GRAY'S BOTANICAL TEXT-BOOK.

Volume II.

PHYSIOLOGICAL BOTANY.

GRAY'S BOTANICAL TEXT-BOOK

CONSISTS OF

VOL. I. STRUCTURAL BOTANY. By ASA GRAY.

II. PHYSIOLOGICAL BOTANY. By GEORGE L. GOODALE.

III. INTRODUCTION TO CRYPTOGAMIC BOTANY, BOTH STRUCTURAL AND SYSTEMATIC. By WILLIAM G. FARLOW. (*In preparation.*)

IV. SKETCH OF THE NATURAL ORDERS OF PHÆNOGAMOUS PLANTS; their Special Morphology, Useful Products, &c. (*In preparation.*)

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GRAY'S BOTANICAL TEXT-BOOK.

(SIXTH EDITION.)

VOL. II.

PHYSIOLOGICAL BOTANY.

I.

OUTLINES OF THE HISTOLOGY OF PHÆNOGAMOUS PLANTS.

II.

VEGETABLE PHYSIOLOGY.

BY

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PREFACE TO THE SERIES.

The first edition of the Botanical Text-Book was published in the year 1842, the fifth in 1857. Each edition has been in good part rewritten, — the present one entirely so, — and the compass of the work is now extended. More elementary works than this, such as the writer's Lessons in Botany (which contains all that is necessary to the practical study of systematic Phænogamous Botany by means of Manuals and local Floras), are best adapted to the needs of the young beginner, and of those who do not intend to study Botany comprehensively and thoroughly. The present treatise is intended to serve as a text-book for the higher and completer instruction. To secure the requisite fulness of treatment of the whole range of subjects, it has been decided to divide the work into distinct volumes, each a treatise by itself, which may be independently used, while the whole will compose a comprehensive botanical course. The volume on the Structural and Morphological Botany of Phænogamous Plants properly comes first. It should thoroughly equip a botanist for the scientific prosecution of Systematic Botany, and furnish needful preparation to those who proceed to the study of Vegetable Physiology and Anatomy, and to the wide and varied department of Cryptogamic Botany.

The volume upon Physiological Botany (Vegetable Histology and Physiology) has been prepared by the writer's colleague, Professor GOODALE.

The Introduction to Cryptogamous Botany, both structural and systematic, is assigned to the writer's colleague, Professor FARLOW.

A fourth volume, a sketch of the Natural Orders of Phænogamous Plants, and of their special Morphology, Classification, Distribution, Products, etc., will be needed to complete the series: this the writer may rather hope than expect himself to draw up.

ASA GRAY

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PREFACE TO VOLUME II.

THE present volume is devoted to a consideration of the microscopic structure, the development, and the functions of flowering plants; that is, to their Vegetable Histology, Organogeny, and Physiology. In the first volume of the Botanical Text-Book these topics were treated only incidentally, or in an elementary manner, as an introduction to Morphology.

Cryptogams, or flowerless plants, are treated in this volume only so far as their study may throw light on certain features of the anatomy and physiology of Phænogams. The simple structure of many of the flowerless plants, especially of those of the lower grades, makes them suitable objects in which to investigate numerous phenomena of vegetable nutrition, growth, and reproduction, and they have been extensively employed as convenient material for this purpose. Reference must therefore be made in the present treatise to some of the more important results.

Vegetable Histology treats of the minute anatomy of plants. A knowledge of its leading facts is indispensable to a clear understanding of Vegetable Physiology, and their presentation must needs precede any satisfactory examination of the latter. The technique of Vegetable Histology requires special treatment, and therefore considerable space has been devoted to its appliances and methods. This special treatment has been supplemented by a series of practical exercises which the student is urged to perform in the order designated. It will be seen that in some cases several examples are suggested: the beginner is advised to examine thoroughly at least one of the examples under each head.

Organogeny, the study of nascent organs, occupies much of the middle ground between Histology, Morphology, and Physiology. The means by which it is investigated are those of Histology, but its answers are given to Morphology. For convenience, the study of the development of each organ of the plant is made to precede the examination of its mature state.

Vegetable Physiology concerns itself with the life of plants. The appliances of which it makes use are taken chiefly from Physics and Chemistry, and facility in their employment demands some practical acquaintance with those departments. To one who has worked systematically in a physical and chemical laboratory, experimental vegetable physiology presents little difficulty. To aid the work of students whose opportunities for experimenting in Physics and Chemistry have been slight, a series of practical exercises in Experimental Physiology has been added. The appliances selected for these examples are not complicated or expensive, and it is hoped that teachers and students alike may find their employment practicable. The Praxis embodies in compendious and convenient form the directions which have been employed by the author in his classes.

The illustrations of tissues and of apparatus have been taken from many sources. They have been selected with reference to the special needs of those students to whom the larger works and the current journals are not easily accessible. The same rule has been largely followed in the treatment of citations from authorities. Where it has been possible to do so without too great sacrifice of space, the phraseology of the original reference has been given.

In the preparation of this volume the author has had at many steps the wise counsel of his teacher and associate, Professor ASA GRAY, to whom he wishes to make his grateful acknowledgments.

In the proof-reading, verification of references, and Index, Mr. W. W. NOLEN, Assistant in Biology, has rendered aid of great value. His painstaking and good judgment have lightened in every way a formidable and burdensome task.

GEORGE LINCOLN GOODALE.

BOTANIC GARDEN OF HARVARD UNIVERSITY,
CAMBRIDGE, MASS., August, 1885.

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PHYSIOLOGICAL BOTANY.

INTRODUCTION.

HISTOLOGICAL APPLIANCES.

The instruments and other appliances used in the examination of minute vegetable structure are, with the exception of a few special ones to be considered later, the following: —

1. **Simple microscope.** For the preliminary preparation of many objects, a simple stage-microscope is indispensable. It should be furnished with only the best lenses, preferably doublets or triplets, magnifying from ten to at least twenty diameters. The glass portion of the stage should be not less than an inch and a half in diameter; supports at the sides of the stage, on which the wrists may rest during dissections, are of considerable use. If the compound microscope described below is provided also with an inverting eye-piece and with an objective of long focus, it can be made to serve for most dissections; otherwise a simple microscope should always be at hand.

2. **Compound microscope.** When reduced to its simplest terms, this consists of a stage, or flat support for the object to be examined, an adjustable tube carrying two combinations of lenses, the objective and the eye-piece, and finally some means of illuminating the object. The desiderata to be borne in mind in the selection of a compound microscope for use in Vegetable Histology, are: excellence in the optical parts, ease and steadiness in their adjustment, and simplicity of construction. Other things being equal, a microscope with a short tube and with a low stand will be most convenient, on account of the large number of cases in which reagents must be employed, their application requiring a horizontal stage.

3. **Three objectives and two eye-pieces,** from combinations of which magnifying powers of forty to eight hundred diameters can be obtained, will suffice for nearly all the histological work described in this volume. Two objectives and a single eye-piece furnishing powers of sixty to five hundred diameters are enough for all ordinary investigations of minute structure. Adequate and convenient illumination is secured by a plane and a concave mirror under the stage. If this is supplemented by an achromatic condenser, so much the better. The stage, preferably thin, should be provided with a perforated revolving disc, or other suitable system of diaphragms, by which its central aperture can be made larger or smaller.

4. The student ought, at the outset of his work, to make himself familiar with the principal effects which are produced in the appearance of the object in the field of the microscope, by changes in the amount and direction of the light thrown by the mirror. Details can sometimes be brought out clearly by oblique illumination, which are only faintly, if at all, seen in direct light.

5. In general, low magnifying powers are to be preferred to higher ones; and combinations of high objectives with low eye-pieces, securing a given magnifying power, are always better than those in which low objectives and high eye-pieces are used to obtain the same enlargement.

6. The slips of glass, or "slides," upon which microscopic objects are commonly prepared and preserved, are three inches (76 mm.) long by one inch (25 mm.) wide. This is for most cases a more convenient size than that frequently employed in Germany; namely, 48 × 28 millimeters. The glass should be free from color and from imperfections. The preparation to be examined under the microscope should be covered with a disc of thin glass before it is brought under the objective. Perfect cleanliness of slide and cover-glass is absolutely necessary in all examinations, and must be secured by the exercise of scrupulous care.[1]

7. **Dissecting instruments.** Sharp delicate needles, by which

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[1] For cleaning glass perfectly, the following preparation may be used:—
A strong solution of potassic bichromate to which about half as much concentrated sulphuric acid is cautiously added. To this mixture add an equal volume of water. The glass slips, or covers, are to be kept in this solution for a short time, and then thoroughly rinsed in pure water, after which they may be dried with cloth or wash-leather. For ordinary use alcohol of usual strength answers the purpose very well.

the parts can be separated by teasing, are often better than any cutting instruments. They are indispensable in the examination of very young flower-buds, and of great use in the isolation of tissues under the dissecting microscope.

8. Sufficiently thin sections of soft parts may be made by any keen-edged knife. A razor of good quality is generally to be preferred to the ordinary dissecting scalpel, since its wide and stiff blade can be held with greater steadiness, and its steel admits of as sharp an edge. As a rule, the razor should be dipped in water before using, as this permits the steel to pass more easily through tissues.[1] If the parts from which sections are to be made are too small to be held in the fingers, they can be firmly seized between slices of pith. It is often convenient to imbed the object in paraffin or in an alcoholic solution of soap.[2] These melt below the temperature of boiling water, but are solid at ordinary temperatures, and the latter, if properly made, is transparent. A little of the melted imbedding substance is poured into a small cone of glazed paper, and when it begins to cool, the object is placed in the middle of the mass. Upon complete cooling it is firmly held therein.

Before putting the object into paraffin it should first be saturated with alcohol, and this replaced by benzol or oil of cloves, in order to enable the paraffin to hold the specimen firmly. The paraffin may be dissolved away from the sections by application of benzol, oil of cloves, or turpentine (see also 110).

9. Thin sections are best removed from the knife by a camel's-hair pencil, and are to be placed at once in water or some other liquid. Except in certain cases, water may be used as a medium for the preliminary examination of sections.

10. **Microtome.** Any of the simpler microtomes, or section-cutters, will be convenient in much histological work, and of great use in the preparation of a series of sections from any very minute object, since this permits them all to be of exactly the same thickness.

11. **Measurements.** Microscopic objects are measured by micrometers. The eye-piece micrometer can be more rapidly used than one on the stage of the instrument; and if its value

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[1] Advantage is frequently gained by moistening the edge of the knife with dilute potassic hydrate before dipping it in water, thus removing traces of oil which may have adhered to it during sharpening. But potassic hydrate should not be used in this way if reagents are to be subsequently employed.

[2] Made by dissolving enough of any good transparent soap in hot alcohol, to form, upon cooling, a firm, clear mass.

for the different objectives and for *the length of* **tube** has been determined accurately, it is usually preferable.

The values of the spaces in the eye-piece micrometer are ascertained by comparison with known values of the spaces on a standard stage micrometer; for example, if one space in the eye-piece micrometer corresponds to five spaces of the stage micrometer, and the latter has a value of one thousandth of a millimeter, each space of the former equals five thousandths of a millimeter.

The unit of microscopic measurement is the "micro-millimeter,"[1] one thousandth of a millimeter. It is expressed by the Greek μ.

12. **Drawing.** An image of the object under the microscope may be cast by reflection upon paper at the side of the microscope, by means of a Camera lucida. Several forms of the Camera lucida are adapted to use with the tube of the microscope in a vertical position, and are more convenient for the majority of cases coming within the scope of the present work. Oberhäuser's, Milne Edwards's, and Abbe's are of this kind.

13. **Polarizing apparatus.** This is of great use in the examination of certain contents of cells. It consists of two Nicol prisms, one below the stage of the microscope and receiving the light which is reflected from the mirror, the other in the eye-piece. Upon turning one of the prisms, distinctive optical characters, not otherwise seen, are presented by grains of starch, etc.

14. **Media and reagents.** The fluid in which a microscopic specimen is submitted to examination is technically known as its medium. Chemical agents subsequently added for the purpose of producing changes by which the chemical character of the objects may be recognized, are termed reagents. Some of the media, however, in common use produce characteristic changes in certain cases, and might be as truly referred to the latter class as several of the reagents themselves. The substances in

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[1] For convenience of reference, the following table of comparative measurements is given: —

μ.	INCHES.	μ	INCHES.	INCHES.	μ.
1	.000039	6	.000236	$\frac{1}{10000}$ =	2.5399
2	.000079	7	.000276		
3	.000118	8	.000315	$\frac{1}{1000}$ =	25.3997
4	.000157	9	.000354		
5	.000197	10	.000394	$\frac{1}{100}$ =	253.9972

One meter = 39.370432 inches.

which microscopic specimens are preserved are termed mounting-media.

15. Media. In all ordinary cases pure water is the best medium in which to place the object for examination. If distilled water cannot be procured, filtered rain-water or melted ice will answer perfectly. In some instances water produces an immediate change either in the cell-wall or in the contents of the cells. For instance, the superficial cells of the coats of many seeds swell up at once when they are placed in water, and lose their former shape; on the other hand, important contents in the seeds of many plants are dissolved immediately when the sections are moistened. Hence, other media must be sometimes substituted for water. Absolute alcohol (see 40) is the most useful for meeting the cases above referred to. Thus, if a section of a seed-coat be first examined in absolute alcohol, and the alcohol be gradually replaced by water as directed in 17, the changes due to water will take place slowly, and can be watched throughout. For the cases in which the cell contents are suspected of undergoing change from water, castor-oil is a useful medium. If thought best, this can be removed subsequently from the specimen by alcohol or ether, and the latter in turn may be made to give place to water, and the changes can be followed with certainty.

16. Glycerin (see 60), either concentrated or somewhat diluted with water, is a highly useful medium, imparting a good degree of transparency to most specimens. It withdraws a part of the water of the cell-sap, and in the case of thin-walled cells this is followed by some change of form. The remarkable effects produced upon some of the contents of cells by the action of glycerin and similar agents will be referred to under Protoplasm.

17. One medium may be replaced by another by the careful use of bibulous paper. Good filtering paper is the best for this purpose. If a little of the liquid which it is desired to place under the cover-glass be put at the edge of the cover, and the opposite edge be then touched lightly with the paper, the liquid will be at once drawn through. By successive applications of the same liquid, the specimen can be thoroughly washed without removal of the cover-glass.

18. Reagents. Four reagents are in very common use in nearly all histological examinations; namely, caustic potash, a solution of iodine, an acid, and a staining agent. Even in ordinary cases, however, it is desirable to have a somewhat wider choice than this, and therefore the following brief hints are

given as to the preparation and employment of some of the most useful reagents. More detailed directions must be sought in special treatises upon micro-chemistry.[1] The list and the general rules here given will serve for most investigations.

19. It is best to try first a very small amount of the reagent, and carefully note its effect before adding more. If it is necessary to increase the amount, draw a little through by means of bibulous paper, as previously directed. Many reagents are slow in producing their effects. Hence some time must be allowed to elapse before one reagent is replaced by another, and it is well in some cases to apply slight heat to accelerate or increase the action; but this must be very cautiously done.

20. If one reagent is to be followed by another, attention must be given to the effects which the reagents have upon each other, or upon the medium, as well as upon the specimen. For instance, small dark crystals of iodine separate from an alcoholic solution when this is brought into contact with water. Removal of the cover-glass is advised in all cases where one reagent is to be washed out before the application of a second, or where one is to be immediately followed by another, provided the specimen is not so delicate as to be disturbed by it. Some parts of the specimen are apt to escape action, if the washing or the introduction of several reagents in these operations is conducted without lifting the cover; but by the exercise of great care both these operations may be carried on successfully by the use of bibulous paper without removing the cover-glass.

21. Owing to their importance, potash and iodine are described first. The other reagents are given in alphabetical order, for convenience of reference.

22. *Potash*, *Potassic hydrate*, *Caustic potassa*, are names interchangeably given to white solid potassa and to its solutions. This substance absorbs carbonic acid so eagerly from the air, that it must be kept in glass-stoppered bottles. To prevent the stoppers from becoming fastened by the action of the alkali on the glass, it is well to smear them with vaseline or paraffin.

23. Solutions of two strengths are used. I. Concentrated. Solid potassa is dissolved in the smallest amount of water (not far from half its own weight) by which it will become liquid. This dense syrupy liquid is too strong for ordinary use. II. A common solution made with one part of solid potassa in three,

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[1] Consult the following: Botanical Micro-Chemistry, by Poulsen, translated by Trelease (Cassino, Boston), 1884. Hilfsbuch by Behrens (Schwetschke, Braunschweig), 1884.

five, or ten parts of water, depending upon the particular case in which it is to be used.

24. For use as a macerating agent in separating cells, a strong solution is preferable, and is more efficient when it is slightly warmed. For dissolving or rendering transparent most of the contents of cells, more dilute solutions are better. Owing to the prompt effect produced on the cell-wall, and upon the contents of cells, especially of young ones, a moderately strong solution of potassa is the most useful clearing agent that we have. After a mass of tissue, for instance an embryo, has been acted on by a solution of potassa until it has become translucent, it is to be cautiously subjected to the action of an acid, preferably acetic or hydrochloric, and then washed. A second treatment, or even a third, may be necessary to make the object sufficiently clear. Sometimes, however, the potassa renders the tissues too nearly transparent, in which case they may be slightly clouded by a little alum-water. This process of clearing tissues was first used by Hanstein in the examination of the tissues at points of growth, and it is of very wide applicability.

25. Some structures are darkened at first by the use of potassa, but cautious treatment afterwards with a dilute acid and a second application of potassa will generally produce a good degree of transparency.

26. Potassa is a solvent for many of the substances which incrust the cell-wall, but in most cases the solutions must be used warm; in a few instances heated even to boiling. The cell-wall, washed after such treatment, will give the cellulose reactions (see 145). Suberin can thus be removed from the cell-walls of cork, forming with the potassa yellowish drops.

27. As the aqueous solution of potassa causes considerable swelling of the cell-wall, it is desirable to have also at hand an alcoholic solution. This is best made by mixing 95 per cent alcohol with a strong aqueous solution of potassa until a cloudiness appears. The mixture is then to be shaken frequently, and, after a day or so, the clear liquid above is to be carefully poured off. This solution may be diluted with alcohol if necessary.[1]

28. Solutions of caustic soda can replace potassa in most of the foregoing reactions. The special cases in which these alkalies are employed for the identification of certain contents of cells will be described later.

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[1] Russow's Potash-alcohol.

29. *Iodine.* This element is only very slightly soluble in pure water. Upon exposure to strong light, however, a somewhat larger amount of iodine passes into solution after a while, owing probably to formation of hydriodic acid. If it is necessary to examine the effect of iodine alone, as in certain parts of Lichens, a fresh solution should be used. In fact, it is recommended that in such cases a minute fragment of solid iodine be placed in pure water under the cover-glass at the moment of examination.

30. But for all ordinary examinations, a solution of iodine in water which contains iodide of potassium is used. The proportions employed vary widely. A convenient strength is obtained by dissolving one gram of iodine and five grams of potassic iodide in enough water to make one hundred cubic centimeters. Even this solution is too strong for some purposes. In a few cases a different solution is advised, made by dissolving five centigrams of iodine and twenty centigrams of potassic iodide in fifteen grams of water.[1] But, in general, dilute solutions are preferable.

31. A solution of iodine and iodide of potassium in glycerin is employed by some. An alcoholic solution is sometimes useful.

32. Iodine is a characteristic test for starch, to which it imparts a blue color, depending for its depth chiefly upon the strength of the solution. Iodine in absolute alcohol gives with dry starch a brownish color; if the alcohol is not absolute, that is, anhydrous, a blue color is given as with ordinary aqueous solutions.

33. In most cases cellulose is colored pale yellow to deep brown by iodine. If the specimen is acted on by concentrated sulphuric acid, either just before or just after the application of the iodine, a blue color appears. This reaction for cellulose is disguised by various incrusting matters, which can be removed by strong acids or alkalies; after their removal the washed specimen will give the characteristic cellulose reaction (see also 143).

34. Iodine and a metallic iodide in a strong solution of chloride of zinc form a very useful reagent for cellulose, to which a blue color is given. The reagent is easily made by dissolving pure zinc in concentrated hydrochloric acid until there is no further action of the acid. The solution, with a little metallic

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[1] Poulsen.

zinc still undissolved, is to be evaporated to a syrupy consistence, saturated with potassic iodide, and lastly enough pure iodine added to render the whole a deep red or brown. Cell-walls that have incrusting matters, for instance, cork-cells and most wood-cells, are turned yellow by this reagent. It is known as Schulze's reagent. Behrens advises the preparation of modifications of this important reagent, all depending on the relative amount of iodine and the degree of dilution. A little practice in their use will suggest the cases to which each is specially applicable. Solutions of iodine color protoplasm, and other albuminoid bodies, yellow to deep brown.

35. Owing to the tendency of iodine solutions to form hydriodic acid, it is recommended by many authors that they be kept out of the light; but this precaution is not necessary unless the investigation calls for pure iodine alone; in such a case it is better to use only freshly prepared solutions.

The following reagents are arranged in alphabetical order.

36. *Acetic acid.* Glacial acetic acid diluted by two or four parts of water, or the ordinary concentrated acid of the shops, is used (1) to neutralize the alkali in Hanstein's method (see 24); (2) to discriminate between oxalates and carbonates, the latter dissolving with effervescence in it, the former remaining unchanged in it, but dissolving quietly in hydrochloric acid; (3) in the study of the nucleus.

37. *Alcohol.* Common strong alcohol, or the so-called "95 per cent," is widely employed for the preservation of microscopic material. In it soft tissues become hardened. This is a great advantage in the case of specimens which are too yielding to be cleanly cut when fresh. If it is desirable to again soften tissues which have been hardened by the action of alcohol, it is merely necessary to soak them for a short time in water, when they will assume nearly the consistence they had when fresh. This reagent produces certain marked changes in the contents of vegetable cells: the protoplasmic matters become more or less shrunken, many oils and fats are dissolved, and certain substances in solution in the cell-sap are separated out (see 183).

38. The air which occurs in intercellular spaces and in all dry specimens is generally removed with ease by the action of alcohol, especially if a little heat is applied.

39. Alcohol is of use also in the preparation of some of the staining agents.

40. Absolute alcohol contains only the merest trace of water. Hence it must be used instead of ordinary alcohol whenever the

specimen is affected by water, as is the case with mucilaginous tissues, crystalloids, etc. As a reagent for use under the cover-glass it is more satisfactory than common alcohol, but in keeping it the greatest care must be exercised to exclude moisture.

41. *Alum.* Either potash- or ammonia-alum may be used to diminish the transparency of cells which have been acted on by potassa (see 24). Alum is a mordant in some of the processes for staining (see 98).

42. *Ammonia.* Aqueous ammonia may replace the fixed alkalies, potassa and soda, but possesses no advantage over them except in its somewhat slower and less violent action. For its use in the examination of albuminoids, see 125. Its principal use in microscopy is in the preparation of certain staining agents (see 77) and cuprammonia.

43. *Anilin chloride.* Dissolved in alcohol, this reagent imparts a pale yellow color to lignified cell-walls. Upon addition of hydrochloric acid, the color is much deepened. This is Höhnel's test for lignin.

44. *Anilin sulphate.* This substance in aqueous or alcoholic solution gives to lignified cell-walls a pale yellow color, which is much deeper when the reagent is followed by sulphuric acid, — Wiesner's test for lignin.

45. *Argentic nitrate*, or nitrate of silver, in extremely dilute alkaline solution freshly made, has been recommended for discriminating between living and dead protoplasm, the former turning dark, the latter remaining unchanged (see details in Part II.).

46. *Asparagin.* A concentrated solution of asparagin is suggested by Borodin for the recognition of asparagin itself when its crystals have been formed in tissues blanched by darkness.

47. *Auric chloride*, long used for staining preparations in animal histology, has been somewhat employed for coloring the cells of certain lower plants, and in the same manner as argentic nitrate, for detecting the condition of protoplasm.

48. *Benzol* is a powerful solvent for various vegetable fats and resins. It is also used for the preparation of benzol-balsam (see 112), and in dissolving paraffin (see 8).

49. *Calcic chloride.* Treub employs this for clearing tissues. The fresh section, after having been moistened by a little water, is covered with dry powdered chloride, warmed until it is about dry, and afterwards placed in a little water.

From this it is to be transferred to glycerin, where it soon becomes clear.[1]

50. *Calcic hypochlorite* in aqueous solution bleaches many tissues without the use of an acid, but, in general, specimens which have been subjected to its action are more thoroughly decolorized if they are subsequently placed in dilute hydrochloric acid, washed in pure water, and finally transferred to glycerin. Preparations which have been bleached by this method are easily colored by some of the staining agents described on page 15. Sodic hypochlorite may replace it in all cases.

51. *Carbon disulphide* is used as a solvent for fats.

52. *Carbolic acid*, or phenol, dissolved in the least quantity of concentrated hydrochloric acid which will take it up, gives a green color with lignified cells. It is better to add to a few drops of the strongest hydrochloric acid a small quantity of crystallized phenol, warm the mixture slightly, and upon its cooling add enough acid to remove any cloudiness.

53. *Chloral hydrate* in aqueous solution is recommended by Arthur Meyer[2] as a clearing agent. Two parts of water are added to five parts of chloral, and used somewhat above the temperature of 15° C.

54. *Chromic acid.* The pure acid, in strong solution, acts promptly on cell-walls, dissolving all except those which are silicified and those which are cutinized. Even the latter yield to prolonged action. If the solution is more dilute, the action goes on only so far as to cause swelling of the cell-wall, bringing out, in special cases, a very distinct stratification. Solutions which are so dilute as to be merely pale yellow cause hardening of soft tissues, and this acid therefore forms an excellent adjuvant to alcohol for this purpose (see Part II.).

55. *Cuprammonia.* To a solution of cupric sulphate add enough soda (or potassa) to produce a precipitate. After removal of the excess of liquid by filtration, place the precipitate in a flask, wash once with water which has been freed from air by boiling, and then dissolve the mass in the least quantity of concentrated ammonia which will take it up. The freshly prepared solution should act promptly on delicate fibres of cellulose, cotton for example, causing them to swell and apparently pass into solution. Lignified and cutinized cell-walls are not acted

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[1] Flahault: Accroissement terminal de la racine. Ann. des Sc. nat., 1878. vi. p. 24.

[2] Das Chlorophyllkorn, Leipzig, 1883.

upon until the foreign matter has been removed by the agents previously spoken of (see 26).

This reagent, known as Schweizer's,[1] possesses its chief interest from the fact that it is the only liquid known in which cellulose appears to dissolve without essential change of composition. It has a limited application in the discrimination of fibres used in the arts.

56. *Cupric acetate* in aqueous solution is used as a preparatory liquid for the examination of resins. The part to be examined is kept in a concentrated solution for some days, and sections are then made from it. If certain resins are present, they will appear of a green color. The above is Franchimont's test based on a reaction discovered by Unverdorben.[2]

57. *Cupric sulphate* in saturated aqueous solution is used for the detection of certain carbohydrates (see 184) and albuminoidal matters (see 124). Commercial blue vitriol, recrystallized two or three times, will answer for all ordinary cases.

58. *Ether* is used as a solvent for fats, etc.

59. *Ferric chloride* in aqueous solution was formerly recommended as a test for the tannins;[3] the tannin of oak-bark becoming bluish-black; that in the leaves of the sumach, greenish-black. But the distinctions are not constant. Ferric acetate and sulphate are now more generally used than the chloride as a test, and are better.

60. *Glycerin.* Only the purest glycerin should ever be employed in microscopic examinations. The following are among the most important of its many applications: 1. In clearing specimens. It is used not only as an adjuvant in the Hanstein and other methods of clearing, but, in many cases, it serves well without any other reagent. 2. To cause withdrawal of water from fresh cells, the degree of effect depending on the strength of the glycerin. 3. In the examination of protein granules (see 175). 4. As a test for inulin; this substance separates sooner or later in the form of sphærocrystals. 5. As a solvent for iodine (see 31).

61. *Hydrochloric acid.* Pure concentrated acid is one of the most satisfactory agents for the maceration of woody tissues. When dilute, it serves for the discrimination between carbonates and oxalates, the former dissolving with effervescence, the latter

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[1] Schweizer: Vierteljahrsschrift natur. Ges., Zurich, 1857.

[2] Behrens: Hilfsbuch, p. 377.

[3] Watts's edition of Fownes's Chem., p. 672.

without. It must be remembered that acetic acid dissolves carbonates, but not oxalates (see 36).

This acid has been used by Pringsheim[1] in the study of chlorophyll grains; fresh sections of tissues containing chlorophyll being exposed to the action of the acid for some hours. From the grains, minute spheres of a brownish color become nearly detached, and these afterwards appear as clusters of acicular crystals (see Part II.). Hydrochloric acid is also of use in the examination of some protein matters (see 124).

62. *Indol* (Niggl's test[2] for lignin) is used in an aqueous solution. The specimen, subjected to the action of the solution for a few minutes, is transferred to sulphuric acid of specific gravity 1.2 (made by adding one part of concentrated acid to four parts of water). Lignified structures become red.

63. *Mercuric chloride*, or corrosive sublimate, dissolved in fifty parts of absolute alcohol renders protein grains insoluble in water. Pfeffer[3] recommends that the specimen should remain in this reagent at least twelve hours. Dippel[4] uses a dilute aqueous solution (1 in 500) to render visible the currents in the most delicate threads of protoplasm (and for the demonstration of the nucleus without affecting the other contents of the cell).

64. *Millon's reagent*, commonly called acid nitrate of mercury, is best prepared, according to its discoverer, by pouring upon pure mercury its own weight of concentrated nitric acid. For a short time the action is violent; when it subsides a little, gently warm the liquid until the metal is completely dissolved. The solution is immediately diluted by twice its volume of pure water. After a few hours the liquid is to be decanted from the crystalline mass which has formed, and it is then ready for use.[5]

This reagent is more efficient when freshly made.

Albuminoid substances are colored red by this reagent even in the cold, but much more readily upon the application of heat. According to Millon, the reaction is due to the presence in the liquid of both mercuric nitrate and nitrite.

This reagent has been employed for the demonstration of the stratification and spiral striation of certain cell-walls.

65. *Nitric acid* gives to protein matters a yellow color, which is intensified upon the subsequent use of ammonia. The

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[1] Pringsheim's Jahrbücher, Bd. xii. p. 294, *et seq.*

[2] Flora, 1881, p. 545, *et seq.*

[3] Pringsheim's Jahrbücher, viii. p. 441.

[4] Dippel: Das Mikroskop, i. p. 281.

[5] Quoted from Behrens: Hilfsb. p. 247.

same treatment, especially if the slide is slightly warmed, colors the so-called intercellular substance yellow. The acid is also used as a test for suberin (see 158).

66. *Osmic acid* (perosmic acid) is very volatile, and therefore is best preserved in sealed glass tubes until wanted for use, when the tube can be broken under water. Even from the aqueous solution the irritating acid escapes in small amount, rendering it a disagreeable reagent to work with. The solutions are usually of one per cent strength.

Oils are colored brown by the reduction of the acid to metallic osmium on the surface of the drops. Living protoplasm is killed at once by even dilute solutions of this acid, and there is usually more or less discoloration of the different parts. Hence it is a useful agent for arresting the processes of cell-division and growth at any desired stage. Advantage is sometimes gained, according to Poulsen,[1] by the combination with it of chromic acid.

67. *Phenol* (see carbolic acid, 52).

68. *Phloroglucin*, used by Wiesner as a test for lignin.[2] The specimen is first acted on by hydrochloric acid, and then moistened by a solution of phloroglucin in water or alcohol. If the cell-walls are lignified, they will at once assume a red color. Höhnel[3] suggests the employment of a strong decoction of cherry wood instead of the phloroglucin. Used in the same way, it imparts a violet color to lignified cells. This test is hardly so satisfactory as the other.

69. *Potassic bichromate* in aqueous solution is used to harden tissues, and is about as good as chromic acid. It has been also employed by Sanio[4] for the detection of tannin.

70. *Potassic chlorate*, used with nitric acid, is the most convenient macerating agent. If a few small crystals of this salt are added to a little concentrated nitric acid in a test-tube containing a fragment of wood, and the liquid is carefully warmed, violent action begins somewhat below the point of boiling, and the wood is speedily disintegrated. By selecting acid of the right strength, and by careful regulation of the heat applied, the action of the liquid can be kept well under control, so that almost any degree of action can be obtained. It is not safe to use this reagent in the room where delicate apparatus is kept,

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[1] Mikrochemie, p. 19.

[2] Sitzungsber. Akad. Wien, 1878, p. 60.

[3] Ib. 1877, p. 685.

[4] Bot. Zeitung, 1863, p. 17.

since the gases evolved act upon metals. This is Schulze's macerating process.

71. *Potassic nitrate*,[1] used in the examination of protoplasm (see Part II.).

72. *Rosolic acid*, or corallin, dissolved in water containing a trace of sodic carbonate, forms a purple fluid which colors vegetable mucus red. It is used also to demonstrate the structure of cribrose-tissue.[2]

73. *Schweizer's reagent* (see cuprammonia).

74. *Sodic chloride* (common salt), used in aqueous solution in the examination of protoplasm (see 120).

75. *Sugar.* Cane sugar dissolved in water to form a thick syrup is allowed to act for some time on tissues containing protoplasm: a drop of concentrated sulphuric acid is then placed on the object, when the protoplasm will take on a faint rose-red color. The reaction is uncertain.

76. *Sulphuric acid.* Pure concentrated acid is used as an adjuvant in many tests, *e. g.*, with iodine solutions in the identification of cellulose, but it is also of great use by itself in breaking down cellulose. By it, a cellulose wall can be destroyed without destruction of the protoplasm within (see 141).

77. **Staining agents.** A few of the chemicals in the foregoing list impart to certain tissues, and certain contents of cells, colors which have a good degree of permanence when the specimens are preserved in a suitable medium. But the colors produced by most reagents are fugitive, and serve only a temporary purpose. When, therefore, it is desirable to stain or tinge a given part of a specimen permanently, recourse must be had to dyes which do not readily fade.

78. Some of these have been long in use in Vegetable Histology for the purpose of preparing attractive specimens for the demonstration of tissues, but it is only within a recent period that they have been successfully employed in the study of cell-division. In the examination of the changes which take place in the interior of cells during division, they are indispensable: in the examination of the tissues themselves, their use is far from satisfactory. As will be specially shown later, the chemical differences between the cell-walls of certain tissues which it is desirable to distinguish from each other under the microscope are not very great, and they often behave alike as respects

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[1] Treub: Naturk. Verh. d. koningl. Akad. vol. xix., 1878, p. 9.

[2] Behrens: Hilfsbuch, p. 313.

staining agents. Hence it is impossible to lay down rules which will apply to all cases in which tissues are to be stained: the staining of the nucleus, however, can be readily secured by following the explicit directions given in the chapter on "Cell-growth."

79. Of the whole class of staining agents, it may be said that exposure to strong light diminishes the brilliancy of the coloring they produce in the specimen, and in many cases completely destroys it. In general, the staining obtained by allowing the specimen to remain for a long time in a dilute solution of a dye is more satisfactory than when a stronger dye is used with haste.

80. CARMIN. Two grades are readily procurable in this country; namely, (1) "No. 40," (2) "Orient." The former is the cheaper, and will answer for all cases described in this treatise; but attention must be called to the fact that it is sometimes adulterated, and hence it may be found necessary to change the proportions given in the following formulas. A good carmin, even of the grade first mentioned, should leave only little residue when placed in strong ammonia. If more than a trace of residue is found, the amount of carmin in the formula must be proportionately increased.

81. *Ammonia-carmin.* Pure powdered carmin is rubbed up with a little water to form a thin paste, enough strong ammonia to dissolve it is cautiously added, and the whole is then filtered. The filtrate is to be evaporated slowly over a water-bath. The dried mass dissolves readily in water, forming a clear liquid which keeps well; but it is better to preserve the mass in a tightly-stoppered bottle, dissolving it only as required (Hartig's carmin).[1]

82. A modification of this carmin is made as follows: .2 to .4 gram of carmin is shaken up with 30 c.c. of water, and a few drops of ammonia added. A part of the carmin dissolves, and is to be filtered. If the filtrate smells strongly of ammonia, it is allowed to stand for half a day under a bell-jar. A drop of ammonia will re-dissolve any slight trace of carmin which may separate. This fluid is to be added to water, drop by drop, until the right color is obtained (Gerlach's ammonia-carmin).[2]

83. If, to the filtrate last mentioned, 30 grams of glycerin

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[1] Dippel: Das Mikroskop, i. p. 284.

[2] Behrens: Hilfsbuch, p. 257.

and 10 grams of strong alcohol are added, a liquid is obtained which is known as Frey's glycerin-carmin.

84. *Beale's carmin* is nearly the same. Ten grains of carmin are placed in a test-tube, and half a drachm of strong ammonia added; the mixture is shaken, and gently heated over a spirit-lamp. The solution is to be boiled for a few seconds and then allowed to cool. In an hour two ounces of glycerin and two ounces of water are to be added, together with half an ounce of alcohol; the liquid is then filtered.[1]

85. *Thiersch's borax-carmin.*[2] 2 grams of borax are dissolved in 28 c. c. of distilled water, and .5 gram of carmin added. The solution is next mixed with 60 c. c. of absolute alcohol, and filtered.

86. *Thiersch's oxalic-acid carmin.*[3] 1 gram of carmin is dissolved in 1 c. c. of ammonia and 3 c.c. of water. Another solution is prepared by dissolving 8 grams of crystallized oxalic acid in 175 c. c. of water. The two solutions are then mixed, 16 c. c. of absolute alcohol added, and the whole filtered. This liquid is violet when ammonia is in excess; orange, if too much oxalic acid is present.

87. *Grenacher's alum-carmin.*[4] Carmin is dissolved in a solution of potash-alum or ammonia-alum until the required color is obtained. This has been modified by Tangl as follows: To a saturated solution of alum, enough carmin is added to give a deep color (1 grm. in 100 c. c. of solution), the whole boiled for ten minutes, and filtered upon cooling.

88. *Woodward's carmin.* "Pulverized carmin 7½ grains, water of ammonia 20 drops, absolute alcohol half an ounce, glycerin 1 ounce, distilled water 1 ounce. Put the pulverized carmin in a test-tube and add the ammonia. Boil slowly for a few seconds, and set aside uncorked for a day, to get rid of the excess of ammonia. Add the mixed water and glycerin, and next the alcohol, and filter."

89. *Carmin with picric acid.* This agent, known as Ranvier's picrocarmin, is made by cautiously adding to a concentrated solution of picric acid enough ammonia-carmin solution (81) to saturate it, and then evaporating to one-fifth the volume.

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[1] Beale: How to Work with the Microscope, p. 125.

[2] Behrens: Hilfsbuch, p. 258.

[3] Behrens: Hilfsbuch, p. 257. In Dippel (Das Mikroskop), p. 285, the proportions are somewhat different.

[4] Archiv. für Mikrosk. Anat., 1879, p. 465. Tangl, in Pringsh. Jahrb., Bd. xii., 1880, p. 170.

Upon cooling, a slight sediment is deposited. After filtration from this sediment the liquid is evaporated to dryness, and afterwards dissolved in water in the proportion of 1 : 100.

Another formula is: 1 gram of carmin and 4 c.c. of concentrated ammonia are mixed with 200 c.c. of water, and 5 grams of picric acid then added. After nearly complete solution the clear liquid is poured off, and exposed to the air for some weeks. The red powder left after this slow evaporation is to be dissolved when required in water in the proportion of 2 : 100, and the solution filtered through two thicknesses of filter-paper.

Cochineal, the substance from which carmin is prepared, may be used in aqueous extract, or with alum. The formula for the preparation with alum is given as follows: Rub to a fine powder one gram of cochineal with one gram of burnt alum; mix with 100 c.c. of water, and boil down to 60 c.c. When cold, filter the solution several times, and add a few drops of carbolic acid.

90. *Hæmatoxylin* (a dye obtained from logwood) is used dissolved in alcohol, or alum-water, according to circumstances.

Frey gives the formula: 1 gram of hæmatoxylin is dissolved in absolute alcohol. This solution is added, drop by drop, to a three per cent aqueous solution of alum, until it becomes deep violet in color. After exposure to the air for a few days, it is to be filtered, and is then ready for use; but a fresh filtration will be found necessary after a time. Poulsen advises that a few drops of a ten per cent solution of alum be added to an aqueous solution of hæmatoxylin (.35 gram in 10 c.c. water).

Aqueous extracts of several other dye-woods can replace hæmatoxylin in some cases, but they have no advantage over it.

91. *Picric acid* (trinitrophenic acid) in aqueous solution is valuable for staining and hardening protoplasm. It may be used alone, combined with carmin (see 89), or with nigrosin.

92. Alkanet-root (alkanna) in alcoholic solution tinges resinous globules and serves to prepare for cutting specimens which contain them. The method of use is described under "Resins."

93. *The coal-tar colors.* Under this name are comprised the anilin derivatives and a few others of a slightly different origin. The following table will indicate to some extent the changes of color which may be expected when these dyes are used with tissues which have a marked acid or alkaline reaction. But it should be observed that the names of several of the dyes are loosely applied, and that the dyes made by different manufacturers are not always of the same character or strength. All of the dyes mentioned below are soluble in water and alcohol.

Name.	Effect of dilute H Cl.	Effect of dilute Ammonia.
	Red dyes.	
Magenta.	Color fades to brown or light purple.	Fades completely.
Safranin.	Color changes to purple, and a brown precipitate occurs.	Little change.
Red anilin.	Deep orange-brown color.	Reddish precipitate.
Acid azo-rubin.	Slight change of tint.	Little change.
Eosin.	Orange precipitate.	No marked change.
Ponceau.	No change of color	No change.
	Yellow and Orange dyes.	
Solid yellow.	Purple precipitate.	Little change.
Orange "R."	Unchanged.	Unchanged.
Gold orange.	Little change.	Color deepens to red.
	Green dyes.	
Methyl-green.	The bluish tint becomes deep green.	Fades out.
Brilliant green.	Fades somewhat.	Whitish precipitate.
Emerald green.	Fades out.	Whitish precipitate.
	Blue and Violet dyes.	
Cotton-blue "B."	Unchanged.	Fades somewhat.
Methyl-violet "BBBBBB."	Greenish precipitate.	Purple precipitate.
Nigrosin.	Little change.	Little change.

94. A solution of any of the above dyes consisting of one gram with enough water to make one hundred cubic centimeters, although too strong for most cases, is very convenient, since it can easily be diluted at will. From even very dilute solutions parts of a specimen, for instance, a cross-section of a stem, will take up some of the color with more or less change. If the staining is too deep, a part of the color can be removed by careful washing in alcohol, or in a very dilute acid or alkali (see above table for each case).

95. *Double-staining.* It is sometimes possible to color different parts of a specimen with more than one dye; for instance, staining the fibres of the bark green, and the wood of the same specimen red. The best results are obtained by the use of an alcoholic solution of one of the dyes and an aqueous solution of the other. The following method proposed by Rothrock[1] gives excellent results. The dyes are Woodward's carmin (see 88) and anilin green (or "iodine green"). The specimen (whether bleached by sodic hypochlorite or left unbleached) is first thoroughly saturated by alcohol, which hardens it, and causes contraction of the contents; it is then kept for a day in a dilute

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[1] Botanical Gazette, September, 1879.

alcoholic solution of anilin green. In a row of watch-crystals the following liquids are placed: (1) water, (2) Woodward's carmin, (3, 4, 5) alcohol, (6) absolute alcohol, (7) oil of cloves. The specimen, taken from the green, is dipped for a moment in water, then for about a minute in the carmin, then successively through the alcohols, in each of which it remains ten to twenty minutes, except in the first, where it remains only long enough to have the unfixed carmin washed away. From the last alcohol it goes into oil of cloves (or benzol), where it should remain long enough to become perfectly transparent. It is then to be mounted in balsam.

96. Double-staining can also be effected by the successive use of hæmatoxylin and an anilin color. By the use of two or more anilin dyes different parts of a specimen may be colored differently; but as a rule all these effects are uncertain, and cannot be relied upon for the positive identification of tissues. In general, however, long bast fibres take characteristic colors.

97. The following combinations for double-staining are recommended by Dr. Stirling,[1] and though originally designed only for animal tissues, serve well with sections of plants:—

1. Osmic acid and picrocarmin. 2. Picric acid and picrocarmin. 3. Picrocarmin and logwood (hæmatoxylin). 4. Picrocarmin and an anilin dye. 5. Logwood and iodine green. 6. Eosin and iodine green. 7. Eosin and logwood. 8. Gold chloride and an anilin dye.

98. In the cases which require special treatment, for instance, the staining of the nucleus, the precautions laid down must be attended to in order to insure success. But in the ordinary instances where it is desirable to stain a specimen merely to bring some part into prominence for purposes of demonstration, the widest choice in dyes and their use is advised. A few mordants have been tried in order to fix the colors, but with little success. The best are tannin in solution, and aqueous solutions of any of the alums. A little practice will show which mordant is best for each case.

99. Specimens stained by nearly all of the above dyes can be mounted securely in balsam, as directed in section 110; but glycerin and glycerin-jelly mounts are apt to become faded or discolored after a time.

100. **Mounting-media.** Pollen and other dry specimens are preserved in shallow cells formed by a thin ring of asphalt-

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[1] Journ. Anat. and Phys., 1881, p. 349.

cement, varnish, or white lead, allowed to dry nearly to hardness, upon which a cover-glass fits firmly, and is retained by a second ring of the same cement. If the precaution is taken to have the cover-glass fit evenly to the first layer of cement, there is little danger that the subsequent layer, which is to hold the cover in place, will creep under it and into the cell.

101. Glycerin, pure water, calcic chloride solution, potassic acetate, and like liquids may be used as mounting-media in cells prepared in the manner just mentioned, but made of greater thickness. Care must be observed to avoid touching the upper edge of the cement ring with the liquid; and yet the cell must be completely filled, in order to exclude air.

102. If a specimen has been prepared in glycerin, and it is not considered well to disturb the cover-glass, a cement ring or square can be built up around the cover at a little distance from it, *provided* the glass slide is thoroughly cleaned at the place where the cement is to be put. After the requisite number of layers have hardened sufficiently, a ring of the same or, better, of a more quickly drying cement may be placed across from the edge of the cell to the cover-glass, to hold it in place. As this, in drying, will contract somewhat, it is a good plan to place two or three fragments of thin glass under the cover, that these may receive the pressure and prevent crushing the specimen.

103. Of the mounting-media, one of the best is glycerin and acetic acid in equal parts, boiled and filtered. It serves well for thin-walled specimens (especially in the lower plants).

104. Specimens of fresh cells or of juicy tissues which are to be mounted in glycerin are best treated in the manner recommended by Beale.[1] "The specimen is first immersed in weak glycerin, and the density of the fluid is gradually increased, either by adding from time to time a few drops of strong glycerin, until it bears the strongest, or by allowing the original weak solution to become gradually concentrated by slow evaporation. In this way, in the course of two or three days the softest and most delicate tissues may be made to swell out almost to their original volume in the densest glycerin or syrup. They become more transparent, but no chemical alteration is produced, and the addition of water will at any time cause the specimen to assume its ordinary characters."

105. It is plain that mounts in any liquid must be liable to injury from displacement of the cover-glass; but this can be

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[1] How to Work with the Microscope, p. 360.

partially guarded against by fastening to the upper surface of the slide, near its two ends, square pieces of pasteboard a little thicker than the cell itself.

106. *Glycerin-jelly*, a mixture of glycerin with pure gelatin, is liquid at the temperature of boiling water, and solidifies again on cooling. Any specimen which is not injured by being slightly heated can be mounted satisfactorily in the jelly, *provided* it is first thoroughly saturated with glycerin. But this precaution is by no means necessary in all cases.

107. A drop of the melted jelly, free from air-bubbles, is placed on the slide (a fragment of the solid jelly can be melted on the slide if preferred), the specimen placed therein, and the cover-glass, previously moistened slightly on the under side with glycerin, is carefully laid on, and the preparation now allowed to cool. When the jelly is again hard, a varnish or cement ring may be placed around the edge of the cover to hold it in place. Asphalt-cement is apt to impart to the jelly a dark tinge, which may sooner or later spoil the mount, and hence the colorless varnishes are better.

108. The edge of the jelly may be lightly touched with a strong solution of a chromate, for instance, bichromate of potassium, and exposed for a while to light. This renders the jelly insoluble, and firmly sets it.

109. The following are among the best formulas for making this useful mounting-medium: —

One part of pure gelatin, three parts of water, and four of glycerin (Schacht, quoted by Dippel). Nordstedt uses the same proportions, and advises the addition of a small piece of camphor or a drop of carbolic acid, to prevent moulding.

One part of gelatin is soaked in six parts of water for two hours, seven parts of glycerin are added, and one per cent of carbolic acid is added to the whole. The mass is heated for fifteen minutes, with constant stirring, and then filtered through glass-wool. All the ingredients must be absolutely pure (Kaiser, Bot. Centrbl., 1880, p. 25).

The proportions employed in the second formula, but without the addition of the carbolic acid, give a clearer jelly; and it has not been apt to mould, especially if the cork of the bottle containing it be wrapped in a thin piece of linen, which has been dipped in dilute carbolic acid.

110. *Canada balsam.* This is used either (1) alone, or (2) in solution. In either case the specimen must be free from water, and permeated by some liquid easily miscible with the balsam.

This is easily effected by first saturating the object with alcohol (beginning preferably with dilute, and then using stronger), in order to expel all water; next placing the alcoholic specimen in oil of cloves, turpentine, or benzol, until the alcohol is in turn expelled. The specimen thus permeated is transferred to balsam which has been previously placed on the slide. Care must always be taken to have the balsam perfectly free from air-bubbles.

111. When used alone, the balsam on the slide may be heated, to drive off a part of its more volatile constituents, and the specimen can then be placed in the warm liquid. But this method is not applicable when the specimen is affected by slight heating; it is best adapted to hard tissues, like woods and fibres. Balsam which has thus been heated hardens on cooling to a good degree of firmness. This firmness is secured with balsam used without heat only after a longer lapse of time, during which the more volatile matters have escaped.

112. If pure balsam is cautiously heated in a capsule until it no longer gives off vapors, the melted mass will cool into a pale amber-colored solid. This solid dissolved in a small quantity of benzol forms a liquid of the consistence of syrup, which is useful for all mounting where heat is injurious. The specimens must be treated successively with alcohol and benzol, and they are then ready to be immersed in the benzol-balsam on the slide. An equally serviceable solution is made by dissolving the mass in chloroform. Chloroform-balsam requires the specimen to be saturated with chloroform before immersion.

113. In all the above cases two precautions will save disappointment: 1st. the slides and cover-glasses should be heated slightly, to drive off any moisture on the surfaces which are to come in contact with the mounting-medium; 2d. the covers should be held in place by means of a slight weight, or by the pressure of a spring clip, until the balsam or its solution has become tolerably firm. A little experience will show that specimens mounted in balsam may require a somewhat different management of the mirror under the stage from those which are mounted in a medium with a different refractive power. *Damar* may replace balsam when the latter, which is the better, is not to be had.

114. *Hoyer's mounting-media* are highly recommended by Strasburger.[1] The one which is preferred for anilin preparations

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[1] Das botan. Practicum, 1884, p. 40.

is made by adding colorless pieces of gum-arabic to a solution of potassic acetate or ammonic acetate, until the liquid becomes of the density of thick syrup, while in that intended for carmin preparations the gum is dissolved in a five to ten per cent aqueous solution of chloral hydrate, and about ten per cent of glycerin added. Either of these media, or a plain solution of pure gum-arabic, will be found to answer admirably for all preparations of woods which are to be photographed.

115. The edges of the cover-glass are usually painted with some varnish of good quality. Those in best repute are: —

1. Asphalt-varnish, to be thinned with turpentine when too thick.
2. Maskenlack, a German preparation, thinned with alcohol.
3. Mikroskopirlack, also thinned with absolute alcohol.
4. Shell-lac in alcohol, tinged with some anilin color. If a few drops of castor-oil are added to the solution, it dries into a less brittle finish.
5. Gold-size.
6. White lead (with oil).

It is a good plan to revarnish slides whenever the varnish first shows any indication of breaking away.

A few works in regard to microscopic manipulation and micro-chemistry which may be advantageously consulted by the student are the following: —

Beale. How to Work with the Microscope (London). This is a large octavo volume, with very minute descriptions of microscopical appliances and manipulation. Several editions have been printed.

Carpenter. The Microscope (London). A small octavo of about 900 pp. This work deals at some length with the structure of animals and plants.

Behrens. Hilfsbuch zur Ausführung Mikroskopischer Untersuchungen im Botanischen Laboratorium (Braunschweig, 1883). This is specially devoted to microscopic manipulation and micro-chemistry. An English translation has appeared.

Poulsen. Botanical Micro-Chemistry. Translated and enlarged by Professor Wm. Trelease (Boston, 1884). An excellent account of the chemicals used in the examination of vegetable structures, together with some directions for their employment.

Strasburger. Das botanische Practicum. See an account of this work on page 165.

Bower and Vines. A Course of Practical Instruction in Botany (London, 1885). A most useful and convenient guide to the study of the histology of flowering plants, ferns, and their allies.

PART I.

CHAPTER I.

THE VEGETABLE CELL IN GENERAL: ITS STUCTURE, COMPOSITION, AND PRINCIPAL CONTENTS.

116. **The unit in Vegetable Anatomy,** the fundamental component of which the fabric of plants is constructed, and from which all the diverse histological elements are derived, is the cell. Even the elements which are the least cellular in appearance, and which have names of their own (as fibres, ducts, etc.), are only transformed cells, or simple combinations of them; so that the cell is the type as well as the unit of vegetable structure, as indeed it is of animal structure also. The name *cell* is one which would not be given to it if the nomenclature were to be founded upon our present knowledge. Cells were originally taken to be only closed cavities in a vegetable mass.[1] We now

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[1] The earliest recognition of cellular structure in plants appears in Robert Hooke's **Micrographia** (1665), p. 113. "Our microscope informs us that the substance of cork is altogether fill'd with air, and that that air is perfectly enclosed in little boxes or cells distinct from one another."

Nehemiah Grew, of London (The Anatomy of Plants, book i. p. 4), under date of 1671, says of the mass through which the framework of a young plant is distributed, "It is a Body very curiously organiz'd, consisting of an infinite number of extreme small bladders," etc.

Malpighi, of Bologna, in a work presented to the Royal Society in the same year, uses nearly the same language: "Exterior etenim cuticula utriculis, seu sacculis horizontali ordine locatis, ita ut annulus efformetur, componitur, etc." (Anatomes Plantarum Idea, p. 2).

As a preliminary study, a beginner should prepare and examine a few sections like the following: —

(1) From the tip of the root of a bean (which has germinated on wet sponge or paper) cut a thin section lengthwise, and carefully examine it under a power of 200–400 diameters. If the section is thin enough, the contents of the cells can be made out, and will be seen to consist of a colorless lining (*protoplasm*), in which one part (*the nucleus*) appears denser than the rest. Next, treat the section with a solution of iodine, and notice what parts are colored, — the protoplasm and nucleus are yellow and brown, but the cells on the looser part of the tip contain bluish granules (*starch*). This starch can best be shown by first dissolving out the protoplasm with dilute potash.

know them to be organs and even organisms. Histology therefore begins with the cell in its independent condition.

117. A complete and living vegetable cell consists of a cell-wall enclosing certain essential contents.

118. In their earliest state some of the lower plants exist as a mass of motile living matter, not bounded by any envelope. But in all plants of the higher grades the living matter of the cell is from the very first protected by a cell-wall.

119. That which is essential to the vital activity of a cell is an apparently half-solid substance, — protoplasm. With the properties of protoplasm as a living thing, Physiology and not Histology is immediately concerned. But it is necessary throughout the study of Histology to make a distinction between the cells which are vitally active and those which serve chiefly or wholly some mechanical end; and hence attention must be called at the outset to the means by which the living matter of the cell can be identified.

120. **Protoplasm** exists in all young cells — for instance, in the soft cone of tissue in buds, in root-tips, and other points of growth — as a nearly transparent or finely granular substance.[1] It completely fills the interior of very young cells, but with increase of the cells in size there arise cavities (*vacuoles*) containing sap, and these by their enlargement and confluence may appear to occupy the entire space within the cell. If, however, such a cell be acted upon by anything which causes contraction

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(2) Make a thin section through the petiole of a begonia or some common house-plant, and observe the granules imbedded in the protoplasm (*chlorophyll-granules*); notice also crystals, either in masses or single.

(3) Examine a thin section through dry pine wood, test with iodine, and observe the absence of protoplasmic matters. Examine in the same way any hard wood.

(4) Make a section through any starchy seed, for instance a common bean, and treat it with a solution of iodine; notice the distribution of protoplasmic matters in the form of thin irregular films throughout the cells. Examine a similar section in oil, and see what differences, if any, can be detected. Probably the presence of *protein granules* will be made out.

From these preliminary examinations a beginner will have demonstrated the protoplasmic matter in its active, resting, and reserve states; he will have seen chlorophyll, the nucleus, and starch, the chief form in which food is stored in plants. He will also have seen a few of the more common crystals.

After such a study the student is urged to examine practically the characteristics of the cell-wall and the cell-contents as they are presented in this chapter.

[1] By the use of staining agents, especially hæmatoxylin, protoplasm can in many cases be shown to possess a complicated mesh of very delicate fibres,

of the protoplasm,[1] as, for instance, a solution of common salt, the protoplasm separates from the cell-wall, and by its contraction shows clearly that it is a closed sac. At a later stage in some cells even this thin protoplasmic sac wholly disappears.

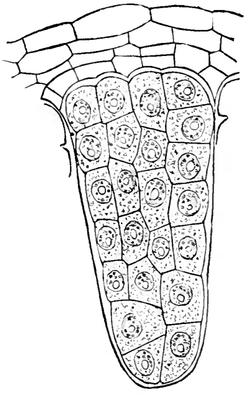

Fig. 1. From developing anther of Orchis maculata, showing young cells completely filled with protoplasm. Observe also the nucleus with its nucleolus, in each cell. (Guignard.)

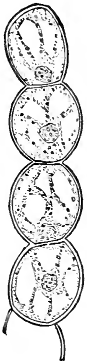

Fig. 2. A hair from the stamen of Tradescantia pilosa, showing the protoplasm in the form of granular threads running from side to side of the cell-cavity. The white spaces between these threads are vacuoles. The nucleus can also be seen in each of the four cells. (Jacobs.)

121. Protoplasm itself must be regarded as essentially transparent and colorless, but it is seldom found without some admixture of other matters, which give it a granular appearance. The granules are generally very small, and as a rule are not found at the periphery of the mass. The limiting surface of the protoplasmic mass is further distinguished by being somewhat denser and firmer than the substance it encloses; and although it cannot be separated from the latter by mechanical means, it is often spoken of as a film;[2]

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which take up the coloring matter readily, leaving the remainder of the mass unstained. It is believed by Schmitz that the unstained mass is a homogeneous liquid filling the meshes (Sitzungsber. der niederrhein. Gesellschaft in Bonn, 1880).

[1] Such substances are termed *plasmolytic* agents.

[2] Of the appearance of protoplasm, the following remarks by Mohl, who first gave it the name in 1846, are of interest. "If a tissue composed of young cells be left some time in alcohol, or treated with nitric or muriatic acid, a very thin, finely granular membrane becomes detached from the inside of the wall of the cell in the form of a closed vesicle, which becomes more or less contracted, and consequently removes all the contents of the cell, which are enclosed in this vesicle, from the wall of the cell. Reasons hereafter to be discussed have led me to call this inner cell the *primordial utricle*. . . . In the centre of the young cell, with rare exceptions, lies the so-called *nucleus cellulæ* of Robert Brown. . . . The remainder of the cell is more or less densely filled with an opaque, viscid fluid of a white colour, having granules intermingled in it, which fluid I call *protoplasm*" (Mohl: The Vegetable Cell, Henfrey's Translation, 1852, pp. 36, 37).

and where there is any break in the continuity of the mass, for instance in the case of sap-cavities, a similar limiting film may be supposed to exist.

122. The consistence of protoplasm depends on the amount of water which it contains. Thus in dry seeds it is nearly as tough as horn, while in the same seeds during germination it becomes like softened gelatin. It absorbs water readily and becomes permeated by it, thereby increasing its apparent fluidity, but it never becomes a true fluid. Moreover, there is a limit to the amount of water which it takes up.

123. Chemically considered, protoplasm is a very complex substance. It belongs to a group of bodies of which the albumin of egg may be conveniently taken as the type. They undergo many slight but sometimes remarkable changes, and have been collectively termed proteids. The terms *albuminoids* and *proteids* may be used interchangeably (see 857).

124. The albuminoids, or proteids, which form with water the bulk of protoplasm proper, are of course associated with the matters which this living substance makes, uses, and discards. But these matters exist in the protoplasm in very different proportions at different times, though never in such amount as to obscure the peculiar reactions of the albuminoids. These are the following: 1. The yellow or brownish color imparted by solutions of iodine. 2. The purple color produced when the specimen first saturated with a solution of cupric sulphate is acted on by potassic hydrate. 3. The rose color, often faint, which follows the successive action of a solution of sugar and strong sulphuric acid. 4. The red color given by Millon's reagent. This test generally requires the cautious application of heat. 5. The yellow or orange color following the application, in succession, of strong nitric acid and ammonic hydrate.

125. Dilute solutions of the caustic alkalies dissolve protoplasm; concentrated solutions do not. If a young cell is acted on by concentrated potash, its protoplasm is not essentially affected; but if water is now added, the protoplasm dissolves at once.

126. The spherical or ellipsoidal mass found in the protoplasm of active cells, and differing from the rest of the protoplasm in its greater density, is the *nucleus*. The sharply defined point often seen in the nucleus is the *nucleolus*.

127. The nucleus undergoes remarkable changes during the earliest stages of the cell, which will be described in the chapter on "Growth." The relations which exist between the proto-

plasm in one cell with that in contiguous cells will be considered in Chapter VI.

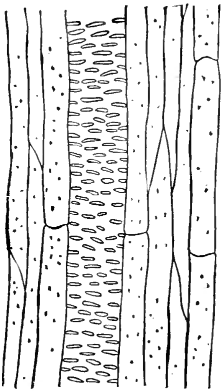
128. **The cell-wall.** The cell-wall is produced from materials contained in protoplasm,[1] and is laid down in intimate contact with it, as an even homogeneous film which exhibits at first no obvious structure, but with increase in size generally becomes modified in appearance, consistence, and composition.

129. Its evenness of surface is in most cases early lost by addition of new matter, giving rise to protuberances or markings of different sorts. Though at first possessing no evident structure, it may become clearly differentiated into layers, and thus become stratified, or striations may appear. Its consistence, at the outset that of the most delicate bleached linen fibre, may soon become changed, on the one hand to that of soft gelatin, or on the other to that of the densest wood. Moreover, although devoid of color when first produced, it may acquire distinct coloration; and, lastly, its chemical character may undergo such important changes that its normal reactions are no longer given.

130. **The markings of the cell-wall.** Uniform thickening of the whole cell-wall is extremely rare; even in the examples which are commonly given to illustrate it, pores or channels, more or less distinctly visible, interrupt its continuity.

131. The thickenings may possess great irregularity, or they may be so strictly localized and regular as to form characteristic features of the widest use in diagnosis. They may project outwardly, forming ridges, spines, and other sculpturings; or, as is most commonly the case, inwardly, giving rise to rings, spirals, etc.

132. If the wall is thickened throughout, except at well-defined points, depressions or pits are produced, varying considerably in outline, but occurring generally as simple dots or lines. In some cases it is not difficult to see that these dots or lines are true pores or fissures running from one cell to the next.



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[1] According to Schmitz, the cell-wall is produced by the conversion of the limiting film of protoplasm into cellulose. That the cell-wall is formed *at* the limiting film admits of no question.

FIG. 3. Pitted duct; from stem of Cichorium Intybus. (Jacobs.)

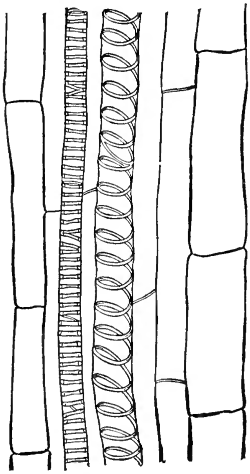
133. Bordered pits are a very common modification of the last. A comparatively large spot remains unthickened, but becomes covered by a low dome which has at its top a small aperture; at a corresponding point of the wall of the neighboring cell another thickening produces a similar dome, so that the two domes constitute a double convex body which appears as a disc with a central perforation. These bodies are known as discoid markings.

134. Sometimes the spot covered by the arched projection or dome is elliptical instead of round. When this kind of marking becomes linear, or nearly so, it is termed scalariform.

135. When annular and spiral thickenings occur the cell-wall lying between them remains so thin that a slight strain suffices to break it, releasing the rings and coils. The number, the direction, and the steepness of the spirals furnish in some cases diagnostic features.

136. Besides spirals and rings, there are intermediate forms, which pass easily over into netted or reticulated thickenings. It happens sometimes that the reticulated markings are so regular that their interspaces appear as regular polygons.

137. The external sculpturing of the cell-wall can be seen in many pollen-grains, and in the hairs of many plants, though in the latter case the projections may be partly due to irregularities in the form of the cell.



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138. **Stratification and striation.** The cell-wall, even at an early stage, frequently exhibits a distinctly stratified structure. In some cases, at least, removal of all the water which forms a constituent of the wall obliterates every trace of stratification, and this fact supports the hypothesis that the appearance of lamination is caused by differences in the amount of water contained in alternating layers of the wall. The less strongly refractive layers are supposed to contain more water than those which are highly refractive. But there are cases of stratification

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FIG. 4. Annular and spiral markings; vertical section through stem of Tradescantia pilosa. (Jacobs.)

which cannot be satisfactorily explained by this hypothesis. There are, besides, numerous instances in which the stratified appearance is not clearly shown until the cell has been acted on by an acid or an alkali; a good example of this is afforded by the firm cells of the albumen of the vegetable ivory (Phytelephas).[1]

139. An appearance of spiral striation,[2] ascribed also to the unequal distribution of water, is often seen, especially in the cells of the liber of Apocynaceæ and allied orders, and in many wood-cells. The striations are not constant as regards the steepness of the spiral; in fact, in a few instances rings instead of spirals are present. A striated appearance is sometimes presented in walls which have been deprived of all their water.

140. Chemically considered, the young cell-wall consists essentially of cellulose, a substance which has the same percentage composition as starch, namely, $C_6H_{10}O_5$. Even in its purest state it is associated with a trace of mineral matters which remain behind as ash when it is burned, and in the living cell it is always permeated by water.

141. **Cellulose** is not soluble in any of the following liquids commonly used in microscopic manipulations, — water, alcohol, glycerin, dilute alkalies, and dilute acids. It is, however, more or less strongly acted on by hot concentrated alkalies, without passing into true solution, and it is apparently dissolved by strong sulphuric acid. Whether cellulose becomes truly dissolved by concentrated sulphuric acid, or merely forms some other carbohydrate under its action, is of little consequence, so far as the destruction of cell-walls is concerned. In nearly all cases its action is so energetic that the wall of a cell can be

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[1] As shown by Mohl, the action of a mineral acid of proper degree of concentration causes the wall to swell up, and the lamellar structure becomes very distinct. "By this means the lamellar structure may be demonstrated even in those cases in which the unaltered membrane appeared completely homogeneous" (Mohl: Vegetable Cell, p. 10).

[2] "The stratification is visible on the transverse and longitudinal sections of the cell-wall, the striation on the surface as well; it is usually most evident there, but is in general less easily seen than the stratification; it depends on the presence of alternately more or less dense layers in the cell-wall, meeting its surface at an angle. Generally two such systems of layers may be recognized mutually intersecting one another. There are thus all together three systems of layers present in cell-wall: one concentric with the surface, and two vertical or oblique to it mutually intersecting, like the cleavage planes of a crystal splitting in three directions (Nägeli); and just as this cleavage is sometimes more evident in one direction, sometimes in another, so it is also with the stratification and striation" (Sachs: Text-book, 2d Eng. ed., p. 20).

wholly removed by this acid, even without destroying the protoplasmic contents; and this fact has been extensively employed in the examination of the continuity of the protoplasm in contiguous cells.[1]

142. The only known solvent from which cellulose can be recovered without change of composition is Schweizer's reagent, ammoniacal solution of cupric oxide. In this liquid, cellulose swells considerably, and slowly disappears. It is thought by some chemists that it does not truly dissolve. From its apparent solution, it can be precipitated in the form of a flocculent mass by acids, salts of many kinds, and even by the addition of a large amount of water (see 55).

143. Freshly prepared aqueous and alcoholic solutions of iodine do not color pure cellulose beyond giving a faint yellowish tint; but if the reagents have been kept for some time, particularly in the light, they may impart a blue color.[2] The latter

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[1] Unsized, well-bleached linen paper is nearly pure cellulose. If it is dipped in a cold mixture of one volume of water and two volumes of strong sulphuric acid, withdrawn after ten to twenty seconds, and washed thoroughly in water, and finally in dilute ammoniacal water, it becomes much like parchment. This "vegetable parchment" is a suitable membrane for certain experiments in absorption. The acid in this experiment is supposed to convert at least a portion of the cellulose into a substance which closely resembles starch in its chemical reactions, termed *amyloid.* Parchment paper can be made also by concentrated zinc chloride, and by a few other agents.

[2] Mohl (The Vegetable Cell, p. 24, Eng. Trans.) says: "When imbued with iodine, it becomes indigo-blue if wetted with water." In a note on pages 28 and 29, he further says: "My researches shewed me that the influence of sulphuric acid was by no means necessary for the production of the blue colour in membranes which are not strongly incrusted, as in the parenchymatous cells of succulent organs, but that iodine and water alone are sufficient; while in full-grown and hardened cells sometimes the primary membrane alone, sometimes even a greater or smaller portion of the secondary layers had through the deposition of foreign substances, altogether lost the property of becoming blue on the application of sulphuric acid and iodine, although they were still composed of cellulose, and iodine alone would very readily produce a blue colour in all their membranes after the infiltrated matters had been removed. The means I employed to remove the infiltrated substances were caustic potash and nitric acid. . . . After this treatment, the whole of the layers of all elementary organs are coloured a beautiful blue by iodine even when they offer so great a resistance to the action of sulphuric acid before the treatment with nitric, as is the case in the outer membrane of wood-cells and of vessels, and in the brown cells at the circumference of the vascular bundles in Ferns."

It is plain that, in the latter cases, the cell-wall had been very powerfully acted on before the application of the iodine, and to this severe preliminary treatment may be ascribed the efficiency of the latter in producing the blue color.

color, however, is given even by fresh solutions of iodine to cellulose which has been previously treated with certain chemical agents, for instance, strong sulphuric acid. A convenient method of employing this reaction as a test for cellulose is to thoroughly moisten the object with a dilute solution of iodine, and then to apply strong sulphuric acid, upon which the cellulose immediately turns bright blue. It is sometimes advantageous to dilute the sulphuric acid employed, either with water or with glycerin; but for most cases the concentrated acid is the best.

Schulze's solution of iodine, better known as chloroiodide of zinc, used alone, gives with pure cellulose a blue color inclining to purple. This reaction, though not always so prompt as the other, is generally more manageable, and, on the whole, more satisfactory.

In a few instances the cell-membrane becomes yellowish-brown throughout, upon the application of an iodine solution, a reaction which might be easily mistaken for that which albuminoids give; that the color, however, is not here due to their presence, appears on subjecting the tissue to the action of Millon's reagent. Vertical sections of the stem of Begonia, as noticed by Nägeli, afford an instructive example of this.[1]

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[1] That the yellow color imparted by iodine has been otherwise interpreted, will appear from the following: —

Harting (Ann. des Sc. nat., sér. 3, tome v. p. 328) states, that "all lignified cells have Protein matters in their walls."

Mohl (The Vegetable Cell, p. 25) says: "Nitrogenous compounds *do not* occur in the membranes of cells which are just at the commencement of their development, for these are not coloured yellow by tincture of iodine, yet hardly a full-grown cell is met with in which this is not the case."

It is held by Nägeli that vegetable cell-membranes consist, in some instances, of two isomeric substances, unequally soluble, which are intimately commingled. One of these is soluble in cold water, more easily in hot water, and sometimes needs for its complete extraction a dilute acid. From the solution iodine throws down a blue or bluish-green precipitate.

A synoptical table, based on differences in solubility of cellulose and its modifications, and in their behavior towards iodine, has been constructed by Nägeli. The part of the table which is given below affords excellent practice for the beginner.

I. DIFFERENCES IN SOLUBILITY.

(1) In cold water, becoming swollen; in hot water, disappearing, *vegetable mucilage; e. g., in the outer layer of the cells forming the testa of quince seeds and those of flax.*

(2) Soluble in concentrated sulphuric acid, and in cuprammonia; *e. g., cotton-hairs, bast-fibres,* etc.

144. The principal modifications of the cell-wall are the following: —

(1) Partial or complete conversion into mucilage (Gelatination); (2) Lignification; (3) Cutinization (or Suberification); (4) Mineralization.

145. All of these, except the first, change the chemical character of the cell-wall only by what may be regarded as infiltration; upon removal of the infiltrated matter by means of proper agents, the cellulose basis of the wall is left behind with very little if any change.

146. It sometimes happens that one part of the membrane of a cell, or even one of its layers, may be modified in one way, and another in another; it is also possible for the same membrane to undergo two of the changes above mentioned; namely, Lignification and Mineralization.

147. **The mucilaginous modification.** Commonly the cell-wall is not much changed by immersion in water. It may become more nearly transparent, but its size and density are not essentially

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(3) Soluble in sulphuric acid, insoluble in cuprammonia (unless previously acted on by acids or alkalies); *e. g., the pith*, and *medullary rays of woods.*

(4) Soluble in concentrated sulphuric acid; insoluble in cuprammonia, but becoming soluble in this upon previous treatment with Schulze's macerating liquid; *e. g., wood-cells of pine, oak, yew*, etc.

(5) Insoluble in concentrated sulphuric acid and cuprammonia, but soluble in boiling concentrated potassic hydrate; *e. g., cuticle*, and *the outer layer of the membrane of older ducts.*

II. Iodine Reactions.

(1) With iodine and water, a blue color: *lichen-filaments*, etc.

(2) With iodine and water, no color; but giving a blue tint with iodine and a metallic iodide; or when iodine is followed by sulphuric acid: —

A. *Thin-walled Parenchyma* (which will often turn blue when a pure iodine solution acts with repeated drying), *older Parenchyma, the inner part of thickened wood-cells of Pinus and Abies*, and *the bast-fibres of hemp.*

B. Only when the reagents have been preceded by the application of nitric acid: *all membranes in the interior of the plant, e. g.*, the outer part of wood-cells and ducts, the brown cells which surround the vascular bundles in ferns, etc.

C. Only when the reagents have been preceded by the use of boiling potassic hydrate: *cork*, etc.

According to Frémy and Urbain, the substances which form the skeleton of plants are principally pectose and derivatives from it, cellulose and its isomers, vasculose, and cutose. These four groups are thus distinguished from one another.

Pectose acted on by alkaline carbonates is changed into pectic acid, and affected. It sometimes happens, however, that the cell-wall acquires wholly new relations to water, and becomes capable of absorbing a large amount of it with great increase of volume and translucency. A cell-wall which has undergone this mucilaginous modification takes on, when placed in water, the consistence of soft gelatin, and if the mass is then warmed it appears to dissolve, forming a thick mucilage. Upon drying, the mucilage hardens into a translucent gum, in which the cellulose character is nearly or wholly lost.

148. Generally the changes produced in such a wall by water are so rapid that it is desirable to place the specimen at first in alcohol, and then to replace this medium cautiously by water or by dilute glycerin, when the variations in shape, size, and consistence can be easily followed. The addition of alcohol will of course arrest the changes at any stage desired.

149. These changes can be easily traced in the outer cells of the integument of a flax-seed. The mucilage appears as an obscurely stratified mass nearly filling the cells, except at their centre, where there is a low-arched cavity. On the cautious

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pectates are formed. These are readily decomposed by hydrochloric acid, and insoluble gelatinous pectic acid is thrown down.

Cellulose and its isomers agree in being soluble in concentrated sulphuric acid, but they differ in the following points: Cellulose dissolves at once in cuprammonia; paracellulose, only after the action of acids; metacellulose, not even then.

Vasculose is not easily soluble in concentrated sulphuric acid, but after the action of oxidizing agents gives rise to resinous acids, which are separable by alkalies from associated cellulose.

Cutose, the transparent film covering the aerial organs of plants, is dissolved neither by concentrated sulphuric acid nor by cuprammonia, but dissolves without change in alkaline liquids. The following results of analyses by Frémy and Urbain (Ann. Sc. nat. bot., 1882) show approximately the amount of these substances in different parts of certain plants.

Root of Paulownia. — (1) Substances soluble in water and in dilute alkalies: cork 45, soft bast 56, body of root 47. (2) Vasculose: cork 44, soft bast 34, body of root 17. (3) Paracellulose: cork 4, soft bast 4, body of root 30.

Stems. — Vasculose increases in amount with the density of the wood. The pith contains: of cellulose 37, paracellulose 38, vasculose 25 per cent. Cork contains: matters soluble in acids and alkalies 5, cutose 43, vasculose 29, cellulose and paracellulose 12 per cent (cutose and vasculose forming together the subérine of Chevreul).

Leaves of Ivy. — Water and substances soluble in neutral solvents 707.7, parenchyma (formed of cellulose and pectose) 240, fibres and vessels (of vasculose and paracellulose) 17.3, epidermis (cutose and paracellulose) 35 parts.

Petals of Dahlia. — Water and soluble matters 961.30, parenchyma (of cellulose and pectose) 31.63, vasculose 1.20, paracellulose 2.27, cutose 3.60 parts.

addition of water, this cavity becomes more clearly defined, the whole mass of the cell swells, and the mucilage can then be made out as a distinctly stratified structure belonging apparently as much to the outer as to the inner face of the cell-wall. But if the action of water is prolonged, the stratified appearance vanishes, and the wall becomes optically homogeneous, with the exception of its middle portion, the so called primary membrane, which remains unchanged. On the addition of iodine and sulphuric acid, the primary membrane, but not the mucilage, becomes blue. Furthermore, the lateral walls of the cells are not converted into mucilage.

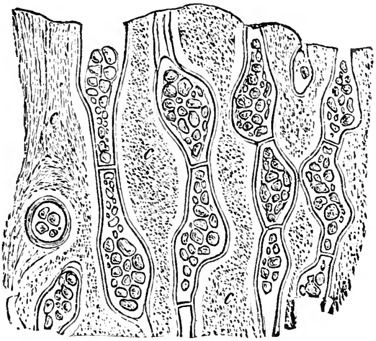

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FIG. 5. Section of the albumen of Ceratonia siliqua, showing mucilaginous modification. (Sachs.)

150. The mucilaginous modification can be examined to advantage in the seeds of some Polemoniaceæ (especially Collomia) and a few Acanthaceæ, *e. g.*, Ruellia. These seed-coats are covered with hairs which break open when wet, and allow not only the mucilage but also slender coiled threads to escape. The achenes of some Compositæ of the Senecio group and the nutlets of a few Labiatæ (the Salvia tribe) exhibit nearly the same phenomenon.

151. **Lignification.** Induration of the cell-wall is caused most commonly by the presence of an incrusting substance known as lignin. Owing to the difficulty of separating it from the cellulose, with which it is associated, its chemical composition must be regarded as uncertain. Although generally spoken of as a single substance, it is probable that the lignin, or incrusting matter, is made up of several different substances,[1]

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[1] Payen (Mém. des savants étrangers, ix., 1846, pp. 68, 5) distinguished four such incrusting matters, differing in their composition and in their behavior to solvents. *Lignose:* insoluble in water, alcohol, ether, and ammonia; soluble in solutions of potassa and soda. *Lignone:* insoluble in water, alcohol, and ether; soluble in ammonia, potassa, and soda. *Lignin:* insoluble in water and ether; soluble in alcohol, ammonia, potassa, and soda.

which occur in different proportions in different plants and in different parts of the same plant.

152. Lignin dissolves readily in Schulze's macerating liquid and in potassic hydrate, but not in cuprammonia, the well-known solvent for cellulose.

153. By the use of Schulze's macerating liquid a lignified cell-wall can be wholly freed from its incrusting substance, and pure cellulose will be left behind. For control, it is well to employ the tests for lignin given below, both with ordinary wood and with similar specimens which have been treated with this solvent.

154. *Tests for lignin.* 1. Salts of anilin. If a lignified cell-wall is subjected to the action of a strong solution of anilin sulphate acidulated with sulphuric acid, or to that of a solution of anilin chloride acidulated with hydrochloric acid, it will at once turn yellow. The depth of the color depends somewhat upon the strength of the solution. The color is destroyed by alkalies, but is restored by acids. Wiesner, who first applied the foregoing reagents to the detection of lignin, has suggested another which is for many cases even more satisfactory; namely, 2. Phloroglucin. In an alcoholic or aqueous solution of this substance (.01 per cent) a lignified cell-wall does not change color; but if the specimen is slightly acidulated with hydrochloric acid, it becomes violet or purple. 3. Carbolic acid (phenol) and hydrochloric acid. The solution described on page 11 imparts to lignified cell-walls, when exposed to a strong light, a green color which is very fugitive. Specimens under examination should therefore be watched from the moment that the reagent reaches them. 4. Indol. An aqueous solution is to be replaced under the cover-glass, after it has moistened the specimen thoroughly, by a little dilute sulphuric acid; lignified cells will become red or reddish-violet. This reagent does not appear to have

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Ligniréose: soluble in all the solvents mentioned above, but only to a slight extent in water.

CHEMICAL COMPOSITION.

	Carbon.	Hydrogen.	Oxygen.
Lignose	46 10	6.09	47.81
Lignone	50.10	5.82	44.08
Lignin	62.25	5.93	31.82
Ligniréose	67.91	6.89	25.20
Cellulose (of cotton)	44.35	6.14	49.51

According to Franz Schulze, the probable composition of lignin is: Carbon, 55.55; Hydrogen, 5.83; Oxygen, 38.62.

any marked advantage over that which gives nearly the same color, namely, phloroglucin.

155. By the employment of these reagents many cell-walls have been shown to be distinctly lignified when the older reagent — iodine in solution — failed to detect the change.

156. **Cutinization.** Ordinary and lignified cell-walls, and those which have undergone the mucilaginous modification, absorb water freely. On the other hand, the walls of certain cells found chiefly on the exterior of organs are repellent. The substance which imparts the repellent character to the cell-wall is known as cutin; when restricted to cork it is called suberin.

157. Cutin and suberin have been described as different substances; but although the former is more generally associated with waxy matters, its reactions are essentially the same as those of suberin. The water-proofing of the cell-wall may be superficial, as in most young epidermal cells, or it may affect the whole structure of the wall, as in the case of cork. If a distinction is made between the two states, the first may be termed cutinization, the second, suberification.

158. Cutin can be removed from the walls with which it is associated, by the use of Schulze's macerating liquid, subsequent treatment with potassa, and careful washing. It is sometimes necessary to heat the section in potassa before the cellulose can be completely freed from the other matters.

159. Höhnel[1] has shown that the wall of a cork-cell, with the exception of the young cork-cells in Coniferæ, is composed of five plates: (1) a middle plate, common to the two contiguous cells; (2) two plates, one on each side of the latter, consisting of cellulose which is both cutinized and lignified; (3) two plates of cellulose forming the inner lining of the respective cells. The latter plates may be more or less lignified. Differences in the relative proportions of these constituent plates give rise to differences in the character of different kinds of cork.

160. As in the case of lignin, the difficulty of extracting cutin renders its chemical composition doubtful. It is usually given as follows: —

Carbon	73–74 per cent.
Hydrogen	10 "
Oxygen	17–16 "

But there is also a trace of nitrogenous matter demonstrable; this probably belongs to residual protein matters which are in

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[1] Sitzungsber. d. k. Akad. Wien, Bd. lxxvi. 1 Abth.

the cell-cavity, and not in the cell-wall. Sulphuric acid and chromic acid, even when concentrated, produce little effect on cutinized membranes, beyond removing traces of cellulose present in the cell-wall. The latter acid, however, increases the transparency of cutinized membranes, especially after prolonged action.

161. Potassic hydrate softens such membranes and colors them yellow; when heated it breaks them into a granular mass which may be removed by careful washing. Cautiously heated with Schulze's macerating liquid, they disintegrate into granules of ceric acid, — a substance which dissolves in alcohol, ether, and benzol. Several of the coal-tar colors stain the cutinized portions of cell-walls very deeply; if the specimen thus colored is placed in absolute alcohol, the cutinized parts alone remain colored.[1] Two points relative to the cutinization of epidermal cells may be noted: (1) the cutin may take on the form of layers, often numerous and conspicuous; (2) there may be a considerable irregularity in the outline of the deposits, sometimes as folds, hooks, and the like, which do not strictly conform to the cellulose wall on which they arise.

162. **Mineralization of the cell-wall.** Although all cell-walls, even the most delicate, can be shown to contain traces of inorganic matter, it is only in a few special cases that such substances appear in a form to be noticed under the microscope. Mineralization of the wall may be general or local, may depend upon the presence of crystals or of amorphous deposits, and these may consist of silicic acid or of calcium salts.

163. General mineralization of the wall depends most frequently on silicic acid, and may be best demonstrated by first boiling the specimen in nitric acid, drying, heating to redness on platinum-foil, and, lastly, treating again with nitric acid. The silicic acid remains behind as a delicate skeleton which copies in all particulars the contour of the wall of which it formed a part. Fine examples are afforded by the harder grasses.[2]

Calcium salts may exist in crystalline or amorphous form, and may be distinguished by the tests to be given for them under the section on "Crystals." That in some cases they constitute an integrant part of the wall itself admits of no question.

164. In the cells of many plants, especially Urticaceæ, pedicellated concretions occur, which, on superficial examination,

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[1] Olivier: Bull. Soc. bot. de Fr., 1880, p. 234.

[2] *Tabasheer* consists of the siliceous substances which occur in the joints of bamboo in large quantities.

appear to be much like the sphere-crystals described in 186. But if they are carefully treated with dilute hydrochloric acid, the chief part of the concretion disappears, leaving behind a delicate trace of cellulose which was intermingled with it. That this cellulose was an intrusive growth into the cell from the wall, is shown by a study of its development. In most cases such concretions (Cystoliths) are plainly stalked, but in some instances they are only obscurely stalked, and are with difficulty distinguished from the ordinary cell concretions. In the leaf of Ficus elastica (see Fig. 6) they are more completely developed than in any other common plant.

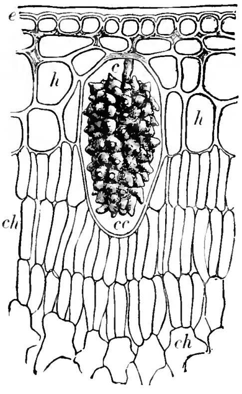

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FIG. 6. Cystolith from the upper part of a leaf of Ficus elastica. *e*, epidermis; *h*, hypoderma; *c c*, cystolith; *ch*, *ch*, cells containing chlorophyll. It will be observed that the pedicel of the cystolith appears to be attached to the lower wall of the upper epidermal cells.

165. Other changes, chiefly those of degradation, may take place in the cell-wall, giving rise to products variously known as gums, resins, &c.; but in all these cases there is such a commingling of the cellulose derivatives with those formed from the contents of the cell, that they cannot be readily distinguished.

166. Protoplasm, as was shown in the previous sections, gives rise upon its exterior to the cell-wall. Inside the cell, likewise, it produces, either directly or indirectly, various substances. In the present chapter these substances are to be considered only so far as relates to their detection and identification. Most of them are to be examined later, with reference to their office in the life of plants.

167. **Plastids.** In the protoplasm of active cells certain granules having substantially the same chemical and, with the exception of their color, the same physical properties as protoplasm, are clearly differentiated. They are imbedded in the general protoplasmic mass, and are not separable from it by mechanical means.

168. Such granules may be conveniently referred to three types,[1] depending upon the color: (1) those which are green, —

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[1] Recent investigations render it probable that these three kinds of granules are derived from a common source, and although hardly distinguishable from

Chloroplastids, or chlorophyll granules, also called chloroleucites; (2) those which have some color other than green, — *Chromoplastids*, or chromoleucites; (3) those which are devoid of color, — *Leucoplastids*, or leucites.

169. *Chlorophyll Granules*, or *Chloroplastids*, are met with in the green parts of all plants; in fact, to them the green color is due. But they are sometimes masked by the presence of color in the cell-sap. Their shape is spherical or spheroidal, and somewhat flattened. They have an average diameter of 2 to 5 μ, but many granules are considerably larger than this. It frequently happens that they become of great size, owing to the presence of solid contents, — for instance, starch, — which may accumulate in large amount.

170. If the granules are subjected to the action of alcohol, their coloring matter is wholly removed; but they retain their former volume and shape, appearing faintly outlined in the protoplasmic mass in which they are imbedded. Hence it is proper to distinguish between the chlorophyll body of the chloroplastid and the chlorophyll pigment which imparts to it its characteristic color.

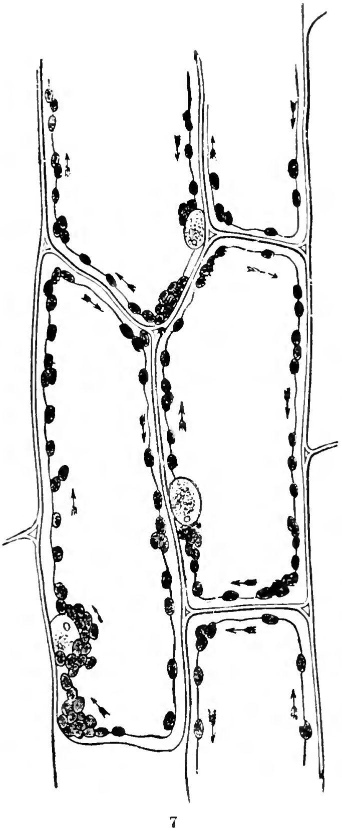

FIG. 7. Chlorophyll granules in the leaf of Vallisneria spiralis. $\frac{400}{1}$. (Weiss.)

The chlorophyll body may be shown, by the process described in 61, to be somewhat spongy in structure, and to have on its

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each other at the outset, become chloroplastids, chromoplastids, or leucoplastids, according to the part which each is to play. Moreover, one kind of granule can, under certain conditions, perform work which properly belongs to another, and hence it is not always easy to identify the different kinds. In most cases, however, their discrimination is very simple.

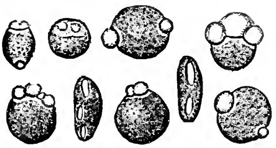
They are also called, collectively, **Chromatophores.**

exterior a delicate film. Meyer believes that the coloring matter takes the form of grains of extreme minuteness which are interspersed through the whole substance, while Tschirch holds that the pigment, dissolved in a liquid similar to the ethereal oils, is diffused through the mass.

171. If starch is present in large amount in chloroplastids, iodine causes at once a deep bluish-brown color; but if the starch is not very abundant, the characteristic blue reaction is concealed by the yellow produced by the protein reaction of the protoplasm. Hence it is well, after having removed the chlorophyll pigment by alcohol and subsequent washing with water, to treat the specimen with moderately strong potassic hydrate in order to dissolve the protein matters. If this has been well done, and the specimen carefully freed from the potash, the protoplasmic mass and its imbedded granules will seem to have completely disappeared; but the skilful use of oblique illumination will show that an undissolved trace of something having the former contours remains behind. Application of iodine brings out minute blue points where the granules were.

Chloral hydrate of the strength recommended in 53 may replace potassic hydrate in this examination.

172. The starch in chlorophyll granules is sometimes wholly within the granule; but it is occasionally — especially in the case of flattened granules — found on their exterior, forming a noticeable protuberance.



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173. When a plant containing chlorophyll granules is kept for a time in darkness, the production of starch is arrested; and if other forms of activity continue, even that starch which has already accumulated in the granules soon disappears. Furthermore, the color of the granules is changed from green to yellow; and if the change is not arrested at this point by bringing the plant again into the light, all the granules will break up and become apparently merged in the

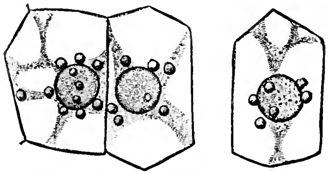

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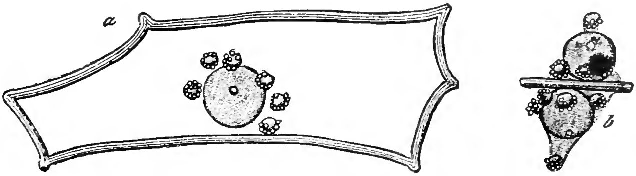
FIG. 8. Chlorophyll granules with protruding starch-grains. From the cortex of Philodendron grandifolium. $\frac{850}{1}$. (Schimper.)

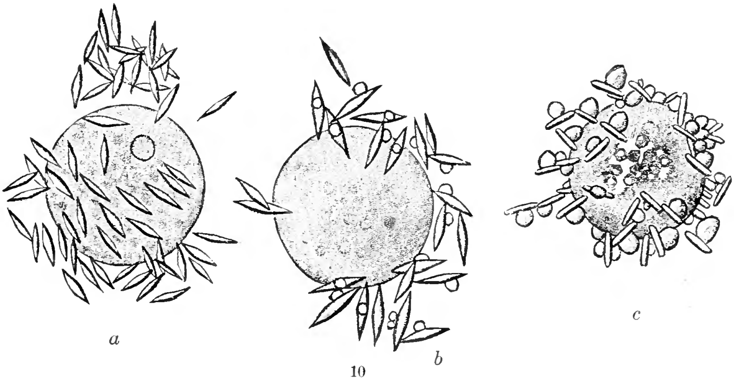
FIG. 9 *a*. From the epidermis of Philodendron grandifolium. Young cell with amylogenic bodies newly formed. $\frac{850}{1}$. (Schimper.)

general protoplasmic mass of the cells, being no longer recognizable. Those, however, which have been changed no further than by loss of color, closely resemble another kind of granule; namely, leucoplastids. (For exceptions see Chapter X).



9 *b*

174. *Leucoplastids.* These are found in parts which are normally devoid of chlorophyll, such as tubers, rhizomes, etc. They may be wholly colorless, or faintly tinged with yellow, and hence are apt to escape detection. They may be considered as the points around which starch accumulates when stored for the future needs of the plant. Schimper,[1] who first accurately described them in all their relations, terms them "starch generators;" they are also known as *amylogenic* bodies, which of course means the same thing. They are seen to the best advan-



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[1] Schimper: Bot. Zeit., 1880, 1881, 1883.

FIG. 9 *b*. Same, more advanced: *a*, the amylogenic bodies are covered with starch-grains; *b*, two nuclei on a cell-wall, each surrounded by amylogenic bodies covered by starch. $\frac{850}{1}$. (Schimper.)

FIG. 10. *a*, Young amylogenic bodies surrounding the nucleus of a cell in the root of Phajus grandifolius; *b*, same, with starch-grains developing; *c*, same, more advanced. $\frac{850}{1}$. (Schimper.)

tage in thin sections of many starchy tissues, by the use of dilute tincture of iodine, which colors them more or less deeply yellow. Millon's reagent colors them red.

Owing to the minuteness of the leucoplastids, the following explicit directions by Strasburger will aid in their detection: Make thin longitudinal sections through the upper part of a young pseudobulb of Phajus grandifolius, taking care that the cut extends to its green surface. Immediately place the sections in an alcoholic solution of iodine diluted with one half its volume of water. (Picric acid may be advantageously used instead of the iodine solution.) In good preparations the leucoplastids will be seen in the inner part of the section as small staff-shaped bodies which, at the first glance, appear to be homogeneous, but are afterwards recognized as somewhat granular in structure. The section is next to be examined nearer its outer part, and it will then be seen that the bodies there possess a green color, are larger, and lenticular in form. They are also plainly porous, their increase in size being apparently associated with a sponginess of their substance. Their size diminishes towards the outer cellular layers, they become somewhat rounded, and finally take the familiar form of chlorophyll granules. Prismatic colorless protein crystals are frequently associated with these bodies. In sections which are placed in water, the leucoplastids disappear almost instantaneously, and even the chlorophyll granules soon begin to disorganize, while the swollen protein crystals then appear as colorless parts of the latter.

In the rhizome of Iris Germanica the sections for examination must be taken parallel to the surface. In uninjured cells the leucoplastids appear as collections of protoplasm at the end of each starch-granule. If the section is in water, the leucoplastids become granular and finally break up into minute granules which show the Brownian or molecular movement.[1]

Chromoplastids, or the color-granules which occur abundantly in flowers and fruits, will be specially treated later.

175. **Protein granules.** The protein matters in plants have been divided into two classes: (1) the *active*, such as active protoplasm, the nucleus, etc.; (2) the *reserve*, which can change their dormant condition and become active when occasion demands. Inactive, amorphous protoplasm, as it sometimes exists in certain cells, where it is simply a tough shapeless mass, does not need further consideration at present; the reserve matters

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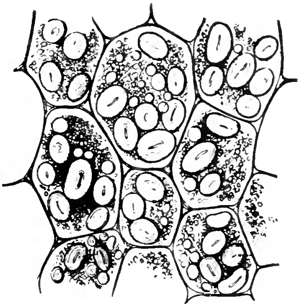
[1] Strasburger: Das botan. Practicum, 1884, pp. 67, 68.

now to be examined being those which take the form of more or less regular grains. These which are known as

176. Protein granules may be either independent, or associated with other substances. In nearly all cases they are more or less soluble in water, and hence require special treatment for their satisfactory examination. Cells supposed to contain them may be placed for examination in any fixed oil, and the granules will remain unchanged. A more practicable method of treatment is suggested by Pfeffer; namely, to subject the granules to the action of an alcoholic solution of mercuric chloride, by which they are rendered insoluble (see 63). The solution is made by dissolving one part of mercuric chloride (corrosive sublimate) in fifty parts of absolute alcohol; in this solution the thin sections of seeds, etc., suspected of containing protein granules, must be kept for at least twelve hours. Upon removal to water, after this period, they remain substantially unchanged. The precaution must be taken not to touch with any metal the sections after they have been placed in the mercuric chloride solution. They must be removed by a camel's-hair brush.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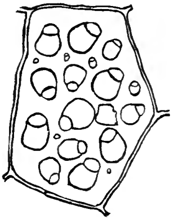
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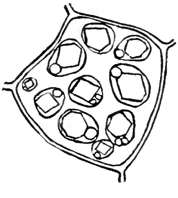
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177. The protein matter of which protein granules consist may be wholly without definite shape, or a portion may assume somewhat the form of crystals. The latter have been called protein crystals or crystalloids, and they are generally associated, in the granules of which they form a part, with inorganic matters either amorphous or crystalline. Hence in some protein granules we have to distinguish between the inorganic contents, the

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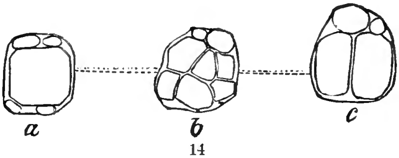
FIG. 11. Cells from cotyledons of Vicia sativa, showing protein matters in a finely divided state, intermingled with starch-granules. (Schmidt.)

FIG. 12. Protein granules from the endosperm of Ricinus communis. The specimen is in oil. $\frac{400}{1}$. (Pfeffer.)

FIG. 13. Protein granules from the endosperm of Ricinus communis. The specimen, first treated with mercuric chloride in absolute alcohol, is now in water. $\frac{400}{1}$. (Pfeffer.)

protein crystal-like bodies, and the protein basis or stroma in which all of these are held.



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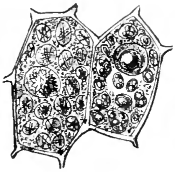
The protein basis sometimes, if not always, appears to consist of two substances, differing in their solubility in water, and commingled as granulose and cellulose are in starch-granules. While the protein basis is generally very soluble in water (not *per se*, but owing to the presence of potassic phosphate), the protein crystals are insoluble, or only slightly affected by it, usually becoming more or less swollen. After solution of the protein basis has taken place, a delicate membrane is left behind, and through this transparent film the protein crystals are clearly seen. The relative amounts of protein basis and protein crystals vary widely; in some cases the former appears to be wanting, the latter wholly filling the interior of the membrane. Such crystals appear in potato-tubers in the form of small cubes. Protein crystals of great beauty are easily demonstrated in the endosperm of the common Brazil-nut (Bertholletia). Very instructive phenomena are presented when different sections of the seed are subjected to the following reagents; (1) osmic acid (one per cent solution); (2) hæmatoxylin



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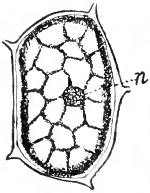

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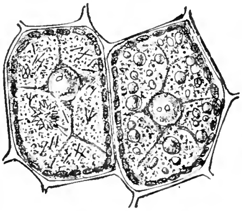

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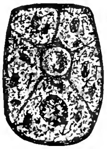

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FIG. 14. Single protein granules treated as in Fig. 12. $\frac{800}{1}$. (Pfeffer.)

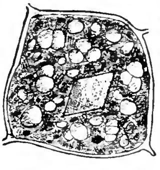
FIG. 15. Protein granules from Silybum marianum. In the cell on the left they have crystalline contents; in that on the right, globoids. This section was taken from the cotyledons of a dormant seed, and after treatment with mercuric chloride in alcohol was placed in water. $\frac{500}{1}$. (Pfeffer.)

FIG. 16. The mesh of the ground mass of the cell has been cleared by dilute potassic hydrate and hydrochloric acid. *n* = nucleus. $\frac{500}{1}$. (Pfeffer.)

FIG. 17. Cells from the cotyledons of a germinating seed which has just ruptured the seed-coat. The protein granules have disappeared, but their contents are recognizable. $\frac{500}{1}$. (Pfeffer.)

FIG. 18. Silybum marianum. Cell from the cotyledon of a nearly ripe seed in which the formation of protein granules has just begun. $\frac{500}{1}$. (Pfeffer.)

in concentrated glycerin; (3) concentrated potassic hydrate, water being added afterwards. Permanent preparations of protein crystals can be made by first acting on the section with mercuric chloride for a day or more, washing in water, staining with eosin, and finally mounting in potassic acetate (101).



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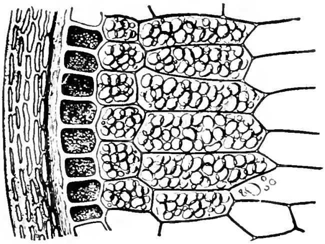
The inorganic matters associated with the protein crystals in protein granules are either (1) amorphous or globular concretions of a double phosphate of calcium and magnesium, known as *globoids*, or (2) crystalline clusters of calcic oxalate.

The protein granules, especially those which are most complex in their composition, are also known as *Aleurone* grains. The protein crystals are generally termed *crystalloids*.[1] For an analytical classification of protein granules in seeds, see pages 182 and 183.

178. **Starch,** the principal form in which the elaborated food of plants is held in reserve, occurs as minute spheroidal or polyhedral granules. Under a sufficiently high power, and with proper management of the mirror of the microscope, the single granules exhibit an appearance of stratification which is sometimes very distinct, but more commonly obscure; in the latter case dilute chromic acid can be used to render the stratification plainer. The layers of stratification are arranged around a point, — often very eccentrically, as in potato



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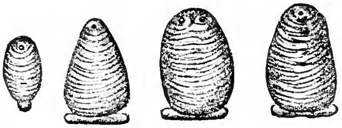
[1] The fact that protein crystals have, as a rule, less constancy in their angles than inorganic crystals, taken together with the fact of their swelling when immersed in water, has led authors to speak of them as **crystalloids** rather than as crystals. But Famintzin has recently shown that certain crystalline forms artificially produced obscure these distinctions, since they agree more closely in some of their physical characters with organic structures than with ordinary inorganic crystals (Ber. der deutsch. bot. Gesellsch., 1884, p. 32).

FIG. 19. A cell from nutmeg lying in oil. In the ground mass are very numerous crystals of fat. Some of the granules are compound starch-granules, but others are protein granules with crystalloids. The rhombic granule has hardly any envelope. $\frac{500}{1}$. (Pfeffer.)

FIG. 20. Globoids of Vitis vinifera. $\frac{500}{1}$. (Pfeffer.)

FIG. 21. Large protein granules from Vitis vinifera. $\frac{500}{1}$. (Pfeffer.)

FIG. 22 Wheat-grain, showing cells containing starch-granules. (Schmidt.)



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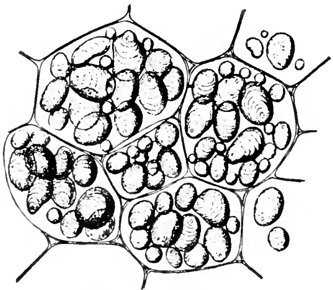
starch, or with great regularity, as in wheat. This point is known as the nucleus, or hilum. If two or more nuclei are discernible, the granule is said to be compound.

Occasionally many small single granules cohere slightly to form an aggregate which can be easily broken. According to Wiesner, there may be as many as 30,000 granules in a single aggregate of this kind.



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Both simple and compound granules may occur in the same cell, but some plants have only simple, and others only compound granules. Canna and Curcuma may be cited as examples of the former; Jatropha, of the latter.

Since starch occurs in every plant in all stages of development, the size of the granules must be extremely variable. Nevertheless, a statement of the more common limits may aid in their identification.

25

Wiesner gives the following limits of size for some of the more common sorts of starch, first grouping them into small, medium, and large granules.

Small granules (from 0.002 to 0.015 mm.): as the simple granules of rice, oats, buckwheat; also the smaller granules of wheat, rye, barley, etc.

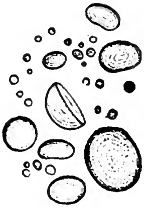
Medium granules (from 0.02 to 0.05 mm.): as the compound granules of rice and oats, the larger ones of wheat, rye, and barley, the simple granules of Indian corn, and of the common leguminous plants.

Large granules (distinguishable as granules to the naked eye): as the simple granules of Curcuma leucorrhiza, Canna edulis, potato, etc.

FIG. 23. Starch-granules from the bulb of Phajus grandifolius, showing the nucleus at the upper part and the starch generator or amylogenic body below. $\frac{850}{1}$. (Schimper.)

FIG. 24. Cells from potato-tuber, showing starch-granules. (Schmidt.)

FIG. 25. Starch-granules from sarsaparilla. (Berg and Schmidt.)



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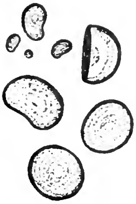

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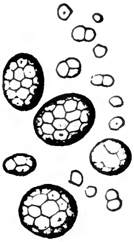
Starch is insoluble in cold water, but forms with boiling water a paste in which all traces of structure are lost. If a specimen of starch be gently heated with water upon a glass slide, the granules will be seen to swell at a temperature of 40°–50° C., and the appearance of stratification will often become plainer. The alkalies and mineral acids generally hasten the



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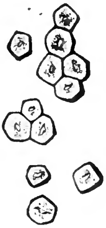

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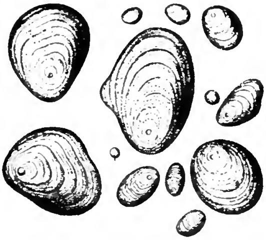

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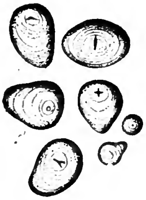

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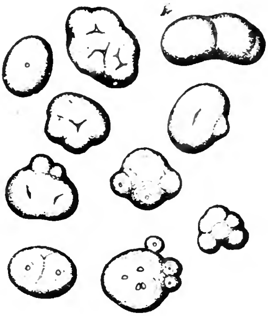

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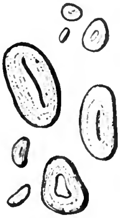

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FIG. 26. Starch-granules of wheat.
FIG. 27. Starch-granules of Indian corn.
FIG. 28. Starch-granules of barley.
FIG. 29. Starch-granules of oats.
FIG. 30. Starch-granules of rice.
FIG. 31. Starch-granules of potato.
FIG. 32. Starch-granules of Maranta (arrow-root).
FIG. 33. Starch-granules of Bomaria (Chili arrow-root).
FIG. 34. Starch-granules of Vicia sativa, var. leucosperma. All the figures of starch are from Berg and Schmidt.

formation of starch-paste, and bring about some other changes, such as its conversion into soluble matters.

179. Starch is usually said to have the following composition, $C_6H_{10}O_5$, and these proportions are doubtless correctly stated; but it is probable that the molecular constitution is more complex than this formula would indicate.[1]

180. When starch is acted on by saliva or pepsin, it is slowly separated into two substances, one of which passes into solution, while the other remains as a skeleton, and with little change of form. This delicate framework, which remains after the soluble matter is removed, is closely related to cellulose, as shown by its behavior with reagents, and has received the name of *starch cellulose*. The substance which is removed by the action of saliva is termed *granulose*.

181. When starch is not associated with too large a proportion of protein matters, it can always be detected by the blue color which it takes with iodine in solution; but if protein substances are present in considerable amount, they may obscure the reaction by the yellowish or brown color which iodine imparts to them. Iodine does not, however, always produce a *blue* color with starch; the shade may vary towards red, forming a purple which may be almost black. Furthermore, as the transient color given by this reagent fades, it may pass through various tints of orange and yellow.

Protein matters which mask the starch reaction may be removed by careful treatment of the specimen with potassic hydrate (not too concentrated), and subsequent washing with pure water. After such treatment it sometimes happens that the starch appears as a diffused mass instead of in minute dots.

182. When starch-granules are seen in polarized light they generally exhibit two crossed lines which appear to turn as the Nicol prism is revolved. Many kinds of starch give under the polarizer characteristic figures, many of them of great beauty.

183. **Inulin,** although occurring in solution in cells, is nevertheless thrown down in characteristic forms by means of the preservative media alcohol and glycerin, and can be examined as a solid. If the root of Dahlia, Helianthus, or any of the common Compositæ which store up their food in fleshy underground parts, be subjected to the action of alcohol for a few days, thin sections will exhibit in the cells peculiar masses of a spheroidal

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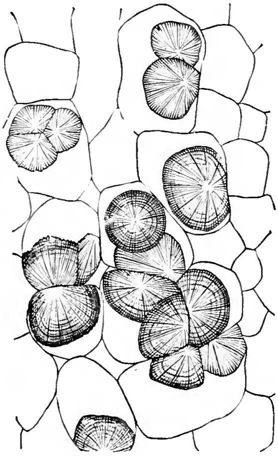
[1] W. Nägeli, however, gives the formula for starch as follows: $C_{36}H_{62}O_{31}$. Beitr. z. näheren Kenntniss der Stärkegruppe, 1874.

form which are distinctly radiating in structure. Occasionally these masses have large rifts which run across the surface of the sphere.

In composition, inulin closely resembles starch, but does not give any color with iodine. To detect it when in solution, a thin section of the plant containing it is moistened on the glass slide with absolute alcohol, when a cloudy precipitate will at once appear; in a short time (the supply of alcohol having been replenished as it evaporates) the specimen grows clearer, and small sphærocrystals of inulin are seen. If now the specimen is carefully washed with water, the smaller granules disappear and the well-defined remain.



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184. **The carbohydrates dissolved in the cell-sap** may be grouped in two classes: (1) those which are isomers of cellulose (*i. e.*, have the same percentage composition, $C_6H_{10}O_5$), and (2) the sugars.

1. The isomers of cellulose are mucilage, gums, and dextrin, all of which are probably derivatives of starch. Various substances intermediate between them have been described, but the above are all that need now be taken into account. (*a*) *Mucilage*, when not plainly resulting from the breaking up of the cell-wall, is colored red by rosolic acid, and the color is not readily removed by alcohol. (*b*) *The gums*, of which cherry gum may be taken as an example, are not tinged by rosolic acid. (*c*) *Dextrin* can be detected by Trommer's test, which Sachs applies as follows: a section which is at least a few cells in thickness is placed in a porcelain capsule with a strong solution of cupric sulphate, and the liquid is heated to boiling; the specimen is then washed in water, and dipped at once in hot potassa. If the cells contain either dextrin or grape-sugar, there will immediately appear a reddish precipitate. To discriminate between dextrin and grape-sugar, it is merely necessary to keep portions of the plant to be examined in 90 or 95 per cent alcohol, which will dissolve out the sugar and leave the dextrin, if any

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FIG. 35. Sphærocrystals of inulin from root of Cichory treated with alcohol. $\frac{480}{1}$. (Jacobs.)

is present. Usually all the grape-sugar is extracted in a day or two.

2. *The sugars.* Grape-sugar has been just referred to as giving the same reaction as dextrin with Trommer's test. Its formula is $C_6H_{12}O_6$. Cane-sugar, which has the formula $C_{12}H_{22}O_{11}$, gives no red precipitate with the same test, but the liquid in the cells becomes bright blue, and quickly diffuses into the potassa.[1]

185. **Crystals** are of such general occurrence in widely different orders of the higher plants, that there are perhaps none in which they may not be detected. They have been found in nearly all parts of the vegetable structure, more commonly in the interior of parenchyma cells, sometimes in specialized crystal-receptacles, occasionally in the very substance of the cell-wall. They occur either singly or in groups; either separate or barely coherent, or in various degrees of combination.

When solitary and simple they are usually octahedra or prisms, and their aggregations are combinations of these. Good octahedral crystals are afforded by the petioles of Begonia; examples of the prismatic form are found in the outer scales of onions, in orange leaves, in the inner bark of maples and apple-trees, and in most of the tissues of Iris and its allies.

When the prisms are very long and slender their angles and faces are seldom well defined.[2] Indeed, the most attenuated forms are usually terete, or slightly flattened, and taper gradually to a point at both ends. To these De Candolle long ago gave the name *Raphides*, — that is, needles.[3] These are generally massed in a compact bundle, like a wheat-sheaf, occupying a large part of the interior of the containing cell.

Raphides are by no means of such general occurrence as are ordinary crystals, but (as Gulliver has pointed out) are seemingly restricted to certain orders.[4] They are universal in Araceæ and Onagraceæ. In the common Arums and Callas, raphides-bearing cells may readily be found in the parenchyma

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[1] Pringsheim's Jahrb., iii. p. 187. In the Sitzungsber. d. k. Akad. Wien, for 1859, Sachs has given colored figures illustrative of these reactions.

[2] When the longer prisms are clearly defined, they are referable to the monoclinic system. Measurements of angles are given by Holzner, in Flora, 1864, p. 292. A paper by Bailey (Am. Journ. of Sc. and Arts, vol. xlviii., 1845, p. 17) also contains determinations.

[3] Organographie, 1827, p. 125.

[4] Gulliver has examined representative plants of all the more important orders of the British Flora, with respect to the occurrence of diagnostic crystals (Annals and Magazine of Natural History, 1863 to 1867).

of the leaves, and detached entire; on becoming turgid when wetted, they will usually discharge their raphides one by one from one or both ends of the cell until the bundle is almost exhausted.[1]

186. When the ordinary octahedral or prismatic crystals are aggregated or combined, they generally compose a spherical mass. Such aggregations are of two principal types: (1) those made up of many small crystals irregularly grouped, and usually presenting sharp points over the surface, as in Fig. 36 *a*; (2) those with a distinctly radiated structure (Fig. 36 *i*). Good examples of the former are abundant in the foliage of Chenopodiaceæ and the stems of Cactaceæ. Clusters belonging to the latter, or stellate, type are not uncommon in Malvaceæ. Both forms have been termed *Sphæraphides*[2] and *Sphere-crystals*. The term *cystolith*, sometimes improperly applied to them, should be wholly restricted to the peculiar bodies described on page 40.

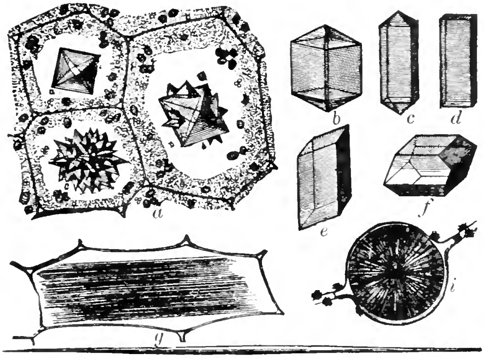

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FIG. 36. The more important forms of crystals of calcic oxalate: *a*, three cells from the petiole of Begonia manicata; *b*, from the leaf of Tradescantia discolor; *c* and *d*, from the leaf of Allium Cepa; *e*, from the inner bark of Æsculus Hippocastanum; *f*, from the leaf of Cycas revoluta; *g*, a cell containing raphides, from the frond of Lemna trisulca; *h*, a single crystal from the same, more highly magnified; *i*, sphæro-crystal from Phallus caninus. (Kny.)

187. Owing to the mechanical difficulty of isolating plant-

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[1] Turpin (Annales des Sc. nat., sér. 2, tome v., 1836) described the raphides-bearing cells of Caladium, in which this discharge takes place, under the name of *biforines*.

[2] "They are most irregularly scattered through the tissues of the plant. . . . I have never failed to find them in a single species of the order Caryophyllaceæ, Geraniaceæ, Lythraceæ, Saxifragaceæ, and Urticaceæ, and believe that few if any orders could be named in which sphæraphides do not exist as part and parcel of the healthy and growing structure of the plant" (Gulliver, in Annals and Magazine of Natural History, vol. xii., 1863, p. 227).

crystals for examination, their chemical composition has not yet been determined with certainty in all cases. That a protoplasmic film usually envelops both solitary and aggregated crystals, can be shown by the method pointed out by Payen:[1] namely, by dissolving the crystal slowly in very dilute nitric acid, and testing with iodine, when the film will become yellowish-brown. It has also been made out beyond question that some crystals have a considerable admixture of cellulosic matter, and that a few others are covered by a membrane of cellulose.[2] But these two substances do not obscure the chemical reactions in ordinary cases, by which it has been shown that the larger number of crystals consist of calcic oxalate, after which, in frequency of occurrence, comes the carbonate of the same metal. These two salts can be easily distinguished from each other by the following simple tests: —

Reagent.	Calcic Oxalate	Calcic Carbonate.
Acetic acid.	No effect.	Dissolves with effervescence.
Hydrochloric acid.	Dissolves without effervescence.	Dissolves with effervescence.

Since these two salts may occur in the same specimen, it is best to use acetic acid first; by this agent all traces of the carbonate are removed, and hydrochloric acid can then be applied in order to detect the presence of oxalates. Sanio[3] and Holzner have shown conclusively that many crystals which have been supposed to be calcic carbonate consist merely of the oxalate.

Crystals of calcic sulphate have been reported as occurring in certain Musaceæ,[4] in the bark of the willow, in the roots of aconite, bryony, and rhubarb; and also in the root of a young bean.[5] Calcic phosphate is said to have been detected in the

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[1] Payen: Mém. des savants étrangers, ix., 1846, p. 91.

[2] Rosanoff (Bot. Zeit., 1865, 1867), Crystals in pith of Ricinus and Kerria. Pfitzer (Flora, 1872), crystals in the leaves of orange and the bark of many trees.

Hilgers has investigated the occurrence of crystals at different periods of growth of different organs. From his results it appears, (1) that in the very youngest parts no crystals are to be found; (2) they appear, however, very early in most parts, and (3) speedily attain their maximum size, after which they undergo no change (Pringsheim's Jahrb., vi., 1867, p. 285).

[3] Sanio: Monatsber. Berliner Akad., 1857.

[4] Van Tieghem: Traité de Botanique, p. 526.

[5] Sitzungsberichte der Wiener Akad., xxxvii., 1859, p. 106.

wood of Tectona grandis (Indian Teak).[1] Holzner[2] uses the following reaction to detect calcic sulphate: a solution of baric chloride (not too concentrated) is brought into contact with the crystal under examination; calcic sulphate soon becomes covered with a whitish deposit of baric sulphate. This test failed to show the presence of calcic sulphate in the plant-crystals hitherto referred to this salt; they all gave, however, the reaction for the oxalate.

188. Crystals closely resembling in most respects those which are found in cells can be produced by Vesque's method.[3] Three test-tubes are placed side by side: in the first is a moderately strong solution of calcic chloride; in the middle one, a five per cent solution of sugar; and in the third, a solution of potassic oxalate. From the liquid in the first to that in the second a short strip of filtering-paper runs, and a similar strip passes from the second to the third test-tube; and thus the liquids in the three tubes are brought into indirect contact. Crystals will be formed in the middle tube, their character depending upon the nature of the liquid there. In a solution of sugar, raphides are produced; in pure water, prisms of small size, but with sharply defined faces and angles.

189. According to Souchay and Lenssen,[4] monoclinic ("Clinorhombic") crystals of calcic oxalate containing two equivalents of water are produced upon quick precipitation, while by very slow action right octahedra with six equivalents of water are formed.

A few works of reference are the following: —

Mohl. Principles of the Anatomy and Physiology of the Vegetable Cell. Translated by Henfrey (London, 1852). An octavo of 158 pages. This is an excellent translation of a classical work.

Hofmeister. Die Lehre von der Pflanzenzelle (Leipzig, 1867). An octavo of 397 pages. The volume treats very fully of the physical properties of protoplasm.

Ebermayer. Physiologische Chemie der Pflanzen (Berlin, 1882). This is the first volume of an expensive work which deals with the relations of plants to soil and climate.

Husemann und Hilger. Die Pflanzenstoffe (Berlin, 1882). Two large volumes. It has very extensive references to the literature of the subject, and most of its abstracts are excellent.

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[1] Ples: Naturkundig Tijdschrift voor Nedrlandsch-Indië, 1858, p. 345. Quoted from Holzner.

[2] Flora, 1864, p. 283. This communication contains a good abstract of the literature of plant-crystals up to 1862.

[3] Ann. des Sc. nat., sér. 5, tome xix., 1874, p. 300.

[4] Annalen der Chemie und Pharmacie, c., 1856, p. 311.

CHAPTER II.

CELLS IN THEIR MODIFICATIONS AND KINDS, AND THE TISSUES THEY COMPOSE.

190. While cryptogamous plants of the lower grade may consist of single cells, or of a series or stratum of simple and undifferentiated cells, phænogamous plants, although equally simple and homogeneous at the initiation of each individual, develop into a more complex organization, at an early period differentiate some of their cells into peculiar kinds, multiply the kinds into tissues or fabric, and of these build up the organs and parts which are familiar in ordinary vegetation.

191. The microscropical study of the parts even of a single herb or tree, and much more that of a variety of plants, reveals numerous forms or kinds of cells, and also (as might be expected from their common origin) brings to view series of gradations between the kinds, sometimes even between those which are, upon the whole, widely differentiated from each other. While, therefore, a general classification of the cells of any ordinary plant into kinds is easy, any classification which shall satisfactorily exhibit our present knowledge of the histological elements, and discriminate their varieties, is very difficult, if not at this time practically impossible. At least, it must be said that the most recent classifications are based upon considerations of a character too recondite and special to be mastered at the beginning by an ordinary student.

192. The most general and obvious division of the histological components of a stem, root, or leaf would be into, (1) fundamental or typical cells, and (2) transformed cells. The first are those in which the normal cellular character persists without profound, if any, alteration or disguise; as in the pulp of leaves, the pith of stems, and in a portion of the bark. The second are those which assume or affect lengthened or fibrous forms and a longitudinal development (at least in all axes, and commonly in leaves and other expanded organs), and, combined into threads, fascicles, bundles, or more massive structures, constitute the framework, which imparts solidity and strength throughout. Some

of these cells are so long in proportion to their breadth, and of such diminished calibre, that they have naturally been called fibres, although all gradations between them and typical cells may be demonstrated. All these cells are interchangeably called woody fibres or wood-cells, and one kind of them takes the name of bast-cells.

193. Others are of larger calibre, are peculiarly marked by thickenings on certain lines or in certain patterns, incline to be developed end to end in a chain or row, and to become confluent at the junctions, so as to form conduits of considerable length; these are called vessels, or ducts. Vessels and fibres are associated in the plant; almost every separate thread of framework consists of both, and so is called a fibro-vascular bundle or fascicle. Moreover, the known gradations between the two are such as to render a complete distinction between them nearly impracticable; so that they form the fibro-vascular, or, when a single word is used, the vascular system. To this system, also, pertain specially differentiated cells, such as cribrose-cells, in the bark, etc.

194. All these are developed in or among the fundamental or untransformed cells, and originate from the differentiation of some of them.

195. The fundamental or typical cells may therefore be said to constitute the fundamental system; which may also be conveniently called the cellular system, in contradistinction to the vascular.

196. In an ordinary leaf it forms all but the framework of ribs and veins; in the stem of a dicotyledon, the outer bark, the pith, and the rays which traverse the wood; in that of a monocotyledon, which generally has a looser texture than the last, it is the common mass through which the definite bundles of the vascular system are distributed. Of the fundamental system, the most typical or unmodified cells are such as the chlorophyll-bearing cells of leaves and of the green bark of stems, as well as those with uncolored contents forming the pith, etc. Borrowing a word from the old anatomists, the early investigators of vegetable structure called tissues composed of such cells *Parenchyma*, perhaps taking the idea of the name from leaves in which the veins are distributed through the softer parts as blood-vessels through the parenchyma of the glands.

197. Parenchyma, therefore, is the name of cellular tissue in contradistinction to fibro-vascular tissue. In its primary sense, only comparatively soft and thin-walled cellular tissue

took this name, and this is indeed typical parenchyma; but the name rightly includes, as species or varieties, thicker-walled and even solidified tissues composed of cells similar in other respects to the type, as those in the hard endosperm of seeds.

198. A counterpart name, *Prosenchyma*, was employed to designate tissues formed of elongated cells, such especially as wood-cells and bast-cells. These being usually thick-walled, and those of typical parenchyma thin-walled, this character was brought into the definition; that is, cells of prosenchyma were said to be thick-walled as well as long and narrow, those of parenchyma thin-walled as well as isodiametric. But this distinction does not hold out well. All fibro-vascular tissues are thin-walled at first, and some remain so; while portions of pure parenchyma may become thick-walled, firm and hard, or take on every intermediate condition. So that prosenchyma may be best held to denote tissue of the fibro-vascular system, and typically that formed of wood-cells.[1]

199. An explanation of the mode of production, multiplication, and transformation of cells is deferred to a later stage. Suffice it here to advert to the fact that every phænogamous plant, originating in the seed, begins as an isolated cell, which develops into a globular cluster of parenchyma cells, and grows into the embryo or rudimentary plantlet, taking on the shape and degree of development characteristic of its kind. In embryos which are considerably developed in the seed, the axis and beginnings of the leaves are already outlined or rudimentarily indicated there; in others the indication takes place in the early stages of germination.

200. From this if not from an earlier period development is no longer homogeneous. A superficial layer of the common parenchyma becomes distinguishable as the epidermis; while in an inner zone, or at special points, certain cells develop into ducts and wood-cells (prosenchyma), and thus are initially delineated the outlines of the systems or regions which are to characterize the whole growth; namely, — taking a dicotyledonous embryo for the type, — an epidermal layer, a cortical layer, a fibro-vascular zone, and a medullary portion. As stem and root develop, these primordial tissues complete themselves and have only to go on growing, each after its kind; but at the developing points (apex of the stem and of the root), as also in special portions or

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[1] "Zu dem Prosenchym im weitern Sinne können wir auch die Gefässe zählen" (Nägeli: Beiträge, i. p. 2).

zones, initial differentiation continues. Here the nascent tissue, consisting of parenchyma cells, multiplying by successive divisions, and also the nascent prosenchyma as it forms and while still capable of further division, has been named *Meristem.*

201. Meristem, therefore, is not a kind of tissue, but the nascent state or early condition of any tissue. It is developing parenchyma, either multiplying as such, or differentiating into elongated forms, as for instance, in cambium.

Leaving the processes of cell-development to be considered under the head of "Growth," and the disposition of cells and tissues in the fabric to be described under the several organs (root, stem, leaf, etc.) which they compose, the kinds of cells are here to be indicated, without particular reference to their arrangement in the plant. In all classifications of objects which are understood to have been developed from one type, intermediate forms of almost every gradation are to be expected. It is specially so with plant-cells; and of them it should be said, once for all, that the kinds which have received distinct names, with or without sufficient reason, are only types, or leading modifications, — some of a very marked, some of a quite subordinate character.[1]

202. Plant-cells are to be described in this chapter under the following classification: —

I. Cells of the fundamental system, or parenchyma cells, — permanent typical cells.
  1. Parenchyma cells, strictly so called, including as modifications collenchyma cells and sclerotic parenchyma cells, or grit-cells, such as the lignified cells of seed-coats and drupes, etc.
  2. Epidermal cells, and their modifications; *e. g.*, Trichomes.
  3. Cork-cells, forming suberous parenchyma, or cork.

II. Cells and modified cells of the fibro-vascular system, — prosenchyma in the widest sense.
  1. Cells of prosenchyma proper.
    a. Typical wood-cells and woody fibres, including libriform cells (Sanio), and the secondary wood-cells (De Bary).
    b. Vasiform wood-cells, or Tracheids.

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[1] Sometimes a single cell in a uniform tissue may develop unlike its neighbors as regards one or more of the following characters: form, size, nature of cell-wall or cell-contents. Such cells are termed by Sachs, idioblasts.

  2. Vessels, or ducts.
    a. Dotted.
    b. Spirally marked.
    c. Annular.
    d. Reticulated.
    e. Trabecular.
  3. Bast-cells, Bast-fibres, or Liber-fibres.
III. Sieve-cells, or Cribrose-cells.
IV. Latex-cells.

Intercellular spaces and canals are neither cells nor tissues, but they require consideration in connection with them.

I. Cells of the Fundamental System, — Parenchyma in the widest sense, including Modifications for Protective Surfaces.

PARENCHYMA.

203. This term is applied at present to all typical cellular tissue except that which belongs to the epidermal system. It therefore constitutes the mass which surrounds fibro-vascular bundles, forming pith, medullary rays, the pulp of leaves and fruits, etc. It occurs in nearly all parts of all plants.

The elements of parenchyma are simple cells more or less separable from each other, in some cases by slight pressure, and in others by the cautious use of a macerating solution. The cells vary greatly in form, but usually are polyhedral or spheroidal. Extended classifications of the cells themselves, based upon form, have been made, but they are of no utility and of small historical interest. Yet three principal shapes may well be distinguished; namely, short or isodiametric, elongated, and flattened.

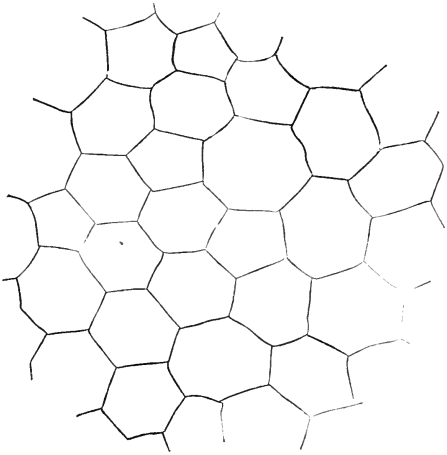

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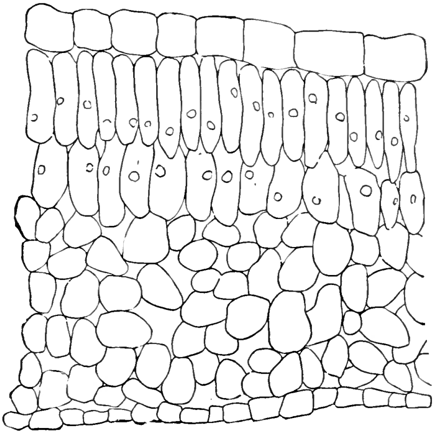
FIG. 37. Parenchyma from stem of Marrubium. $\frac{110}{1}$. (Jacobs.)

204. In the youngest state of organs short parenchyma cells form the whole mass; here they are relatively small, filled with protoplasm, and have no intercellular spaces. Later they are changed in shape and size, may have conspicuous intercellular spaces, and the protoplasm may be replaced, at least in part, by other matters.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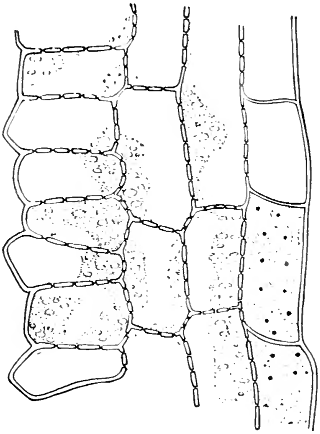
205. If the cells are loosely aggregated and have conspicuous intercellular spaces, the tissue is called *spongy parenchyma.* The cells in such cases are apt to be more or less branched, and in some plants assume regular stellate forms.

206. Elongated parenchyma cells are generally more compactly combined than the short ones. They are well seen in the upper part of most leaves, where they have received the significant name *palisade-cells.*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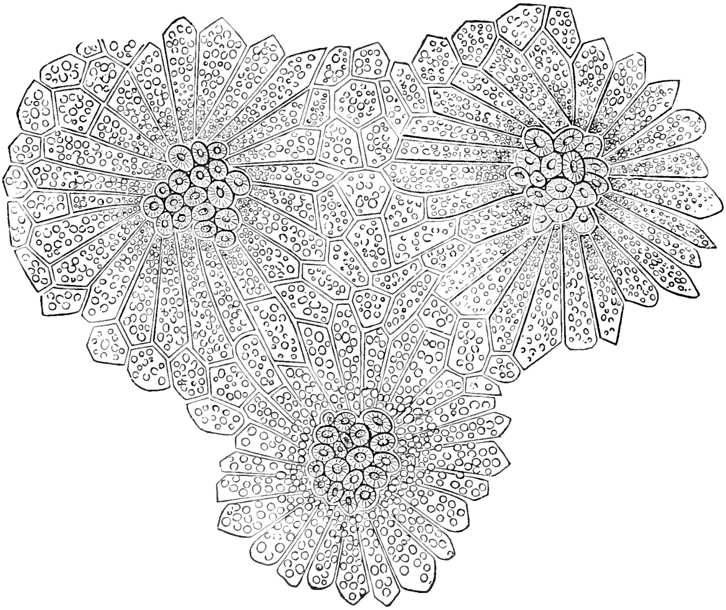
207. Flattened parenchyma cells are the common form in the vertical plates (medullary rays) which radiate from the pith to the bark in woody plants.

208. The walls of typical parenchyma cells are thin, and may be variously marked with pits, especially at the points of contact with other cells. Thickening threads forming reticulations and spirals are not uncommon; the latter occur in the aerial roots of Orchidaceæ. A crumpling or folding-in of the wall is seen in some of the cells of pine leaves.

FIG. 38. Forms of parenchyma in leaf of Pyrus communis. (Jacobs.)
FIG. 39. From pith of Sambucus nigra, showing pitted walls. (Gris.)

209. Thin-walled parenchyma cells play an important part in assimilating and storing, and special names are given to cells which have these offices, such as chlorophyll parenchyma, starch parenchyma, etc. In the tissues of most succulents, and in the leaves of a few plants, some of the parenchyma cells are filled with clear sap and more or less mucilaginous matter, and constitute the so-called water tissue.

210. The walls of typical parenchyma cells consist of ordinary cellulose; but even slight deviations from the type furnish good illustrations of lignified and of cutinized membranes.



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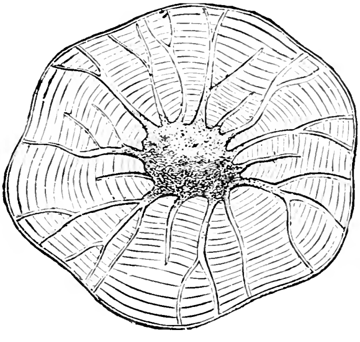
211. Lignification may increase the thickness of the cell-wall, greatly reducing the cell-cavity, or it may merely harden the membrane without much thickening. The parenchyma cells found associated with other elements in woody tissues have walls of the latter character; the grit-cells in pears and many other fruits show good examples of the former. Such hardened cells are called sclerotic parenchyma cells.

FIG. 40. Sclerotic parenchyma cells from fruit of the pear. (Weiss.)

In many cases it can be shown that canals run through these thickened walls, as shown in Fig. 41.[1]

212. Certain modified parenchyma cells are often united to form sheaths around fibro-vascular bundles. These cells are prismatic, and in close apposition. Their walls are thin, except at their faces of mutual contact, where they are conspicuously thickened, and often plicate, and nearly all parts of the membrane are more or less cutinized.



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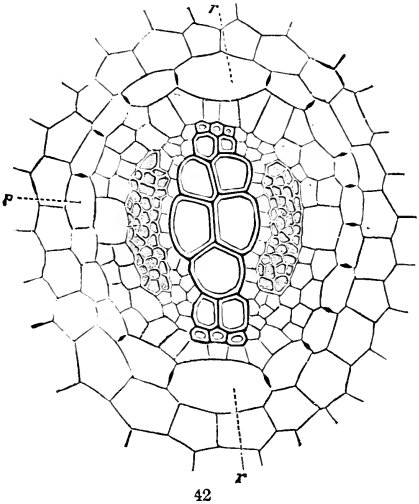
213. These cells constitute the *endodermis*. They generally contain a large amount of starch.

214. Parenchyma cells may undergo the mucilaginous modification (see 147), as in the conductive tissue of the style of many flowers and the albumen of many seeds. This change is common also in the lower plants.

215. An appearance closely resembling in some points that produced by the mucilaginous modification is pre-



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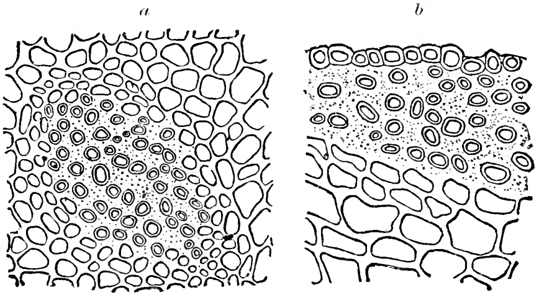
[1] A second kind of sclerotic parenchyma sometimes accompanies the longer sclerotic cells in a few ferns and some monocotyledons. Its cells appear as if segments of a jointed fibre, somewhat flattened on the side next the long cells, and decidedly convex on the other. Such flattened cells are unequally thickened on the two sides, and the walls are somewhat silicified. But the most striking feature in many cases is the deposition within the cavity of the cell of a mass of silicic acid; this is well seen in the hard cells which accompany the fibro-vascular threads in the leaves of some palms.

FIG. 41. A sclerotic cell from the nutshell of Juglans regia. (Reinke.)

FIG. 42. Section through the central cylinder of a binary root of a vascular cryptogam (Cyathea medullaris). *p*, *r*, *r* = *endodermis*. (Van Tieghem.)

sented by the parenchyma cells just under the epidermis, or outer layers of cells, in many plants. The cell-wall is thickened very considerably at the angles, and upon the application of dilute acids swells greatly, but without becoming clearly mucilaginous. When moist, such cells have a bluish-white color and a marked lustre. They are known as



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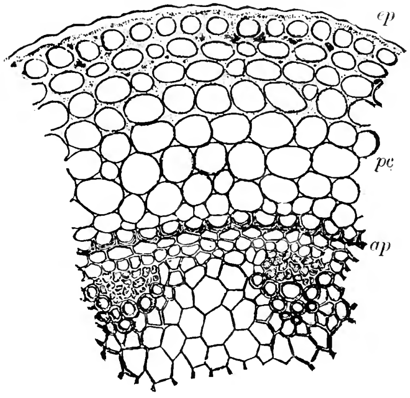

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216. Collenchyma cells. They are generally somewhat elongated, and so united as to form threads which possess great strength, and are believed to serve an important mechanical office in the plant. Good examples of these are afforded by the stems of many Umbelliferæ.

EPIDERMIS.

217. This is the outermost layer of cells covering the surface of the plant. In some of the higher plants it persists with little change throughout the life of the organism; in others it is

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FIG. 43. Parenchyma with walls which have undergone the gelatinous modification: *a*, from the centre of the style of Salvia scabiosæfolia; *b*, from the stigma of Gesneria elongata. (Capus.)

FIG. 44. Transverse section of root-stock of Smilacina bifolia, showing collenchyma cells just under the epidermis, *ep*. Note also the ordinary parenchyma at *pc*, and the endodermis at *ap*. (Van Tieghem.)

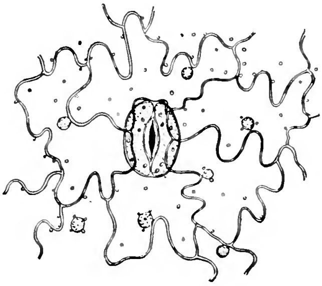
sooner or later thrown off, and replaced by a subjacent protective tissue, — cork.

218. Except at peculiar openings (stomata, etc.), the epidermal cells are in close apposition. Upon their exposed surface they are cutinized, and thus a continuous hyaline film is formed, known as the *Cuticle*.[1]

219. Sometimes the epidermis may be torn off without much disturbing the underlying tissues.

220. Besides the cells which compose the proper tissue of the epidermis, there are certain appendages or accessory structures, mainly hairs or analogous productions (together called trichomes), and peculiar cells which constitute the stomata.

221. **Epidermal cells proper** are in uninterrupted contact. They are usually of a tabular or prismatic form. The lines which mark their outlines as viewed from above are sometimes straight, but oftener sinuous, at least on the longer sides of the cell, which here as elsewhere correspond with the direction of growth. Near stomata and trichomes the cells frequently assume very irregular forms.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222. Their upper or free surface is generally slightly convex, and often has minute outgrowths, for instance, in velvety petals; when these are larger and longer, they constitute the simplest form of plant hairs.

223. Delicate epidermis possesses thin walls; but in a large number of fleshy and tough plants the walls have considerable thickening, yet not always on the same part. Thus in the leaves of Cycads the upper wall is the thicker; in many Bromeliaceæ, the lower and side walls. In a few cases the cell-cavity is nearly filled by the thickening material. Stratification, striation, and pitting of the cell-wall may also occur, great diversity existing in all these respects.

224. When the epidermis is very delicate, the demonstration of the thin film of cuticle requires great care in the employment

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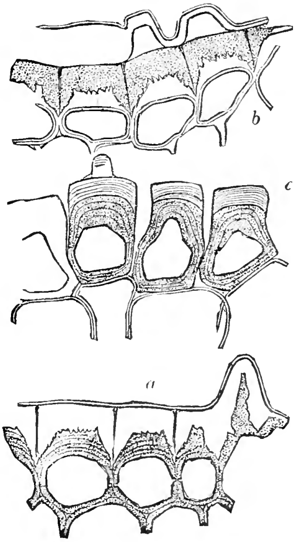
[1] By De Candolle the term *cuticle* was applied to the layers of epidermal cells, and not restricted to the cutinized film (Physiologie, 1832, p. 109).

Fig. 45. Stoma of Sambucus nigra surrounded by epidermis.

of the reagents. According to de Bary,[1] the cuticle merely covers the pure soft cellulose membrane of the epidermal cells when these are thin-walled; but when the walls are thicker, especially in epidermis which is long-lived, that part of the cell-wall which borders on the cuticle becomes infiltrated with cutin, and thus there arise one or more layers of modified cellulose, each of which exhibits the reactions of cutin. When such cells are treated with warm potassic hydrate (a ten per cent solution is, on the whole, strong enough), the cutin is slowly removed, and the cellulose wall remains, although with considerable loss of substance. Walls which are thus impregnated with cutin in strata form *cuticularized layers*.[2] The management of a warm solution of potassic hydrate, in order to obtain satisfactory results in the demonstration of the fine stratification, demands much care. It is advisable to apply very gradual increments of heat to the glass slide in the case of the more delicate specimens.



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225. Waxy and resinous matters are frequently associated with the cuticle. In some cases the amount of such substances is large, and assumes commercial importance. The young leaves of the wax palm (Ceroxylon andicola) are said

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[1] Vergleichende Anatomie, p. 80.

[2] This division into apparent lamellæ can be easily demonstrated in some cases by the application of chloroiodide of zinc, which imparts a yellowish color to the thick film, except at its outer surface. Mohl explained the structure of the exposed cell-wall in Viscum album, where the film is very thick, as follows: "The epidermis cells consist here of two or three generations enclosed one within another, of which all the thickened walls on the outer side have become blended together into a membrane composing the cuticle. These layers are to be called the cuticular layers of the epidermis, to distinguish them from the mass secreted on the outside of the cells, the true

FIG. 46. Transverse section of the leaf of Aloe verrucosa: *a*, section in water, — the non-cuticularized parts of the membranes shaded; above these are the cuticular layers covered by the cuticle proper; *b*, section heated in potassic hydrate; the cuticle proper has been raised from the cuticularized layers; *c*. section boiled in potassic hydrate; cuticle proper removed, epidermal cells separated, cuticular layers distinguished by finer stratification.

to yield twenty-five pounds of wax to each tree. Bayberry wax is a more familiar example.

226. To such waxy coatings is due the glaucous appearance of the leaves and fruits of many plants. The coatings are chiefly of the following kinds (de Bary[1]): —

1. Coherent layers or incrustations upon the epidermis. 2. Crowded vertical rods of considerable length, as, for instance, those on the internodes of Saccharum officinarum, from ten to fifteen hundredths of a millimeter in height. 3. Very short rods or rounded grains. These, on the leaves of Tropæolum, are not very near together, but on those of the cabbage, tulip, etc., are more crowded. 4. When the grains are more minute, and have the shape of needles irregularly massed together, they constitute the peculiar bloom of the leaves of Eucalyptus, Ricinus, etc.

227. Between the above kinds there are many intermediate ones, Agave Americana, for instance, furnishing forms between the two last named.

228. Epidermal cells proper have a delicate lining of protoplasm and a distinct nucleus. The cell-sap is generally colorless and transparent, allowing light to pass with very little obstruction to the layers beneath the epidermis; but in some cases it is so colored as to impart a conspicuous hue to the plant. In many water-plants there is no well-marked distinction between epidermis and the subjacent tissue, even the cells of the upper layer containing chlorophyll, but epidermal cells are mostly free from either chlorophyll or starch. Brongniart has shown that some amphibious plants have chlorophyll in the epidermal cells of the aquatic but not of the terrestrial form. That the rule is not universal is shown by Callitriche, which, according to Hegelmaier, has epidermis without chlorophyll in both forms.

229. Epidermis usually consists of only one stratum of cells, but it may be made up of two, three, or even more layers. Division of the original epidermal cells by one or more partitions parallel to the surface of the leaf gives rise to superposed cells; and thus *multiple epidermis* results, as in the upper surface of

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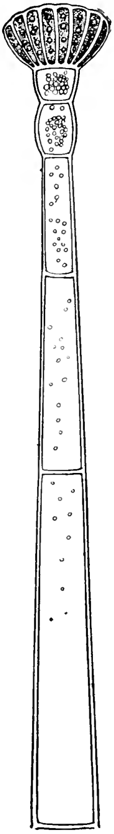
cuticle, which is soluble in caustic potash, and in most cases forms but a very thin coating over the epidermal cells" (Veg. Cell, Henfrey's trans., p. 35). Good examples for study of the different kinds of cuticular infiltrations are afforded by the following, — leaves of Dianthus caryophyllus, Galanthus nivalis, Ilex, Pinus, Hoya, Sassafras, and Taxus, and twigs of Viscum and of Oleander.

[1] Botanische Zeitung, 1871.

the leaves of many species of Peperomia, Ficus, and Begonia. Multiple epidermis is not always of even thickness throughout; sometimes a portion may be only one or two cells thick, while adjacent portions are composed of many layers. Such differences are generally associated with the occurrence of stomata, hairs, etc. The subjacent cells in some forms of multiple epidermis are smaller than those above them, and in these cases the arrangement of the cells in the successive layers presents striking inequalities.



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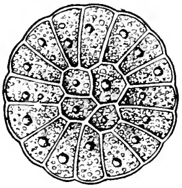

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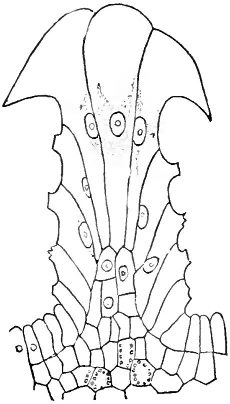

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230. **Trichomes.** Under this term are included the multifarious forms of hairs, scales, bristles, and prickles. *Hairs* are sometimes of diverse forms on the same plant, and even on the same part, but sometimes so peculiar and uniform throughout large genera, or even orders, that they aid in their identification; as, for instance, in Malpighiaceæ, Loasaceæ, and Elæagnaceæ.

231. Simple hairs, whether branched or unbranched, are formed by the prolongation of a single epidermal cell, either slight, forming a mere papilla, or to a great length, as in the so-called fibres of cotton. Simple hairs are abundant upon the rootlets of most plants at a little distance behind the advancing tip, where they play an important part.

232. Compound hairs are of all degrees of complexity. They may start from a single cell, or from a group of cells, and may have the derivative cells arranged in many ways. The cells at or near the

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Fig. 47 *a*. Upper portion of a glandular hair of Martynia proboscidea. $\frac{160}{1}$. (Martinet.)

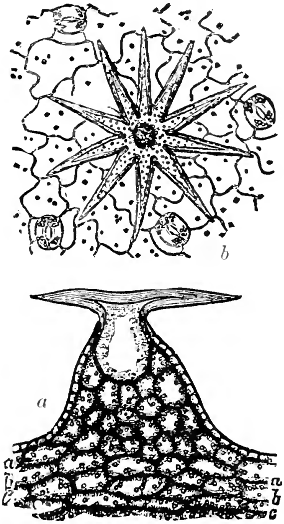
Fig. 47 *b*. View from above, of the upper portion of the same. $\frac{320}{1}$. (Martinet.)

Fig. 48. Cynoglossum officinale. Longitudinal section through a young angular bristle at the beginning of the thickening. $\frac{240}{1}$. (Strasburger.)

foot of the hair may differ somewhat in shape, size, and arrangement from the other epidermal cells. They may form an eminence upon which the foot rests, or they may be somewhat sunken so that the body of the hair hardly reaches the general surface of the epidermis; but usually the hair projects for a considerable distance above the border of the depression.

Both simple and compound hairs may be variously curved and branched, giving rise to stellate and many other forms.

233. *Scales* are trichomes which are mostly compound, and consist of discs borne by their edges or centres, either with or without a short foot or stalk. If the disc is composed of radiating cells, the scale becomes stellate, a form which resembles or passes into the stellate and tufted hairs common in Malvaceæ, etc. Well-marked stellate scales are met with in Oleaceæ and Elæagnaceæ.



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234. *Bristles, prickles and epidermal spines* are firmer or stouter outgrowths. When such outgrowths are truly epidermal, they come off with the epidermis.

Hairs, scales, and prickles differ very greatly as to their persistence, some being exceedingly short-lived, as, for instance, the hairs which occur on roots; while others, for instance the prickles on the rose, last for long periods.

235. In certain outgrowths from the edges of leaves or elsewhere the structure is complicated by the presence of a portion of the underlying framework. This is notably the case in the fringe upon the leaves of Droseraceæ. There are all degrees of variation between such trichomatous outgrowths and spinulose teeth, or lobes.

236. The consistence of the cell-wall in trichomes varies widely, from extreme tenuity to the density of a silicified wall. The more delicate hairs are transparent, so that the contents

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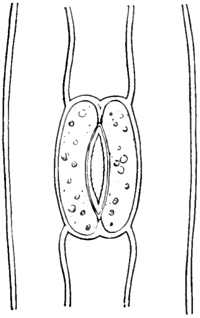
FIG. 49. Branching unicellular hairs: *a*, from Humulus (the hop); *b*, stellate hair of Deutzia. (Van Tieghem.)

can be plainly seen, thus affording opportunity for examining the movements of protoplasm, and for the study of the effects of reagents upon the contents of cells.

Young hairs contain much protoplasmic matter; at a later stage they have a large proportion of cell-sap; still later many are filled only with air.

237. At first the epidermis is always completely continuous, the cells being in close contact with each other; but soon there appear, especially in leaves, guarded openings through which the interior of the plant is brought into communication with the surrounding atmosphere. These apertures are of two principal kinds, the most important and widely distributed being

238. **Stomata.** These are combinations of epidermal cells of a peculiar character, between which a narrow slit extends directly through the epidermis to an intercellular space below. The cells bordering the slit are well termed guardian cells, on account of their opening and closing under certain circumstances. The neighboring epidermal cells are frequently arranged in a definite order; and the position of the stoma has in many cases a plain relation to the underlying framework.



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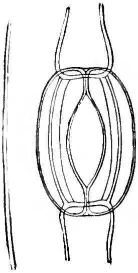

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Stomata belong especially to green organs exposed to the air; but they have been detected on all superficial parts of the plant, with the exception of roots.[1]

239. Viewed from above, stomata appear generally as elliptical bodies through which runs a narrow slit in the direction of the longer diameter. Each guardian cell is therefore half the ellipse. The cleft varies in width according to certain external condi-

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[1] The following cases are cited by de Bary (Vergl. Anat., p. 49): On rhizomata and tubers (young potatoes), on the perianth, the anther (in Lilium bulbiferum), on the pistil, on the seed-coat (Canna). Plants destitute of chlorophyll may also be destitute of stomata, as in Monotropa Hypopitys; or have them only on the pistil, as in Lathræa.

FIG. 50. Adult stoma of Hyacinthus orientalis, seen from above. (Strasburger.)
FIG. 51. The same, seen from below.

tions hereafter to be described, the stoma being in fact a delicately balanced valve. A vertical section shows that the outer part of the opening is wider than the narrow passage farther down, and that the space below this widens somewhat towards the intercellular cavity.[1]

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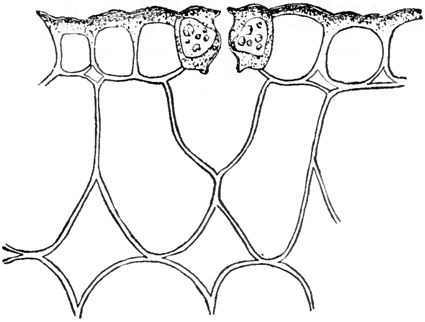
[1] The following table, compiled from figures given by Weiss, gives the number of stomata on the upper and under sides of the leaves of various plants for the most part readily procurable by students. To show the wide differences in size, the longer and shorter diameters have been added, and, finally, the fraction of a square millimeter covered by a single stoma.

Name of plant.	Number in sq. mm.		Length.	Breadth.	The space in a sq. mm. covered by a stoma.	
	Upper side.	Under side.			Upper side.	Under side.
Abies balsamea	0	228	0.047	0.031	0	0.2660
Abies nigra	31	82	0.042	0.027	0.0276	0.0731
Acer Pseudoplatanus, L.	0	400	0.024	0.017	0	0.1280
Amarantus caudatus, L.	171	193	0.012 0.026	0.012 0.017	0.0195	0.0672
Anemone nemorosa, L.	0	67	0.045	0.040	0	0.0947
Asclepias incarnata, L.	67	191	0.026	0.018	0.0247	0.0702
Avena sativa, L.	48	27	0.054 0.060	0.035 0.050	0.0706	0.0554
Berberis vulgaris, L	0	229	0.033	0.022	0	0.1305
Betula alba, L.	0	237	0.029	0.018	0	0.0972
Brassica oleracea, L	219	301			0.1137	
Buxus sempervirens	0	208	0.032	0.031	0	0.0942
Caltha palustris, L.	—	43	0.042	0.034	0	0.0482
Euphorbia Cyparissias, L	0	259	0.027	0.018	0	0.0989
Ficus elastica	0	145	0.028	0.019	0	0.1187
Galanthus nivalis, L	30	55	0.034	0.022	0.0176	0.0323
Geranium Robertianum	—	297	0.045	0.032		0.3356
Helianthus annuus, L.	175	325	0.034	0.023	0.1074	0.1995
Hydrangea quercifolia, Bertr.	0	330	0.020	0.019	0	0.1015
Ilex Cassine	0	212	0.029	0.025	0	0.1206
Juglans nigra, L	0	461	0.024	0.018	0	0.1563
Lilium bulbiferum, L.	0	62	0.071	0.050	0	0.1751
Maclura aurantiaca, Nutt.	0	251	0.022	0.016	0	0.0695
Mimosa pudica, L.	138	302	0.017 0.026	0.009 0.015	0.0164	0.0927
Morus alba, L.	0	480	0.018 0.029	0.008 0.021	0	0.0547
Nymphæa alba, L.	460	0	0.026	0.022	0.2070	
Pinus Strobus, L.	142	0	0.054	0.032	0.1945	
Pinus sylvestris, L.	50	71	0.034	0.023	0.0307	0.0436
Pisum sativum, L	101	216	0.024	0.017	0.0323	0.0691
Pittosporum Tobira, Ait.	0	382	0.031	0.027	0	0.2494
Populus dilatata, Ait.	55	270	0.035 0.033	0.024 0.021	0.0363	0.1471
Ribes aureum, Pursh	0	145	0.036	0.025	0	0.1025
Secale cereale, L.	—	25	0.051	0.029	0	0.0269
Sequoia gigantea (young plants)	0	82	0.053	0.033	0	0.1434
Silene inflata, Sm	71	166	0.033	0.021	0.0386	0.0905
Solanum Dulcamara	60	263	0.021	0.014	0.0139	0.0607
Stellaria media, Sm.	128	—	0.029	0.026	0.0758	
Syringa vulgaris, L.	0	330	0.028	0.016	0	0.1162
Vinca minor, L.	0	477	0.029	0.018	0	0.1961
Vinca minor, var. variegata	0	405	0.024	0.016	0	0.1223
Zea Mais, L.	94	158	0.037	0.029	0.0792	0.1332



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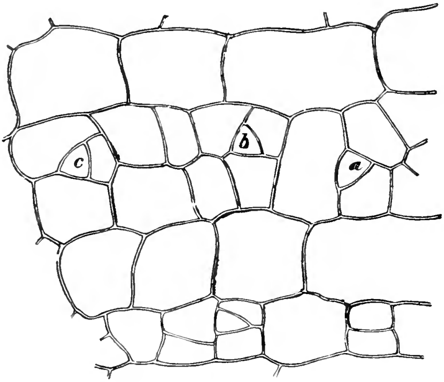
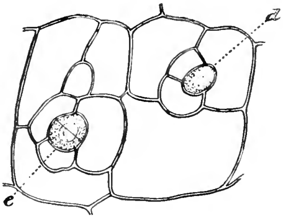
240. As appears from the following figures, the first stage in the development of an ordinary stoma is the separation of a part of an epidermal cell by means of a vertical partition, thus forming the mother-cell of the stoma. This next divides by a vertical plane which soon exhibits a narrow chink. The cells thus slightly separated at their common wall may by subsequent growth bring about changes in the relations of the neighboring cells.

In Sedum, as shown by Strasburger, there are preparatory divisions in different directions, while in some monocotyledons there are simultaneous divisions in contiguous epidermal cells.

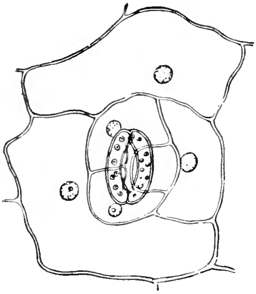


53 *a*

241. Stomata are not present, at least in a perfect form, in any submerged plant. In aquatics with



53 *b*

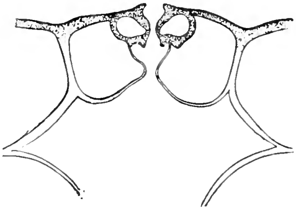


53 *c*

Fig. 52. Vertical section of stoma of Hyacinthus orientalis. (Strasburger.)

Fig. 53 *a*, *b*, *c*. Three stages in the development of the stomata of Sedum spurium. Fig. 53*c* shows the narrow slit made by the neighboring epidermal cells. (Strasburger.)

floating leaves they are confined to the upper surface of the leaf. The leaves of certain plants, as those of monocotyledons and those which take a vertical position, have them in nearly equal numbers on the two sides; but in most cases the number on the under exceeds that on the upper surface, as will be seen from the table on page 71. As regards the approximate number on leaves of average size in some of our common plants, the following figures may be of interest: —



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Nymphæa	7,650,000
Brassica oleracea	11,540,000
Helianthus annuus	13,000,000

242. *Water-pores.* Directly over the extremities of the fibres of the framework of many green leaves are found apertures in the epidermis which have no true guardian cells,[1] but which closely resemble ordinary stomata in most other respects. Owing

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[1] That is, the bordering cells do not close under external influences.

FIG. 54. Vertical section of stoma of Sedum spurium. (Strasburger.)

FIG. 55. Water-pores in leaf of Rochea coccinea. The left-hand figure shows both an ordinary stoma (the lower one) and a water-pore (the upper), as seen on upper surface of leaf. The right-hand figure shows the structure displayed by a vertical section. (Van Tieghem.)

to the fact that their cavity answering to the intercellular space of a stoma is often filled with water instead of air, these have been called water-pores. At certain times liquid water passes through these pores, collecting at the opening and sometimes leaving there, upon evaporation, slight incrustations of calcic carbonate. Water-pores assume different forms and vary much in size. Good examples are afforded by many Aroideæ, by the teeth of the leaves in some species of Fuchsia, the leaf-margins in Tropæolum, etc.[1]

Small rifts of nearly the same shape can be found in certain grasses; but in these the aperture comes from a mechanical rupture,[2] and the underlying structure is very simple.[3]

CORK.

243. This protective tissue is formed beneath and replaces epidermis in the older superficial parts of plants; it also constitutes the films by which wounds are healed. Only the inner layers of cork-tissue possess cellular activity, those which lie outside of them having perished: the former contain protoplasm and are capable of cell-division; the latter contain air, and occasionally small clusters of crystals. The inner, active, and growing layers are known as cork meristem, cork cambium, or *Phellogen;* the outer, produced from this and no longer living, make up the bulk of the outer bark, and are ordinarily called cork. Although the older cork-tissues must be further described in Chapter III., under "Bark," their elements may be conveniently treated of now in connection with the cells which produce them.

244. Origin. Cork may arise from several different sources, the principal of which are the following: (1) from division of cells in the epidermis (*e. g.*, species of Pyrus, Salix, Viburnum, etc.); (2) more commonly from underlying parenchyma, in a few cases even from that which occurs in the inner bark (the bast parenchyma), as in Vitis and Spiræa; (3) from parenchyma at injured surfaces, as in the healing of wounds.

245. It is normally produced upon the stems and roots of flowering plants, especially dicotyledons. Its cells are generally

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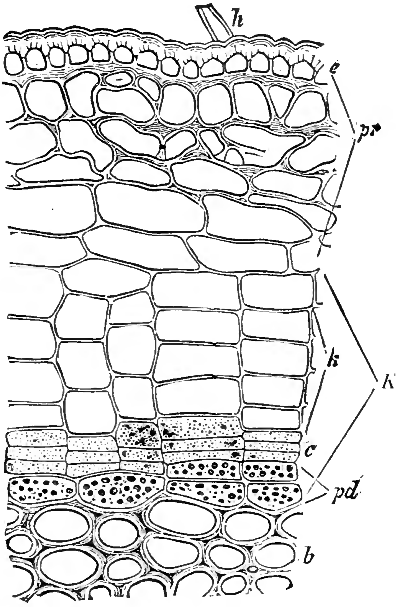
[1] For a full account of water-pores, see de Bary's Anatomie, p. 54, and Jahrb. konigl. botan. Garten, Berlin, 1883.

[2] De Bary: Anatomie, p. 57.

[3] Gardiner: Proceedings Camb. Phil. Soc., 1883.

formed by the division of the mother-cell into two tabular cells, by a partition parallel to the surface of the organ. In most cases the outer cell becomes cork, while the inner retains its power of division and in turn produces new cells. But with the first appearance of the cork-layer a change takes place in all layers lying to the outside of it: they are cut off from nutritive supplies and soon die. The continuous layers of cork are called, collectively, *Periderm*, a name restricted by Mohl to tough cork in distinction from soft cork, but now employed with a wider signification.



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246. Cork meristem gives rise to successive layers of cork-cells: if the new layers differ much from the preceding in the shape and size of their cells, an appearance of stratification naturally results. Cork meristem may, in exceptional instances, produce on its inner side permanent parenchyma, the cells of which contain chlorophyll; these green layers are called *Phelloderm*, and are observed well in the beech, willow, etc. (see Chapter III.).

247. Cork-cells are tabular, or sometimes cubical, and with few exceptions have no intercellular spaces. In the case of very flat cells which cohere more firmly laterally than in the line of the radius, the cork-tissue may be readily separated in films or sheets.

248. The walls of older cork-cells are cutinized or suberized throughout. The demonstration of cellulose in cork-cells is not possible unless the cells have been first acted on by solvents,

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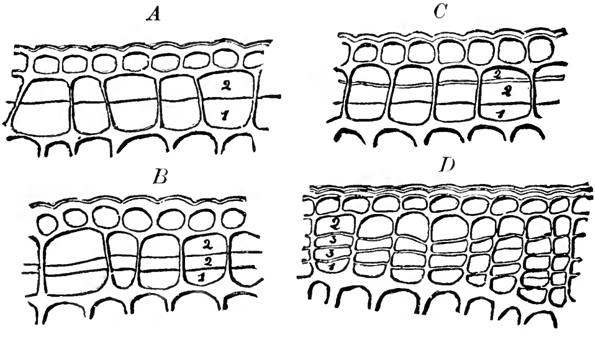
FIG. 56. Formation of cork in a branch of Ribes nigrum, one year old; part of transverse section: *h*, hair; *e*, epidermis; *pr*, cortical parenchyma, somewhat distorted; *K*, the total product of the phellogen *c*; *k*, cork-cells; *pd*, phelloderm; *b*, bast-cells. (Sachs.)

such as caustic potash, and the like. But sometimes the cell-wall seems to be completely changed into cork-substance.

249. Cork-substance behaves towards reagents in nearly all respects as cutin does (see 157).



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250. Cells which have been completely suberized can be separated from each other by the gradual action of Schulze's macerating solution.[1]

251. The color of cork-cells is not dependent upon the amount of the change of the wall into cork-substance. The walls of the cells in some species of willow are colorless, while those in other species are distinctly yellow; and yet the former have been as thoroughly changed into cork-substance as the latter.

II. Cells of the Fibro-vascular System,—Prosenchyma in the widest sense.

252. The cells and modified cells of this system constitute the framework of a plant. In a few of the higher and in many of the lower plants it is barely if at all developed, the entire structure consisting, in such cases, of a mass of parenchyma covered by epidermis. But in most plants it exists as a skeleton

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[1] This fact has led to the belief that there exists in such cases an intermediate plate which differs in its character from the rest of the cell-wall; but prolonged action of the same reagent, especially with warming, causes the cells to break down and ultimately form a disorganized mass.

FIG. 57. Formation of cork and secondary cortex in Betula verrucosa. *A*, *B*, *C*, *D*, successive stages; 1, first layer of secondary cortex; 2, layer which divides in *B*, to give outside the first layer of cork (shown in *C*), and a layer, 3, within, which again divides in *D*. (Sanio.)

bringing all parts into closer relations, and strengthening the whole.

253. The cells are normally of considerable length in proportion to the transverse diameter, and are generally more or less sharply pointed (prosenchyma proper). The most important of the modified cells belonging to this system unite to form long rows in which the terminal partitions are nearly or quite obliterated, throwing the cavities into one, and thus forming a cylinder, termed a *duct.* Between proper prosenchyma cells and ducts there are numerous connecting forms which render impossible any attempt at classifying them exactly.[1]

Associated with these cells, but differing in some important particulars, are cribrose and latex cells, which for convenience are here to receive separate treatment.

254. Before developing the provisional classification given on page 59, attention must first be directed to the peculiar transitional forms constantly met with, which belong as much to parenchyma as to prosenchyma, but are more conveniently examined in connection with the associated wood-elements.

Chief among these intermediate forms must be mentioned those of which Fig. 58, No. 9, may be taken as a representative. Here the whole structural element is isolated as an elongated combination of three cells, one of which has flattened ends, while the other two, attached to these ends, have their free extremities pointed. In spite of their form, such cells are usually described as wood-parenchyma cells. When their walls are thicker, they are not easily distinguishable from septate libriform cells (see 263).

255. The forms shown in Fig. 59, No. 19, are common in the wood of many plants, notably the oaks. They are relatively small, have rather blunt extremities and thin walls. They occur with these characters especially in the autumnal wood of the oaks (see 395), while in the spring wood they are apt to

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[1] For the satisfactory study of the relations of the elements of prosenchyma, very thin sections are necessary; but for the examination of the elements themselves, recourse to some process of maceration, by which they can be isolated, is always desirable. In general, there is nothing preferable to Schulze's solution in any strength adapted to the special case; it must be remembered that the slow action of a dilute solution gives better results than the more rapid action of a concentrated one. If the section to be examined is first subjected to the action of the macerating solution of proper strength and then thoroughly washed, it can be dissected at pleasure under a high power of a simple lens. This method is always to be preferred to the ordinary one of disintegrating the whole specimen and obtaining a confused mass of separated cells.

pass over into the variety shown in Fig. 59, No. 18. The latter are known as "conjugate cells."

PROSENCHYMA PROPER.

256. **Typical wood-cells.** These are best illustrated by elongated, often pointed cells, of which good examples are found in the cambium layer (that is, the layer of merismatic or formative

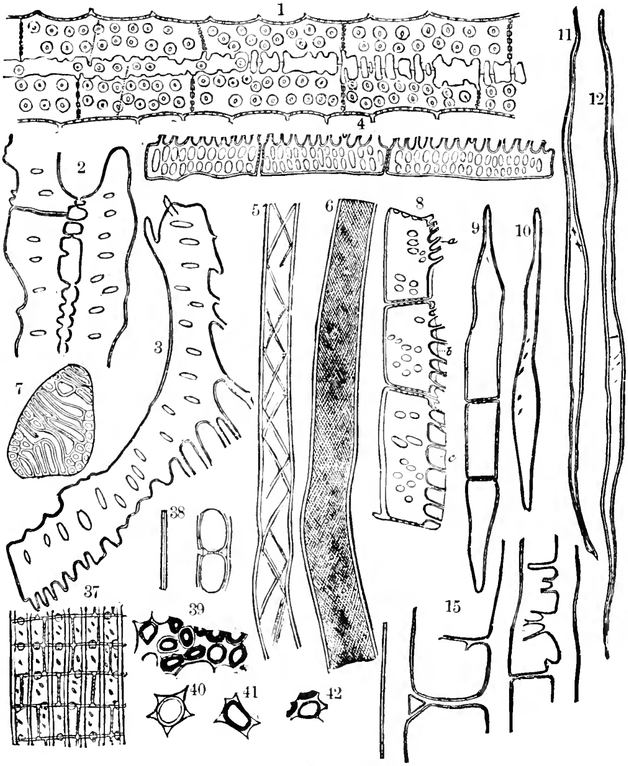

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FIG 58. Drawings of wood-elements. 1-7. Avicennia sp. 1. Wood-parenchyma cells united with each other; tangential section. 2, 3, 4. Conjugate wood-parenchyma cells isolated by Schulze's solution. 5, 6. Portions of spirally striated libriform fibres isolated by Schulze's solution. 7. The septum of a duct. 8-12. Tectona grandis; the elements separated by maceration. 8. Conjugate wood-parenchyma cells. 9. Ordinary wood-parenchyma fibre. 10. Substitute fibre. 11. Simple libriform fibre. 12. Septate libriform fibre. 15. Porlieria hygrometrica; conjugate substitute fibres seen in radial section. The wood-cells are omitted in order not to confuse the diagram. 37. Radial section through the wood of Jatropha Manihot. 38. Tangential section through a libriform fibre and two cells from a medullary ray of the same plant. 39-42. Bast-cells of Cytisus Laburnum. 39. Cross-section through a part of a young bast-bundle acted on by chloroiodide of zinc. 40, 41, 42 Cross-sections through young bast-cells, acted on by chloroiodide of zinc. (Sanio.)

tissue just under the bark of dicotyledonous plants). Their walls are thin, and at first nearly or quite free from pits or other markings.

They grade into three constantly recurring forms; namely, (1) parenchyma (see 254); (2) attenuated forms, often so slender as to deserve the name of fibres; (3) forms with peculiar markings at most points of contact, and thus much resembling ducts or vessels.

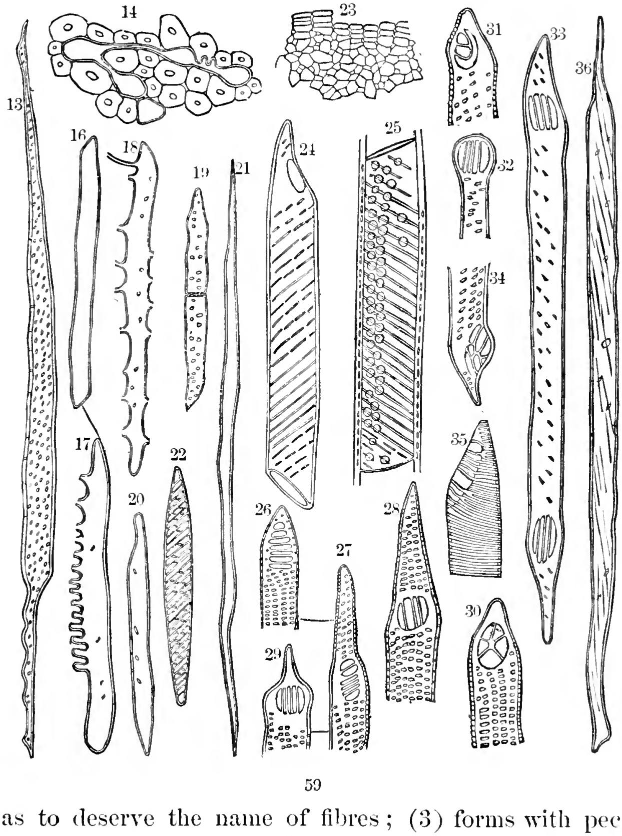

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FIG. 59. Drawings of wood-elements. 13. Tracheïd from Tectona grandis. 14-18. Porlieria hygrometrica. 14. Conjugate substitute fibres seen in transverse section. 16. Ordinary substitute fibre after maceration. 17, 18. Conjugate substitute fibres after maceration. 19-22. Cytisus Laburnum; the elements separated by maceration. 19. Wood-parenchyma fibre. 20. Substitute fibre. 21. Simple libriform fibre. 22. Tracheïd. 23. Cross-section through the cambium and youngest wood of Cytisus Laburnum. 24-25. Ducts from Mahonia Aquifolium. 24. After maceration. 25. Longitudinal section. 26-31. Ducts from Hieracium, separated by maceration; showing the extremity only. 32-34. Ducts from Onorpordon acanthium, separated by maceration. 35. Spirally marked duct from Vitis vinifera, after maceration. 36. Libriform fibre from Jatropha Manihot. (Sanio.)

257. The drawings of wood-elements represented in Figs. 58 and 59 are from Sanio's work, and are given with his nomenclature. The cells figured in Nos. 10 and 16, termed by Sanio substitute fibres (German, Ersatzfasern), answer well to the type of prosenchyma. When these cells are much reduced in calibre, they are known as libriform fibres.

258. Ordinary prosenchyma cells usually have simple pits, but no true spirals. The pits may be round, and of the same size as those on the ducts with which they may be in contact, but sometimes they are elongated slits, and run obliquely, as shown in Fig. 59. If two of these cells are in contact, processes may extend from one cell to corresponding protrusions in the other, and thus one cell is united with the next. By careful maceration such cells can be separated, and then each appears to have one or more rows of square teeth or short tubes. It sometimes happens that the wall at the end of these intrusive tubes is broken down, thus allowing free communication between the cells.

Good examples of substitution cells are to be found in the wood of Magnolia, Liriodendron, many Leguminosæ, etc. They are not so common, however, as conjugate parenchyma cells (see Fig. 58).

259. **Woody fibres** are of two chief classes: (1) those in which the narrowed cavity is continuous throughout the whole length, and (2) those which have partitions dividing it (septate fibres).

The first class has been again divided into two groups depending upon the presence of starch, but the division is not wholly satisfactory. The first group comprises all those fibres which have a trace of protoplasm, while those of the second have also more or less starch, and generally some tannin.

All of these woody fibres resemble the bast-fibres of the inner bark of dicotyledons so closely that they have been well called libriform. They are described by Sanio, from whose paper on the subject most of these names are taken, as being always spindle or fibre-form, relatively strongly thickened, and occasionally furnished with bordered pits which somewhat resemble those of vasiform elements (264), but are smaller and less clearly defined. They never have true spiral markings, and very seldom any spiral striation. They contain during the periods of rest of vegetation in winter more or less starch, and perhaps some chlorophyll and tannin, but at other times only air.

260. The unseptate fibres, the true libriform cells, are only sparingly pitted, except in a few species like Oleander, where they are pitted on both the radial and tangential walls. The pits are generally elongated and oblique, and according to Sanio always running from left to right.

261. The cell-wall of these fibres is always lignified, and presents three layers; and in some instances there is also a layer which is plainly gelatinous, *e. g.*, in Betula and Alnus. These gelatinized fibres are not found in all of the annual rings, nor in all parts of even one ring.

262. Libriform cells are variable in length in different plants; some of the shortest occurring in Daphne Mezereum, .14 mm., and the longer in Avicennia, 2 mm. In all cases they are the longest elements in the mass of wood. They are generally simple, but occasionally branched cells are met with, as in Tilia and Cladrastis. They are sometimes irregularly grouped together, sometimes radially arranged. Species of Magnolia exhibit the latter, Ulmus the former, mode of arrangement.

263. Septate libriform cells have sometimes been confounded with wood-parenchyma; but Sanio points out the following distinctive characters: (1) they are always thicker walled; (2) they have oblique slits, while wood-parenchyma has only roundish pits; (3) they become septate only after the thickening has progressed to some extent, while in wood-parenchyma the divisions begin before the cambium cells[1] from which it is derived have begun to thicken.

Septate libriform cells are less common than any other woody element; examples, however, are not rare in Vitis, Hedera, and Rubus.

264. Vasiform elements. Neither of the two forms already considered — namely, typical wood-cells and woody fibres — has distinctive spiral markings or true bordered pits (that is, discoid markings); but another important class of wood-elements, of which mention must next be made, is characterized by such thickenings.

265. To this class of elements it is difficult to give any satisfactory name. They have been collectively termed vascular, but a large part of them are comparatively short and closed, and cannot be properly known as ducts or vessels; the name Tracheal (or Tracheary), more widely employed, is open to

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[1] The immediate derivatives from the cambium, which are partly formed woody fibres, have been termed cambium fibres (Sanio: Bot. Zeit., 1863).

the objection that while it is a significant term when applied to trachea-like bodies (ducts) it is a misnomer when applied to an elongated cell wholly free from annular or spiral markings.

266. Tracheal cells are of two chief kinds: (1) those which are closed throughout, — at least until a very late stage of development; (2) those formed by rows of cells which lose their intervening partitions, and hence are thrown into a long canal, or vessel. The former are known as *Tracheïds*,[1] the latter as *Tracheæ;* for which terms may be substituted the following, applicable in nearly all cases, — *Wood-cell* and *Duct.*

The distinctive markings of tracheïds and tracheæ are bordered pits, or discoid markings, and various thickenings of which the spiral may be taken as an example.

Tracheïds and tracheæ further agree in the following point: when complete, the protoplasmic mass disappears, leaving generally no trace. The cavity is filled in a few cases with watery fluid, in some with water and air, but in most with air alone. Occasionally other matters may be found in the tracheæ, for instance, latex; but these are so exceptional as to need no further mention at this point.

267. **Vasiform wood-cells,** or **tracheïds,** are elongated and tapering cells, more or less lignified, and having peculiar markings, the principal kinds of which, although previously referred to in 133, require a more extended treatment here.

268. **Bordered pits,** called also **areolated dots** and **discoid markings,** are very common, especially in wood of gymnosperms, where they form a characteristic feature both in fossil and

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[1] But the term *tracheïd,* as usually understood, is applied to wood-cells with peculiar markings, next to be described.

The following measurements by Sanio show the difference between the length of some tracheïds and the libriform cells in the same plant: —

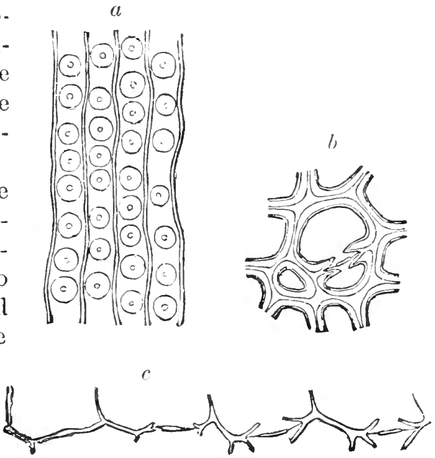
	Tracheïds.	Libriform cells.
Rhamnus catharticus	.28 mm.	.52 mm.
Æsculus Hippocastanum	.26 "	.43 "
Daphne Mezereum	.15 "	.21 "
Ribes rubrum	.49 "	.47 "

Where, however, the tracheïds alone are present, they are sometimes much longer; for instance, in Staphylea pinnata, 1 mm., and in Philadelphus coronarius, .85 mm.

According to Sanio, the bordered pits of ducts are the same as those of the tracheïds, as regards size, form, and usually as regards frequency.

Occasionally tracheïds are found which are plainly septate. It thus appears that the tracheïds form a gradation between true ducts and libriform cells with bordered pits.

recent plants. When the wood in a pine stem is cut radially, the flattened sides of the wood-cells exhibit the dotted appearance seen in Fig. 60. The number and mode of distribution of the markings in the wood-cells or tracheïds of Coniferæ are so nearly constant, that they may be used with considerable certainty in the discrimination of a few genera.



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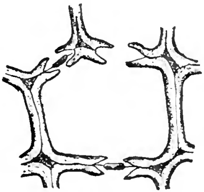
269. In a transverse section of the mature tracheïds the discoid markings are plainly seen to be pits having an arched border or incomplete dome, and it is also seen that the thin spot or pit is common to two contiguous cells. Hence the two domes, being on opposite sides of a partition-wall, have a lens shape, and the central perforations are nearly or exactly opposite each other (Fig. 62). Even in the same specimen the bordered pits vary within comparatively narrow limits both as regards the size of the disc and that of the central aperture.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62

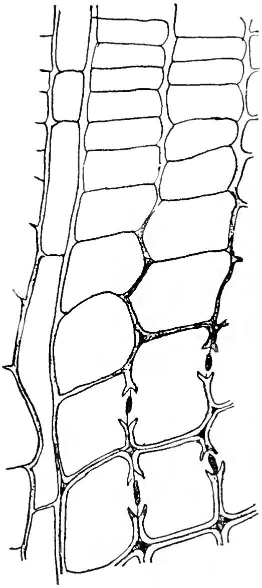
The two domes making up a single discoid marking are at first separated by a delicate plate of unequal thickness; but later this middle lamella may be broken down, and then a free passage extends from one cell to the other.

The character of the domes and the middle plate can be understood from the accompanying figures of sections of the stem of Pinus sylvestris (Figs. 62 and 63). According to Sanio, the sections should be boiled in acetic acid, in order to remove all cell-contents.

FIG. 60. Areolated or disciform markings of the wood-cells (tracheïds) of Pinus Laricio: *a*, aspect of radial walls; *b*, a transverse section; *c*, development of the markings in Pinus sylvestris. (Sanio.)

FIGS. 61 and 62. Pinus sylvestris. Transverse sections of nearly perfect and perfect discoid markings. (Strasburger.)

The cambium-cells and the youngest tracheïds have uniform and smooth walls, but in those next older there appear thin spots, which are well defined above and below, but not on the sides, for here they grade off into the thicker part of the wall. In the cells which are still older the thin places take the shape of discoid markings, and are clearly seen in any radial view. Comparison of radial with transverse sections shows that at the margins of the thin places a portion of the wall extends as a slight projection upwards, and partly over the spot. In the more mature form the thin place is still retained as a delicate plate separating the two cells, but easily broken down perhaps in further growth.



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270. *Scalariform markings* (see 134) are especially abundant in ferns. The bordered pits are much elongated, and appear as clefts with only narrow portions of the wall between them (Fig. 64 *l*). They often follow each other with as much regularity as the "rounds" of a ladder, whence the name (from *scalaria*, — a flight of steps). They are more commonly found in

DUCTS.

271. Ducts, or Tracheæ, are variously marked by pits, and by the thickenings described in Chapter I. Some of the more common forms of dots are shown in Fig. 64.

Spiral, annular, and reticulated markings are all formed by the thickening of parts of the wall by which narrow lines or bands are produced on the inner surface. In these cases the portions of the wall which are not thickened are often of extreme tenuity, and break upon slight pressure or strain, permitting the spiral to uncoil or the rings to separate (Fig. 64, *s s'*).

272. **Spiral markings.** The number of threads or narrow bands varies from one to fifteen or even twenty, the latter in the petioles of Musa.[1] They wind, as a rule, from right to left;

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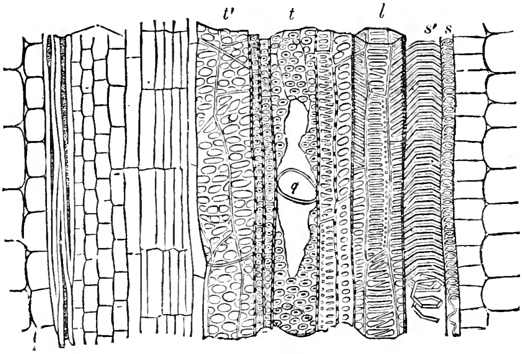
[1] De Bary: Vergleichende Anatomie, 1877, p. 163.

FIG. 63. Pinus sylvestris. Cross-section through the cambium and young wood-cells. (Strasburger.)

but, according to Mohl, from left to right in a few plants. Thus in the wood of Vitis vinifera, Berberis vulgaris, and some others, they run from left to right in the ducts first formed, but in the reverse direction in those which are produced later. And by interruption of the spiral it may have two directions in the same duct, as in those of Cucurbita.[1] The steepness of the spiral depends in part on the age of the cell, or vessel, — at least in some cases. According to Mohl, "if the vessel is developed in an organ which has already completed its longitudinal growth, the turns of the spiral lie close together; but if the organ undergoes elongation after the completion of the development of the vessel, the turns of the fibre are drawn far apart by the stretching which the vessel suffers; consequently very loosely wound spiral vessels are usually found in the posterior first-formed portion of the vascular bundle nearest to the pith, while those lying nearest the bark have close convolutions."[2]



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273. **Annular and reticulated markings** have been regarded as mechanical modifications of spirals, and it is true that intermediate forms exist between these types. For instance, tightly wound spirals are nearly annular, and in some cases there are threads which run either vertically or obliquely from one part of a spiral to the contiguous thread. But even in the youngest states of some ducts the markings appear as rings or as a net-

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[1] Mohl: Vermischte Schriften, 1845, pp. 287, 321, Ueber den Bau der Ringgefässe.

[2] Mohl: Vegetable Cell, Eng. Trans., 1852, p. 19.

FIG. 64. Vertical radial section of hypocotyl of Ricinus communis, illustrating different markings of ducts; *t' t*, pitted; *l*, scalariform; *s' s*, spiral, the spirals beginning to uncoil. (Sachs.)

work. While, therefore, they may and probably do have a common origin with spirals, it is not necessary to assume, nor is it probable, that they have resulted from mechanical displacements of them. The relative positions of the separate rings may be explained in the same way as the steepness of the spirals.[1]

274. Cases are met with, in which projections from the wall may extend nearly or quite across the cell-cavity, somewhat after the manner of beams. Such cross-beam cells or ducts are called trabecular. A good example can be found in some of the tracheïds of the leaf of Juniperus communis.[2]

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[1] "The notion was extensively held that the spiral fibre could not follow the expansion which the vessel underwent during its growth, and tore up into fragments which were again united into rings, and thus brought about the formation of annular vessels. Completely as this idea, which was a contradiction to all observation, had been refuted by Moldenhawer, it remained a standing article in all phytotomical writings up to Meyen's Physiologie" (Mohl: Vegetable Cell, p. 21).

[2] De Bary: Vergleichende Anatomie, p. 171.

The following measurements of wood-cells and ducts are given by Wiesner (Die Rohstoffe des Pflanzenreiches, 1873, p. 525): —

	Average diameter of wood-cells.
Rhus Cotinus	7.5 μ.
Lonicera Xylosteon	9.8 "
Salix Capræa	11.0 "
Viburnum Lantana	22.0 "
Alnus glutinosa	25.0 "
Fraxinus excelsior	28.0 "

	Average diameter of ducts.
Hæmatoxylon Campechianum	112 μ.
Cæsalpinia Sappan	120 "
Ochroma Lagopus	140 "
Fraxinus excelsior	140 "
Ulmus campestris	158 "
Tectona grandis	160 "
Juglans regia	220 "
Carya alba	248 "
Quercus sp.	200 to 300 "

The ducts in the foregoing examples are so large that in cross-section they can easily be seen by the naked eye. The following are considerably smaller: —

Tilia sp.	60 μ.
Acer sp.	71 "
Alnus sp.	76 "
Rhus Cotinus	80 "
Betula sp.	85 "

275. **Tyloses.** If a cell still growing is in contact with a duct at one or more of its perforations, the cell may intrude into the cavity of the duct, and to a considerable extent. Such intrusive growths are known as Tyloses (German, Thyllen).

If the intrusive portion of the tylosis further multiplies, producing new cells, the cavity of the duct may contain a confused mass of irregular cells of various shapes and sizes. Such masses are often found in the ducts of Quercus alba, Q. castanea, Q. macrocarpa, Q. tinctoria, Q. virens, Castanea vesca, Carya alba, C. olivæformis, C. amara, Juglans nigra, Sassafras officinalis, Morus rubra, Maclura aurantiaca, and Robinia Pseudacacia. In the latter they are especially striking.[1]

BAST-FIBRES (LIBER-FIBRES).

(Sclerenchyma of many recent German authors.)

276. The name *bast* was originally given to the inner bark of the linden (bass-wood), and hence originated its use as a prefix in "bast-matting," etc.; the name *liber* was applied in a more general way, namely, to any smooth inner bark (upon which one could write). That which imparts strength to inner bark, making it of use in the arts, consists of long and tough cells with very much reduced calibre; but these are not confined by any means to inner bark. Owing to this fact, some have thought best to abandon the terms bast and liber for such cells, and adopt, on account of their firmness, a term formerly given to grit-cells, namely, sclerenchyma; the older terms, however, are not likely to lead to confusion, whereas the other might. It is in the bark of dicotyledons that liber-cells or liber-fibres occur most abundantly.

Their prevailing shape is that of a slender spindle, which may taper simply, or may be somewhat forked at the extremity.

The following can be seen only under a lens: —

Euonymus Europæus	20 μ.
Fagus sp.	28 "
Cratægus sp.	30 "
Ligustrum sp.	36 "
Pyrus communis	40 "

[1] Mr. P. H. Dudley, who communicates some of the names in this list, adds in his note: "So far I have never found any tyloses in ducts with scalariform markings."

Occasionally fibres which are very much branched are met with, notably in the leaves of Camellia, for instance common tea; see Fig. 68. Generally the walls are thickened unevenly, even forming conspicuous projections into the cavity of the cell; while some fibres have regular and characteristic markings, a few of which are shown in Fig. 65. Septate forms are occasionally found. The change in the character of the cell-wall which accompanies the thickening is essentially lignification, like that observed in wood-cells and ducts. It is generally said that the walls of liber-cells are less brittle than those of the elements of wood, and this is commonly so; but there are some flexible wood-elements, and there are, on the other hand, some very brittle fibres of sclerenchyma. The thickening of the wall in liber-cells takes place not only in different degrees, but with variations in the amount of infiltration of foreign matters, which give rise to differences in the behavior of the fibres with reagents. In a few cases the inner part of the wall is somewhat gelatinous

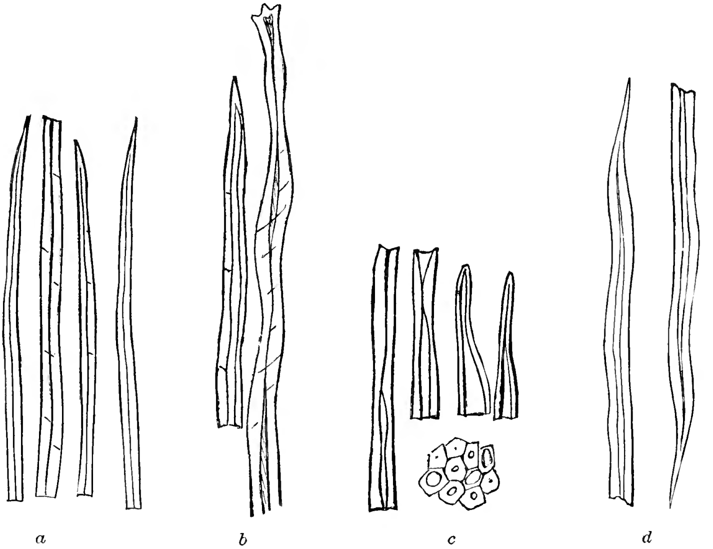

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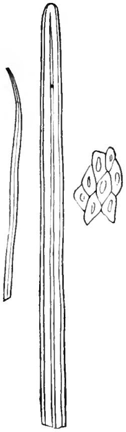
FIG. 65. Fragments of some of the more common bast-fibres used in the arts. $\frac{200}{1}$.

a, Flax, Linum usitatissimum. (Wiesner)
b, Hemp, Cannabis sativa. (Schacht.)
c, Jute, Corchorus capsularis. (Wiesner.)
d, China-grass, Bœhmeria nivea.

and possesses the power of swelling in water and in dilute acids (compare Collenchyma); in some others the outer part of the wall is gelatinous, while the inner is hard. Morus alba, Gleditschia triacanthos, and Robinia Pseudacacia are examples of the first, Astragalus falcatus of the second, condition (Sanio).

277. One of the most striking characters of the bast-fibres of many plants is the abundance of crystals found therein. Excellent examples are afforded by the inner bark of some of our ligneous plants (294).



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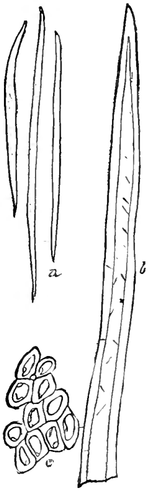

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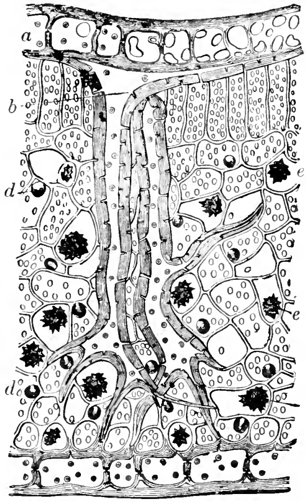

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278. The firm attachment of fibres to those above and those below them has given rise to erroneous ideas relative to the length of single fibres, as the table on the following page shows.[1] By careful management it is possible to isolate a connected thread of fibres of great length; the value of fibres for textile purposes depends largely upon this fact.

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[1] The table on page 90 has been compiled from data given by Wiesner and also by Vetillart, which are here rearranged for greater convenience of reference.

FIG. 66. Fibre of Agave Americana: *a* and *b*, $\frac{60}{1}$; *c*, $\frac{250}{1}$. Only the upper part of each fibre is shown in the left-hand figures. The right-hand figure shows a cross-section of a group of cells.

FIG. 67. Fibre of Coir (Cocos nucifera): *a* and *c*, $\frac{60}{1}$; *b*, $\frac{250}{1}$. *a* shows three separate and complete fibres, *b*, the upper part of a single one, *c*, a cross-section of a group of cells.

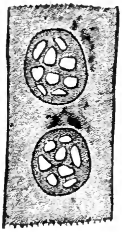
FIG. 68. Transverse section through leaf of Camellia (Thea) viridis, showing: *a*, epidermis; *b*, branched liber-cell; *d*, oil-drop; *e*, crystals. (Mirbel.)

THE CHARACTERISTICS OF FIBRES.

Name of Fibre.	Reaction with Cuprammonia.	Reaction with iodine and sulphuric acid.	Reaction with anilin sulphate.	Length of raw fibre, cm.	Width, mm.	Length of the bast-cells composing the fibre, mm.	Width of the bast-cells composing the fibre.	
							Limit of size, mm.	Average size, mm.
Raw flax fibre (Linum usitatissimum).	Soon attacked and almost entirely dissolved.	Colored blue.	Remains uncolored or nearly so.	20–140	.04–.62	20–40	0.012–0.026	0.015–0.012
Raw hemp fibre (Cannabis sativa).	Clean fibre dissolved.	Greenish-blue to pure blue.	Colored faint yellow.	100–300		10+	0.015–0.028	0.016–0.019
Raw jute (Corchorus capsularis).	Bluish color and more or less distinct swelling.	Yellow to brown.	Golden-yellow to orange.	150–300	.03–.14	0.8–4.1	0.010–0.021	0.016
Raw esparto fibre (Stipa tenacissima).	Bright green.	Rusty red.	Egg-yellow.	10–40	.09–.5	0.5–1.9	0.009–0.015	
Bromelia Karatas.	Bluish color and marked swelling.	Reddish-brown.	Golden-yellow.	120	.15-1.2	1.4–6.7	0.027–0.042	
Raw fibre of aloe (Aloe perfoliata).	Bluish color and feeble swelling.	Reddish-brown.	Golden-yellow.	40–50	.075–.105	1.3–3.7	0.015–0.024	
New Zealand Flax (Phormium tenax).	Bluish color and more or less distinct swelling.	Varies with purity of fibre, being yellow, green, or blue.	Remains uncolored or nearly so.	80–110	.042–.12	2.5–5.6	0.008–0.019	0.013
China grass (Bœhmeria nivea).	When "cottonized," quickly acted upon and almost completely dissolved.	Copper red to blue.	Remains uncolored or nearly so.			Up to 220	0.040–0.080	0.050
Ramiefibre (Bœhmeria tenacissima).	When "cottonized," quickly acted upon and almost completely dissolved.	Copper red to blue.	Remains uncolored or nearly so (hardly perceptible yellow).			Up to 80	0.016–0.126	
Coir (Cocos nucifera).	Perceptible swelling and pronounced blue color.	Reagent not applicable on account of the color of the fibre.	Not applicable on account of the color of the fibre.	15–33	.05–.30	0.4–0.96	0.012–0.020	0.016
Agave (Agave Americana).	Swells and becomes somewhat blue.	With iodine solution yellow, on the addition of sulphuric acid greenish or brownish.	Yellow.	100	.10–.46	1.02–2.2	0.016–0.021	0.017
Musa (Musa textilis).	Blue color and feeble swelling.	With iodine solution yellow, on the addition of sulphuric acid golden-yellow to greenish.	Pale yellow.	750	.010–.28	2 0–2.7	0.012–0.046	0.029

III. Cribrose-cells, Sieve-cells, or Sieve-tubes.

279. In the inner bark of stems of dicotyledons with normal structure certain long cells of peculiar character are found associated with bast-fibres. They are of tubular or prismatic form, and are characterized by the presence of circumscribed panels in the walls, in which are numerous fine perforations permitting communication between contiguous cells. The panels are known as sieve-plates; the perforations, as sieve-pores. These cells constitute an essential, though by no means always a conspicuous, element of fibro-vascular bundles. Taken collectively, they may be known as cribriform tissue. By their union end to end they appear like long tubes with the continuity interrupted here and there by cross partitions. These partitions which separate the individual cells are sometimes nearly horizontal, but more generally oblique, as shown in the annexed figures where they mostly cut the lateral wall of the cell at a sharp angle.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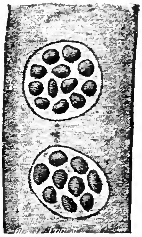
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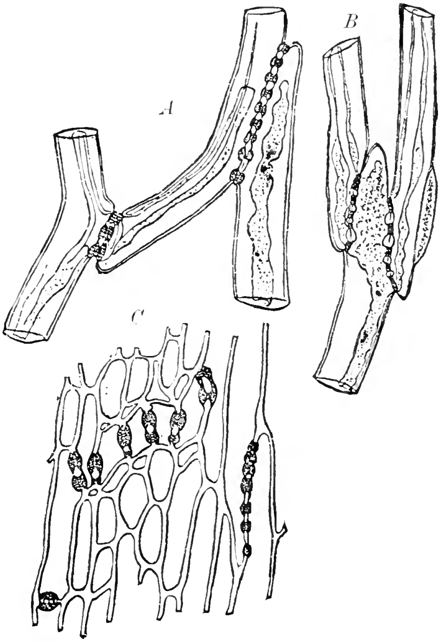

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280. The walls of cribrose-cells are never lignified; on the contrary, they are

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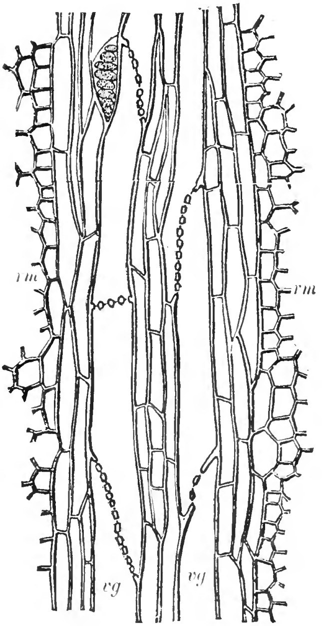
FIG. 69. Pinus sylvestris. Face view of radial wall containing two cribrose-plates wholly deprived of callus. $\frac{1165}{1}$. (Janczewski.)

FIG. 70. Pinus sylvestris. Radial wall of a young tube, face view. The future cribrose-plates are composed of callus-cylinders, filling the meshes of a cellulose network. $\frac{1165}{1}$. (Janczewski.)

FIG. 71. Cribrose-cells in Vitis vinifera: *A*, transverse anastomosis of two cribrose-

very soft and colorless. Owing to their yielding character, it is not easy to make satisfactory sections for their demonstration, from fresh material; it is better to keep the material in alcohol for a while, or to dry it carefully, as Russow advises. All sections, to show the sieve-cells, must be very thin. The following measurements of single large cells given by de Bary serve to indicate their wide range in size:



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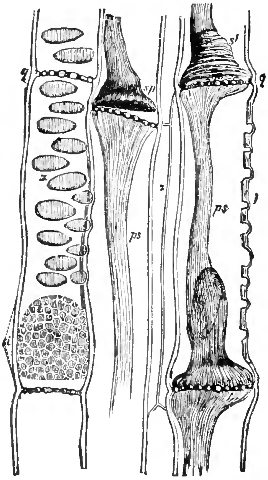

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	Length, mm.	Transverse diameter, mm.
Cucurbita Pepo	.370 –.450	.045
Calamus Rotang	2.000	.030 –.050
Potamogeton natans	.275	.025
Vitis vinifera	.6	

281. The sieve-plates occur at the points of contact of sieve-cells. They are always found at the ends of the cells, and may

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cells isolated by maceration; the septa are in their winter state. *B*, branching of cribrose-cell isolated by maceration. *C*, tangential section across a medullary ray, showing the transverse anastomosis of cribrose-cells; the callus at the septa is in its winter state. (Wilhelm.)

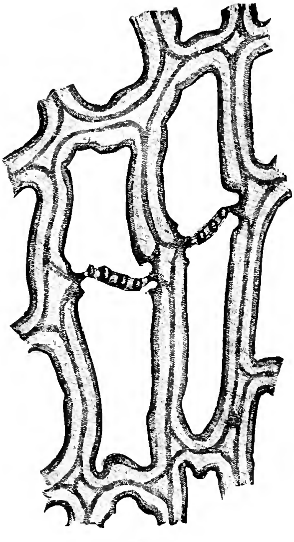
FIG. 72. Cribrose-cells in Vitis vinifera. Longitudinal tangential section (beginning of July) through the bast of a stem 1 cm. thick; *vg*, cribrose-cells, the oblique as well as one horizontal perforated septum cut longitudinally. The face of one septum, however, is shown at the upper part of the figure; *rm*, medullary rays. (De Bary.)

FIG. 73. Cucurbita Pepo Longitudinal section showing terminal sieve-plates at *q*, *q*, and a lateral one at *si*: *ps*, contracted protoplasm. (Sachs.)

likewise appear upon the lateral walls. When the terminal partitions are horizontal, or nearly so, they are cross-plates, the whole partition forming one plate; but on very oblique ends the plates may be separated and lie in one or more rows. The plates on the walls are smaller and irregularly distributed. On parts of the wall contiguous to cells of any other kind there may be dots; there is yet some doubt as to whether they are perforations.

The diameter of the sieve-pores is given by Mohl as not far from 2 μ; but although some are even 5 μ in diameter, the former figure is too high for the average.

282. That which is characteristic of sieve-plates, in distinction from groups of perforations elsewhere found, is a thickening mass, of bluish lustre and apparently homogeneous structure, known technically as the *callus*. It is best shown at the terminal plates, especially after the application of a solution of iodine which turns it yellow, and makes it more sharply defined. In concentrated sulphuric acid and in the strong alkalies this mass swells up so as to be several times its original size; and in the former it soon dissolves, leaving only slender threads in its place. The character of the callus



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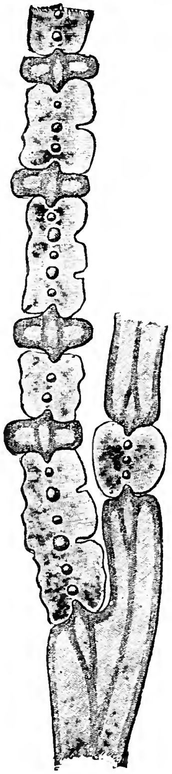

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FIG. 74. Pinus sylvestris. Transverse section across four entirely passive tubes, which are somewhat compressed laterally. $\frac{1165}{1}$. (Janczewski.)

FIG. 75. Pinus sylvestris. Terminal partition. A tube inserted upon the radial wall. The pores of the terminal partition are filled with warty callus, in the midst of which the cellulose network may always be seen; in the pore of the radial wall the callus is completely smooth and round. Tangential section. $\frac{1165}{1}$. (Janczewski.)

varies with the age of the cell and with the time of year, as shown in the figures.

283. Anilin blue is the best pigment for bringing out the form of the callus clearly. If, as Russow[1] recommends, its use be supplemented by that of Schulze's iodide, the callus may be seen to be made up of at least two portions, distinguished by the depth of color. In young and active cribrose-cells the callus usually appears to be a gelatinous layer on each side of the sieve-plate; in most old cells it is no longer seen.

284. Contents of the cells. In the younger and active state just referred to, the cells contain a watery liquid which holds more or less granular matter, and the walls are lined by a delicate film of protoplasmic substance. That the callus is also of a protoplasmic nature is not clear, although some of its reactions suggest this. It frequently contains minute granules of starch, which sometimes give a bluish-brown color with iodine, like starch which has been acted on by diastase. Russow thinks that a ferment is present in the cells in their active state. When old, most cells lose not only the callus but also the greater part of their other contents. In active cells there are frequently found very small but brilliant globules which are albuminoidal. All the contents above mentioned vary within certain limits at different periods of the year.

285. The sieve-cells of the higher cryptogams have been shown by Janczewski[2] to be nearly if not quite imperforate at all seasons. In gymnosperms, they pass through two periods: the first, or the evolutive, in which the plates produce the callus, the cells themselves containing parietal protoplasm; the second, or passive, stage, in which the protoplasm disappears entirely, and communication between the contiguous cells occurs. In monocotyledons and dicotyledons the cells have four periods; namely, the evolutive, the active, the transitory, and the passive.

IV. Latex-cells, Latex-tubes.

286. Certain plants when wounded exude a milky juice known as latex. They belong to widely separated orders; for instance, to Papaveraceæ, Campanulaceæ, Asclepiadaceæ, Urticaceæ, etc.

The cells in which latex occurs are characterized by a softness of cell-wall which renders them easily compressible; hence,

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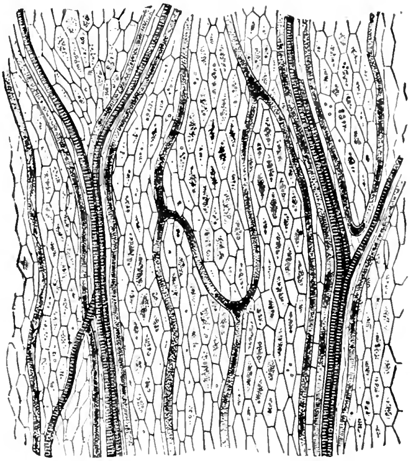
[1] Annales des Sc. nat. bot., sér. 6, tome xiv., p. 167.

[2] Annales des Sc. nat. bot., sér. 6, tome xiv., p. 50.

bounded by turgescent tissues, their contents readily escape through any incision.



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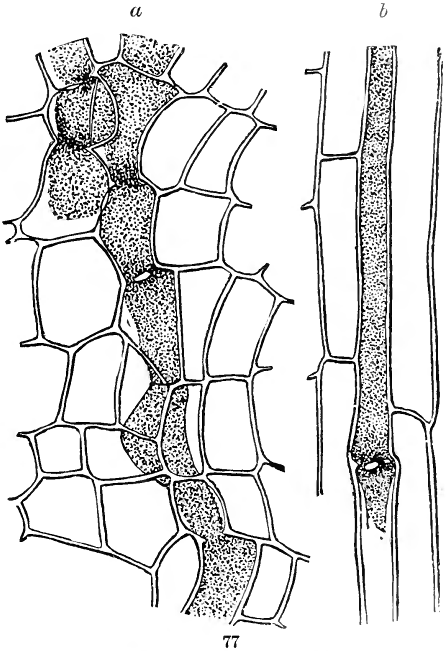
Latex-cells are not restricted to any one organ of the plant, but may, and generally do, occur in all parts, and may be associated with more than one tissue-system. They are, however, usually found in parenchyma, and run in the same general direction as the fibro-vascular bundles near which they lie. For convenience, they may be divided into the simple and the complex.



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287. The simple forms are single cells, which may be much and variously branched. Subsequent to the development of one of these cells in a plant, and when it has extended its ramifications throughout the different organs, a new cell may independently give rise to new branchings, and to a new system, some of the branches of the two cells perhaps becoming confluent. Good examples of the simple forms are af-

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FIG. 76. Longitudinal section through a sepal of Chelidonium majus, showing latex-tubes. (Weiss.)

FIG. 77. Latex-tubes composed of confluent cells: *a*, in the root; *b*, in the stem of Chelidonium majus. (De Bary.)

forded by the following orders, — Asclepiadaceæ, Apocynaceæ, and Euphorbiaceæ.

The complex forms consist of rows of cells which coalesce to form a latex-system. The individual cells may have their partition-walls broken down very early, a mere vestige of them remaining; or the partitions may be simply perforated, so as to allow a free communication between contiguous cells. Moreover, the confluent cells may be conjoined laterally, thus constituting a complicated network which runs through the plant.

288. Occasionally roundish groups of perforations resembling in a few particulars those of sieve-plates are found in the latex-cells of Papaver and some Cichoraceæ; but they are coarser and more irregular, and are devoid of the peculiar sieve-plate structure. Moreover, no true intermediate forms have been proved to exist between the two kinds.[1]

289. The wall of a latex-cell is often very thin, and free from any markings; but with even slight increase of thickness, striations and stratification make their appearance, projections may extend into the cavity of the cell, or even spirals may be present. In character, the cell-wall possesses many of the peculiarities of collenchyma, especially in its behavior with iodine.

290. That the cells contain a protoplasmic lining is highly probable, but this has not yet been satisfactorily demonstrated. The liquid in the cells consists of granular matters suspended in a watery fluid, and imparting to it a milky appearance. Often the color of the liquid is yellow, as in Argemone, or orange, as in Chelidonium. The watery fluid contains in solution sugar, gums, resins, traces of albuminoid matters, and various principles, for instance, alkaloids (like morphia), and organic acids.

The suspended matters are of minute size, with the exception of peculiar forms of starch-granules. When perforation is made in the latex-system of a turgescent stem, these granules can be seen to move towards the point of injury. The same movement can be observed when the pressure on one part of the stem is materially increased; and hence arose the erroneous belief that there is a circulation of latex.[2]

291. Upon exposure to the air latex coagulates, and forms upon drying a sticky, elastic mass, which in some plants is sufficiently abundant to furnish the india-rubber of commerce.

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[1] D. H. Scott: On the development of articulated laticiferous vessels. Journ. Mic. Science, 1882, p. 144. An interesting account is also given by de Bary, from notes by Schmalhausen, Vergleichende Anatomie, p. 205.

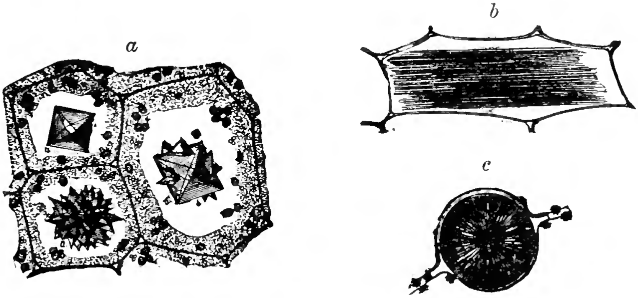
[2] Schultz: Die Cyklose des Lebenssaftes in den Pflanzen, 1841, p. 282.

RECEPTACLES FOR SECRETIONS.

292. Individual cells (idioblasts) may differ greatly from their neighbors as respects their contents. Such cells may be well named after their characteristic contents; as crystal-cells, resin-cells, mucilage-cells, tannin-cells, etc.

293. They vary much in shape and size. Frequently they are not readily distinguishable from their immediate neighbors by anything except their contents. In other cases, however, they may assume forms widely different from those of the cells around them, and may also be distinguished by their size. They are often so associated together as to form "glands."

294. *Crystal-cells.* These sometimes, as de Bary points out, curiously resemble the shape of the crystal or groups of crystals which they contain. Thus globular clusters are generally contained in spherical cells, elongated prisms in elongated cells (as in Quillaja). "In many trees each cambium-cell (as it develops into a bast-fibre) may be divided by diagonal partitions into numerous (20 to 30) chambers, the height of which is about the same as the width, and each is filled by a crystal or a small cluster. In this case the general outline of the original cambium-cell remains unaltered, and the whole row of compartments may be isolated as a chambered fibre."[1] The bast-cells containing crystals have been already noticed.



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295. *Resin-cells.* In a large number of plants soft viscid substances are present, which exude when the tissues are wounded. They may be roughly classed into (1) *Balsams*, in which resinous matter is mixed with a considerable proportion of

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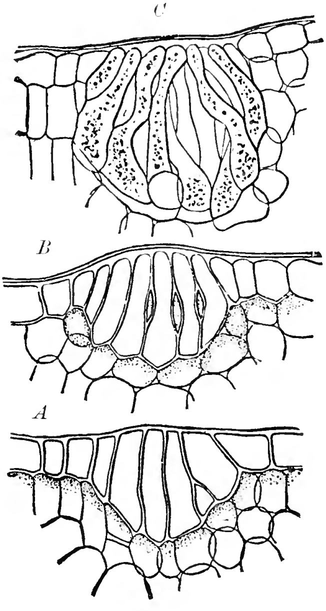
[1] De Bary: Vergleichende Anatomie, p. 145.

FIG. 78. Crystal-cells: *a*, from the petiole of Begonia manicata; *b*, a cell with raphides, from Lemna trisulca; *c*, from Phallus caninus. (Kny.)

one or more essential oils, forming a thickish liquid; (2) ***Resins,*** which have comparatively little essential oil commingled, and are of various grades of hardness; (3) *Gum-resins*, or resins having more or less mucilaginous or gummy matters. To the latter class are sometimes referred the products left by the drying of many milky juices (latex); of such, caoutchouc is an example. All the foregoing substances may be found in single cells, which are of very diverse forms.



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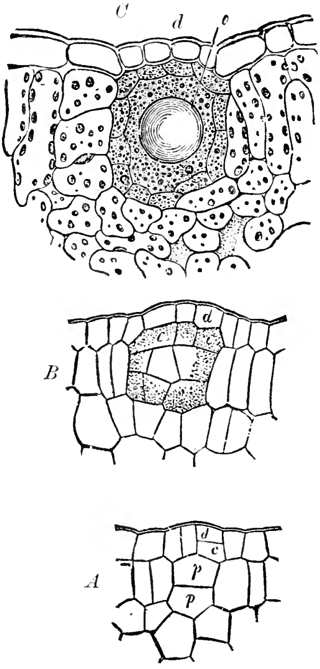

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296. Roundish cells of this character are found in the Magnoliaceæ and some Compositæ, etc. Long cells are to be detected in some Liliaceæ, etc., and they are connected by many intermediate forms with resin-ducts arising from the confluence of several cells. On the other hand, they pass by various gradations into structures which are generally referred to the latex-

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FIG. 79 Transverse section through the leaf of Psoralea hirta; the epidermis consisting of one layer with some of the tissue shown on both sides of the gland: *A*, very young state in which the secretion is not yet present; *B*, somewhat older, secretion commencing; *C*, mature state. (De Bary.)

FIG. 80. A "gland" in Dictamnus Fraxinella: *A*, *B*, early stages; *C*, mature state; *p*, *p*, *c*, mother-cells of the gland-tissue; *d*, the covering layer forming a continuation of the epidermis; *o*, a large drop of oil. (Rauter.)

system. To this system should perhaps be referred also numerous cases of pigment-cells, like those in the roots of madder and rhubarb; also the peculiar bodies seen in the periphery of the pith of Sambucus, and the milk-sacs of some species of Acer.

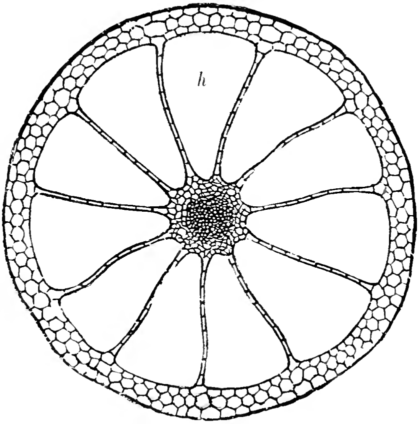
297. *Mucilage-cells* are larger than the surrounding cells, and sometimes closely resemble intercellular spaces filled with mucilaginous matter. In some instances the mucilage is distinctly referable to changes in the contents of the cell, in others to a disorganization of a portion of the wall, while in still others both sources may be recognized.[1]

298. Cells containing tannin in very large amount are frequently met with, but they do not call for special remark.

299. Resins and the like are found not only in single cells but also in spaces formed by the breaking down of the intervening walls of cell-clusters of various shapes; hence various forms of receptacles for these substances may be looked for.

INTERCELLULAR SPACES.

300. The walls of cells still capable of division are generally in unbroken contact; but as differentiation goes on they may become separated more or less by unequal growth or by a breaking down of intermediate cells.[2] The intercellular spaces thus formed may be mere chinks, or they may become chambers of large size. They may contain merely air, or air and watery sap, or most of the matters described in the previous sections.



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Air-spaces in the looser tissues of plants are generally so con-

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[1] The details of this subject can be found in Prings. Jahrb., v. 161 (Frank), and Annales des Sc. nat., sér. 6, tome i. p. 176 (Prillieux).

[2] The first mode of development of intercellular spaces has been termed *schizogenic*, the latter *lysigenic*; moreover, a distinction may be made between those intercellular spaces which are formed when the tissues begin to differentiate, —*protogenic*, — and those formed in older tissues, — *hysterogenic*.

FIG. 81. Transverse section through the stem of Elatine Alsinastrum, showing large intercellular spaces, *h*, containing air. (Reinke.)

nected throughout the plant, and communicate so directly with the stomata, that they constitute an apparatus for bringing the interior of the structure into close relations with the outer air. Sometimes the aggregate volume of the air-spaces is very large in proportion to the volume occupied by the cells themselves.[1]

In composition, the air within the plant usually differs from that of the atmosphere in containing a larger proportion of nitrogen. If the air-spaces are much smaller than the cells which surround them, they are termed *interstices;* if about as large as the cells, *lacunæ;* if conspicuously larger, *air-passages* or air-chambers. Two chief forms of lacunæ are distinguished by de Bary; namely, cavities surrounded by cells which are more or less branched, and those surrounded by plates of cells. Good examples of the former are afforded by many water-plants, rushes and the like; of the latter, by the stems of many Araceæ, for instance, Acorus Calamus.

301. The continuity of the larger air-passages may be interrupted by plates crossing at an angle (generally slightly oblique). Such dividing plates, termed *diaphragms*, are frequently complicated in their structure.

302. Hairs, sometimes much branched, are found in the larger air-passages of many plants. These form the stellate structures in the Nymphæaceæ, and the "H-like" cells in some Araceæ.

303. Intercellular spaces, usually those of small size, may contain water together with air. This is the case in the cavities under the water-pores of Fuchsia, etc.

304. When intercellular spaces contain resins, oils, and the like, they constitute, together with the simple cells described in 295, the structures loosely called *internal glands.* Often these are merely irregular spaces left by the breaking down of one or

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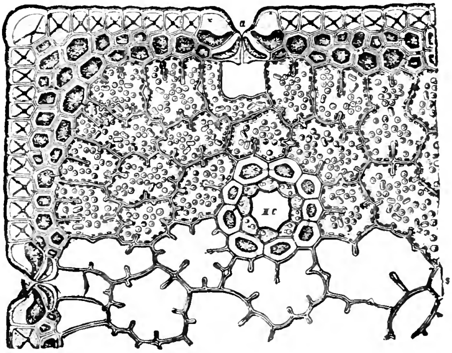
[1] The following measurements are taken from Unger (Sitzungsb. d. Wiener Akad., xii. 373).

Name of plant.	Parts examined.	No. of parts by volume of air in 1000 parts of the plant.
Paspalum setaceum.	Four leaves with their sheaths.	68
Musa sapientum.	Piece of the leaf-stalk.	480
Nicotiana Tabacum.	Leaf with leaf-stalk.	256
Brassica Rapa.	Leaf with leaf-stalk.	175
Begonia manicata.	One leaf with its stalk.	66
Camellia Japonica.	Two leaves with their stalks.	224
Prunus Laurocerasus.	One leaf with its stalk.	219
Aucuba Japonica.	One leaf with its stalk.	273
Ardisia crenulata.	Four leaves with short stalks.	220

more cells, but they sometimes have a remarkable regularity of form and clearness of outline.

It has been observed that these spaces filled with resinous and other matters are not, as a rule, met with in the plants which are provided with the simpler receptacles, consisting of single cells or small groups. De Bary classifies these resin-passages and spaces as follows: (1) those passages which contain mucilage and gums, as those in the Cycads, species of Canna, Opuntia, and some Araliaceæ; (2) resin-canals and cavities containing resins, ethereal oils, emulsions of resinous gums, etc., variable in quality in different cases; *a*, passages or canals, as those in Coniferæ, Alismaceæ, Aroideæ, the tubuli-flowered Compositæ, Umbelliferæ, Araliaceæ, Anacardiaceæ; *b*, short cavities, as in species of Hypericum and the true Rutaceæ, many species of Oxalis and Myrtaceæ, and some species of Lysimachia. The cells which surround the more complete cavities are so different from the neighboring parenchyma that they have been termed, collectively, the *epithelium* of the spaces.



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It is not fully known in what way the various resinous and mucilaginous matters are produced in the cavities. In some instances, at least, the matters appear at a very early stage of the development of the cells which are afterwards broken down to form the cavity. The special cases, like those of the Myrtaceæ, in which the cavities contain oil, are best for purposes of study, because they are so frequently to be found in the thinnest leaves, and at an early stage of development.

FIG. 82. Transverse section of part of leaf of Pinus Laricio, showing a resin-passage, *HC*. (Kny.)

CHAPTER III.

MINUTE STRUCTURE AND DEVELOPMENT OF THE ROOT, STEM, AND LEAF OF PHÆNOGAMOUS PLANTS.

GENERAL CONSIDERATIONS.

305. THE tissue elements, described in the preceding chapter, are arranged in various ways to form and connect the organs of the plant. If elements of the same kind are united, they constitute a *tissue*, to which is given the name of those elements; thus parenchyma cells form parenchyma tissue or simply parenchyma; cork-cells form cork, etc. A tissue can therefore be defined as a fabric of united cells which have had a common origin and have obeyed a common law of growth.

Tissues are united to form *systems;* systems, to form *organs*.

306. In nearly all plants with which the present treatise deals there is some kind of framework consisting mainly of the more elongated cells and ducts. This framework runs throughout the entire organism. It is surrounded by parenchyma, in which other tissue elements may also occur; the epidermis in some of its modifications covers the whole.

307. The three chief systems found in plants are, therefore, the fascicular, the cellular, and the epidermal; and these correspond in a general way to three classes of functions. In the cellular system are found the active cells by which assimilation, the proper work of the plant, is effected; the fascicular system is largely conductive, and serves also important mechanical ends; the epidermal system brings the assimilative apparatus of the plant into safe relations with the surroundings.

No discussion of the cellular and epidermal systems, introductory to a special consideration of them as they occur in the different organs, is needed; but some general statements relative to the fascicular system will obviate repetitions later.

308. The fascicular system, in its most complete development, comprises the following tissue elements, which occur in very different proportions in different cases, — prosenchyma in the widest sense, including wood-cells of all kinds, ducts, fibres, and cribrose-cells; together with some commingled parenchyma. With

the exception of the parenchyma, all these elements are elongated and are arranged in various sorts of fascicles or bundles, whence the name, the *fascicular system.* Since fibres and vessels play such an important part in the composition of this system, it has been also called the fibro-vascular system, and the bundles, fibro-vascular bundles.

309. When reduced to its lowest terms, a fibro-vascular bundle consists of two tissue elements, namely, cribrose-cells and tracheal cells, the latter being sometimes replaced either wholly or in part by ducts.

310. The two elements are usually associated with some parenchyma and with a considerable proportion of long bast-fibres; but, while preserving a general uniformity of structure throughout, a bundle may become considerably changed in composition during its course. This is well shown by comparing sections taken at some distance from each other; for instance,

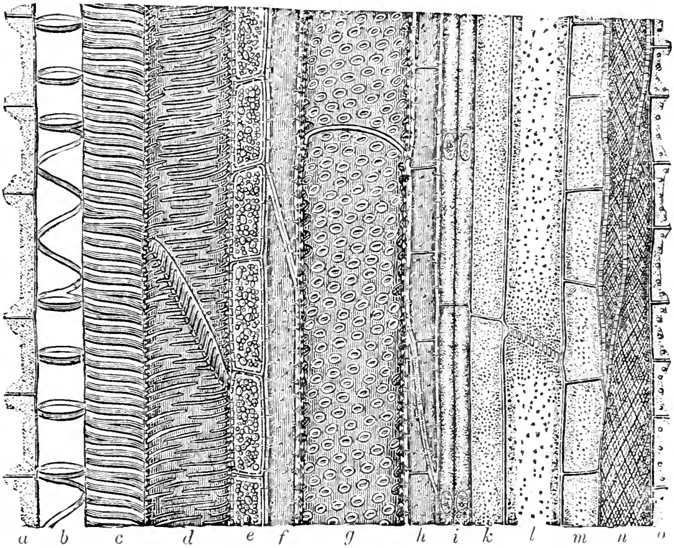

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FIG. 83. Longitudinal radial section of a collateral fibro-vascular bundle, from the stem of a dicotyledon: *b—i*, wood; *i—n*, liber; the wood comprises, *b*, a narrow annular duct, *c*, wider spiral duct, *d*, a duct with septum, *e*, woody parenchyma, *f*, woody fibre, *g*, wide duct with areolated pits, *h*, septate woody fibres; the liber comprises, *n*, liber-fibres, *m*, short parenchyma, *l*, cribrose-cells, *i*, cambium, *k*, long parenchyma or cambiform. (Kny.)

one made in the middle of the course of a bundle with one near its extremity.

311. The cribrose part of the bundle may also be termed its liber-portion or bast-portion; the tracheal, its woody portion. These terms are not liable to be confounded with any others, since it is with the cribrose portion that the well-known bast-fibres or liber-fibres are associated, while it is in the tracheal portion that all the constituents of wood are found.

312. For the first term (bast-portion), Nägeli has introduced the word Phloëm; for the second (wood-portion), Xylem. In this treatise these terms will be used interchangeably with the others. But the woody portion of a bundle is sometimes very far from being conspicuously lignified, and the bast-portion may be much reduced.

313. The three principal ways in which the elements of bundles are arranged are: 1. A single strand of liber has one side in contact with a single strand of wood, the two running side by side, — the *collateral* bundle. This mode of arrangement is common in the stems of phænogams. A variety of the collateral bundle has a strand of liber on each side of the wood, or, conversely, a strand of wood on each side of the liber, — the *bicollateral* bundle. 2. The strands of liber and wood are in different radii, — the *radial* bundle. This is the most common mode of arrangement in roots. 3. A strand of one element is wholly enveloped by the other element, — the *concentric* bundle. These modes of arrangement will be further discussed under "Roots" and "Stems."

314. The bundles are surrounded by parenchyma; but this is very frequently limited at the periphery of the bundle by a cylinder formed of closely united parenchyma cells, which contain considerable starch. The *endodermis* is a special case of this structure, in which the cells are more or less distinctly cutinized. When this enveloping cylinder is well defined, it is known as the bundle-sheath.[1]

315. At first, each bundle consists of similar cells (*procambium*), some of which differentiate into fibres, vessels, etc. Bundles in which all the procambium cells become permanent cells are *closed;* those which retain an inner portion (*cambium*) capable of further differentiation are *open*.

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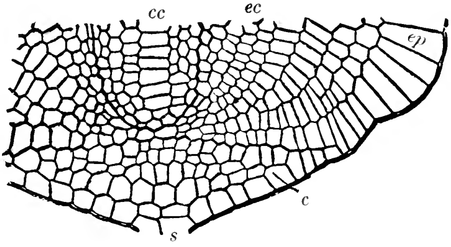
[1] In a great number of instances it is convenient to refer to the same structure the long and firm bast-cells which are found at one side of the bundle; but the subject, when examined from the point of view of development, especially when the vascular cryptogams are taken into account, presents so many difficulties that it may be here left without further treatment.

316. As regards the course of the bundles through the plant, it is sufficient to note here that they are variously combined in the different organs, sometimes forming compact masses of tissues, and at others running as slender and delicate isolated threads.

317. It has been seen in 201 that meristem is the nascent state of any tissue, and that it may multiply as such, or first become differentiated into elongated forms (cambium). For convenience of reference, the meristem at the growing-points of the axis of the plant is given special names: *Dermatogen*, the layer of nascent epidermis; *Periblem*, the layer of nascent cortex just beneath the epidermis; *Plerom*, the cylinder or shaft of nascent fascicles. The cells from which these primordial layers or masses of nascent tissues arise are known as *initial cells*.[1]



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The initial cells produce primordial layers or masses of tissues; by their further development the primordial layers or masses give rise to the early distinctive tissues of an organ. The tissues thus early formed constitute the *primary structure* of the plant.

318. In the further growth of an organ, especially in plants which are to live more than a single year, or which have a well-defined period of rest, remarkable changes may take place in its structure, especially by the introduction of new elements. Such changes are known as secondary, and give rise to the *secondary structure* of the organ. From the nature of the case, it is impossible to draw a sharp line between the primary and secondary structure; but the division is nevertheless useful in the examination of the minute anatomy of the plant.

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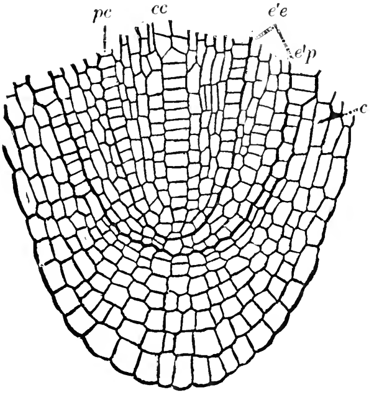
[1] Hanstein: Die Scheitelzellgruppe im Vegetationspunkt der Phanerogamen, 1868; also in Botanische Abhandlungen, 1871, p. 3.

The distinction between meristem proper and cambium is insisted on by Nägeli in his Beiträge (1858).

FIG. 84. Longitudinal section through the middle of the root-tip of the embryo of Pontederia cordata. The lower initial cells produce the cap, *c*; the middle, the nascent cortex, *ec*; the upper, the nascent central cylinder, *cc*. The nascent epidermis, *ep*, of the stem is continued down to the cap; *s*, the point to which the suspensor was attached. In other terms, *cc* is the plerom, *ec*, periblem, *ep*, dermatogen. (Flahault.)

THE ROOT.

Primary Structure.



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319. It was stated in Vol. I., p. 27, that the root, or descending axis, "normally begins in germination at the root-end of the caulicle, or so-called radicle; but that roots soon proceed, or may proceed, from other parts of the stem, when this is favorably situated for their production."

320. A longitudinal section through the tip of a germinating radicle exhibits only parenchyma cells. Slight differences exist between these cells, both as regards shape and size; at the very end of the radicle they are relatively large, and form a sort of cap-like covering (*root-cap*) for the smaller cells lying directly back (*the growing-point*). If the section is thin enough, it will be seen that at the growing-point numerous rows of cells appear to converge, the fact being that all the cells of such rows are derived by multiplication from those at the growing-point.

321. Certain differences in the arrangement of these rows can be seen upon comparing the radicles of plants of different classes.

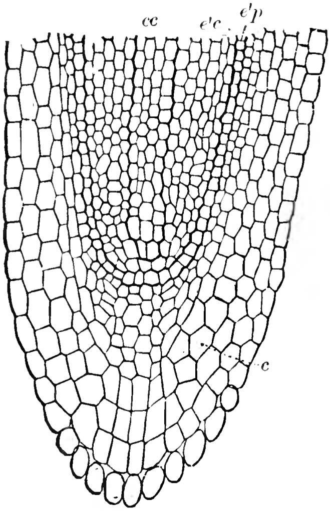

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Fig. 85. Longitudinal section through the middle of the root-tip of Fagopyrum esculentum. The lower initial cells give rise to the cap *c*, and the epidermis *e'p*; the middle produce the cortex *e'e*; *pc*, peripheral layer of the central cylinder *cc*, which comes from the upper initial cells. (Janczewski.)

Fig. 86. Longitudinal section through the middle of a lateral root of Pontederia crassipes: *cc*, nascent central cylinder (plerom); *e'c*, nascent cortex (periblem); *e'p*, nascent epidermis (dermatogen); *c*, root-cap. (Flahault.)

Thus in most cases the group composing the point of growth consists of three kinds of superposed cells, so arranged in layers that each gives rise to a determinate portion of the forming root: (1) the outer or lower layer, to the root-cap and the rest of the *epidermis;* (2) the middle, to the cells which are immediately under the epidermis, — the *cortex;* (3) the inner or upper layer, to the *central cylinder.* But in some plants [1] there are more than three layers of initial cells (*e. g.*, Sparganium, Raphanus, etc.), while in others there are less than three (*e. g.*, only one in Cucurbitaceæ, two in Triticum).

322. **The Root-cap.** The growing-points of nascent roots originate just below the surface of the organ whence they proceed; hence roots are said to be formed endogenously. In emerging, they rupture the layer of tissue by which they had been covered, but are from the first protected at the end by a thicker or thinner mass of parenchyma, — the root-cap.[2]

323. It does not always have the same origin, as will be seen by the notes,[3] nor has it the same shape and size in all plants.

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[1] Janczewski (Ann. des Sc. nat., sér. 5, tome xx., 1874) describes six types of development of the tissues of the root: —

1. Four distinct layers of meristem; namely, Plerom, Periblem, Dermatogen, and Calyptrogen; *e. g.*, *Hydrocharis.*

2. A distinct Plerom and Calyptrogen, but the Periblem and Dermatogen have initial cells in common; *e. g.*, *Gramineæ.*

3. A distinct Plerom; the Periblem, Dermatogen, and Calyptrogen have common initial cells; *e. g.*, *Iridaceæ.*

4. A distinct Plerom and Periblem; the Dermatogen and Calyptrogen have common initial cells; *e. g.*, *Helianthus annuus.*

5. All four layers have common initial cells; *e. g.*, *Phaseolus* and *Pisum.*

6. Only a distinct Plerom and Periblem; therefore there is neither true epidermis nor root-cap, since these are formed simply by outer layers of the Periblem; *e. g.*, *Gymnospermæ.*

Treub (1876) and Eriksson (1878) distinguish seven types.

[2] According to Olivier, a part of the tissue thus broken through by the advancing radicle of grasses remains at its base, as the coleorhiza, while the rest becomes the root-cap (Ann. des Sc. nat., sér 6, tome xi., 1881, p. 19).

[3] According to Flahault (Recherches sur l'accroissement terminal de la racine chez les Phanérogames, Ann. des Sc. nat., sér. 6, tome vi., 1878), who bases his opinion on an examination of three hundred and fifty species of Phænogams, the terminal growth of the root may be referred to two structural types which are characteristic of monocotyledons and dicotyledons.

In monocotyledons the epidermis is generally formed by the initial cells of the cortex. The epidermis never gives rise to a root-cap; the root-cap once formed is continually renewed by the activity of its internal layers. In dicotyledons, on the other hand, the epidermis is almost always independent of the cortex; the root-cap is continually renewed by the activity of the cortex and epidermis.

Roots which grow in the earth seldom have it much developed; but in many aquatics it becomes of large size, though it is always thin. In some species of Pontederia the cap envelops the root for the length of half a centimeter; but it is free at its upper part, and is in contact with the root only at its very tip. The roots of Typhaceæ and Lemnaceæ exhibit nearly the same structure. The cap consists in these cases of only one or two layers of thin-walled cells.

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The aerial roots of some plants have large root-caps composed of firm-walled cells. This is well shown in Pandanus, where the cap consists of many layers of cutinized cells. The cap in all cases exfoliates on its exterior, and is as constantly renewed by the cells within. Nearly all of its cells contain starch-granules in abundance.

324. *The peripheral tissue* in the rootlet does not always have the same origin; it may in some cases be regarded as true epidermis, in others as the outermost portion of the cortical parenchyma. In the vast majority of cases this young superficial tissue is furnished with *root-hairs*; it is therefore designated the piliferous layer.[1]

325. **The piliferous layer** has no intercellular spaces (a few cases of aerial roots of Orchids excepted). The hairs are confined to a narrow zone a short distance behind the tip, although in Triglochin they have been found on the edges of the cap, and in Philodendron very near its edge. When first formed they have delicate transparent walls, and are filled with protoplasm. By the advance of the growing-point and with the formation of new hairs, the older become less active, their walls thicken and turn brown, their contents disappear, and they fall off, generally leaving a nearly glabrous surface.

326. The hairs are generally simple, but in the adventitious roots of some Bromeliaceæ[2] compound hairs are also found.

Branched hairs are seen on the roots of Saxifraga sarmentosa, Brassica Napus, etc.

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[1] Olivier (Ann. des Sc. nat., sér. 6, tome xi., 1881, p. 19), according to whom it is never homologous with the epidermis of the stem (p. 28).

[2] Jorgensen, Botanisk Tidsskrift, 1878, p. 144.

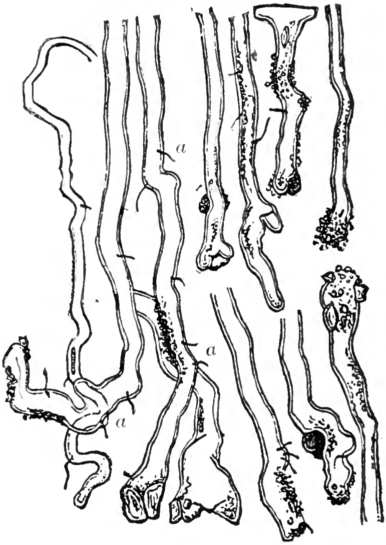
FIG. 87. Seedling of Sinapis alba, showing root-hairs.

FIG. 88. Seedling of same, showing the manner in which fine particles of earth cling to the root-hairs. (Sachs.)

327. Root-hairs are best obtained for study by cultivating seedlings on moist glass, or with the rootlets in water. It is well to compare the forms thus obtained with those found on roots of the same plant grown in loam, sand, fine clay, etc. Masters has shown that the development of the hairs is favored by many conditions, such as porosity of the soil, moisture, etc.; and this fact should be borne in mind in the examination of the root-hairs of any plant.

328. The walls of root-hairs are only slightly cutinized, but there is a great difference in this respect in different plants.

329. The cells of the superficial layer of the rootlet, other than those with hairs, are more or less cutinized, the degree of infiltration depending upon their age. In some cases (*e. g.*, Asphodelus) the thickening is very considerable.



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330. On a few plants[1] no root-hairs have been detected, as Crocus sativus, Cicuta virosa, Abies pectinata and many other gymnosperms.

331. **Roots of orchids.** The newer parts of the aerial roots of Orchids have an epidermis consisting of nearly spherical tracheïds, which, except sometimes in the outermost layers, cohere without intercellular spaces. The walls of these cells are colorless, though in mass they may have a silvery lustre, and when immersed in water they soon become sufficiently transparent to permit the subjacent green tissue to be seen.[2]

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[1] Duchartre (Éléments de Botanique, 1867, p. 214) cites other plants.

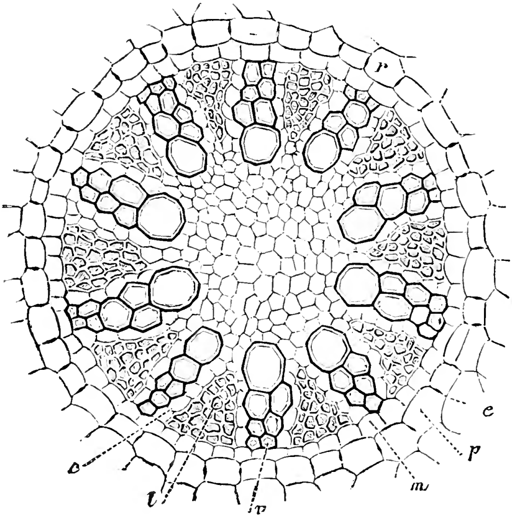
See also a valuable paper by Schwarz in Untersuchungen aus dem bot. Inst., Tübingen, 1882.

[2] According to Leitgeb, the old roots of Vanda furva are green because their tracheïds contain minute Algæ (De Bary, Vergl. Anat., p. 238).

FIG. 89. Root-hairs distorted by contact with the soil. Four in the right-hand upper corner, Selaginella; three in lower corner, Trifolium; the others, Avena. The dark points indicate the attached particle of soil. *a*, *a*, *a*, minute prolongations of the cell-wall. (Sachs.)

332. Sometimes there are papillar outgrowths from these tracheïds, which are to be regarded as root-hairs. They occur chiefly on younger parts of the roots which are in contact with a moist support, or which are kept wet. They cling tenaciously to moist surfaces, and may become much widened and flattened.[1]

333. The **cortex** of different plants varies greatly in thickness and compactness, and in the thickness of the cell-walls. In a few cases remarkable lacunæ are to be seen (*e. g.*, Menyanthes).



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334. The cells bounding the inner layer of the cortex have the general characters described under "Endodermis;" their radial walls are generally more or less plicate, and there are no intercellular spaces.

335. In the primary cortex of roots all the various kinds of secreting cells and receptacles for exudations described on p. 97 may be looked for; but as a rule they are less developed than in the stem. Collenchyma occurs sometimes in roots; *e. g.*, Raphidophora.

336. The **central cylinder** has, at first, a peripheral layer of

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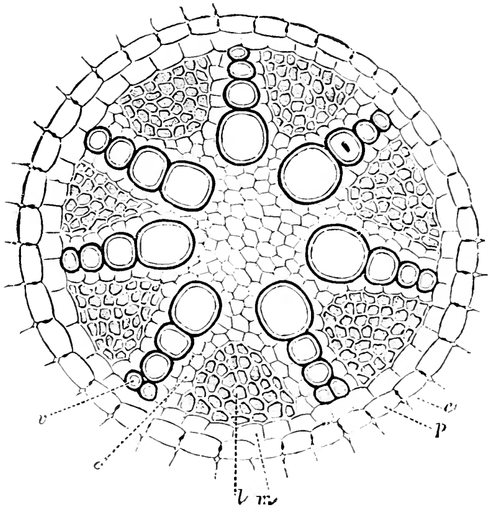
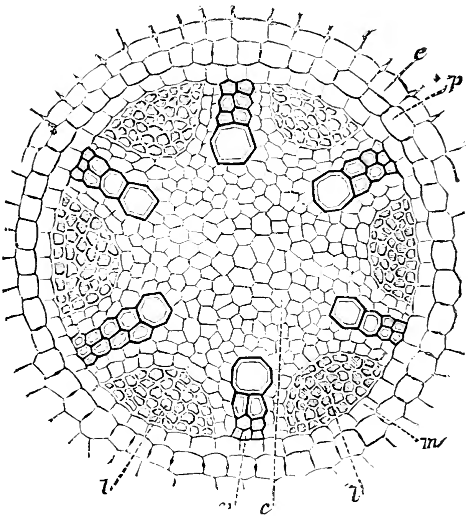
[1] Leitgeb: Die Luftwurzeln der Orchideen, Wien Akad. Denkschr., xxiv., 1865, p. 179.

FIG. 90. Transverse section of the central cylinder of a root of a vascular cryptogam (Marattia lævis): *e*, internal layer of the proper cortex; *p*, endodermis; *m*, peripheral layer of the cylinder; *l*, liber fascicles; *v*, woody fascicles; *c*, conjunctive parenchyma (pith and medullary rays). (Van Tieghem.)

thin-walled cells in close union with the endodermis; at certain points on this layer the woody and the liber fascicles appear, the latter alternating with the former throughout the circle, and the spaces between them being filled with parenchyma.



337. The number of fibro-vascular bundles in the central cylinder varies according to the class of plants, and in the same plant according to the age and size of the root. There are generally two in Cruciferæ, often three in Ervum Lens, four in Ricinus, five in Vicia Faba, six in Alnus, and eight in Fagus; but these numbers are by no means constant.



338. The woody part of the bundle may become re-

Fig. 91. Transverse section of the central cylinder of a root of a monocotyledon (Colocasia antiquorum): *e*, internal layer of the proper cortex; *p*, endodermis; *m*, peripheral layer of the cylinder; *l*, liber fascicles; *v*, woody fascicles; *c*, conjunctive parenchyma (pith and medullary rays). (Van Tieghem.)

Fig. 92. Transverse section of the central cylinder of a root of a dicotyledon (Artanthe elongata): *e*, internal layer of the proper cortex; *p*, endodermis; *m*, peripheral layer of the cylinder; *l*, liber fascicles; *v*, woody fascicle; *c*, conjunctive parenchyma (pith and medullary rays). (Van Tieghem.)

duced to a single duct, as in some Carices, or there may be a large duct surrounded by smaller ones with or without intervening cells, or many large and small ducts variously conjoined. Moreover, there are all degrees of compactness in the union of the different bundles of woody tissue with each other.

339. The cribrose part of the bundle may be reduced to a single cribrose tube (*e. g.*, Anacharis), or two or three (*e. g.*, Pontederia); but usually there are many, which may be variously disposed.

340. Bast-fibres may be associated with the cribrose-cells in the primary structure of the root, and they may be scattered (and occasionally with some sclerotic parenchyma) in the cortex. In Philodendron these scattered groups of bast-fibres frequently contain oleo-resin canals.

SECONDARY STRUCTURE.

341. The older parts of roots, even the recently formed portions lying just back of the root-hairs, may undergo changes either by the alteration of their existing tissue elements or by the introduction of new elements. Some roots, however, do not suffer much change from first to last. Their cells may become more strongly cutinized or lignified as the case may be, but no new elements are brought in. This is true of the roots of many monocotyledons, but in dicotyledons the secondary changes are generally very marked. The changes may affect either the cortex or the central cylinder; in some cases the former more than the latter.

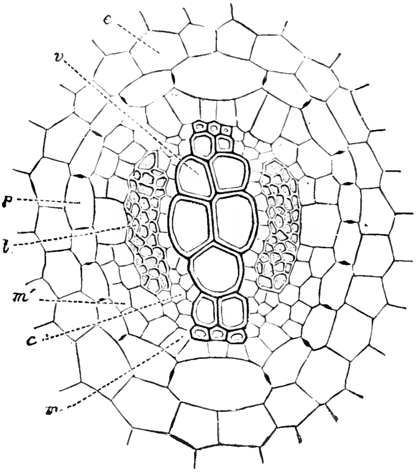


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FIG. 93. Section through the central cylinder of a binary root of a vascular cryptogam (Cyathea medullaris): *e*, internal layer of the proper cortex; *p*, endodermis; *m*, peripheral layer of the cylinder; *l*, liber fascicles; *v*, woody fascicle; *c*, conjunctive parenchyma (pith and medullary rays). (Van Tieghem.)

342. In the **cortex,** according to Olivier,[1] the secondary tissues are either parenchymatous or suberous (corky). The secondary parenchyma of the integument proceeds from the peripheral layer of the central cylinder. The suberous tissue in gymnosperms and in dicotyledons with caducous primary cortex is derived from the pericambial layer; it is composed of tabular cells with very short radial walls, and begins to form outside of the primary liber. In the case of woody dicotyledons with late-formed secondary vessels, and in monocotyledons, it is produced in the external zone of the cortical parenchyma, and is composed of cubical cells.

343. In a given species the level of the root where cork appears depends on the transverse diameter of the root, and also on the surroundings; in roots of the same size the cork generally appears earlier, and is more abundant in aerial than in earth roots.

The cortical parenchyma is renewed by layers of cells just outside of the sheath of the central cylinder, and its development is wholly centrifugal.

344. **The central cylinder** undergoes its most remarkable changes as the root grows older, in the group of dicotyledons. There is very little change, if any, in monocotyledons, but in a few of the latter some of the secondary changes now to be described can be observed (*e. g.*, Dracæna).

345. In dicotyledons, including gymnosperms, the thin-walled cells of the central cylinder are in contact with the inner face of the endodermis, and are known collectively as the *pericambium.* Touching this pericambium like the two ends of a bow, there runs a mass of delicate cells behind each liber bundle. At the point where these bows touch the inner face of the liber bundle a group of cells divides tangentially, forming a cambium layer, which soon gives rise within to new woody elements (often coalescent with those of the primary woody bundles), and on the outside to new liber elements. These new productions are called *secondary wood* and *liber.*

346. In some cases — for instance Pinus — the cells of the pericambium outside of the primary woody bundles produce new wood and new liber. The wood is in contact with the primary wood, while the liber may serve to connect the bundles of primary liber, thus bringing about a union more or less complete between similar elements. From these secondary pro-

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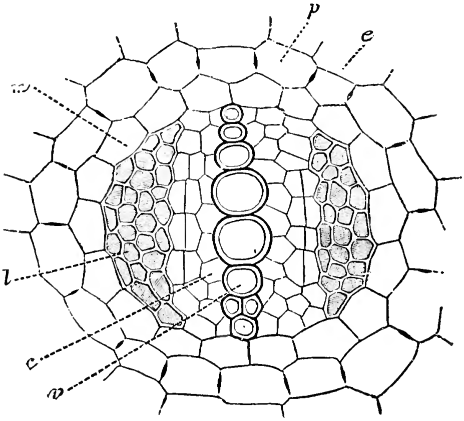
[1] Annales des Sc. nat., sér 6, tome xi., 1881, p. 129.

ductions come, of course, the apparently unbroken rings of liber and the solid masses of wood in old roots. If this development of new wood and liber in a perennial dicotyledonous plant proceeds uninterruptedly, there will exist at the end of the first year secondary elements in large amount. After a period of rest, a perennial root resumes growth at the points where it was suspended, and the formation of new cork, cortex, liber, and wood goes on as before, until it receives further checks. Owing to conditions to be explained later, the character of the woody elements is not the same at the beginning and end of an active period; hence there is generally a clearly defined outline bounding the product of growth of successive years.



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347. More or less of the parenchyma of the original cylinder may remain in the form of radial lines or of bands (medullary rays), some of the same sort of tissue may be subsequently produced from new points of activity, and hence long and short radii will be met with.

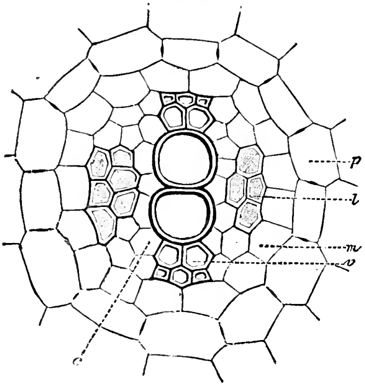

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Fig. 94. Section through the central cylinder of a binary root of a dicotyledon (Beta vulgaris): *e*, internal layer of the proper cortex; *p*, endodermis; *m*, peripheral layer of the cylinder; *l*, liber fascicles; *v*, woody fascicle; *c*, conjunctive parenchyma (pith and medullary rays.) (Van Tieghem.)

Fig. 95. Section through the central cylinder of a binary root of a monocotyledon (Allium Cepa): *e*, internal layer of the proper cortex; *p*, endodermis; *m*, peripheral layer of the cylinder; *l*, liber fascicles; *v*, woody fascicle; *c*, conjunctive parenchyma (pith and medullary rays). (Van Tieghem.)

348. The distinction of texture marking the periods of rest is not clear in the liber, though even here it may sometimes be detected. The cork of the root frequently exhibits such distinction, but never so clearly as does the cork of stems.

349. It is a familiar fact, that the fleshy roots of many plants — beets, and the like — exhibit in the first year from seed concentric rings, which resemble those found in perennials. This appearance is due, according to de Bary,[1] to the fact that at an early stage of development (when the root is only about half a millimeter thick) a new cambium zone is formed in the parenchyma on the outer part of the central cylinder, and this divides tangentially, extending therefore in a radial direction, producing woody and liber elements, and at the same time divides laterally, so that the whole constitutes a zone hardly broken by the rays. Soon a second zone is produced in like manner, and afterwards others. In all these cases the elements are usually not much lignified, but the whole mass remains succulent.

It happens sometimes that tertiary formations are produced in the root, bearing somewhat the same relation to the secondary as these do to the primary. Even formations of higher order are sometimes met with. But the elements of all of these are easily identified, and their mutual relations can generally be so clearly understood that they do not need special description. The following enumeration embraces the most important of these formations: tertiary cork and cortex; fibro-vascular bundles in secondary cortex; tertiary liber and wood in secondary wood. Such anomalies are more frequent in the stem.

350. Roots branch by the development of certain cells at the peripheral layer of the central cylinder, and just in front of the woody fascicles.[2]

The root branches only laterally in flowering plants; in the Lycopodiaceæ there appears to be terminal bifurcation, and here each branch shares with its fellow the tissue elements of the root from which they both come.

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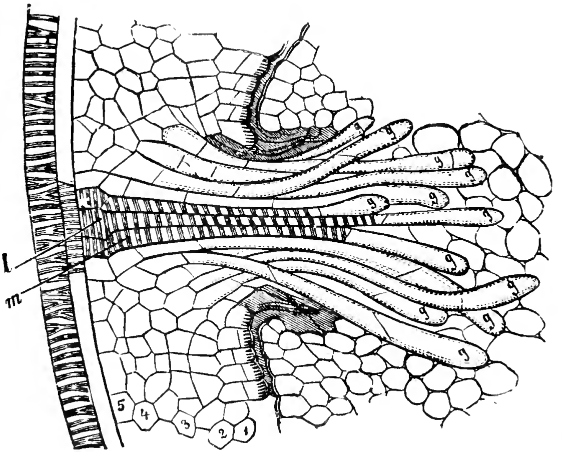
[1] Vergleichende Anatomie, p. 616.

[2] Three types of branching are described by Janczewski: 1. The mother-cells of this layer (the so-called Rhizogenic cells) most frequently give rise to all the tissues of the rootlet. 2. They produce only the central cylinder and cortex, but not the root-cap and piliferous layer, these being furnished by the endodermis of the root. 3. They produce only the central cylinder, the other tissues coming from the endodermis or from the layers immediately outside of it. The subsequent growth of the rootlet both in length and thickness is like that of the root.

351. **Parasitic roots,**[1] or those which fasten themselves for nourishment on other plants, are so much modified by the peculiar conditions under which they live, that they require special mention. Their structure can be best understood by a section through the root of Cuscuta.

Here there is no central cylinder, properly so called, nor is there anything answering to the root-cap. The cortex is regarded as reduced to a piliferous layer, since some of its cells are prolonged to form a fascicle of long hairs in intimate contact with the tissues of the host upon which it has fastened. In the centre of this fascicle of hairs some of the elements are tracheïd-like cells, which are in contact with ducts.



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352. The roots of many plants have distinctive colors: in some the color belongs to the wood (see 402); in others it is due to the cell-sap; in others, for instance, the common carrot, to orange-colored crystalline bodies. The crystalline forms found in the parenchyma of the roots of the carrot are minute rhombs, or sometimes rectangular plates to which starch-granules are attached. They are associated with small quantities of protoplasmic matter. (See Chapter IV., for an account of somewhat similar bodies occurring in flowers and fruits.)

353. **The roots of the higher Cryptogams** (such as Ferns and

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[1] An exhaustive paper on this subject will be found in Pringsheim's Jahrb., 1867: Ueber den Bau und die Entwicklung der Ernährungsorgane parasitischer Phanerogamen, von Hermann Grafen zu Solms-Laubach. Koch's paper is in Hanstein's botan. Abhandlungen, vol. ii., 1875.

FIG. 96. Vertical section of an haustorium of Cuscuta perforating the host-plant. *g*, *g*, absorbing hairs; the central cells are thickened at the base, where they are in contact with the ducts. (Koch.)

their allies) do not differ essentially from those of Phænogams; in most cases, however, the terminal growth, except in the order Lycopodiaceæ, is from a single apical cell instead of a group of cells. The apical cell produces not only the tissue of the body of the root as it extends in length, but gives rise also to the superficial cells at the extremity which constitute the root-cap. Lateral roots start from the interior layer of the cortical parenchyma, and not from the pericambium (see 345).

354. The fibro-vascular bundles are concentric (see 313), as indeed they are in the stems of most of these plants; that is, the bast part surrounds the wood part, as if with a sheath, even where the latter part is rudimentary. There is a tendency in the root, less marked than in the stem, to the production of sclerotic cells of a dark color.

The roots of the higher cryptogams do not materially increase in thickness after they are first formed.

355. Proper roots are not found in Muscineæ (the mosses and hepatics); the absorbing organs here are more strictly root-hairs. These arise as papillæ from the outer cells, and speedily develop into tubular and frequently complex bodies. They often become branched in a remarkable manner, twisting and coiling around one another like the fibres in a thread. They, as well as the somewhat simpler organs of the same nature, found in the Thallophytes (such as Algæ, and the like), are termed *Rhizoids.*

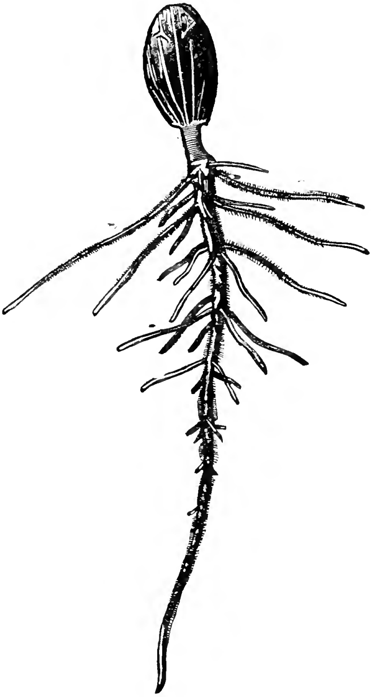

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Fig. 97. Seedling of Cucurbita Pepo, showing the main root, side roots, and root-hairs. (Sachs.)

Neither in Muscineæ nor Thallophytes are fibro-vascular bundles found, although in the former the arrangement of elongated cells sometimes resembles that of the constituents of a simple fascicle. The root-like bodies by which large sea-weeds cling to their supports are *hold-fasts*, rather than true roots; the whole surface of the plant being bathed in water, all parts can probably absorb equally well.

THE STEM.

356. That part of the axis of the embryo which is below the cotyledons is known as the radicle. It is more properly termed caulicle (that is, stemlet), for its mode of growth is not like that of the root, but like that of the stem above the cotyledons. The name *radicle* should be restricted to that which is the beginning of the root, namely, the free end of the caulicle. The caulicle is termed also the hypocotyledonary stem, or hypocotyl; while for the axis which is developed above the cotyledons, that is, from the plumule, the name epicotyledonary stem may be used. A large hypocotyl, which has begun to germinate, displays the structure of the stem to good advantage; but the initial cells and the nascent tissues of the stem must be sought at an earlier stage, for instance, in the plumule of a well-formed embryo, as that of Phaseolus or Faba. A vertical section through the plumule, made transparent by a clearing agent (see 24), shows that the cells have much the same arrangement as in the root-tip, except that no protective cap is present.

357. The outer layer has divisions only at right angles to the surface; it is continuous with the epidermis further back, and is easily recognizable as nascent epidermis (Dermatogen). Enclosed by this are layers which form an arch, the nascent cortex (Periblem). This encloses a mass of tissue from which the fascicular system is derived (Plerom). These tissues are essentially the same in character and development as the corresponding nascent tissues of the root.

358. As the tissue elements develop from these nascent tissues, the stem is produced; its structure is, however, generally complicated by the early formation of lateral appendages, — leaves in some of their modifications. Moreover, the tissues of the stem are continuous with the tissues of the leaves, and it is therefore necessary to take into account the mutual relations of these two organs. The problem becomes still further complicated, in a large number of cases, by the production of branches of some

kind, the tissues of which are of course intimately united with those of the main axis from which they are given off.[1]

PRIMARY STRUCTURE.

359. In the stem, or ascending axis, the distribution of tissue elements is similar to that in the descending axis, — the root. There is a more or less transient epidermis, a cortical substratum, and a central cylinder of some kind.

360. **The epidermis** of stems presents few peculiarities of structure beyond those already described in Chapter II. In most herbaceous plants it persists with little change, except in the matter of trichomes, throughout the life of the plant; but in most ligneous plants it is replaced, often early, by other protective tissues. Persistent epidermis is found in many woody and half-woody plants; for instance, Russelia juncea, Leycesteria formosa, and Ptelea trifoliata.

In Palms[2] "the epidermis exists in old age only in the cane-like and calamoid stems; in the rest it is more or less destroyed by the action of the weather. In Calamus it consists of a simple layer of minute cells elongated in the direction from without inward, and forms a stony, brittle, shining layer."

361. **The primary cortex**[3] consists essentially of parenchyma in which isolated cells of a peculiar character may often be found, such, for instance, as crystal cells, laticiferous cells, tannin cells, and the like (see 292); and its intercellular spaces sometimes serve as receptacles for the various exudations. The parenchyma cells generally contain more or less chlorophyll, and some starch.

362. Immediately beneath the epidermis, and not easily distinguished from multiple epidermis, is a portion of the cortex known as Hypoderma.[4] It is rarely sclerotic parenchyma, more

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[1] In the plumule and other buds all these parts exist potentially; and the sequence of their development can be successfully followed out by the employment of seeds in different stages of germination, or buds collected on successive days in spring and preserved at once in alcohol. In all cases care must be taken to have the date of collection of each specimen recorded in such a manner that no confusion can afterwards arise.

[2] Mohl: Ray Society, Reports and Papers in Botany. The Palm-stem, Henfrey's Translation, 1849, p. 14.

[3] Vesque (in Ann. des Sc. nat., sér. 6, tome ii., 1875, p. 82) gives a very full treatment of the subject.

[4] The word Hypoderma was introduced by Kraus (Pringsheim's Jahrb., 1865–66, p. 321), to designate the layer of colorless cells under the epidermis of leaves, "das Analogon des Rindencollenchyms." It has since been extended to apply to the external cortex just under the epidermis of stems.

frequently it is collenchyma. Excellent illustrations of the latter kind of hypoderma are furnished by most Malvaceæ and Labiatæ.

363. Schleiden[1] distinguished four types of external cortical layers in dicotyledonous stems: 1. That existing as a perfectly closed layer (penetrated in some cases only by small canals opening into stomata); as in most of the Cactaceæ, Rosa, Begonia, etc. 2. That divided into many bundles, so that the green cortical parenchyma reaches the epidermis; *e. g.*, in Malvaceæ, Solanaceæ, etc. 3. That which may be quite distinctly recognized as a special layer, but still grading into parenchyma at the borders; *e. g.*, in Pyrus Malus, Hedera, Ficus, etc. 4. That more completely merging into cortical parenchyma, and therefore less distinct; *e. g.*, in Populus, Salix, Sambucus, etc. There are some plants in which it is not distinguishable; *e. g.*, in Cheiranthus, Mesembryanthemum, etc.

In Papaver and species of Thalictrum the cells of the cortex next to the epidermis have thin walls, while the zone next to the central cylinder may be sclerotic.

The inner boundary of the cortex of the stem is, as in the root, the endodermis. The thin-walled cells just within it form the peripheral layer of the central cylinder, or shaft.

364. Variations in the cortex consist chiefly in one of the following modifications: 1. Increase of its layers, sometimes to an extraordinary extent, and often accompanied, especially in water-plants, by the formation of large air-bearing intercellular spaces. The student should examine the peculiar structure of the cortex at the nodes, in these cases of spongy cortex. 2. It has been previously shown (215) that collenchyma is a common modification of cortical parenchyma. A variation in structure reaching the same end as collenchyma, namely, strengthening the stem, is found in a great number of plants; the cortical parenchyma, especially at the outer part, becoming conspicuously sclerotic, and the tissue very compact. 3. Fibres may occur in the cortex, either isolated or in small fascicles.

365. **The primary fibro-vascular bundles** of the stem are developed at definite points in the peripheral layer of the central cylinder. Their structural elements, wood and liber, vary as regards their relative amount, even in the same plant. A given bundle may and generally does change much during its course, interlacing here and there with other bundles, and giving off branches at different points.

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[1] Principles of Scientific Botany, p. 240.

When corresponding bundles of plants of different groups are compared together, some diversities as regards the arrangement of the wood and liber elements are exhibited; but most of the cases can be referred without difficulty to the class of

366. *Collateral bundles* (see 313) of the ordinary type; namely, those having liber on the external aspect and wood on the internal aspect. In some cases, however, this order may be exactly reversed; *e.g.*, in the cortical fascicles of Calycanthaceæ. The wood-elements in collateral bundles are generally arranged in radial series; the inner ducts or their equivalents (tracheïds) being more slender and having more closely coiled spiral markings than those nearer the periphery of the bundle. The radial series may be in close contact, separated by very thin plates of parenchyma, or may have a large amount of this tissue between them. In dicotyledons, as a rule, the ducts at any given distance from the centre of the stem have a noticeable uniformity, so that a cross-section of the primary tissue shows a number of concentric circles of ducts of the same size. Sometimes, however, the ducts in a radial series may be reduced to one. In stems of monocotyledons there is less regularity in the arrangement of the wood-elements, but there is a substantial likeness in their structure in any group. They are generally in the form of a blunt wedge, the apex towards the centre of the stem, the space between the inclined sides of the wedge being mostly occupied by small ducts, wood-cells, and fibres.

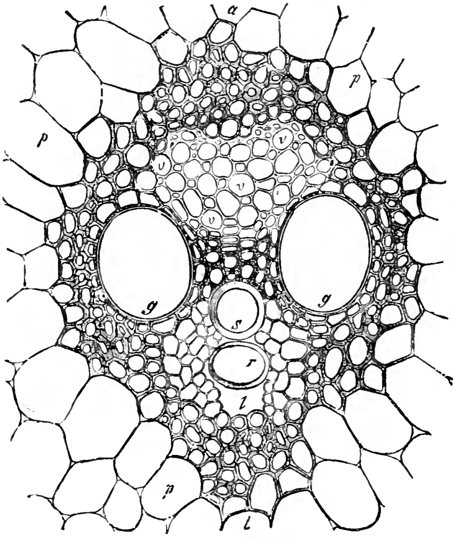

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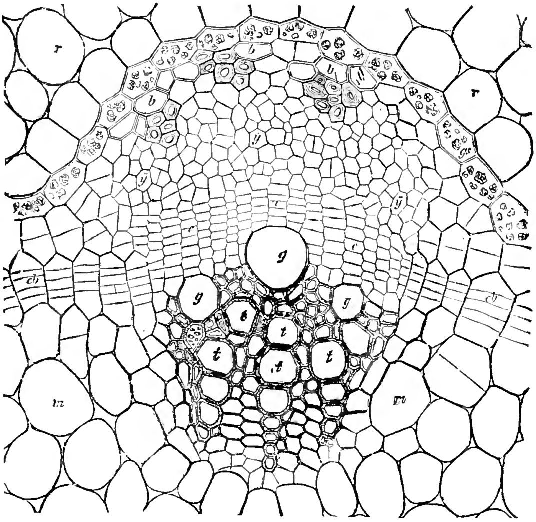
FIG. 98. Transverse section of a collateral fibro-vascular bundle of the stem of Indian corn: *p, p*, conjunctive parenchyma; *a*, outer face; *i*, inner face of the closed fibro-vascular bundle, which consists of a xylem portion (*g, g*, two large pitted ducts; *s*, spirally thickened duct; *r*, isolated ring of an annular duct; *l*, aeriferous lacuna, caused by splitting resulting from growth) and a phloëm portion, *v, v*. The whole bundle is surrounded by a bundle-sheath of thick-walled cells. (Sachs.)

367. The cribrose portion of a collateral bundle often has, in addition to true cribrose-cells, prismatic, thin-walled cells, known as *cambiform cells.*[1]

368. According to Vöchting[2] the cambiform and cribrose cells appear in some cases to have a common mother-cell, which divides obliquely in the direction of its length. The cambiform cells may divide by transverse partitions, and if the cells are moderately large the last divisions may be parenchymatous. In most monocotyledons and dicotyledons the cribrose-cells are much larger than the cambiform ones, and their cross-sections are distinguished by being less sharply quadrangular. In many succulents there are also very small cells resembling undeveloped cribrose-cells.



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369. The cribrose and woody parts of a collateral bundle are generally distinguishable from each other by the lignified char-

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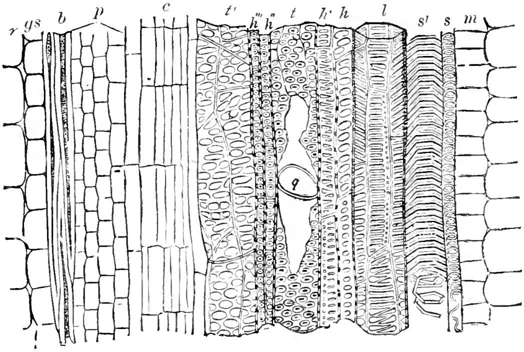
[1] De Bary reserves for these cells the term *Cambiform*, which was used by Nägeli in a wider sense.

[2] Beiträge zur Morphologie und Anatomie der Rhipsalideen, Pringsheim's Jahrb., 1874, p. 327.

FIG. 99. Transverse section of a part of the central cylinder of the mature hypocotyledonary portion of the stem of Ricinus communis: *r*, parenchyma of the primary cortex; *m*, of the pith; between *r* and *b* is the simple endodermis containing starch-grains; the fibro-vascular bundle is made up of the phloëm *b*, *y*, the xylem *g*, *t*, and the cambium *c*, *c*; *cb*, interfascicular cambium. In the phloëm are the bast-fibres *b*, *b*, the soft bast *y*, *y* (partly parenchyma and partly cribrose-tubes); in the xylem, small pitted ducts *t*, *t*, wider pitted ducts *g*, *g*, and between them wood-fibres. (Sachs.)

acter of the latter and the softer texture of the former. As has been before noticed (see 345), in dicotyledons and gymnosperms in which there is annual increase in diameter there is a layer of peculiar merismatic tissue (cambium) between the two parts. It is generally easy to identify the cells of this cambium layer, on account of their elongated form and intimate contact with each other. Their development gives rise (1) to new cells like themselves, (2) to cribrose and (3) to woody elements; all of which are to be examined later, under "Secondary Structure."



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370. The sheaths of collateral bundles may have the character of typical endodermis and envelop the single bundles, or may consist of strands of long fibres (hard bast), which are on one side of the cribrose portion, and accompany the bundle through its whole course in the stem. The strands of fibres frequently encroach upon the cribrose part of the bundle so much as to be more or less commingled with it (see 311).

371. The stem may sometimes have *bicollateral* bundles either (1) with the woody part on the interior as well as on the exterior aspect (*e. g.*, Cucurbitaceæ), or (2) with an envelope of wood surrounding the liber; this envelope is seen at the extremities of the bundle, while the rest of it has the ordinary character (Iris).

372. The bundles of the stem may be *concentric* (see 313); a

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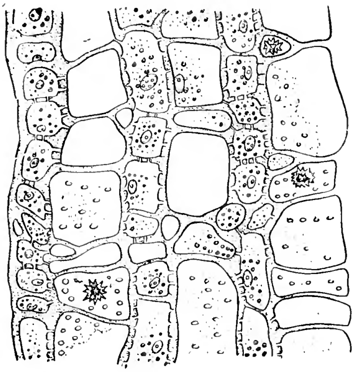
FIG. 100. Longitudinal section of a fibro-vascular bundle of Ricinus (the cross-section being shown in Fig. 99): *r*, cortical parenchyma; *gs*, bundle-sheath; *b*. bast-fibres; *p*. phloëm-parenchyma; *c*, cambium (the row of cells between *c* and *p* develops afterwards into a cribrose-tube); in the xylem portion of the bundle the elements are developed successively from *s* to *t'*; *s*, the first slender and long spiral duct; *s'*, wide spiral duct, the spiral band uncoiling; *l*, duct, thickened partly in a scalariform, partly in a reticulate manner; *h*, *h'*, *h''*, *h'''*, wood-cells; *t*, pitted duct; *q*, absorbed septum; *t'*, pitted duct, still young; in *l*, *t*, and *t'* the boundary lines of the adjoining cells which have been removed are shown in the wall of the ducts; *m*, parenchyma of the pith. (Sachs.)

ring of liber may surround the whole of the woody portion, or the wood may surround the liber. The former of these arrangements is common in the vascular cryptogams (see 354).

373. The pith of the stem consists of parenchyma frequently intermingled with other structural elements in small amount,[1] especially long fibres, woody prosenchyma, and latex-cells.

The parenchyma cells of pith have been classified in the following manner: (1) active cells, having the office of storing starch and other assimilated products for a time; (2) crystal-cells, in which crystals are formed; (3) inactive cells, which, having lost the power of receiving starch or other products, remain empty.

These apparently unimportant distinctions have been shown by Gris [2] to be valuable in the identification of considerable groups of plants. Pith composed of active or inactive cells alone is termed by him homogeneous; that which contains more or less of both kinds of cells, heterogeneous. The arrangement of the elements in heterogeneous pith is so nearly constant as to have much interest for the systematist.



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374. The medullary rays comprise the conjunctive parenchyma, which lies between the bundles in the stems of normal dicotyledons. The cells are for the most part much flattened radially, always so in those cases where the bundles are closely approximated (see also 207).

375. The stem develops from the bud by extension of its internodes. When these have attained a certain length, different

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[1] The peculiar structures found occasionally in the periphery of the pith of Sambucus, and sometimes in the bark, have been mistaken for fungi, but have been shown by Oudemans and by Dippel to be receptacles for a very heterogeneous mixture of tannin and other matters (Verh. d. Nat. Vereins d. Preussens, Rheinlande und Westphalens, 1866, p. 1).

[2] A detailed account of the orders of plants examined by Gris will be found in Nouvelles archives du Muséum, t. vi. fasc. 3, 4, p. 201 (9 plates). An extract from the same is given in Ann. des Sc. nat., sér 5, tome xiv., 1872, p. 34.

FIG. 101. Clethra alnifolia. Longitudinal section through the reticulated pith of a young branch; each active cell contains a nucleus and chlorophyll grains, December. (Gris.)

for different stems, and depending often on some external conditions, they do not further elongate; but those tissues of the internodes by which growth in length has taken place become gradually firmer, and constitute permanent tissue. It sometimes happens that the nodes and internodes of the stem are not plainly distinguishable from each other. This is the case in most palms, where the growth takes place from the terminal bud alone.

376. Even a cursory examination of the structure of a stem which has thus unfolded from a bud shows that the number and the distribution of the bundles have much to do with the number and the arrangement of the leaves. Comparative investigations[1] of large orders of vascular plants have shown that the number of the bundles of the stem always bears some relation to that of the leaves at a given portion of the axis, and to the arrangement of the leaves. "The more bundles in a given leaf, and the greater the number of leaves in a cycle or whorl, the more numerous will be the bundles in the stem at that level. In monocotyledons with a large crown of leaves these two conditions are met with, and in these stems are found the greatest number of bundles."[2]

377. **Course and distribution of the bundles in the stem.** In the internodes, the bundles mostly run parallel to the axis, or in curves of very long radius; at the nodes, they may interlace transversely. If a bundle is followed through its course from below upwards, it will be found to branch at some of the nodes; the branch of the bundle going directly into the leaf at that point, or else passing upwards through other nodes until it reaches a leaf, the number of nodes traversed varying according to the kind of plant and the region of the stem.[3] More than one branch of the bundle may, however, go to a single leaf.

378. If, now, the course of the bundle be examined from above downwards, it can be seen that each leaf contributes its simple or compound fascicle to the larger bundle with which that from the leaf sooner or later becomes confluent. The fascicle from the leaf can frequently be followed down for several internodes as a separate thread, the so-called *foliar trace*. If such foliar traces are nearly isolated in their course, a cross-section of the stem will give a ground-plan of the leaf-arrangement. Usually, however, there is much complexity in the distribution

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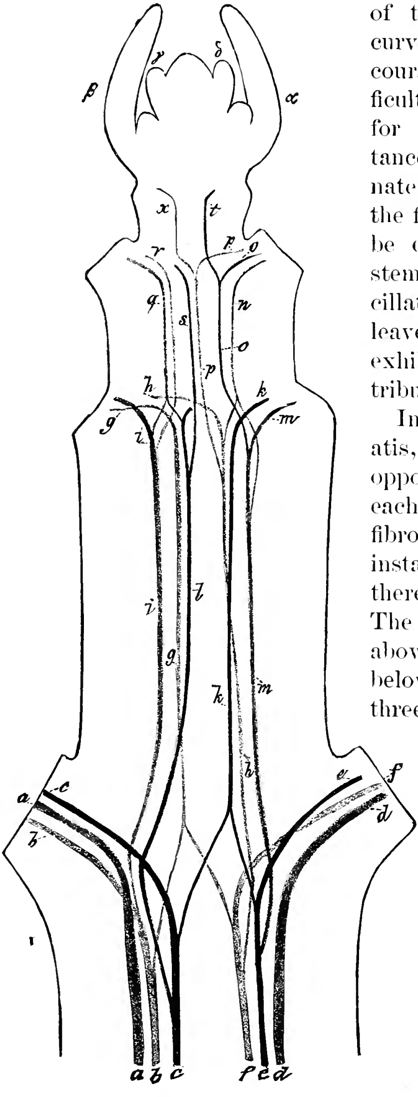
[1] Nägeli: Beiträge zur wissensch. Botanik, 1858, and Hanstein: Pringsheim's Jahrb., 1858.

[2] Van Tieghem: Traité de Botanique, 1884, p. 746.

[3] Van Tieghem: Traité de Botanique, 1884, p. 733.



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of the fascicles, and they curve considerably in their course, so that it is often difficult to follow the foliar trace for more than a short distance. If the stem has alternate leaves, the direction of the foliar traces will of course be different from that in a stem with opposite or verticillate arrangement of the leaves. The following figures exhibit the course and distribution in a few cases: —

In the leafy shoot of Clematis, Fig. 102, the leaves are opposite and decussate. From each leaf there descend three fibro-vascular bundles; for instance, at the lower node there are *a*, *b*, *c*, and *e*, *f*, *d*. The leaves at the node next above decussate with those below; each of them has three fibro-vascular bundles, respectively, *i*, *g*, *l*, and *k*, *h*, *m*, which become somewhat smaller as they descend to the next node, where they become blended with the bundles there. An examination of the third node shows that the two leaves there contribute bundles to the axial cylinder; there is again a blending of the bundles at the node below.

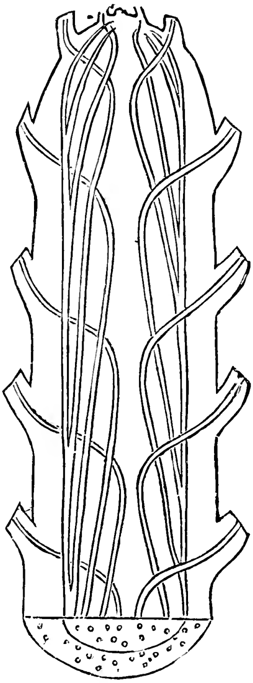
FIG. 102. Diagrammatic view of a leafy stem of Clematis, showing the arrangement of the fibro-vascular bundles: *a*, *b*, *c*, — *e*, *f*, *d*, the fascicles from the lower pair of leaves; *i*, *g*, *l*, — *k*, *h*, *m*, the fascicles from the second pair of leaves; *q*, *r*, *s*, — *p*, *n*, *o*, the

Both lateral strands of a leaf in such a case as this run down through one internode, bend outwards at the node below, and attach themselves to the lateral strands belonging there.

Suppose, now, that a cross-section of the stem of Clematis is made at the lowest node represented in Fig. 102; all the fibro-vascular bundles at that point will be seen in their relative positions, some of them cut squarely off, others obliquely, according to curves which they make. A cross-section in the internode above would show slenderer bundles, but all arranged in much the same manner as in the thicker internode below; that is, in a circle.[1]

The circle is made up of fibro-vascular bundles which have an inner portion of wood; within the circle is parenchyma (the pith), and outside of it more parenchyma (the cortex), which can be stripped off with the bast-portion of the central cylinder as bark.

Compare Fig. 102 with Fig. 103. In the latter, the stem does not exhibit in cross-section the fibro-vascular bundles arranged in a circle: they are more or less scattered; there is no clearly defined central portion nor well-marked outer portion free from them. Hence it cannot be said that such a stem has any distinction of pith, wood, and bark.



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A further distinction may be here noted; namely, that the bundles in Fig. 102 have the power of increasing in thickness, adding new wood and new bast to the primary struc-

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[1] Another feature must be attentively studied; namely, the relation of the forming bundles to the young leaves at the upper part of the stem. One may say the bundles descend from the leaf to the stem, or ascend from the stem to the leaf. But since the development of the leaf part and the stem part of a bundle goes on together, these terms, *ascend* and *descend*, should be understood to refer to our method of tracing the bundles out, and not to the method of their development.

fascicles from the third pair of leaves; x, t, fascicles of the fourth pair of leaves; β, α, — γ, δ, pairs of undeveloped leaves not as yet having fascicles. The diagram illustrates both Clematis Viticella and C. Vitalba. (Nägeli.)

FIG. 103. Longitudinal section through the stem of Aspidistra elatior, showing the curved course of the fibro-vascular bundles in the simplest palm-type. (Falkenberg.)

ture (see 390); but in Fig. 103 the bundles are *closed* (see 315), and incapable of further increase in thickness. Hence any further growth in thickness of the stem shown in Fig. 103 must be by the intercalation of new bundles.

379. It was held by Desfontaines[1] that the new vascular bundles in Palms originate in

Another illustration of the arrangement of fibro-vascular bundles is here given:—

The stem of the Vitis vinifera is usually regarded as sympodial; that is, it is composed of internodes belonging to different axes (see vol. i. pp. 54 and 154). In this species of grapevine two leaves in succession have a tendril on the opposite side, then follows a leaf without any tendril, next the sequence of two with

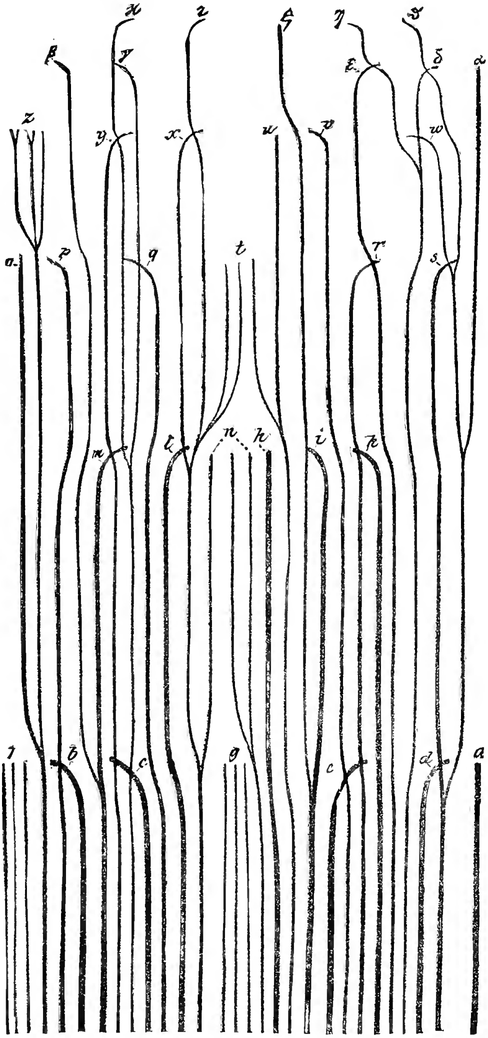

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FIG. 104. Diagrammatic projection, showing the disposition of the fibro-vascular bundles in a leafy shoot of Vitis vinifera. Each leaf has five fascicles, which are unsymmetrically arranged: *a, b, c, d, e; h, i, k, l, m; o, p, q, r, s; u, v, w, x, y; α, β, γ, δ, ε; η, ζ, θ, ι, κ*. Each tendril has three fibro-vascular bundles passing in from the stem, *g, t, z*; the axillary buds have also three, *f* and *n*. (Nägeli.)

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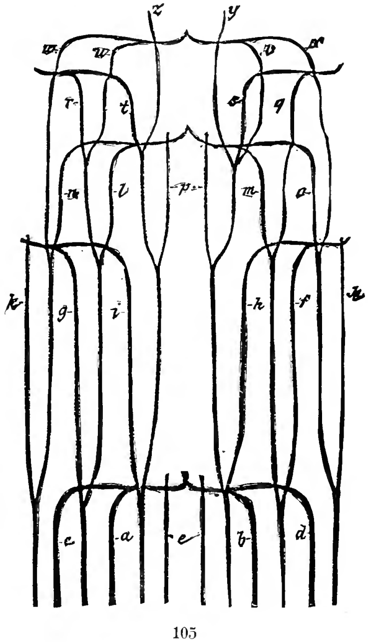
[1] Quoted by Mohl, in The Structure of the Palm-Stem (The Ray Society, Reports and Papers on Botany; London, 1849).

the centre of the stem, and that the hard and thick vascular bundles, situated at the periphery of the stem, are older than the softer ones occupying the centre. For stems like those of Palms he used the term *endogenous*, giving the name *exogenous* to the other class, in which new layers are added to the outside of the wood. The terms endogenous and exogenous were adopted by De Candolle, and have played an important part in Systematic Botany. Comparative researches have shown that the term endogenous as applied to the growth of stems like those of Palms is not appropriate, and hence the correlative words have been generally abandoned as names of the two great groups of plants. They are now generally replaced by the words monocotyledonous and dicotyledonous (see Vol. I. p. 69).

Moreover, it is now generally admitted that, although the distinctions pointed out in 366 — namely, those relating to the arrangement and course of the bundles — are valid for most plants of the two great groups, monocotyledons and dicotyledons, they do not hold for all.

380. Instead of describing the numerous exceptions to both of these groups *as* exceptions, many authors have endeavored to construct some new classification which shall embrace most of the anomalies in one or more co-ordinate divisions. Of these attempted



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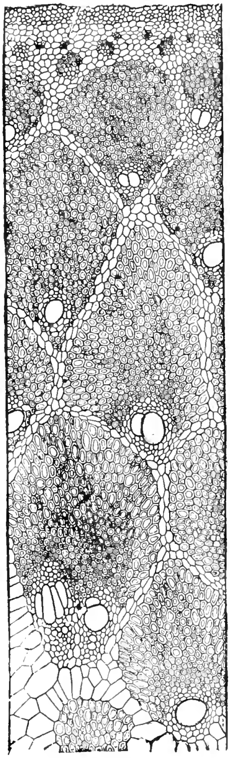
tendrils is resumed. Every leaf has five fibro-vascular bundles, which are arranged unsymmetrically, as shown in the figure. The long distance through which some bundles can run before uniting with any others, and the differences in structure at the successive nodes, are clearly exhibited in the diagram.

FIG. 105. Diagrammatic projection of the disposition of the fibro-vascular bundles in Phaseolus vulgaris. This diagram, like Fig. 104, superposes two longitudinal sections, both seen from the axis: *a*, *b*, *c*, *d*; *f*, *g*, *h*, *i*; *l*, *m*, *n*, *o*; *q*, *r*, *s*, *t*; *u*, *v*, *w*, *x*; the successive leaf-traces, each with four fascicles. Of the upper leaf-trace, the first two fascicles, ***y***, ***z***, are visible. *e*, *k*, *k*, *p*, fascicles for the three leaves below. (Nägeli.)

classifications only one will be given here, and that only in part and somewhat rearranged; namely, de Bary's: —

I. The palm-type. A cross-section of most monocotyledons shows that the bundles are not arranged in a simple ring, but that they are irregularly scattered or more or less crowded to form a shaft, which may be hollow as in most grasses, or filled in the centre with parenchyma through which scattered bundles run. The periphery of this cylinder or shaft is not a true bark, nor is the middle a true pith. In the simple palm-type, all the bundles are leaf-strands.



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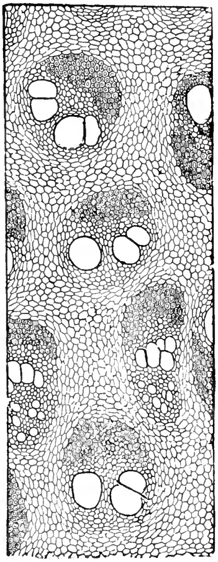

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II. The dicotyledonous type, in which all the primary bundles are leaf-trace threads. The bundles are arranged in a simple circle within which is pith, outside of which is cortex; medullary

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FIG. 106. Transverse section through the outer part of the stem of Kunthia montana, a Palm. (Mohl.)

FIG. 107. Transverse section through the middle part of the stem of Corypha cerifera, a Palm. (Mohl.)

rays run between the parenchyma of the pith and that of the cortex. To this type belong most dicotyledons, Coniferæ, and Gnetaceæ (with the exception of Welwitschia[1]).

III. Anomalous dicotyledons, differing from the last in not having all their primary bundles arranged in a simple circle. The extra bundles may either be in the cortex, as in some Melastomaceæ and Rhipsalideæ, or they may lie in the pith either scattered or arranged in rings, as in Cucurbitaceæ, the herbaceous Berberidaceæ, species of Papaver, Thalictrum, Amarantus, and Phytolacca, many Nymphæaceæ, some Begoniaceæ, and a few species of Aralia.

De Bary's other classes comprise anomalous monocotyledons and certain higher cryptogams.

381. To make clearer the somewhat complicated structure of palm-stems which have unfortunately been selected in many text-books to illustrate the histology of monocotyledons, a few general statements are now given as introductory to the special treatment in the note.[2] That portion of a palm-stem which lies above the lowest active leaves (better called *fronds*) is of a conical shape, is often much elongated, and carries all the new and forming

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[1] For a description of this interesting plant, and an account of its peculiarities of structure, consult J. D. Hooker on Welwitschia.

[2] The exposition by de Bary of the structure of the simpler forms of Palms is given nearly in full in the translation which follows: —

"Since the appearance of Mohl's Palmenanatomie, the following main characters have been recognized as belonging to the simple palm-type.

"All the bundles in the cylinder (with some doubtful and certainly extremely insignificant exceptions which will be mentioned later) are leaf-traces. The base of the leaf includes the whole circumference of the stem, or at any rate the greater part of it. The leaf-trace is always several threaded: generally it consists of many threads, in stout stems even of a couple of hundred; its width is nearly the whole of the circumference of the stalk. From the base of the leaf the threads curve down into the cylinder, within which they descend, some in its outer surface and nearly radial and perpendicular, others radial and oblique, first pressing inward toward the long axis of the cylinder in a curve which is convex towards the upper and inner side of the stem, then curving outward, and gradually passing towards the outer surface of the cylinder, and in proportion as they approach this, approximating towards a perpendicular position. All threads descend through many internodes, and unite at last in the outer portions of the cylinder with others which enter it further down, attaching themselves to these in a direction which is sometimes tangential, sometimes radial, and sometimes oblique. Until this attachment of their lower ends, the bundles run independently. The union of the lower ends of bundles with others that enter the cylinder lower down generally takes place in such a way that the whole number of the bundles in successive internodes of equal circumference remains about the same. As the successive internodes and leaves

leaves. It is known as the *Phyllophore*. The newest leaves are formed nearest the apex of this cone; and here, as before shown, all the fibro-vascular bundles common to the leaves and stem originate. In most cases there is absolutely no increase in thickness of the stem below the base of this cone; but as the apex of the cone is developed and extends further upwards, thus elongating the stem, there is also a growth in thickness of the part of the cone just above its base. Thus a uniform size of the cylindrical stem is kept. But such increase in thickness cannot continue below the point at which there are active leaves.

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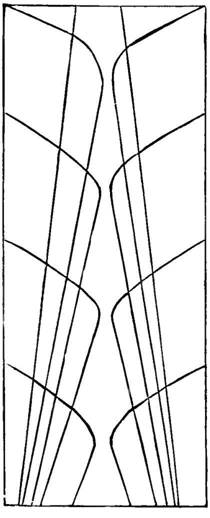
increase in size, the number of bundles grows larger, and conversely. The number of internodes through which a bundle passes cannot be fixed with exactness.

"Those bundles in a leaf-trace which curve like a bow towards the middle of a cylinder do not penetrate to equal depths; as a general thing, the median bundle of a series lies deepest, and the others lie less deep in proportion to their distance from this; the marginal ones descend nearly perpendicularly in the outer surface of the cylinder. Where there are several series of bundles, those in the inner series generally penetrate more deeply than those in the outer ones which lie at an equal distance from the median thread.

"The necessary consequences of the course described are: first, that in the cross-section of an internode the bundles stand closer together in proportion as they are nearer to the outer surface of the cylinder, — a phenomenon which is especially noticeable when the bundles are distributed over the whole surface of the cross-section of the cylinder; second, the successive traces dwindle, and their curving threads cross each other. Mohl's celebrated plan, which is here reproduced in Fig. 108, exhibits this latter relation in a radial longitudinal section, being based on the untenable assumption that all the threads of a trace are nearly equally curved, and are placed in a tangentially perpendicular direction, so that they form in the outer surface an open curving cone. If it



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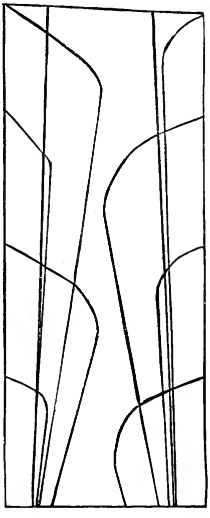

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FIG. 108. Mohl's diagram of the course of the fibro-vascular bundles.

FIG. 109. Diagram of the course of fibro-vascular bundles in a palm-stem with distichous leaves. (De Bary.)

382. Branner[1] has shown that the bundles in Palms do not end blindly at their lower extremities upon the surface of the stem, but that they are connected in sections or divisions from base to summit one with another, and one on top of another. He has further shown that each bundle lies in a spiral curve within which it grows; and whether it returns to the surface upon the side in which it originated or upon the opposite side, it is always in this curve.

383. The structure and development of monocotyledons have received much attention during the last few years, and the results obtained have caused some modification of previously existing classifications. Two of the proposed methods of rearrangement are herewith given: —

384. Falkenberg recognizes the three following types of stems of monocotyledons.

I. The tissue of the central cylinder is not plainly separable even in its mature state into conjunctive parenchyma and fibrovascular bundles. (To this type belong the water-plants, Zostera, Potamogeton, and probably all submerged monocotyledons.)

II. The bundles and the fundamental tissue are plainly differentiated; the former extending almost horizontally from the leaves to the middle of the cylinder, then curving downwards, running outwards, and finally terminating in the superficial

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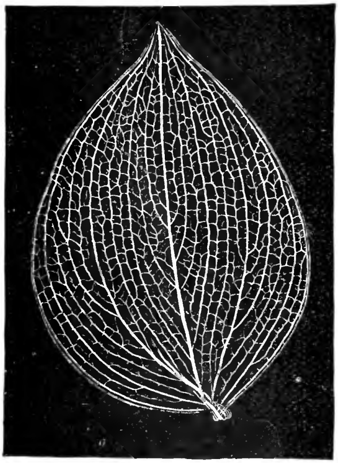
is assumed that the leaves alternate with precisely one half divergence, and include the stem, and that the threads stand tangentially perpendicular, then the actual course in the stem will be shown in the plan of a radial section through the median thread of a leaf given in Fig. 109. But the assumption of a radially perpendicular course is valid only for those bundles which are also tangentially perpendicular. As was first observed by Meneghini, admitted afterwards by Mohl (Verm. Schriften, p. 160), and more minutely shown by Nägeli, each radially curving thread runs also in a tangentially oblique direction, and in spiral curves which are proportionate to the radial curving. Nägeli found the median thread of a leaf of Chamædorea elatior, Mart., for example, making $1\frac{1}{8}$ revolutions in six internodes; in the sixth, it had not, in its outward course, quite reached the middle point between the centre of the stem and the inner surface of the bark. In stems with very short internodes and closely crowded bundles the spiral curves are at once perceptible in the cross-section, being plainest in the bundles of the stem of Xanthorrhoea, which press almost horizontally towards the centre of the stem, this peculiarity giving to its cross-section the strange appearance which has been frequently mentioned.

"Finally, many variations from that course of a thread which has here been described as typical may occur; there may be curvings alternately toward the outside and the inside, etc., which are not constant."

[1] Proceedings of American Philosophical Society, 1884, p. 459.

layers of the central cylinder. (The Mohl-Mirbel Palm-Type, illustrated by Asparagus, Iris, Canna, Aspidistra (see Fig. 103), Acorus, Scirpus, Zea, etc., the underground parts of Lilium, Tulipa, etc.).



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III. The bundles and the fundamental tissue are plainly differentiated; the bundles running downwards, and gradually converging at a point in the middle of the central cylinder, here blending with the leaf-traces of older leaves, without again curving outwards. (Examples are afforded by Tradescantia, the parts above ground of Lilium, Tulipa, etc.).

385. Guillard[1] describes six types of structure in the stems of monocotyledons which depend chiefly upon the relations of a central zone (called "intermediate") to the fibro-vascular bundles in the remaining portions of the stem. The classification has no substantial advantage over that of Falkenberg.

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[1] These types will be better understood after some peculiarities in the terminology are explained. By "pith," in monocotyledons, Guillard means the central region of parenchyma; by "intermediate zone," the active zone immediately surrounding the central region; by "cortical zone," the zone outside the external circle of bundles and the products of the intermediate zone. The six types are the following: —

1st Type. No intermediate zone between the pith and cortical zone; *e. g.*, Polygonatum vulgare.

2d Type. An intermediate zone represented by different tissues: —

1. Consisting of cauline bundles; *e. g.*, Iris florentina.
2. Consisting of meristemiform tissue (that is, tissue which produced from secondary meristem retains the shape but not the activity of meristem); *e. g.*, Chamædorea elatior.
3. Consisting of a fascicular sheath; *e. g.*, Epipactis palustris.
4. Consisting of the three foregoing; *e. g.*, Acorus Calamus.

3d Type. A single external zone of bundles, with a potential intermediate zone; *e. g.*, Luzula campestris.

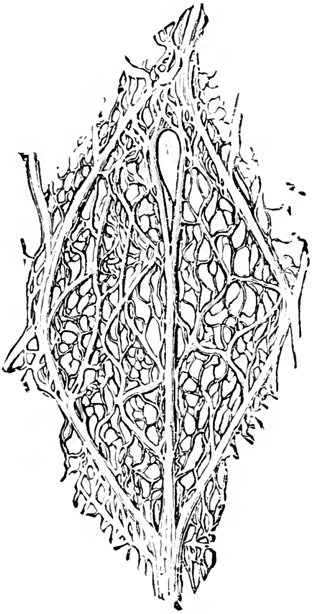
4th Type. Common bundles in two groups: one at the centre of the stem, the other forming the ordinary circle, separated from the first by a potential intermediate zone; *e. g.*, Tradescantia Virginica.

Fig. 110. Distribution of the fibro-vascular bundles in the leaf-shaped *branch* of Ruscus hypoglossum. (Ettingshausen.)

Secondary Structure.

386. It has been noticed that the fibro-vascular bundles of monocotyledons differ from those of dicotyledons chiefly in the possession by the latter of a layer of merismatic tissue (cambium) between the cribrose and woody portions. The stems of perennial dicotyledons increase in thickness from year to year chiefly by the annual production of a new mass of wood upon the inside of this layer, and of liber upon the outside; but the stems of most monocotyledons have no provision for annual increase in diameter. Hence it is convenient, in spite of numerous anomalies, to consider the secondary structure of the stem under these two heads.

387. **Secondary structure of monocotyledonous stems.** As has been already observed, the primary bundles in palms run from the leaves in curves of long radius until they again approach the surface of the stem, and their fullest development is found in the middle part of their course. While a cross-section exhibits these bundles as scattered without much order in a mass of parenchyma, a vertical section shows that they have entered the stem at different heights (since the leaves with which they were developed were at different points on the stem). A vertical section can display only parts of most of these curved bundles. At the stem of a palm just below the crown of leaves there are as many bundles seen in a cross-sec-



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5th Type. A central mass of secondary tissue, formed from central meristem. Intermediate zone well developed; *e. g.*, Triglochin maritimum.

6th Type. Bundles having several distinct liber elements; *e. g.*, Tamus communis. (Anatomie de la tige des Monocotylédones, Ann. des Sc. nat., sér. 6, tome v., 1878, p. 1.)

Fig. 111. A diamond-shaped mesh of primary fascicles intermingled with secondary fascicles in the stem of an Opuntia. (Reinke.)

tion as have been derived from the leaves at that point; and since these bundles do not possess a cambium layer, they have no power of increasing in size. The only changes therefore to be looked for in the stem of a palm from year to year are those in the ragged exterior from which the leaves fall, and the possible increase in firmness of the individual elements of the older bundles. The stems of most palms are as thick when they begin to ascend from the ground as they will afterwards be, their bundles early becoming permanent tissue throughout.

388. The presence of obscure nodes in the stem may complicate its structure somewhat by the introduction of horizontal interlacing bundles; but there is in these cases, as in the former, no provision for increase in thickness.

389. In some monocotyledonous stems new bundles can arise in a merismatic layer just within the cortex, and therefore cause an increase in the diameter of the stem.

A similar mode of increase in thickness is met with in the stems of many dicotyledons; as those of Nyctaginaceæ, many Chenopodiaceæ and Amarantaceæ, etc. Secondary bundles are formed in a merismatic layer outside the primary bundles, and in contact with their liber.

390. The **secondary structure of normal dicotyledonous stems** (see 369) is easily understood when it is remembered that the cambium of their primary bundles possesses the power of forming the following kinds of tissue: *a*, new wood on the outside of that which was last produced; *b*, a layer of new liber; *c*, fresh cambium for subsequent activity; and *d*, continuations of the medullary rays.

The cambium layer in the stems of most dicotyledons is composed of extremely delicate, thin-walled cells, which are filled with protoplasm and building materials. In the spring, when the bark is readily stripped from the wood, this layer appears as a thin film of mucilaginous matter, showing, to the naked eye, no cellular structure. In the case of such plants as the maple, birch, and pine, this juicy mass possesses a very sweet taste, owing to the large amount of organizable nutrient matter which it contains.

391. The cambium layer exposed by removal of the bark soon dies, and of course all further increase in diameter is impossible unless the wound is healed in some way (see 421).

392. The growth in size of the stems of normal dicotyledons depends therefore upon the existence and activity of cambium cells between the wood and bark. The juxtaposition of the

primary bundles brings the cambium into the form of a circle, sometimes broken, but frequently uninterrupted. If the cambium circle is substantially unbroken, a new compact ring of wood is laid upon the wood of the primary bundle, and a new ring of liber forms within the older liber. This action may be indefinitely repeated; and in a climate where there are notable differences either in temperature or moisture between the seasons, the concentric circles are records of the years.

If the primary bundles are not in contact, the new wood added year by year simply increases the size of the wedges at their outer part.

393. New bundles may be intercalated directly between those already present, and grow in much the same manner as the primary ones; or they may arise at new points of activity and produce great changes of form. In the same way tertiary changes and those of a higher order may follow the secondary ones, giving rise to stems which have a very complicated structure. The most puzzling

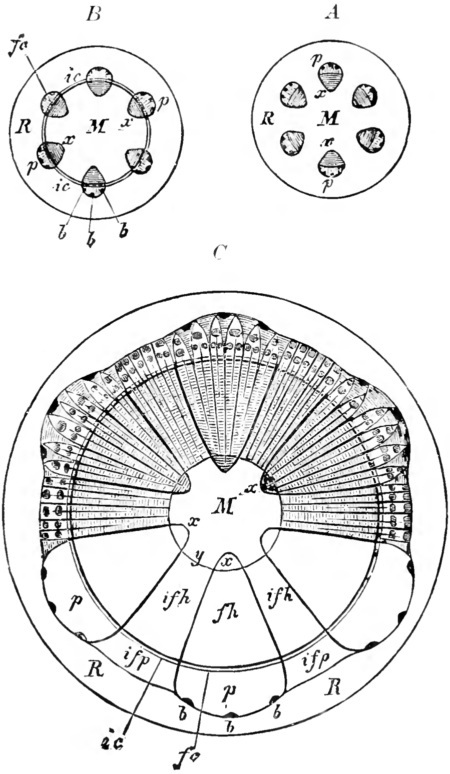

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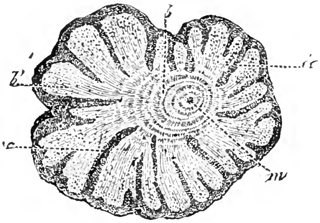
FIG. 112. Diagrams showing the secondary increase in thickness of a normal dicotyledonous stem: *R*, cortex; *p*, phloëm with three fascicles of hard-bast fibres; *x*, xylem; *M*, pith. *A* shows only primary structure; *B* exhibits formation of the ring of cambium; *fc*, fascicular cambium; *ic*, inter-fascicular cambium; *b*, *b*, *b*, fascicles of hard bast; *C*, at the end of the year, after the formation of the secondary fibro-vascular ring; *p*, liber; *fh*, secondary wood of the bundle; *ifp*, inter-fascicular liber; *ifh*, inter-fascicular secondary wood; the entire ring is subdivided by medullary rays of different lengths. (Sachs.)

cases can generally be referred to eccentric growth of some one or more parts, as in flattened stems, or explained by the introduction and more vigorous growth of supernumerary bundles.

394. Extraordinary anomalies are afforded by the *lianes* of tropical countries, woody climbers with distorted stems. They belong chiefly to a few orders; namely, Bignoniaceæ, Malpighiaceæ, Menispermaceæ, and Aristolochiaceæ. A few interesting cases are shown in the accompanying figures, and are sufficiently explained in the descriptive letter-press.



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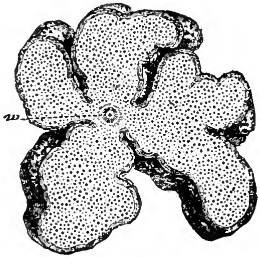

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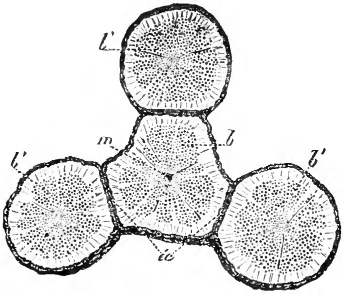

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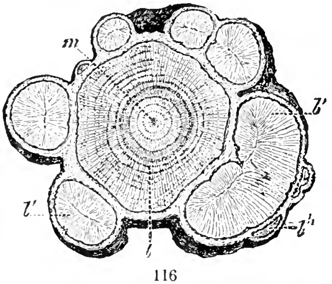

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395. **Spring wood and autumn wood.** The secondary wood annually produced in a temperate climate like ours exhibits certain differences between the inner and the outer portion of the year's

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FIG. 113. Transverse section of the stem of a liane belonging to the order Malpighiaceæ: *m*, pith; *b*, the central portion of the wood, arranged in concentric layers around the pith. (Duchartre.)

FIG. 114. Transverse section of the stem of a liane belonging to the order Malpighiaceæ: *m*, the pith. The bark follows all the irregularities of the wood. (Duchartre.)

FIG. 115. Transverse section of a liane belonging to the order Sapindaceæ: *b*, primary woody body having its own pith *m*, and bark *c'c*; *b'*, *b'*, *b'*, three secondary woody bodies without pith, but having as thick a bark as the primary body. (Duchartre.)

FIG. 116. Transverse section of the stem of a liane belonging to the order Sapindaceæ: *b*, the primary or central woody body having its own pith *m*; *b'*, *b'*, *b'*, *b'*, a circle of unequal secondary woody bodies; *b''*, tertiary woody bodies. (Duchartre.)

ring. That which is produced earliest (spring wood) has somewhat larger ducts and wood-cells than that which is formed later (autumn wood). The difference is not very striking when the wood of a single year is examined, for the diminution in size is gradual from within outwards; but if the autumn wood of one year is compared with the spring wood in the next ring, the difference is very marked. The cause of the difference in character between the early and later wood formed during a single season is supposed to be the greater pressure exerted by the tense bark in autumn. The experimental evidence in favor of this view will be presented in the chapter on "Growth."

396. In climates where there is no marked arrest of vegetative activity during the whole year, for instance, in that of the equatorial zone, the secondary wood seldom presents any clearly defined annual rings. In the wood of warm, temperate zones, however, well-marked annual rings are not uncommon.

397. It has long been known that in temperate climates a tree may exceptionally form a double ring in a single year. The cause of this in cases which have been carefully examined appears to be: (1) a partial cessation of activity owing to injury, followed by (2) a renewal of activity in the same season. Thus an elm may be stripped of its leaves in early summer and suffer a temporary check; but the buds already formed for another year develop into full leaf in a short time, the assimilative activity is resumed, and two rings are formed as a result of this cessation and renewal. Kny[1] has found this to be the case with several trees which had been deprived of their foliage at the end of June. Wilhelm has found by experiment that a tolerably well-defined double ring was formed in Quercus sessiliflora, from which he removed all the leaves on the 7th of June; while in a second case, where the foliage was removed later (July 10th), the duplication of the ring was not apparent.

398. From this statement it would appear that even in temperate climates, where there is a prolonged period of complete inactivity due to the cold, the number of rings shown in the cross-section of a stem may not exactly coincide with the number of years through which the tree has lived. But, as matter of fact, the lines of limitation in the intercalated rings are so much less distinct than those on either side, that the two lesser rings would be counted as one, and therefore be credited to the growth of one year instead of two.

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[1] Verhandl. d. botan. Vereins der Prov., Brandenburg, 1880.

[2] Child: Popular Science Monthly, December, 1883.

The largest number of rings yet reported in any case appears to be that given for the great trees of California; namely, "2,100, with a probability that others considerably exceed this."[1] Other higher numbers of rings or estimates of age are, however, given in some works.[2]

399. That it is unsafe to base any calculation of the age of a tree upon its diameter follows from the fact that its growth during one year differs from that during another (see 400). Even the use of De Candolle's modification of Otto's rule,[3] which is perhaps the best yet given, leads to erroneous results. The method assumes that the number of rings averages nearly the same to any given unit of thickness in the outer as in the inner part of the stem. Having determined the number of rings in an inch just under the bark, this number is multiplied by the radius in order to obtain the whole. For example: Extract from opposite sides of a tree two pieces having a depth of two inches each. Suppose the number of rings in the two-inch piece on one side to be 20, while in the other there are 32, the average per inch will be 13. Deduct twice the thickness of the bark from the whole diameter of the tree, to obtain the diameter of the wood in inches, and multiply one half of the diameter by 13.

400. The woody rings annually formed in a stem differ considerably in size; a narrow ring being the growth of a cold

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[1] S. Watson, in Addendum to Botany of California.

[2] The following estimates cited by De Candolle (Physiologie Végétale, p. 1007) are believed to range altogether too high: —

The Linden of Neustadt, in Würtemberg, 1147 years.

The Oak of Bordza (on the Baltic), 710 distinct rings counted and 300 indistinct rings estimated = 1010 years. (By Otto's rule this would be 1080 years.)

The Yew of Crow-Hurst (Surrey), measured by Evelyn in 1660, 1458 years.

The Yew of Braburn (Kent), measured by Evelyn in 1660, and said by him to be *superannuated*, 2880 years.

The estimate given by De Candolle, of the age of trees of Adansonia (Baobab); namely, 6,000 years, has been shown by Dr. Gray (North American Review, 1844) to be wholly erroneous.

[3] Otto's rule is thus given by De Candolle: Ascertain the diameter at the height of about five feet, and make a notch at the same point on the circular surface, to count a certain number of annual layers which we measure. We then find the annual growth of those trees which have left off growing in height by the formula $\frac{4\,d\,(D - d)\,V}{n\,D^2}$, and of those which continue to grow in height by the formula $\frac{D^3 - (D - 2\,d)\,3\,V}{n\,D^3}$; D being the diameter of tree; V, volume of same; d, thickness of annual layers which have been counted; n, the number of these layers (Physiologie Végétale, p. 981 .

season, a broad ring of a warmer one. Their width varies also in the same species in different localities: thus, in Pinus sylvestris, grown between 50° and 60° north latitude, in Europe (the space occupied by the British Isles), the annual layers are very seldom less than $\frac{1}{3}$ of a millimeter in thickness; while in the same tree, grown far north, the thickness is not $\frac{1}{16}$ of a millimeter.[1] The width varies also in different parts of the same ring. For instance, in the case of Pinus sylvestris, Bravais and Martins found the two opposite radii in a stem to have the ratio of 9 to 19, the side having the greatest thickness being that which had its foliage best exposed to air and light. The eccentric growth of the wood of branches has been often noted; the longer radii are those on the lower side.

401. **Sap-wood** (Alburnum). The new and soft wood contains a larger proportion of soluble organic matters, of nitrogenous substances, and, when fresh, of water, than the older, harder wood lying just within. The "sap" of the tree is found in largest amount in the newer wood. The name *alburnum* was given to the sap-wood by the early histologists on account of its white or pale color. Contrasted with it, but not always very sharply, is the harder substance, **Heart-wood,** or Duramen.[2] The latter was given its name because of its greater hardness, or durability. Generally there is some distinction in color between the sap-wood and heart-wood, owing to the presence of peculiar coloring-matters lodged in the texture of the latter.[3]

402. **Color of wood.** The deep colors which characterize many kinds of wood are contained chiefly in the walls of the cells and ducts. In Hæmatoxylon Campechianum the coloring-matter sometimes occurs also in crystals inside the cells themselves or in clefts of the wood. The wood of Pterocarpus santalinus (Red Sanders-wood) consists of libriform cells intermingled with small groups of very large ducts, both of which contain the ruby coloring-matters in large amount. Many Berberidaceæ, Cladrastis tinctoria, Cercis, etc., have yellow coloring-matters in the wood; in Guaiacum the color is greenish; in black walnut, brown; in ebony, nearly black.

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[1] Bravais and Martins: Ann. des Sc. nat., sér, 2 tome xix., 1843, p. 129.

[2] The word *Duramen* is used by some writers to denote merely that heart-wood which has become very dense by peculiar infiltrations (Saunersdorfer, in Sitzungsber. d. k. Akad. Wien., 1882).

[3] The following figures, giving the proportion of sap-wood to the entire volume of the trunk, are from Tredgold (Principles of Carpentry, Section X., cited by Rankine): Chestnut, 0.1; Oak, 0.294; Scotch Fir, 0.418.

403. It may be here mentioned that many woods have characteristic odors; for instance, sandal-wood, violet-wood, and many of the coniferous woods.

404. The presence of resinous matters in wood, particularly when these are evenly although sparingly distributed through the mass, exerts a marked effect in retarding decay. The durability of the wood of Southern Cypress, even when exposed to the joint action of the warmth and moisture of a greenhouse, is usually attributed to their presence. But there are some cases of great resistance to the influences producing decay, which cannot be referred to the same mode of protection; for instance, those of Robinia Pseudacacia (or common "Locust") and Catalpa.

405. Various processes have been tried for destroying the putrescible matters in cells, or so modifying the character of the cell-wall that the wood can be protected against decay.

406. The oldest known method of preserving wood is carbonizing, or charring, by which those constituents of the wood specially liable to decay are so changed as to be no longer liable to putrefaction. The wood-preserving processes known as Burnettizing and Kyanizing have for their object the coagulation of protein matters in wood-cells, thus retarding if not preventing putrefaction.

407. In Kyanizing, a solution of mercuric chloride is forced into the texture of the wood; but the cost of this substance is so great, that it has led to a general abandonment of the process.

408. In Burnettizing, the wood is impregnated with a solution of zinc chloride containing about fifty-five per cent of the dry chloride. This is forced into the wood under pressure.

409. Another process — creosoting — depends upon the introduction into the wood of a solution of impure creosote, a pressure of about one hundred and fifty pounds to the square inch being maintained until the wood has absorbed a sufficient amount of the antiseptic liquid. Some of the antiseptic matters obtained by a rough distillation of coal-tar are also used for preserving wood.

It is an interesting fact that even wood which in the air is specially liable to decay can be preserved for a long time if deeply submerged in water.

410. There is an appreciable difference, especially in length, between the wood-cells of the earlier annual rings and those which succeed them; and Sanio has shown that an increase of length of the cells occurs up to a certain period of growth, when

an average appears to be established. This fact is illustrated by the following table, based on measurements of tracheïds of Pinus sylvestris.[1]

Number of the annual ring.	Medium length of the tracheïds.	Medium width of the tracheïds.
1	.95 mm.	.017 mm.
17	2.74 "	
19	3.13 "	
31	3.69 "	
37	3.87 "	
38	3.91 "	
39	4.00 "	
40	4.04 "	
43	4.09 "	
45	4.21 "	
46	4.21 "	
72	4.21 "	.032 mm.

From this table it is seen that the increase can be traced up to the forty-fifth year, but that from that time on, the tracheïds in one ring have the same length as those in the next. Those in the forty-fifth annual ring have an average length of about five times that of those in the first. In the wood of oak, the libriform cells exhibited the greatest difference in length. Thus Sanio found that in a stem of Quercus pedunculata, with 130 rings, the medium length of these elements in the ring of the first year was .42 mm., and in the three outer rings 1.22 mm. Tracheïds in the same rings measured, however, only .39 mm. and .72 mm. respectively. With this increment in the length of wood elements in successive rings, Haberlandt associates a fact noticed by Alexander Braun;[2] namely, that the wood elements in some stems and branches stand not parallel with the axis, but

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[1] Ueber die Grösse der Holzzellen bei der gemeinen Kiefer, Prings. Jahrb., viii. 409.

[2] Ueber den schiefen Verlauf der Holzfäser, und die dadurch bedingte Drehung der Bäume, Berlin, 1854.

It is proper to refer at this point to an instructive paper by Abromeit upon the histology of the oaks, in which the most marked characters of the North American species are fully treated (Pringsheim's Jahrb., 1884, p. 209). According to Abromeit, the oaks can be plainly classified as follows: —

I. With wide well-marked medullary rays.
  A. The annual rings distinctly defined by the concentric circles of the larger ducts of the spring wood, and seen by the naked eye. The smaller ducts are arranged in radial rows in the autumn wood.
    α. With thin-walled ducts.
      a. The radial rows of small ducts touch each other tangentially: Quercus lyrata, alba, Durandii, stellata, macrocarpa, Wislizeni Prinus, Garryana, bicolor (var. Michauxii).

somewhat oblique thereto. The degree of obliquity is generally from 4° to 5°, but it is sometimes much higher than this; for instance, 10° to 20° in horse-chestnut, 30° in Syringa vulgaris (Lilac), 40° in Sorbus aucuparia, and 45° in Punica Granatum.

411. **Density of wood.** Owing to its greater firmness and smaller amount of putrescible substances, heart-wood is economically of far greater value than sap-wood; and hence nearly all determinations of density, strength, etc., are made upon it,

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- β. The radial rows of the smaller ducts are relatively narrow and for the most part isolated tangentially: Quercus bicolor, sessiliflora, Iberica, grosseserrata, castaneifolia, pedunculata, Thomasii, undulata (var. grisea), Mongolica, macranthera, heterophylla.
- γ. The radial rows of the smaller ducts are very narrow, and the ducts differ somewhat in width. The large ducts are in groups in the concentric circles: Quercus lobata.

b. With thick-walled ducts.

- α. The large ducts in the concentric circles are indistinctly grouped, while the small ducts are crowded in narrow radial rows: Quercus rubra and the var.? Texana. Quercus tinctoria.
- β. Large ducts, as in the previous group. The radial lines of the smaller ducts wide, and the ducts themselves visible to the naked eye: Quercus imbricaria, hypoleuca, laurifolia, Kelloggii, palustris, falcata, Catesbæi, aquatica, nigra.
- γ. With distinct radial grouping in the circles of the larger ducts of the spring wood. The radial rows of smaller ducts narrow and straight. The small ducts visible to the naked eye: Quercus Cerris, serrata, Phellos, coccinea.

B. Having thick-walled ducts of one kind, and these arranged in radial rows or groups. The annual rings are not distinct to the naked eye, and are defined chiefly by the thick-walled wood-cells of the outer layers of the autumn wood. They are easily made out under the microscope.

- α. The radial rows of ducts are for the most part wide: Quercus virens, oblongifolia, chrysolepis, rugosa, Ilex, coccifera, Calliprinos, lanuginosa, paucilammellosa, glabra, Burgeri, gilva, thalassica.
- β. Radial rows of ducts mostly narrow: Quercus Suber, agrifolia, glauca.

II. The wide medullary rays appear under the microscope to be somewhat interrupted by wood-cells, so as to appear like groups of narrower rays: Quercus dilatata.

The principal kinds of wood-cells in oaks, according to the nomenclature of Abromeit, are: first, the "pointed," of which there are two varieties, the septate and the unseptate; and, second, the "blunt," which are of comparatively wide caliber, and have thin walls. The length of the pointed cells in an average of 171 measurements was found to be 1.224 mm.; that of the blunt cells only .1 mm. Besides these two chief kinds, there are transitional forms of every sort.

rather than upon the latter. The lightest wood is probably the so-called "cork-wood" of the West Indies (Ochroma Lagopus), with a specific gravity of .25; the heaviest is Condalia ferrea, specific gravity 1.302.[1] The specific gravity of pure cellulose is given by authors variously as 1.25 to 1.52;[2] hence the figures noted above for the extremes of wood-density show indirectly the degree of buoyancy imparted by the air entangled in the tissues.[3]

412. Wood-fibre used for paper-pulp. The longer wood-cells of many common ligneous plants can be profitably separated

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[1] Tenth Census of the United States, vol. ix., p. 272.

[2] Ebermayer: Chemie der Pflanzen, 1882, p. 164. Husemann and Hilger: Die Pflanzenstoffe, 1882, p. 108.

[3] The following determinations were made under the direction of Professor C. S. Sargent, for the Tenth United States Census.

Botanical name.	Common name.	Region.	Av. sp. gr.	Wt. cu. ft. in lbs.
Sequoia gigantea.	Big Tree.	California.	0.2882	18.20
Pinus Strobus.	White Pine.	North Atlantic.	0.3854	24.02
Tsuga Canadensis.	Hemlock.	North Atlantic.	0.4239	26 42
Liriodendron Tulipifera.	Whitewood.	Atlantic.	0.4230	26.36
Taxodium distichum.	Cypress.	South Atlantic.	0.4543	27.65
Castanea vulgaris, var Americana.	Chestnut.	Atlantic.	0.4504	28.07
Abies nigra.	Black Spruce.	North Atlantic.	0.4584	28 57
Populus grandidentata	Poplar.	North Atlantic.	0.4632	28.87
Pinus resinosa.	Norway Pine.	North Atlantic.	0.4854	30.25
Pinus rigida.	Pitch Pine.	Atlantic Coast.	0.5151	32.10
Acer dasycarpum.	Silver Maple.	Atlantic.	0.5269	32.84
Pyrus Americana.	Mountain-Ash.	Atlantic.	0.5451	33 97
Betula nigra.	Red Birch.	Atlantic.	0.5762	35.91
Platanus occidentalis.	Sycamore, Buttonwood	Atlantic.	0.5678	35.38
Juglans nigra.	Black Walnut.	Atlantic	0.6115	38.11
Larix Americana.	Larch.	North Atlantic.	0.6236	38.86
Ulmus Americana.	White Elm.	Atlantic.	0.6506	40.54
Fraxinus Americana	White Ash.	Atlantic.	0.6543	40.77
Quercus rubra.	Red Oak.	Atlantic.	0.6540	40.75
Acer saccharinum.	Sugar Maple.	Atlantic.	0.6912	43.08
Fagus ferruginea.	Beech.	Atlantic.	0.6883	42 89
Quercus alba.	White Oak.	Atlantic.	0.7470	46.35
Betula lenta.	Cherry-Birch.	Atlantic.	0.7617	47.47
Quercus virens.	Live Oak.	South Atlantic.	0.9501	59.21
Guaiacum sanctum.	Lignum Vitæ.	Semi-tropical Florida.	1.1432	71.24

The specimens used in the above determinations by Mr. S. P. Sharples were dried at a temperature of 100° C. until they ceased to lose weight, when the specific gravities were obtained by measurement with micrometer calipers and calculation from the weights of the specimens.

For the purpose of utilizing histological features in the identification of woods, classificatory tables have been prepared by many authors. One of the most useful of these is given in Schacht's work, Die Pflanzenzelle, in which the different wood-cells of Coniferæ are described, in order to aid in the recognition of the genera. Another is de Bary's (Vergleichende Anatomie, p. 509, from each other by mechanical or chemical means for use in the manufacture of paper-pulp. The woods which appear to have

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translated in Sachs's Text-book, 2d Eng. ed., p. 651), in which the structural characters of many kinds of wood are given. The table will be found convenient for reference.

1. Wood consisting only of tracheïds with bordered pits : —
    Wintereæ (Drimys Winteri, Tasmannia aromatica ; also Trochodendron aralioides) : (Conifers).
2. Wood consisting of vessels, tracheïds, parenchyma, and intermediate cells ; that is, substitute or replacing cells or fibres (ersatzfasern) : —
    a. With no intermediate cells ; Ilex aquifolium, Staphylea pinnata, Rosa canina, Cratægus monogyna, Pyrus communis, Spiræa opulifolia, Camellia, etc.
    b. With no parenchyma ; Porlieria.
    c. With both parenchyma and intermediate cells ; Jasminum revolutum, Kerria, Potentilla fruticosa, Casuarina equisetifolia and torulosa, Aristolochia Sipho, etc.
3. Wood consisting of vessels, tracheïds, fibres, parenchyma, and intermediate cells : —
    a. With no intermediate cells ; fibres unseptate ; *e. g.*, Sambucus nigra and racemosa, Acer platanoides, Pseudoplatanus, and campestris.
    b. With both parenchyma and intermediate cells ; fibres unseptate ; Berberis vulgaris, Mahonia ; (Ephedra).
    c. With no intermediate cells; fibres septate and unseptate ; Punica, Euonymus latifolius and Europæus, Celastrus scandens, Vitis vinifera, Fuchsia globosa, Centradenia grandifolia, Hedera Helix, etc.
    d. With all four kinds of cells ; Mühlenbeckia complexa, Ficus.
4. Wood consisting of vessels, tracheïds, fibres, parenchyma, and intermediate cells. This is the most common, and may be taken as the typical structure:
    a. With no intermediate cells ; Sparmannia Africana, Calycanthus, Rhamnus catharticus, Ribes rubrum, Quercus, Castanea, Carpinus sp., Amygdaleæ, Melaleuca, Callistemon sp., etc.
    b. With no parenchyma ; Caragana arborescens.
    c. With both kinds of cells ; most foliage-trees and shrubs ; *e. g.*, Salix, Populus sp., Liriodendron, Magnolia acuminata, Alnus glutinosa, Betula alba, Juglans regia, Nerium, Tilia, Hakea suaveolens, Ailanthus, Robinia, Gleditschia sp., Ulex Europæus, etc.
5. Wood consisting of vessels, fibres, parenchyma, and intermediate cells : —
    a. With no parenchyma ; Viscum album.
    b. With no intermediate cells ; Avicennia.
    c. With both kinds of cells ; Fraxinus excelsior, Ornus, Citrus medica, Platanus, etc.
6. Wood consisting of vessels, fibres, and parenchyma : —
    Cheiranthus Cheiri, Begonia. Also many Crassulaceæ and Caryophyllaceæ.
7. Wood consisting of vessels, fibres, parenchyma, and true woody-fibres : —
    Coleus Macraei, Eugenia australis, Hydrangea hortensis.
8. Wood consisting of vessels, tracheïds, woody fibres, septate fibres, parenchyma, and intermediate cells : —
    Ceratonia siliqua, Bignonia capreolata ; it is, however, still doubtful if true woody-fibres are present.

been most extensively employed up to the present time are some of the species of Abies, Betula, Populus, Tilia, and Liriodendron Tulipifera (in the United States sometimes called "Poplar"). The chemical processes depend (1) upon the solvent power of caustic soda under pressure, and with heat, upon the so-called intercellular substance which unites the cells, or (2) upon the similar power of a sulphite, preferably magnesic, also under pressure and with heat.

413. **Bark. A, Secondary liber.** Each yearly addition to the inner surface of the bark is seldom plainly distinguishable from those which have preceded it, and hence we cannot determine positively the age of an old tree by the layers of its inner bark. The bast-fibres of a single year often cling together in a striking manner, forming bands or strips of considerable strength, and in a few cases, notably that of Daphne Lagetta, there are fine meshes between the fibres, so that the inner bark seems to be composed of layers of delicate lace.

A piece of thick bark of linden macerated for a while in water becomes so softened that the younger portion of the inner bark can be easily separated into the annual layers. Strips of the coherent fibres form the Russia matting of commerce. The strips often measure 2 – 3 meters in length, 2 – 5 cm. in width, and .04 – .08 mm. in thickness. Scattered among the individual hard-bast fibres there are many parenchyma cells, some of which plainly belong to the medullary rays, and others to the fibro-vascular bundles.

414. The bast-fibres, in a few instances, instead of being retained upon the stem for an indefinite period, are separated early, leaving the newer bast exposed. This is the case with some of our species of Vitis, in which the bast becomes detached in the form of long, loose shreds after the first year.

415. The crystals found in bast are very abundant. They are chiefly monoclinic, and occur both singly — arranged in rows — and in clusters.[1]

416. The appearance and distribution of the fibres of bast

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[1] De Bary gives the following list, taken chiefly from Sanio : —

Clusters of crystals in bast of Juglans regia, Rhus typhina, Viburnum Oxycoccus, V. Lantana, Prunus Padus, Punica Granatum, Ptelea trifoliata, Ribes nigrum, Lonicera Tatarica.

Single monoclinic crystals in bast of species of Acer, and the Pomaceæ, Robinia, Cladrastis, Ulmus campestris, Berberis, etc.

Single monoclinic crystals and clusters in bast of Quercus, Celtis, Æsculus Hippocastanum, Hamamelis Virginica, Morus, Salix, Fagus, Populus, Carpinus, Betula, Tilia, etc.

are so characteristic in certain kinds of bark that they may be used for identification. An example is given below.[1]

417. **B, Cork,** which has already been described in part in Chapter II., plays a very important part in the structure of older bark. Its relations to the cells which produce it, and to the epidermis which it displaces at an early period of its growth, will be plain from an examination of Fig. 117. In its production there are periodic arrests of activity just as in the case of wood, and hence in cork-tissue of firm texture it is possible to detect the lines of annual demarcation. When the cork of the cork-oak has reached a merchantable thickness (usually in ten to fifteen years), it is removed down to the phellogen, or cork cambium, and from this tissue new growths begin.[2]

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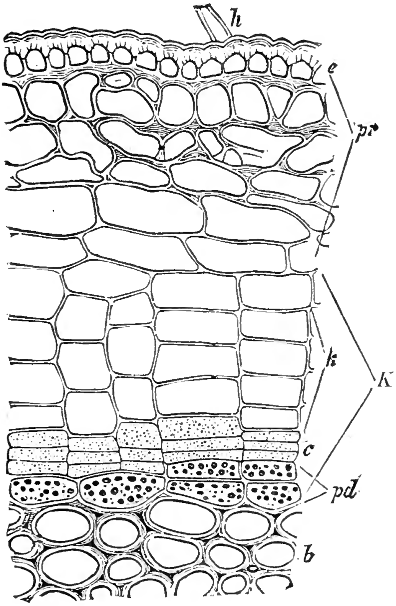
[1] "The liber is traversed by medullary rays, which in cinchona are mostly very obvious, and project more or less distinctly into the middle cortical tissue. The liber is separated by the medullary rays into wedges, which are constituted of a parenchymatous part, and of yellow or orange fibres. The number, color, shape, and size, but chiefly the arrangement of these fibres, confer a certain character common to all the barks of the group under consideration.

"The liber-fibres are elongated and bluntly pointed at their ends, but never branched, mostly spindle-shaped, straight, or slightly curved, and not exceeding in length 3 mm. They are consequently of a simpler structure than the analogous cells of most other officinal barks. They are about $\frac{1}{4}$ to $\frac{1}{3}$ mm. thick, their transverse section exhibiting a quadrangular rather than a circular outline. Their walls are strongly thickened by numerous secondary deposits, the cavity being reduced to a narrow cleft, a structure which explains the brittleness of the fibres. The liber-fibres are either irregularly scattered in the liber-rays, or they form radial lines transversely intersected by narrow strips of parenchyma, or they are densely packed in short bundles. It is a peculiarity of cinchona barks that these bundles consist always of a few fibres (three to five or seven), whereas in many other barks (as cinnamon) analogous bundles are made up of a large number of fibres. Barks provided with long bundles of the latter kind acquire therefrom a very fibrous fracture, whilst cinchona barks, from their short and simple fibres, exhibit a short fracture. It is rather granular in Calisaya bark, in which the fibres are almost isolated by parenchymatous tissue. In the bark of C. scrobiculata a somewhat short fibrous fracture is due to the arrangement of the fibres in radial rows. In C. pubescens the fibres are in short bundles, and produce a rather woody fracture" (Flückiger and Hanbury, Pharmacographia, p. 317).

[2] As noticed in 246, the inner layer of cork-meristem may give rise to parenchyma cells containing chlorophyll. Of these cells Sanio says: "They never become cork-cells, but are truly parenchymatous; they are filled with chlorophyll, starch, and sometimes with crystals. They never become lignified, but the wall remains as unchanged cellulose, and, in short, they are true cortical cells. Since, then, they owe their origin to the activity of the cork-meristem, but behave throughout their whole subsequent development precisely like the cells of the cortex, they may be called cork-cortex cells. When they form a distinctly defined layer, the term Phelloderm is appropriate" (Pringsheim's Jahrb., 1860, p. 47).

418. In some plants, notably the birch, papery layers exfoliate from time to time, while in some other plants, *e. g.*, the shag-bark hickory, large strips of irregular form and thickness are detached. Owing to the mode of their formation, such separated pieces may contain very heterogeneous elements. Of them Sachs says:[1] "Not unfrequently the formation of cork penetrates much deeper [than the periderm]: lamellæ of cork arise deep within the stem as it increases in thickness; parts of the fundamental tissue and of the fibro-vascular bundles, or of the tissue which afterwards proceeds from them, become, as it were, cut out by lamellæ of cork. Since everything which lies outside such a structure dies and dries up, a peripheral layer of dried tissue collects, which is very various in its form and origin. This structure, abundant in Coniferæ and in many dicotyledonous trees, is the *bark*, the most complicated epidermal structure in the vegetable kingdom."



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419. **Injuries of the stem.** The stem, especially in the case of plants living many years, is particularly liable to injuries, the most frequent of which are of course the wounds left by the falling of the lower limbs. It is proper to treat here of the natural repair of such injuries.

420. When any part of a plant suffers serious mechanical injury by which the deeper tissues are exposed, the surface of

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[1] Text-book, 2d Eng. ed., 1882, p. 95.

FIG. 117. Formation of cork in a branch of Ribes nigrum, one year old; part of a transverse section; *e*, epidermis; *h*, hair; *b*, bast-cells; *pr*, cortical parenchyma distorted by the increase in the thickness of the branch; *K*, total product of the phellogen *c*; *k*, the cork-cells radially in rows, formed from *c* in centrifugal order; *pd*, phelloderm (parenchyma containing chlorophyll formed centripetally from *c*). (Sachs.)

the wound exhales moisture very rapidly, and under ordinary circumstances, except in spring, soon becomes dry. As Hartig[1] has shown, the drying of the exposed tissues is fatal to their component cells, and the organic contents speedily undergo chemical decomposition. The products of this decomposition have been further shown by him to be fatal to neighboring cells, and under certain conditions the mischief may progress to an irreparable extent. But usually there is an arrest of the destructive action either from lack of the free oxygen necessary for the putrefactive process, or by the protection afforded by tissues for repair. Wounds in resinous trees are measurably hindered from effecting much damage, owing to the exudation of liquid resins which exclude air.

421. The smaller wounds of a plant are generally healed by cork or by callus. 1. By cork. The superficial layer of cells at the surface of the wound is destroyed by the injury, and dries at once. In soft tissues the layer just below this immediately becomes merismatic, and behaves precisely like normal cork-meristem, covering the entire wound with a grayish or brownish film, which is in unbroken connection with the edges of the wound. Extreme dryness of the air, or, on the other hand, extreme humidity, hinders repair by cork. 2. By callus. This is best studied in leaves and in "cuttings." When a young, juicy leaf is wounded by an incision, some of the cells at the exposed surface may give rise to elongated sac-like bodies, which fill up the greater part of the injured cavity, and, according to Frank,[2] serve as a new epidermis. Or small cells in close apposition may be at once formed, and completely protect the tissue below. In "cuttings" the callus immediately forms a swelling near the wound. A portion of the callus may by continued cell-division extend over the cut end, everywhere bounded on its exposed surface by a cork layer. Activity of the cells in the callus and around the fibro-vascular bundles soon gives rise to new parts, for instance, roots.

422. It often happens under favorable conditions that a large mass[3] of tissue is gradually formed around, and finally over, a large injured surface.

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[1] Zersetzungserscheinungen des Holzes, Berlin, 1878. (Quoted by Frank.)

[2] Die Pflanzenkrankheiten, 1879.

[3] Usually when a branch dies it remains attached for a while to the stem; and no wound is in fact caused until the slow desiccation of the deeper tissues has gone on to a considerable extent, and without exposure to atmospheric air or outside moisture. When the branch at last falls off, the tissues around

423. **Lenticels** are peculiar breaks in the continuity of the periderm of dicotyledons. In some cases they can be detected under minute elevations of the epidermis of the first year, which split open either at the end of that season or during the next, forming a rift running lengthwise of the stem. Through this cleft underlying tissues appear, protruding in an irregular manner, the whole structure constituting a lenticel. According to Stahl,[1] there are two types of lenticels: 1. Those with loose cells in the rift, alternating with denser lines of cells. This is the most common type, good examples being afforded by Alnus, Prunus, Æsculus, etc. 2. Those with closely united cells and with no alternating denser lines. Illustrations can be found in Sambucus (see Fig. 118), Salix, Cornus, etc. The same authority states that in winter both of these kinds form an impervious periderm-like layer. It appears from Stahl's examination that in their complete and open state they aid in the exchange of gases between the interior and exterior of the stem. Klebahn[2]

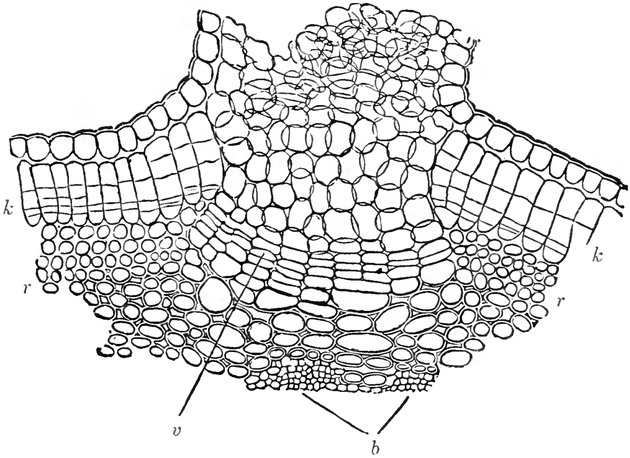

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FIG. 118. Section through a lenticel in the periderm of Sambucus nigra: *k*, periderm; *r*, primary cortex; *v*, meristem, above which are the cells therefrom produced; *b*, liber. (Stahl.)

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its base are in a healthy condition, while the internal shaft of wood is dry, and not liable to undergo rapid decay. The formation of a separative mass over the wood can therefore go on to completion.

[1] Bot. Zeit., 1873. Compare Haberlandt: Sitz. d. k. Akad. Wien, Band lxxii. Abth. i., 1875.

[2] Berichte der deutschen botanischen Gesellschaft, 1883, p. 119.

has lately shown that even in stems with the periderm free from lenticels, provision for exchange of gases is secured by certain intercellular spaces at or near the points where the medullary rays come to the periphery of the stem.

424. **Grafting.** If the cambium tissue of a young shoot is retained for a time in close apposition with that of a nearly related plant, union of the two parts may take place, and the wound may heal by the natural process before described. Success in this operation depends upon selection of suitable stock and scion, choice of the proper season, freshness of the cut surfaces, and, generally, exclusion of air from the wound. The methods of bringing the surfaces of the stock and scion together in this operation of grafting are innumerable, but for the present purpose may be referred to two principal types: (1) that in which the scion, wholly separated from the plant on which it grew as a branch, is placed in some sort of a cleft of the plant which is thenceforth to furnish it with nourishment; (2) that in which the scion is still retained in its connection with the parent plant, but is bent over and a freshly cut surface kept in contact with a cut surface of another plant, until the scion has fairly become attached by organic union. When this is accomplished, it is cut off from the parent plant. This type of grafting, in its many varieties, is known as "approach grafting." It takes place in nature, as shown in the following paragraph.

425. Two branches of one plant may become united when, after removal of a section of bark from each, the two denuded surfaces are kept in apposition for a time. Such unions of axial organs are not rare. Occasionally they may take place between two shoots at a point near the root, so that the trunk will ultimately consist of a single deeply grooved stem. The union may be between two plants of the same species, or even between plants of different species. The attrition of two branches which have grown against one another may suffice to wear off the bark on both down to the cambium, and then, if their exposed surfaces are held together for a while, union will follow. Such natural grafts are met with frequently at the borders of forests.

426. In the kindred operation of budding, a bud with a little of the tissue behind it is placed in a cleft in the bark of the stock, so that the cambium layer of the two may come into close contact.

427. The stem may be invaded by parasitic roots at any part, and its subsequent development seriously affected thereby. Such invasions often give rise to swellings, distortions, etc., by which

the structure of the stem becomes much disguised. In the case of parasites like Phoradendron, which live for several years, a vertical section through the stem of the host-plant shows how complete the union is between the host and parasite. The junction has been well compared to that which takes place between a scion and its stock, since the newer-formed tissues of both plants become perfectly united, and their subsequent growth goes on together.

428. The relations of the root to the stem are not complicated, except as regards the bundles at the "crown" of the root, or the point where it meets the stem. When the primary structure of dicotyledons in which the liber of the root is arranged in one way and that of the stem in another, as shown in Figs. 92 and 112, pages 111 and 137, is followed by the formation of a true cambium ring, the subsequent growth of root and stem is alike. Yearly additions are made in the root in the same way as in the stem; but owing to the unequal resistance exerted by the soil, such increments are often very irregular.

Roots may be produced at any part of a stem where adequate moisture and warmth are furnished; but they strike off chiefly at nodes, and, in the case of cuttings, also at the seat of injury where the callus is formed. Such secondary roots form on stems in much the same manner as root-branches do upon roots.

429. **Rudimentary and transformed branches** present few anatomical difficulties. In the structure of a branch tendril, or runner, it is generally easy to recognize the degree of reduction which the normal fibro-vascular system has undergone. In the case of underground stems and branches there are often puzzling anomalies, but they can mostly be explained by the following facts brought out by Costantin,[1] who has made a special study of a large number of rhizomes: 1. The epidermis, if present, is modified by becoming cutinized first on its outer walls, where it may acquire considerable thickness, and later on its lateral and internal walls. 2. The cortex increases either by enlargement of its cells or by their multiplication, the collenchyma diminishing or completely disappearing. 3. A cork-layer is sometimes produced at an early period, from different points in the epidermis, in the cortical parenchyma, in the endodermis, in the peripheral layer of the bundles, or, lastly, in the liber. This replaces to a great extent the fibrous layer which is so common in aerial, but never much developed in underground stems.

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[1] Ann. des Sc. nat., sér 6, tome xvi., 1883, p. 164.

4. The cortex is developed largely at the expense of the pith. 5. There is only slight lignification of the elements. 6. There is a great accumulation of reserve materials.

430. The relations of a branch to the main axis of the stem seldom present any histological difficulties, the tissues of the former being continuous with those of the latter. When a branch breaks off close to the stem, and the portion remaining becomes buried by stem-tissues which are subsequently produced, a *knot* is formed.

431. **Stems of vascular cryptogams.**[1] The following outline indicates the principal points of difference between the stems of Phænogams and those of Ferns, Equisetaceæ, and their allies.

I. In vascular cryptogams the fibro-vascular bundles are closed and as a rule are concentric. 1. In Equisetum they are slender and are arranged in a circle. From the median line of each tooth of the "sheath" (see Gray's Manual) a fascicle descends perpendicularly through one internode and divides at the one below into two branches, which unite with the lateral ones next to them. 2. In Osmundaceæ the arrangement of the constituent parts of the central cylinder is not unlike that in certain Coniferæ. 3. Lycopodiaceæ have the bundles largely dependent upon the arrangement of the leaves, but the axial cylinder is essentially cauline. 4. Ferns proper may have (*a*) an axial cylinder, or (*b*) several concentrically curved bundles. In either case there may also be isolated and rather slender bundles. In both cases above mentioned the bundles coalesce to form a very complicated network, which apparently is not dependent for its character upon the distribution of the leaves upon the stem.

II. In vascular cryptogams the parenchyma in certain places may become largely sclerotic, forming dense and often brown masses, the constituent cells of which are sometimes considerably elongated.

III. The epidermis in Equisetaceæ is strongly silicified. The stomata in these plants are in the grooves; their development is peculiar in that from one epidermal cell four guardian cells are formed in one plane; but soon the two outer cells grow more rapidly and crowd down the two inner ones, so that the latter afterwards become distinctly below them. The epidermal cells of Ferns frequently contain chlorophyll granules.

432. **Stems of mosses.** Here no true fibro-vascular bundles are met with, but elongated cells fill their place, forming what

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[1] De Bary: Vergleichende Anatomie, p. 289 *et seq.*

has been termed a fascicle. Comparison of these threads — if such they can indeed be called — with the rudimentary fibro-vascular bundles of some water-plants suggests that the former are bundles of the simplest possible kind.

The parenchyma cells are bounded in true mosses by smaller, thicker-walled cells, which do not contain chlorophyll.

THE LEAF.

433. It was shown in 322 that roots are formed under the superficial tissues of the stem, and have these outer layers, or derivatives from them, as coverings during at least a portion of their growth. But leaves are never thus covered by layers of stem-tissue ; hence they are termed *exogenous* productions, while the term *endogenous* is applied to the manner in which roots are formed.

434. **Development.** In the earliest stage of its development the leaf is a mere papilla consisting of nascent cortex (periblem) and nascent epidermis (dermatogen). As soon as the papilla elongates, or becomes flattened, some of its interior cells, making up procambium tissue (see 315), differentiate into fibro-vascular bundles. But the procambium of the nascent leaf and that of the cone of soft tissue constituting the growing-point of the stem are in unbroken connection with each other; in like manner the bundles which are derived therefrom are continuous, and it is not possible to detect any line of demarcation between them. In fact, the newly formed bundles in a young leaf appear as if they are merely the slender prolongations and terminations of those in the young stem.[1]

435. With the transverse and longitudinal enlargement of the nascent leaf there is generally more or less curvature, so that the outer, lower, and earlier leaves infold the upper leaves and the growing-point of the cone. In most cases, some of the lower leaves which thus envelop the growing-point become modified to form protecting scales; such is the ordinary structure of buds (see "Structural Botany," page 42, fig. 83).

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[1] It should be remembered, however, that some of the bundles in the stem (see 365) may be derived from procambium peculiar to the stem, and which does not extend into the leaf. Hence it is necessary to distinguish between stem-bundles, common bundles, and leaf-traces. The former belong to the stem alone; the common bundles are common to stem and leaf; the leaf-traces are leaf-bundles which are in the stem and which at some point unite with other bundles of the same kind to form common bundles.

436. The growth of the young leaf is plainly terminal at first, — that is, new cells are added just in front of the older ones; but it soon becomes intercalary as well, new cells being introduced between those previously existing. According to the seat of activity, this growth may be basipetal (the zone of growth being near the base of the leaf-blade) or basifugal (the zone nearer the apex of the leaf). In most cases the base of the leaf-blade and the stipules early attain a good degree of development, after which the petiole appears.

For the purpose of noting the peculiar mode in which the leaf-blade expands, the simple device suggested by Hales[1] is perhaps as good as any. Through a piece of stiff pasteboard sharp pins are thrust, and fastened at equal distances from each other; for instance, so as to form little squares of $\frac{1}{4}$ inch side. By this simple instrument a young leaf is pierced through with holes at equal distances; then if the leaf elongates more than it widens in the space thus covered, the holes will separate in the direction of the length of the leaf more than in that of its width. The injury done to the leaf by these small perforations does not appear to check or otherwise much modify its growth.

437. **Fibro-vascular bundles.** The distribution of fibro-vascular bundles in leaves has been considered in Vol. I., under "Venation." The two principal types of distribution of the bundles, there spoken of as "veins" or "nerves," were shown to be (1) parallel, (2) reticulated. *Parallel* venation (see Fig. 119) is characterized by having large "veins" or "nerves" running free through the leaf (that is, not connecting with each other), or without any obvious anastomosis; while in *reticulated* venation the veins form a more or less complicated network.

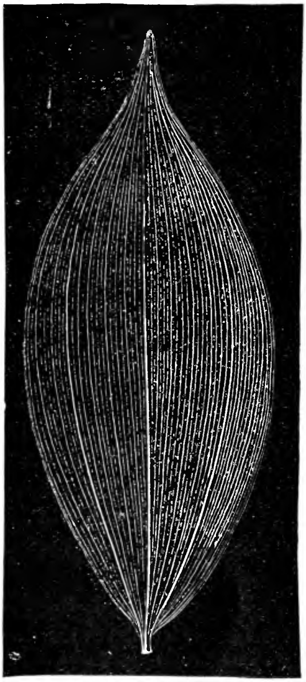

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FIG. 119. Venation of the leaf of Convallaria latifolia. (Ettingshausen.)

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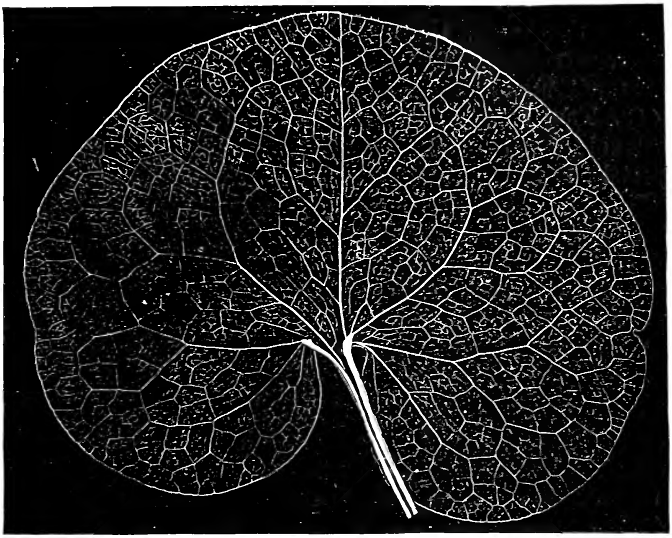
[1] Statical Essays, vol. i., 1731, p. 344.



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438. Parallel venation is of two principal kinds: (1) that in which large nerves run in long curves from the base to the apex of the leaf; (2) that in which smaller nerves run generally at right angles from a main nerve (or *midrib*) to the edges of the leaf. In both these kinds of parallel venation the veins are more or less connected by means of inconspicuous cross-veinlets and by the anastomosing extremities, but some of the veins may be *free*.

439. Reticulated venation is likewise of two principal kinds: (1) palmate (Fig. 120), in which relatively large veins diverge from each other at the base of the leaf; (2) pinnate (Fig. 121), in which

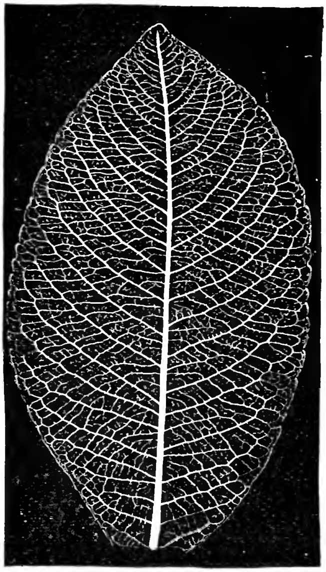

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FIG. 120. Venation of the leaf of Asarum Europæum. (Ettingshausen.)
FIG. 121. Venation of the leaf of Salix grandifolia. (Ettingshausen.)

side veins strike off through the whole length of a strong midrib. In both these cases the veins divide and subdivide and have numerous cross-connections both large and small, until the ultimate ramifications are in great part *free*.

440. Thus it appears that in both types there is abundant communication between the veins of leaves; but in some cases, especially in rudimentary and submerged leaves, in the leaves of Coniferæ, etc., the veins are very generally free, and few if any cross-veinlets are met with.

441. The fibro-vascular bundles of leaves are essentially like those of stems (see 365), and need no special description here. Their extremities are for the most part tracheïds, often arranged in double rows, but their diversities of structure and arrangement are innumerable. One of the more striking special cases of these has been already shown in the illustration of a water-pore (*v*, Fig. 55); others will be considered later (see "Insectivorous Plants"). The tracheïds which terminate the final ramifications of the veins in leaves are in close contact with parenchyma cells.

442. According to Casimir De Candolle, the leaf may be regarded histologically as a branch with its upper, that is its posterior, side atrophied.[1]

443. The stipules have the same arrangement of elements in their fibro-vascular bundles as the blade, — that is, liber below (outside), wood above (inside). But in ligules (organs which are formed by radial deduplication) the arrangement is just the reverse of this, — the liber is above, the wood below.

444. **Parenchyma.** The forms of the parenchyma cells which constitute the pulp of leaves are: (1) spherical or nearly so; (2) ellipsoidal, sometimes much elongated; (3) branched, sometimes stellate. Examples of these three are often met with in the structure of a single leaf; the upper layers generally being composed of ellipsoidal cells, the lower layers of more nearly spherical ones, intermingled with some which are branched.

445. The arrangement of the parenchyma of the leaf-blade is referred by de Bary[2] to two chief types: (1) the *centric*, in which the chlorophyll parenchyma is uniformly disposed throughout the whole organ; (2) the *bifacial*, in which there is a decided difference between the compact tissue of the upper and the spongy tissue of the lower side of the leaf.

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[1] Archives des sciences de la Bibliothèque universelle, 1868, tome xxxii. p. 32, "un rameau à face posterieure atrophiée."

[2] Vergleichende Anatomie, p. 423.

446. The centric arrangement has two modifications: (1) that in which the whole pulp is composed of chlorophyll parenchyma, but towards its middle plane has larger cells with less chlorophyll, and sometimes has conspicuous lacunæ (many grasses, Yucca filamentosa, Crassula, etc.); (2) that in which it is composed of layers which are uniformly distributed above and below a middle layer of colorless cells free from chlorophyll, but, in succulents, very rich in sap (Aloe, Mesembryanthemum, etc.). In both the foregoing modifications the upper layer of the parenchyma may be composed of somewhat longer cells than those below, and to them can be applied the term more generally given to those in the next type, namely, *palisade-cells.*

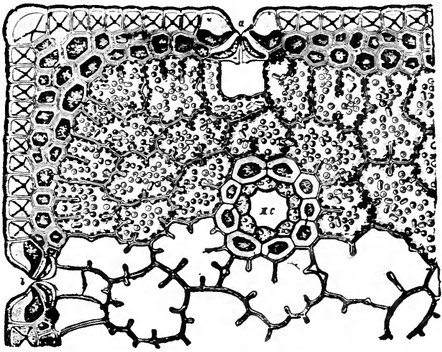

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Fig. 122. Leaf of Pinus Laricio. Cross-section of a part of the leaf, showing the stomata, hypoderma, and parenchyma. The folded walls of the parenchyma-cells (see 208) are plainly shown in the cells below the resin-passage (*HC*), where they have been emptied of their contents. (Kny.)

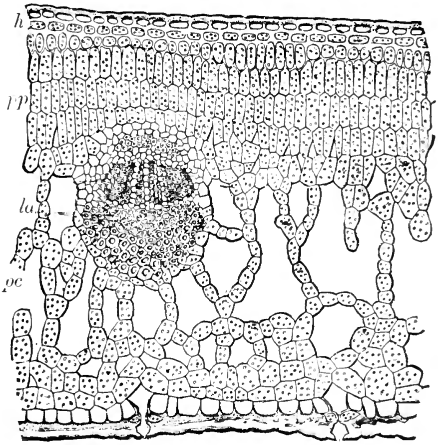

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Fig. 123. Transverse section of a leaf of Ilex Aquifolium, showing arrangement of the parenchyma: *pp*, palisade parenchyma; *pc*, spongy parenchyma; *h*, hypoderma; *la*, fibro-vascular bundle. Stomata are found only upon the lower surface of the leaf. (Areschoug.)

447. The bifacial arrangement has the denser tissue in that part of the leaf which is exposed to the light. This usually consists of several layers of palisade paren-

chyma; but the aggregate thickness of these may not be so great as that of the spongy parenchyma on the other side of the leaf (see 205).

448. In some plants the palisade parenchyma is found almost as abundantly in the under as in the upper portions of the leaves. Bessey[1] has shown that this is the case in the leaf of the Compass plant (Silphium laciniatum): "Its chlorophyll-bearing parenchyma is almost entirely arranged as palisade tissue, so that the upper and lower portions are almost exactly identical in structure." Another plant possessing substantially the same leaf-structure is Lactuca Scariola. When its leaves are grown in the light, they take a vertical position (and generally stand north and south); but if grown in the shade, they are horizontal. The leaves which are developed in the light have palisade parenchyma on both the upper and under portions;[2] but those which are developed in the shade have ordinary parenchyma above and more or less stellate parenchyma below.

449. According to Stahl,[3] exposure of a leaf to light or shade during development has very much to do — in the plants thus far examined — with the form and arrangement of its parenchyma. The leaves of the common beech afford good material for the study of the subject. In some cases, at least, those which are grown in the deep shade of a grove are different in texture from those which are formed in bright sunlight.

450. The parenchyma of the petiole is generally much like that of the stem to which it is attached; layers or lines of thin-walled collenchyma sometimes extending without interruption from the stem into the petiole. In the petioles of Cycads sclerotic elements like those of the stem are often abundant, and are continuous with them.[4]

451. In some leaves which have the power of movement the petiole is much enlarged at its base, forming what is known as the pulvinus. The parenchyma of this structure is sometimes peculiar in being thick-walled on the upper side of the petiole and thin-walled on the under. Other peculiarities will be described under "Movements."

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[1] See also American Naturalist, 1877.

[2] Pick: Botanisches Centralblatt, 1882, vol. xi. p. 441.

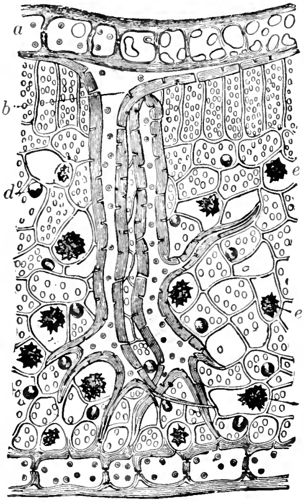
[3] Stahl: Ueber den Einfluss des sonnigen oder schattigen Standortes auf die Ausbildung der Laubblätter, Jena, 1883.

Haberlandt, on the other hand, does not think the effect of light in controlling the character of leaf-structure is well marked.

[4] Kraus: Pringsheim's Jahrb., 1865, vol. iv. p. 305.

452. The **epidermis** of the leaf is continuous with that of the stem. Its principal features have been described in Chapter II., and only the following need now be recalled. 1. It may be simple, that is, composed of one layer of cells; or multiple, — of more than one. 2. Immediately below it may be found in some cases one or more layers of cells known as the hypoderma. 3. The epidermal cells are in unbroken contact with each other except at (1) rifts, (2) water-pores, (3) stomata. 4. Their surfaces may exhibit nearly every form of trichome.

453. Glands secreting nectar are found on different portions of the leaves of various plants; for example, at the junction of the petiole with the blade (Poplar), at the base of the petiole (Cassia occidentalis), on the lower side of the midrib of the leaf (cotton-plant), or scattered over the lamina (turban squash). Such glands are particularly noticeable in insectivorous plants, as Sarracenia and Nepenthes (see Part II.). On making a section of one of the nectar-glands found on a young poplar leaf, the epidermis will be seen to be transformed into a double layer of thin-walled, elongated cells forming the secreting surface, which is charged, together with the parenchyma lying below it, with a syrup derived from the transformation of starch. At times the secretion from a gland is so abundant that drops of considerable size collect upon the surface of the leaf, and if rapid evaporation takes place, crystals of sugar are deposited at the gland.[1]



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454. The leaves of submerged phænogams, for example those of Potamogeton and Myriophyllum, possess no true epidermis; the parenchyma is therefore in direct contact with the surround-

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[1] Trelease: Nectar and its Uses, in Report on Cotton Insects (United States Department of Agriculture, 1879), and Nectar-Glands of Populus, Botanical Gazette, vol. vi. p. 284.

FIG. 124. Transverse section through leaf of Camellia (Thea) viridis, showing: *a* epidermis; *b*, branched liber-cell; *d*, oil-drop; *e*, crystals. (Mirbel.)

ing water. On the external surface its thin-walled cells are in close contact (there being nothing answering to stomata); but in the interior of the leaf there are often lacunæ filled with air. These were thought by Brongniart to be essentially the same as those cavities found in the parenchyma of many marsh plants.

The veins of submerged leaves have no true ducts; the elongated fascicles generally consisting merely of rows of elongated cells.[1]

455. Roots may be produced from leaves in much the same way as they are from stems; that is, some of the cells at the liber may divide in such a manner as to form a protuberance which pushes before it a part of the endodermis. As the root thus formed emerges, the tissues are speedily produced, the wood being continuous with the wood of the leaf, the liber with its liber. Roots may arise naturally in some leaves by simply placing them in contact with moist earth, or they may be produced artificially by mutilation of the petiole or lamina. Bryophyllum calycinum affords a good example of the former; Begonia, Peperomia, etc., of the latter mode of origin.

456. Buds may form spontaneously on the margin of leaves, especially those in contact with a moist surface, or they may grow from the cells under the scar where a mutilated leaf has healed.

457. In some of these cases only the epidermal cells take part in producing the meristem from which the bud is developed; in others the parenchyma just below the epidermis also divides, or the cells under the scar may produce all the axial tissue elements. Begonia is an example of the first method of production, Bryophyllum of the second, Peperomia of the third.

It is interesting to observe that in all these cases the bud forms without the intervention of the fibro-vascular bundles of the leaf. The newly formed axis has fibro-vascular bundles, which may anastomose with those pre-existent in the leaf, but usually they are entirely distinct. The axis is, however, provided with its own root-system, and after a time it becomes severed by a plane of cork from the leaf which produced it.

458. **Fall of the leaf.** In deciduous plants the leaf separates from the stem or twig by the formation of a plane of cells[2] cutting sharply through the petiole at or very near its base. The dividing plane may be partially formed early in the growing

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[1] Brongniart: Ann. des Sc. nat., tome xxi., 1830, p. 442.

[2] Called by Mohl the separative layer (Botanische Zeitung, 1860, p. 1).

season, but generally it is not far advanced in development until near the end of summer. The leaflets of the larger compound leaves — for instance, those of Ailanthus, Gymnocladus, Juglans, etc. — afford excellent material for examining the process of defoliation. Strong leaves of any of the plants mentioned are to be kept between damp (not wet) paper in a warm place for a number of hours, when the formation of the dividing plane can be observed. The plane is so far completed by the end of the second or third day that the leaflets fall with the slightest touch.

459. The strong leaves of horse-chestnut are employed by Strasburger as material for demonstrating the process of defoliation. He says that alcoholic material answers very well for the purpose, but that it happens occasionally that the distinctive brown color of the cells adjoining the cutting plane is nearly or quite lost. The petiole is to be cut through in its median line, and then several very thin longitudinal sections parallel to this are to be carefully made and placed at once in water. In a good preparation the cells making up the cutting plane should be clearly seen extending from the epidermis of the petiole to the fibro-vascular bundles. If the leaf was taken at just the right time, the preparation should show also that the cutting plane has invaded even the tissue of the fibro-vascular bundles. The plane consists of one to several layers of cells, some of which are plainly cutinized; thus, as a rule, the place of separation is a scar healed before the leaf falls.

It happens frequently that changes take place at the middle portion of the cutting plane, by which its layers near the leaf are forcibly separated from those nearer the stem; in such cases the leaf falls because it is forced off.[1]

460. The excision of the leaf usually takes place at the base of the petiole, so that the surface of the scar is even with the

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[1] "The provision for the separation being once complete, it requires little to effect it; a desiccation of one side of the leaf-stalk, by causing an effort of torsion, will readily break through the small remains of the fibro-vascular bundles; or the increased size of the coming leaf-bud will snap them; or, if these causes are not in operation, a gust of wind, a heavy shower, or even the simple weight of the lamina, will be enough to disrupt the small connections and send the suicidal member to its grave. Such is the history of the fall of the leaf. We have found that it is not an accidental occurrence, arising simply from the vicissitudes of temperature and the like, but a regular and vital process, which commences with the first formation of the organ, and is completed only when that is no longer useful" (Dr. Inman, in Henfrey's Botanical Gazette, vol. i. p. 61).

surface of the stem; but it may occur a little higher up, so that some of the petiole remains attached to the stem[1] (Rubus, Oxalis, etc.).

461. Evergreen leaves are those which remain upon the stem without much apparent change during at least one period of suspension of vegetation. The leaves of some evergreens persist through only one year, falling off as soon as those of the succeeding year have fully expanded. It is not unusual in warm temperate climates to have trees and shrubs which are normally deciduous in colder regions retain their leaves until new ones are produced.

Pines and spruces lose some of their oldest leaves every year, but new ones are as regularly formed. Their branches are never completely defoliated, but may bear at one time the leaves which have been formed during several years.

462. The colors assumed by leaves before they fall can be better examined after the subject of the pigment of chlorophyll-granules has been treated in Part II.

463. The fronds of ferns and the leaves of their allies present few peculiarities, and do not need to be here examined. The formation in ferns of the *sori*, or spore-dots, the *sporangia*, or spore-cases, and the *spores* themselves falls properly within the province of Volume III.

464. The leaves of mosses are characterized by great simplicity of structure. For their study any of the species of Polytrichum, or Hair-cap Moss, will answer. In these there is no true fibro-vascular bundle; a series of somewhat elongated and rather firm cells, known as the conducting thread, takes its place. Upon this conducting thread the parenchyma cells are distributed more or less regularly, on one side forming slender elevations four or five cells in height. The cells contain chlorophyll, and generally much starch.[2]

465. In the thallophytes there is no clear distinction of leaf and axis; the tissue consists throughout of parenchyma more or less modified. In some algæ there is often a lateral parting of the frond into segments resembling leaves; but as they are not leaves morphologically, they need no further consideration here.

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[1] For full and interesting accounts of the changes which cause the fall of the leaf, see Mohl's paper in Botan. Zeitung, 1860, p. 1, and also Van Tieghem and Guignard in Bull. Soc. bot. de France, 1882.

[2] In Strasburger's Botanische Practicum, p. 304, the student will find a full and interesting account of the structure of the leaves of Polytrichum and Mnium.

In the examination of the tissues of the organs of vegetation the student is referred to the following works: —

DE BARY. Vergleichende Anatomie (Leipzig, 1877). An octavo volume of about 660 pages, of which an excellent English translation is newly published under the title, "Comparative Anatomy of the Vegetative Organs of Phanerogams and Ferns," by A. De Bary. Translated by F. O. Bower and D. H. Scott, 1884. This exhaustive treatise gives all needful references to the literature of the subject up to 1876.

MOHL. Vermischte Schriften. This is a collection of Hugo von Mohl's most important works, which have appeared from time to time in various journals.

STRASBURGER. Das botanische Practicum (Jena, 1884). This work, of which an English translation is promised, is of very great use both to beginners and advanced students of Histology. The directions for procuring, preserving, and using material are explicit, and for the most part are conveniently arranged. The volume, of more than 600 pages, is divided into separate studies, such as the structure of the bast and wood of the pine, the anatomy of a few common leaves, etc.

OLIVER. Bibliography of the Stems of Dicotyledons (Natural History Review, 1862 and 1863). A citation of the more important works on the stems of different dicotyledons, arranged according to the natural families.

For a treatment of the anatomy of the organs of aquatics and parasites, the fully illustrated work of Chatin may be consulted.

Those curious to examine the diverse and now mostly abandoned views regarding the growth and structure of the stem, will find much of interest in the works of Du Petit Thouars and of Gaudichaud. An account of these and other views will be found in Schleiden's "Principles of Botany" (1849).

CHAPTER IV.

MINUTE STRUCTURE AND DEVELOPMENT OF THE FLOWER, FRUIT, AND SEED.

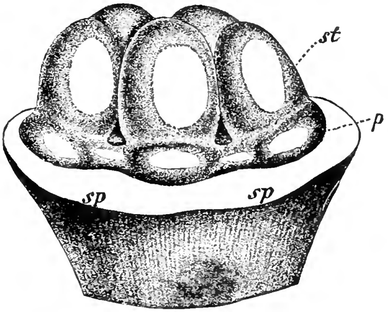
THE FLOWER.

466. In Volume I. Chapter VI., it has been shown that a flower is to be regarded as a modified branch with very short internodes and with the foliar expansions assuming forms unlike those of ordinary leaves. In the outer circle — the calyx — the parts have frequently the texture and color of foliage; but in all the other circles of the flower they are notably metamorphosed. Notwithstanding their disguises, the parts of the flower are identifiable as leafy structures arranged upon an axis. On the careful examination of flower-buds the homology between all their parts and those of a leaf-bud becomes evident. In fact, in their earliest state it is impossible to discriminate between these two kinds of buds. Each has a rounded or cone-like extremity, upon which are disposed at definite points the papillæ which are to develop into foliar organs. In one, these papillæ become green leaves; in the other, the parts of a flower.

467. Two features in the development of flowers require special attention; namely, the sequence in which the organs are produced, and the order in which the histological elements make their appearance. But it is not well in any given case to undertake the examination of the development either of the organs or of the tissues which compose them, until the student has made himself familiar with the characters of the full-grown flower.

468. Undeveloped racemes afford the best material for the study of the developing organs of the flower, and it is generally possible to find in a single young cluster flowers in all the earlier stages of development. There are two good methods of preparing the material for the compound microscope: (1) the whole raceme, first decolorized by absolute alcohol and then softened by glycerin, is to be dissected under a simple lens, and the separate flowers are to be bleached with sodic hypochlorite; or (2) the

very tip of the raceme is to be cut squarely across and placed with a drop of water under a cover-glass, when some of the youngest flowers can be seen either standing vertically or slightly inclined. The air can be drawn out from the specimen by placing the slide for a minute under the air-pump; the outlines of the floral organs will then be distinct.



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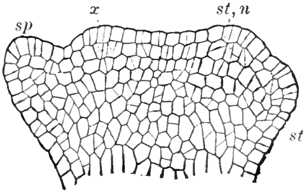
469. A still better method is to make tolerably thick vertical sections of separate flowers, one of which in each flower must be through the median line; and then, arranging the sections[1] in their proper sequence, clear them for examination either by the use of potassic hydrate (as directed in 24), or by the following method, recommended by Strasburger as applicable to many cases of thick masses of soft tissues: Treat the part first with absolute alcohol for a day or two, and then place it in concentrated carbolic acid, after which it becomes clear. For the carbolic acid either of the following may be substituted, — (1) three parts of oil of turpentine and one part of creosote, or (2) equal parts of alcohol and creosote.



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By any one of these methods it is generally possible to obtain preparations of sufficient clearness to exhibit in optical section all the internal tissues.

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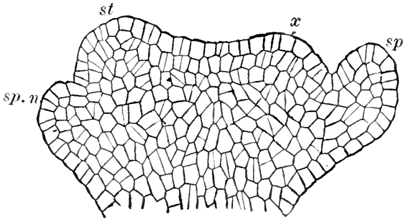
[1] Pfeffer advises that the young flowers should first be tinged with anilin blue, and then imbedded in a strong solution of gum-arabic (to which a little glycerin has been added to prevent brittleness of the mass on drying). Then, when the gum is dry, sections can be easily cut in any direction.

FIG. 125. Lysimachia quadrifolia. Flower seen from the side, and somewhat obliquely, the calyx being removed. At this period the parts of the corolla have not coalesced: *sp*, place where the excised sepals were; *p*, petal; *st*, stamen. (Pfeffer.)

FIG. 126. Lysimachia quadrifolia. Thin longitudinal section through the median line of a flower, in which the organs are beginning to form. Before the sinuses of the calyx, as well as before its lobes, cell-division has taken place on all sides; for instance, at *st*, *n*, and *x*. (Pfeffer.)

470. The fully grown flower of Lysimachia quadrifolia is thus characterized: Calyx hypogynous, deeply 5-parted, the lobes valvate or very slightly imbricated in the bud; corolla hypogynous, wheel-shaped, and deeply 5-parted with hardly any tube, its lobes convolute in the bud; no teeth between the lobes of the corolla; lobes of the corolla longer than the narrow lanceolate lobes of the calyx; stamens of unequal length, plainly united at the base, inserted opposite the lobes of the corolla, glandular; anthers barely oblong; ovary one-celled, surmounted by an undivided style and stigma,. and containing 10–15 ovules on a central placenta.



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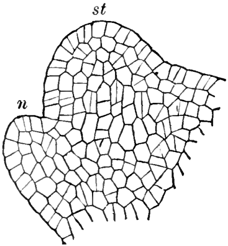

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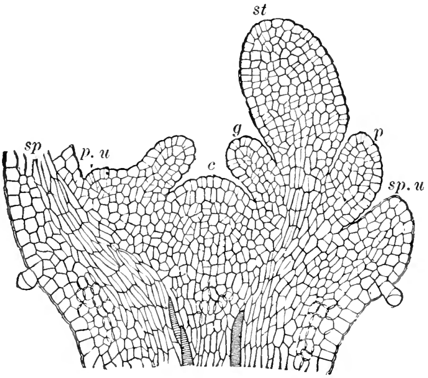

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Fig. 126 shows the appearance of a very young flower of this species; on the rounded or somewhat flattened apex of the axis minute elevations are seen, the outer being the nascent sepals. Fig. 127 shows the flower in a more advanced stage. Fig. 128 represents a portion only, the right, in a still more advanced condition. Fig. 129 exhibits all the organs of the flower, so far as they can be shown

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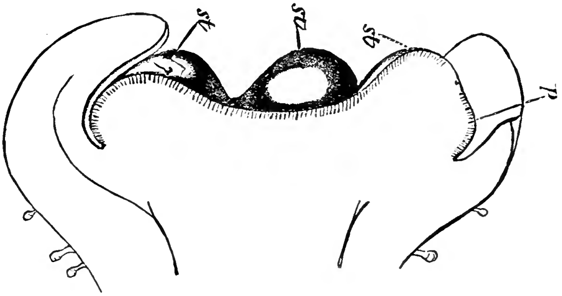
Fig. 127. Lysimachia quadrifolia. A longitudinal section through a flower somewhat more advanced than in Fig. 126; the letters are the same as in Fig. 128. (Pfeffer.)

Fig. 128. Lysimachia quadrifolia. Longitudinal section through an elevation which is considerably advanced before the appearance of the petals: *st*, stamen; *n*, cells where the petals will appear. (Pfeffer.)

Fig. 129. Lysimachia quadrifolia. A longitudinal section through a flower in which all the organs are well developed, and even the parts of the ring by which the corolla-lobes are to coalesce have begun to grow: *sp*, sepal; *p*, petal, or corolla-lobe; *st*, stamen; *g*, ovary; *c*, placenta; *sp. u*, and *p. u*, the tissue uniting the parts of the calyx and corolla respectively. (Pfeffer.)

in a single longitudinal section. Comparison of these figures gives a clear idea of the sequence in which the organs make their appearance; namely, in acropetal succession, — that is, the younger or newer are always nearest the extremity.

471. According to Payer, the sepals always precede the petals, the petals the stamens, and the stamens the pistils, in time of appearance. But in a few cases, of which Lysimachia is one, it may happen that a given circle of organs is somewhat delayed in forming; for instance, in the figures the stamens are seen as considerable protuberances before the petals are clearly outlined. This fact has been considered by some to indicate that the corolla in such cases consists of an intercalated whorl between two other whorls already somewhat developed. But a careful examination of Lysimachia and most other cases shows rather that the petals or the corolla-lobes are laid down in their proper sequence, but that they are temporarily outstripped by the sepals and the stamens.



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The appearance of the forming flower when seen in vertical section is shown in Fig. 130, and a perspective view is given in Fig. 125, exhibiting the late-appearing petals and the much larger stamens.

472. Since the several organs of the flower are modified leaves symmetrically arranged on an axis, the histological constituents of a leafy branch will be found in the flower, albeit much modified in some of their characters. These constituents are, (1) a framework of fibro-vascular tissue, upon which is extended (2) parenchyma, covered by (3) epidermis.

FIG. 130. Lysimachia quadrifolia. Longitudinal section through a flower in which the corolla is just appearing. The elevation on the right has been cut through exactly in the median line, while that on the left has been cut on its edge. Letters the same as in Fig. 129. (Pfeffer.)

473. The **fibro-vascular bundles** of the flower are essentially the same as the collateral bundles found in ordinary green leaves, except that their elements are usually more delicate in texture, and in the inner whorls of organs very much reduced.

474. The **parenchyma** calls for no special remark beyond allusion to the fact that some one of the different kinds of internal glands is frequently associated with it.

475. The **epidermis** has stomata, — which are generally rudimentary, — and most of the forms of trichomes. One of the most interesting peculiarities of structure presented by the parts of the flower is found in the papillar outgrowths alluded to in 222. These are of course minute and short hairs, which, owing to their abundance, impart a velvety appearance to the part on which they occur. This appearance is well shown by the petals of a very large number of the flowers most common in cultivation.

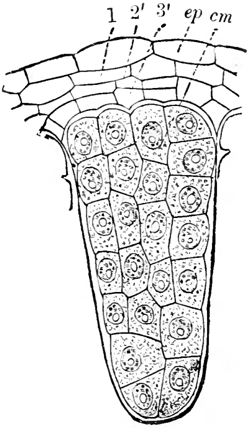
476. The cuticle of the epidermal cells of the more delicate petals is sometimes very distinctly striated in an irregular manner. The walls of the cells generally have a sinuous outline.

477. The colors of petals and other colored parts of the flower are dependent either on the presence of corpuscles (the colored plastids) or of matters dissolved in the cell-sap. The following account of the coloring-matters in the very common Viola tricolor is condensed from Strasburger.

A vertical section through a petal exhibits the epidermis of the upper side as consisting of elongated papillæ, while that of the lower side has only slightly rounded ones. Just below the epidermis of the upper side there is a layer of compact cells, under which are several rows of smaller cells with conspicuous intercellular spaces. The cells of the epidermis of both sides contain violet sap and yellow granules; the layer of compact cells under the epidermis of the upper side contains only yellow granules. The striking diversities in color presented by different parts of a given petal depend wholly upon combinations of these two elements of color; namely, violet sap and yellow granules. In some places which are devoid of either of these elements there are white spots; at these places the light is refracted and reflected by the intercellular spaces which contain air. If the air is removed by pressure, the spots will become transparent.

478. The cell-sap in the parts of the flower may have almost any color, especially shades of red and blue; from this sap the coloring-matter sometimes crystallizes in the form of short and slender needles; for instance, in Delphinium Consolida.

479. **Development of the stamens.** The following outline may serve as an introduction to the study of the development of the stamens. At first, the stamen exists as a mass of homogeneous parenchyma; later, a delicate fascicle, continuous with one in the filament, becomes differentiated in one part of the stamen, the connective. Four longitudinal ridges appear on the anther, which coincide with four lines of large cells within. These cells give rise to the mother-cells of the pollen and to the very delicate pollen-sac.[1]



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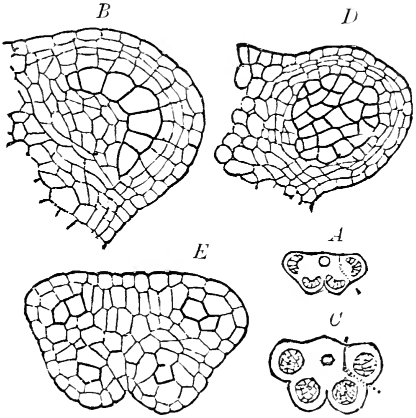
480. The mother-cells of the pollen have at first thin walls, but later these become irregularly thickened. In a large number of cases — many monocotyledons, and most if not all dicotyledons — the nucleus of a mother-cell divides into two nuclei, which themselves divide at right angles to the plane of the first division, thus producing four nuclei forming a tetrahedron. Cell-walls are next formed, and four cells are produced, which are called the *tetrad*. After the mother-cells of the pollen have been changed into tetrads, the mass of protoplasm in each of the cells of a tetrad becomes covered, as Strasburger has shown, with a new



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[1] The cells which make up the layer forming the pollen-sac are known, collectively, as the *Archesporium*. The epithelium which lines the pollen-sac has been termed the *Tapetum*.

FIG. 131. Orchis maculata. A pollen-mass in process of enlargement, with the anther-wall on the outside: *ep*, epidermis; 1, layer of cells under the epidermis remaining undivided; 2′ and 3′, layers arising from division; 3′, the endothecium. The little mass *cm*, formed by the mother-cells, is surrounded by a thickened wall. $\frac{340}{1}$. (Guignard.)

FIG. 132. *A*, transverse section of a young anther of Mentha aquatica; *B*, a fourth of this magnified; *C*, section through a young anther of Symphytum orientale; *D*, a fourth of this magnified. The dotted lines in *A* and *C* show the part taken for examination. *E*, section of a young anther of Leucanthemum vulgare. (Warming.)

cell-wall, the proper cell-wall of the pollen-grains. This wall may be variously marked, sculptured, and cuticularized, giving rise to the characteristic forms and features of the grains as they are met with in the mature flower. In gymnosperms, the development of pollen-grains differs from that described in some particulars which are interesting chiefly from their resemblance to what occurs in the higher cryptogams.

481. The stigma is a surface formed of peculiar cells which secrete a viscid, saccharine matter, slightly acid in reaction. In some cases the walls of the stigmatic cells undergo the mucilaginous modification (Solanum, etc.). The wide differences which exist in the character of the cells of the stigma are illustrated by the following examples: (1) cells with no marked papillæ, as in Umbelliferæ; (2) papillose, as in Salvia, Convolvulus, Spiræa; (3) hairy, as in Hypericum, Geranium; (4) with compound hairs, as in Reseda. In some of the above the cells are rather loosely aggregated, while in others they are much more compactly combined. Below the stigma the style often has collecting hairs, as in Compositæ, Campanulaceæ, etc. (see Volume I. page 222).

482. The style is a prolongation of the ovary, and shares with it its fascicular system. In the interior there is a slender thread of loose tissue made up of thin-walled cells containing considerable food-material, starch or oil, etc. The cell-walls often pass into the mucilaginous condition. The style is sometimes tubular, and lined with the tissue just described.

483. The simple ovary is a modified leaf-blade provided with epidermis, parenchyma, and a fascicular system. The epidermis of the outside of the ovary, and that which lines its cavity, may have all the characters of ordinary epidermis; stomata and hairs may be present, the latter often being mere papillæ, which upon the ripening of the ovary into the fruit become long hairs.

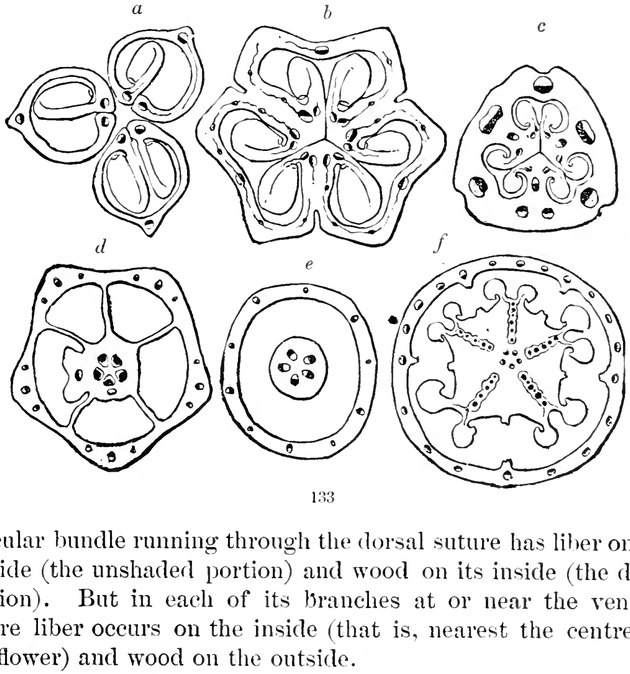
484. In the interior of the ovary there is frequently a peculiar modification, either of the epidermis itself or of the subjacent parenchyma as well. In such cases very loose tissue, sometimes appearing as if composed of felted hairs, lines the cavity of the ovary (or is found at some one portion of it). The walls of this tissue may undergo the mucilaginous modification either in whole or in part. Its cells contain a considerable amount of food-materials (oil and starch). This loose tissue, together with that of the same character found in the style, is known as conductive tissue, and serves as a path of least resistance for the penetrating pollen-tube (see Part II.).

485. The distribution of the fibro-vascular bundles in ovaries

is of much interest, and can best be examined under the two heads of "Simple Pistils" and "Compound Pistils."

486. **Simple Pistils.** The fibro-vascular bundle consists of wood and liber running through the median line of the carpellary leaf, — that is, through the dorsal suture. Two branches are given off by this bundle not far from the base of the leaf, near its two united margins, — that is, at the ventral suture.

487. The folded carpellary leaf has incurved margins; so that whatever the arrangement of the wood and liber may be in the median line of the leaf, the reverse will be found at the margins. Thus in each of the three carpels shown in Fig. 133 *a*, the fibro-vascular bundle running through the dorsal suture has liber on its outside (the unshaded portion) and wood on its inside (the dark portion). But in each of its branches at or near the ventral suture liber occurs on the inside (that is, nearest the centre of the flower) and wood on the outside.



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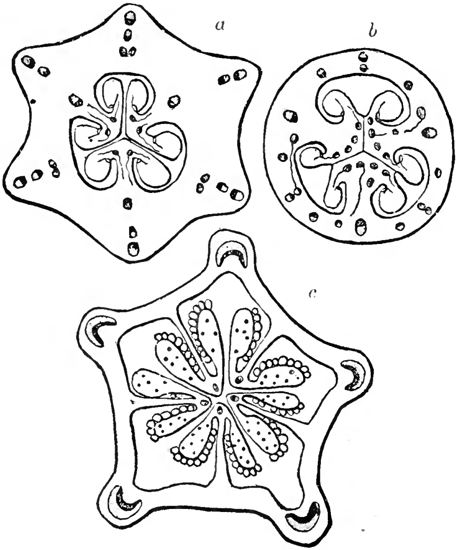
488. **Compound Pistils.** If several carpels unite to form a compound ovary, the same inversion of the order of the parts of the bundles (as shown in Fig. 133 *a*) will be seen when the bundles at the centre of such an ovary are compared with those at its periphery (see diagrams *b* to *f*, Fig. 133).

Fig. 133. Transverse section of superior ovaries, showing the arrangement of the fibro-vascular bundles of carpels: *a*, Eranthis hyemalis; *b*, Hyacinthus orientalis; *c*, Tulipa Gesneriana; *d*, Impatiens tricornis; *e*, Anagallis arvensis; *f*, Lychnis dioica. (Van Tieghem.)

489. But if the ovaries, instead of being superior, as those in Fig. 133, are inferior, as those in Fig. 134, further complications are caused. The fibro-vascular bundles of the several floral whorls united with the pistil are distributed in circles in the parenchyma tissue of the ovary. Thus in Fig. 134 *a*, we find five such circles, corresponding to the calyx, corolla, stamens, and dorsal and ventral sutures of the carpel. The bundles in Fig. 134 *a* are arranged in radial lines from the centre outwards; the six bundles nearest the centre of the ovary are those of the ventral sutures, and have wood outside and liber inside; in the next circle the three with reverse arrangement of elements are those of the dorsal sutures from which the bundles just spoken of branched. In Fig. 134 *b*, all the fibro-vascular bundles save those of the carpels are united to form a single circle, thus giving rise to the three circles of bundles seen in the cross-section, and at the base of the ovary even these did not exist separate. In Fig. 134 *c*, the bundles of all the floral whorls are blended for a considerable height in the ovary; finally, the bundles of the ventral sutures become separated from the rest, which continue united throughout, forming the large bundles seen on the periphery of the ovary in Fig. 134 *c*. The arrangement of the bundles in this figure should be compared with that in Fig. 133.



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490. The structure of the peduncle and the pedicels is substantially the same as that of the stem, and the structure of

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FIG. 134 Transverse section of the inferior ovary, showing the arrangement of fibro-vascular bundles both in the carpels and the external parts of the flower: *a*, Alstrœmeria versicolor, the fascicles of the whorls independent; *b*, Galanthus nivalis, the fascicles no longer so distinctly radial; *c*, Campanula Medium, the fascicles of the whorls blended. (Van Tieghem.)

the bracts is much like that of the leaf; therefore these need not be specially considered here.

491. Ovules are normally formed at definite points or lines upon the ovarian wall, which answer to the edges of the carpellary leaves. The funiculus arises as a slight elevation produced by the multiplication of a cell or a group of cells under the epidermis; in the centre of this elevation, and also under the epidermis, further development produces a spheroidal or cone-like mass, — the nucleus. Then, a little later, cells at the base of the nucleus begin to produce a cylinder (the inner integument), and shortly after, a second one is formed below and outside this (the outer integument). Subsequent development carries the outer integument quite up and around the inner one, and the nucleus; leaving a small opening (the foramen). For peculiarities in the morphology of the ovule, and for cases in which one or both integuments may be wanting, see Volume I. page 278.

492. The funiculus has a collateral fibro-vascular bundle, having its median plane coincident with that of the ovule. The bundle is surrounded by parenchyma and epidermis. It is frequently prolonged into the integuments, being there more or less branched.

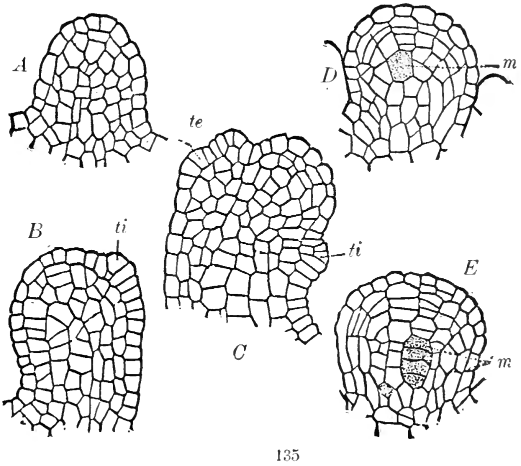

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Fig. 135. Development of the ovule of Aristolochia Clematitis. *A*, young ovule in vertical section; *B*, same, more advanced; *ti*, internal integument forming; *C*, a later stage of same; *ti*, internal integument; *te*, external integument forming; *D* and *E*, later stages of nucleus, to be described in Part II. (Warming.)

THE FRUIT.

493. The fruit is the ripened pistil. But, as shown in Volume I., "it is a loose and multifarious term, applicable alike to a matured ovary, to a cluster of such ovaries, at least when somewhat coherent, to a ripened ovary with calyx and other floral parts adnate to it, and even to a ripened inflorescence when the parts are consolidated or compacted."

494. Histologically considered, fruits present few difficulties, although the changes in form which a pistil undergoes as it ripens are not greater than the changes which it may suffer in minute structure. These histological changes are referable to a few simple kinds: (1) a great development of sclerotic elements, seen in the harder dry-fruits and in the putamen of all stone-fruits; (2) a large increase in the amount of soft-walled parenchyma, containing sap, as in the pulp of all fleshy fruits; (3) a considerable development of color, especially in the superficial parts.

495. Sections to exhibit the structure of the very hard parts of fruits are made most easily by carefully grinding the parts on a fine oil-stone. First, a fragment of the hard shell of a nut or of the putamen of a drupe is obtained by means of any strong cutting instrument, and a flat surface parallel to the plane of the section desired made by a clean file. On a glass slide a drop of Canada balsam is placed, and heated until the more volatile portion is expelled (see 111). Then the flat side of the object just prepared is held upon this balsam until the latter becomes cool and hard; and when thus securely fastened, the specimen is rubbed down on an oil-stone to any required degree of thinness. It is removable from the slide by oil of turpentine, and can afterwards be mounted in a fresh portion of balsam or of benzol-balsam (see 112).

496. The contents of the parenchyma cells of fruits depend very largely on the degree of maturity of the fruit. Changes in the contents go on from the formation of the fruit until it is fully ripe. In some of the more common cases these consist largely in the production of various sugars, especially that which is known as fruit-sugar; and organic acids, for instance, citric, tartaric, and malic acids. A consideration of these changes belongs to Part II.

497. The coloring-matters in fruits, like those in flowers, are either color-corpuscles (chromoplastids), or substances dissolved in the cell-sap. In a few cases the walls of the cells themselves have more or less color.

498. The berries of a common house-plant, Solanum Pseudocapsicum, furnish excellent material for the examination of the coloring-matters of fruits. The following account, condensed from Kraus,[1] will show the essential characters of the color-granules in this case, and it should be compared with what has been already said about the structure of chlorophyll granules and leucoplastids (168 *et seq.*), as well as with the account of the chromoplastids in the parts of flowers (477).

A section through the ripe pericarp shows that it consists of twenty to thirty or more layers of cells, in most of which color-granules occur. In the outermost cells the granules closely resemble both in form and structure ordinary granules of chlorophyll. In some of the granules the coloring-matter is evenly diffused through the whole mass, while in others it is confined to some one part, the rest of the granule remaining without color of any kind. In these cases the colored and the uncolored parts are not very sharply divided from each other.

499. Other granules less like chlorophyll-granules occur, in which there is a sharp demarcation between the colored and uncolored parts; such have been shown to be vacuolar, the vacuoles assuming widely different shapes. These are abundant in the cells which lie five to eight layers, or rather more, from the outside.

In some of these the colored portion appears spindle-form or sickle-form, in others curved twice, like the letter S. It frequently happens that several of these long granules are placed end to end, forming an irregular chain.

500. In the part of the berry which envelops the seeds the color-granules are extremely slender, and needle-shaped.[2] All of the granules lie in the protoplasm; usually in greatest number in that lining the walls, and immediately around the nucleus.

501. Occasionally in the larger pericarp-cells roundish colored objects are met with, which close examination shows are nothing but vacuoles in the protoplasm of the cell filled with colored sap; sometimes these have been mistaken for the granules themselves, but they can usually be distinguished from them without difficulty, on account of the distortion which they undergo upon slight pressure.

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[1] Kraus: Pringsheim's Jahrb., 1872, p. 131.

[2] Trécul: Ann. des Sc. nat., sér. 4, tome x, 1858, p. 154. Weiss: Sitz. d. k. Akad. Wien, 1864 (Band l.), and 1866 (Band liv.)

THE SEED.

502. The ripened ovule is the seed. In ripening, the ovule undergoes changes in the structure both of the integuments and the nucleus. The integuments of the seed answer morphologically to the primine and secundine of the ovule; the outer being the testa, or seed-shell, — also called spermoderm or episperm, — the inner the tegmen, or endopleura. The nucleus of the seed also answers to the nucleus of the ovule. The morphological relations of the different parts of the seed have been sufficiently treated in the first volume, "Structural Botany," and therefore only the histological features will now be presented.

503. Considered as a whole, the testa varies greatly in consistence; it is in some cases as dense as any sclerotic tissue, while in others it is pulpy, and in others still, membranaceous. But it is usually divisible under the microscope into two or more layers, which are not constant in their characters.

504. The ordinary layers met with in the seeds of most agricultural plants have been described by Nobbe[1] in the following terms: 1. The hard layer, composed generally of palisade or staff-like cells of considerable firmness. In Leguminosæ it is the external layer, and its exposed surface is cuticularized. In flax and species of Brassica, it is the second, in cabbage and mustard, the third layer. In a few cases the cells of this layer are tabular instead of staff-shaped. 2. The mucilaginous layer, not present in all the common agricultural seeds, is composed of cells whose walls have the power of swelling greatly when they are placed in water. This layer is sometimes found in the outer part of the testa, sometimes in the inner. 3. The pigment layer, which imparts characteristic colors to the coats of the seeds of many plants, is not constant in the form of the cells. The color may reside in the cell-wall, or in the dried contents of the cell. Sometimes a few pigment-cells are scattered among others of a neutral tint, and even among those which cannot be said to have any proper color at all. In some cases one of the other layers may contain more or less color. In a few other instances the color is not dependent on a pigment layer; for, as Frank[2] has shown, in the steel-blue seeds of species of Pæonia the color is purely a result of reflected light, and is in no wise due to the presence of any true coloring-matter. The dried seeds are dark red or dark brown; but when thoroughly moist-

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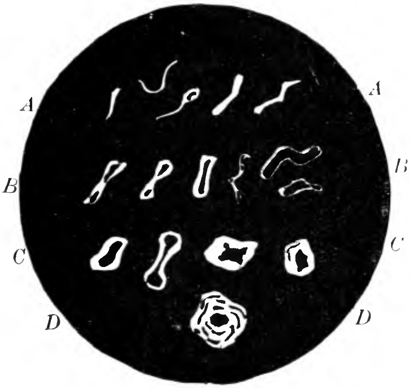
[1] Handbuch der Samenkunde, p. 73.

[2] Botanische Zeitung, 1867.

ened with water (or better still in a fresh state), they are distinctly blue. 4. The protein layer, the cells of which contain granular albuminoid matters.

The layers just described are different in different seeds, and sometimes different in different parts of the same seed-coat, so that the division has really little utility.



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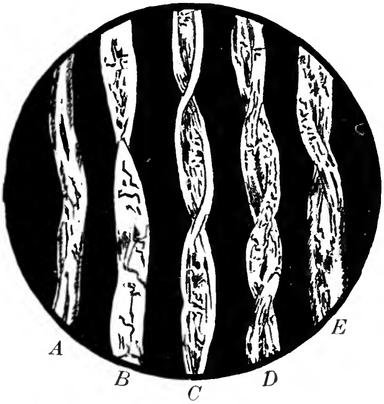
505. The external integument or testa may have well-developed hairs, as has been shown in Volume I. p. 306. Only one of these cases of hairs can be here described; namely, those which form the felted covering of cotton-seeds, and which are the "cotton" of commerce. These are slender cells with collapsed walls. As they approach maturity, the cells become more or less twisted; the resulting spiral is that which imparts to cotton its value as a material for spinning. Some other seeds, notably those of species of Asclepias, have long and strong hairs, but none of these have any spiral twist which fits them for textile purposes.



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Regarding the size of cotton "fibres" (hairs of the seed), the following measurements by Ordway are of interest: Maximum length in the "sea-island" variety, about two inches (five centimeters); in

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FIG. 136. Cross-sections of cotton-fibres. *A A*, unmature fibres; *B B*, half-mature fibres; *C C*, fully mature fibres; *D*, section of fibre, showing laminated cell-walls. (Bowman.)

FIG. 137. *A*, Glassy, structureless fibre; *B*, thin, pellucid, immature fibre; *C*, half mature fibre, with thin cell-wall; *D* and *E*, fully mature fibre, with full twist and well-defined cell-wall. (Bowman.)

upland or "short-staple" cotton, a little over one inch and a half (three and three-fourths centimeters). The greatest width of fibre was found to be .0013 inch. A single fibre sustained without breaking a weight of 150 grains.[1]

506. It has been shown in Volume I. that the seed-coats of many Polemoniaceæ, etc., are furnished with microscopic hairs, "which come usefully into play in arresting farther dispersion at a propitious time or place. . . . The testa is coated with short hairs, which when wetted burst, or otherwise open and discharge along with mucilage one or more very attenuated long threads (spiricles) which were coiled within. These protruding in all directions, and in immense numbers, form a limbus of considerable size around the seed, and evidently must serve a useful end in fixing these small and light seeds to the soil in time of rain, or to moist ground, favorable to germination, to which they may be carried by the wind." The best example of this structure is afforded by the genus Collomia; in this the spiricles are long and very numerous.

507. The nervation of the seed-coats furnishes in many cases excellent diagnostic characters, but they need no special remark histologically. The forms of branching of the fibro-vascular bundle of the funiculus indicate that the ovule and seed are of the nature of leaflets on the margin of the carpellary leaf.[2]

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[1] The above measurements are approximate; those which follow are the exact determinations as they are given by Professor Ordway in the Tenth Census of the United States.

Length of fibre. Maximum length found in the "sea-island" variety of South Carolina, where it was 1.996 inches. The maximum length of the upland or "short-staple" cotton was 1.669 inches. The minimum of length (0.695 inch) was found in North Carolina cotton, grown on a light, sandy loam soil.

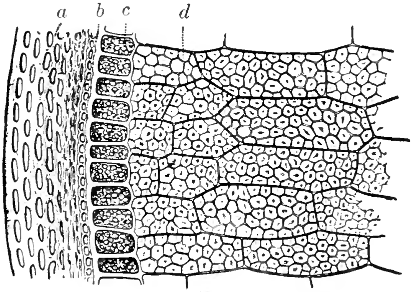
Width of fibre. The widest ($\frac{1308}{1000000}$ inch wide) was quite short (0.945 inch). By far the largest number of wide fibres come from uplands. The "sea-island" variety had a width of $\frac{878}{1000000}$ inch.

Strength of fibre. The strongest specimen examined had a breaking weight of 149.4 grains. Professor Ordway mentions some instances which lead him to think that the strength of the fibre may hold some relation to the amount of phosphoric acid in the soil where it is grown.

Weight of seeds and lint. (Maximum weight for five seeds with lint attached, 22.14 grains.) Light-weight seeds appear to come from sandy soils, heavy-weight seeds from heavy and productive soils.

[2] The reader is referred to a memoir by Le Monnier, in Ann. des Sc. nat., sér. 5, tome xvi., 1872, p. 233, and one by Van Tieghem in same Journal, 1872.

508. The so-called "grains" of the cereals are fruits instead of seeds; the accompanying figures exhibit, therefore, not only the structure of the integuments of the seeds, but also of the ripened ovarian wall.



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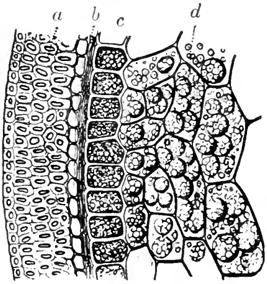

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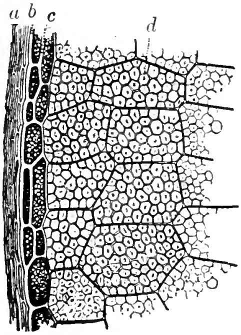
509. As shown in the "Structural Botany," page 309, the nucleus of the seed consists of the embryo and its supply of food. If the store of food is wholly within the tissues of the embryo, the seed is said to be exalbuminous; if partly outside of the embryo, as, for instance, in the cereals here figured, it is said to be albuminous. The albumen is the supply of food in the nucleus of the seed which is not stored in the embryo itself.



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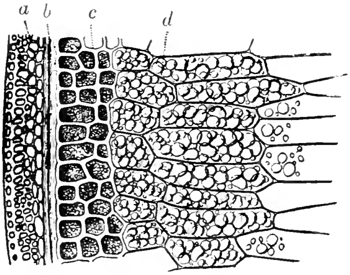

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FIG. 138. Cross-section from the periphery of the fruit of Zea Mais, highly magnified: *a*, fruit-capsule; *b*, seed-coat; *c*, adherent cellular layer; *d*, starch containing albumen of seed. (Berg and Schmidt.)

FIG. 139. A cross-section from the periphery of the fruit of Avena sativa, highly magnified: *a*, chaff; *b*, fruit-capsule with the seed-coat; *c*, adherent cellular layer; *d*, starch containing albuminoid parenchyma. (Berg and Schmidt.)

FIG. 140. Cross-section from the periphery of the fruit of Oryza sativa, highly magnified: *a*, chaff; *b*, fruit-capsule with seed-coat; *c*, adherent cellular layer; *d*, starch containing albuminoid parenchyma. (Berg and Schmidt.)

FIG. 141. Cross-section from the periphery of the fruit of Hordeum vulgare, highly magnified: *a*, chaff; *b*, fruit-capsule with the seed-coat; *c*, adherent cellular layer; *d*, starch containing albuminoid parenchyma. (Berg and Schmidt.)

510. The embryo may exist as a cluster of parenchyma cells without any clear distinction of parts, or it may possess a definitely formed axis and leaves (see "Structural Botany," p. 311). The microscopic structure of the nucleus has been illustrated in part by the figures of the grains of cereals (see also Fig. 22, on page 47), and it has been considered also to some extent in the descriptions of the nascent root and the nascent stem in the embryo. The study of the development of the embryo within the seed belongs to a special subject, which will be treated in Part II. under "Reproduction." It therefore will suffice here to state that the parenchyma cells of which the nucleus is composed contain food materials and protein matters in large amount.

511. The proper food materials in seeds are chiefly oils and starches. The seeds of a large number of plants have been examined by Nägeli[1] with reference to the occurrence of starch, and the following facts are taken from his extensive treatise: —

Phænogams containing		Gymnosperms, Families	Monocotyledons, Families.	Dicotyledons, Families.	Total, Families.
No starch in the seed	In all species .	3	20	190	213
	In a majority .	. . .	. . .	10	10
	In half	. . .	. . .	10	10
	In a small number	. . .	1	2	3
Starch in the albumen, not in the embryo	In all species .	1	17	16	34
	In a majority .	. . .	1	1	2
	In half	. . .	. . .	3	3
Starch in the embryo, not in the albumen	In all species .	. . .	. . .	2	2
Starch in the albuminous embryo	In all species .	. . .	4	11	15
	In a majority .	. . .	. . .	1	1
	In half	. . .	. . .	5	5
	In a small number	. . .	. . .	13	13
Starch in the embryo and albumen	In all species .	1	. . .	1	2
	In a majority .	. . .	. . .	1	1
Starch in the seed throughout	In all species .	2	21	30	53
	In a majority .	. . .	1	3	4
	In half	. . .	. . .	8	8
	In a small number	. . .	. . .	13	13

512. The protein granules in seeds are classified by Vines[2] as follows: —

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[1] Die Stärkekörner, 1858, p. 387.

[2] Proceedings of the Royal Society, vols. xxviii., xxx., and xxxi. On page 62 of the volume last mentioned the following table of seeds and their aleurone grains is given: —

I. Soluble in water: Pæonia officinalis (type), Ranunculus acris, Aconitum Napellus, Nigella damascena, Helleborus fœtidus, Amygdalus communis, Prunus cerasus, Pyrus malus, Leontodon Taraxacum, Dipsacus Fullonum, Ipomœa purpurea, Phlox Drummondi, Vitis vinifera.

II. Completely, and more or less readily, soluble in ten per cent NaCl solution.

I. Soluble in water; *e. g.*, Pæonia officinalis.

II. Completely, and more or less readily, soluble in ten per cent NaCl (sodic chloride) solution.

a. Grains without crystalloids.

(*α.*) Soluble in saturated NaCl solution after treatment with alcohol or ether; *e. g.*, Pisum sativum.

(*β.*) Soluble in saturated NaCl solution after treatment with alcohol, but not after ether; *e. g.*, Helianthus annuus.

b. Grains with crystalloids.

(*α.*) Crystalloids soluble in saturated NaCl solution after treatment with alcohol or ether; *e. g.*, Bertholletia excelsa.

(*β.*) Crystalloids soluble in saturated NaCl solution after alcohol but not after ether; *e. g.*, Ricinus communis.

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a. Grains without crystalloids.

(*α.*) Soluble in saturated NaCl solution after treatment with alcohol or ether: Lupinus hirsutus (type), Vicia Faba, Pisum sativum, Phaseolus multiflorus, Allium Cepa, Iris pumila (var. atrocœrulea), Colchicum autumnale, Berberis vulgaris, Althæa rosea, Tropæolum majus, Mercurialis annua, Empetrum nigrum, Primula officinalis.

(*β.*) Soluble in saturated NaCl solution after alcohol, but not after ether: Helianthus annuus (type), Platycodon (Wahlenbergia) grandiflora, Sabal Adansoni, Delphinium cardiopetalum, Trollius Europæus, Actea spicata, Caltha palustris, Aquilegia vulgaris, Dianthus Caryophyllus, Brassica rapa, Lepidium sativum, Medicago sativa, Larix europæa, Cynoglossum officinale, Spinacia oleracea.

b. Grains with crystalloids.

(*α.*) Crystalloids soluble in saturated NaCl solution after treatment with alcohol or ether: Bertholletia excelsa (type), Adonis autumnalis, Æthusa Cynapium, Digitalis purpurea, Cucurbita Pepo.

(*β.*) Crystalloids soluble in saturated NaCl solution after alcohol, but not after ether: Ricinus communis (type), Datura Stramonium, Atropa Belladonna, Elaïs Guineensis, Salvia officinalis, Taxus baccata, Pinus Pinea, Cannabis sativa, Linum usitatissimum, Viola elatior, Ruta graveolens, Juglans regia.

III. Partially soluble in ten per cent NaCl solution.

a. Entirely soluble in one per cent sodic carbonate solution: Pulmonaria mollis, Omphalodes longiflora, Borago caucasica, Myosotis palustris, Clarkia pulchella.

b. Entirely soluble in dilute potassic hydrate.

(*α.*) Grains without crystalloids: Anchusa officinalis, Lithospermum officinale, Echium vulgare, Heliotropium Peruvianum, Lythrum Salicaria.

(*β.*) Grains without crystalloids: Cupressus Lawsoniana, Juniperus communis, Euphorbia Lathyris.

III. Partially soluble in ten per cent sodic chloride solution.
  a. Entirely soluble in one per cent sodic carbonate solution; *e. g.*, Clarkia pulchella.
  b. Entirely soluble in dilute potassic hydrate.
    (*α.*) Grains without crystalloids; *e. g.*, Lythrum Salicaria.
    (*β.*) Grains with crystalloids; *e. g.*, Juniperus communis.

513. The appendages of the seed known as the strophiole (at the base of the seed), the caruncle (at the micropyle or orifice), and the membranaceous and pulpy forms of arillus (see Volume I. pages 308, 309) do not call for further remark.

The separation of the fruit at maturity, and the separation of the ripened seed as well, are due to changes analogous to those described in 458, under the "Fall of the Leaf." Some of the special forms of mechanisms by which the detachment occurs may be examined in Part II., under "Dissemination."

CHAPTER V.

PHYSIOLOGICAL CLASSIFICATION OF TISSUES.

DIVISION OF LABOR IN THE PLANT.

514. The simplest plant, a green cell living in water, possesses all the appliances needful for the work of vegetation; namely, a protoplasmic body containing chlorophyll, and a cell-wall protecting it. It finds in the water in which it floats, and in the sunlight to which it is exposed, everything requisite for its full activity.

515. Its work is twofold: First, that which it does not share with the animal, and which may therefore be called the proper office of the plant, — the production of organic matter out of inorganic materials, under the agency of light. This work is dependent upon the presence of chlorophyll in the cell, and is known as Assimilation. Second, that which the animal likewise can perform, — the conversion into various forms of activity of the energy stored up in food. This takes place in the protoplasm, whether chlorophyll be present or absent.

516. In a spherical cell isolated from others and leading an independent existence, floating free in the water, and therefore presenting no one part exclusively to the light, there is very slight if indeed any division of labor. One part of its cellulose, protoplasm, or chlorophyll has the same work to perform and is substantially under the same conditions as any other part. But if the cell becomes one of many aggregated to form a mass of tissue, its relations to its surroundings are not the same as before, for its exterior is no longer equally exposed either to water or to light. The cells in the interior of such a mass must derive their supply of material from without through the agency of the neighboring cells; hence division of labor begins. Inspection of the mass shows that some of its cells have the office of absorption, others that of assimilation, others that of treasuring up the products of manufacture, etc. With this incipient division of labor there are also notable changes in the form of cells, by which a more complete adaptation to a particular kind of

work is secured. These adaptations are as marked in the internal anatomy as in the external configuration.

517. The parts of a living being which have definite kinds of work to do are known as organs[1] (cf. ἔργον, work). Since they

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[1] The organs of the higher plants are reducible to three members; that is, three types of structure, which bear to each other definite relations of position and sequence of appearance. These members are the root, stem, and leaf, — to which some add also the plant-hair. In Sachs's Vorlesungen, the number of members is given as two; namely, root and shoot.

In their very youngest state all the modified leaves upon a given plant are indistinguishable from each other; the leaves which are to become petals, stamens, leaf-traps, or tendrils, are like those which are to be ordinary foliage. The same is true of modified stems and modified roots; however diverse in shape and function the modified stems or branches of a plant may finally be, they are at their very beginning precisely alike.

In the determination of the rank of an organ, that is, its reference to one of the three plant-members already enumerated, the following criteria are employed: (1) its position with respect to other parts; (2) its nascent condition; (3) its presence or absence in organisms obviously allied to the one in which it occurs, its rank in these not being obscure.

So far as the organs seen by the naked eye are concerned, it is seldom that any serious difficulty exists in the application of at least one of these criteria to the determination of their rank, and it is generally possible to use more than one. But it is different in the case of the histological organs, for (1) the position can be made out only in sections of the given part; (2) their early nascent condition is the simple cell, common to all tissues; (3) it is not easy to determine whether an organ exists in a rudimentary form in allied organisms or is wholly absent from them.

It is so difficult to apply these criteria to the study of tissues, and the results obtained are so contradictory, that there is no complete agreement among botanists as to what constitutes a histological member except the simple cell itself. In fact, as stated in 191, it is doubtful whether with the material now at hand it would be possible to construct a satisfactory system of tissue elements or histological organs upon a purely morphological basis. Even in the systems which most nearly approach this there are some physiological notions which have affected a few of the minor divisions.

A classification of tissues upon the basis of physiology alone is open to serious objections; one kind of work in the plant can be performed by diverse tissues, and on the other hand one kind of tissue can perform more than one kind of work. This is illustrated by the structural elements through which mechanical ends are reached; the long bast-fibres, woody fibres, collenchyma, and short sclerotic parenchyma, — very diverse elements, but accomplishing the same result. Yet one of these, namely, the woody fibres, is among the most important of the elements by which crude liquids are carried through the plant.

Moreover, in the examination of the minute structure of a part it is not easy to discriminate between the different offices which one of its given elements may fill, because the element is associated with so many others in the formation of a complex organ.

are parts of a whole, — the organism, — they must have definite relations to each other as regards position and office.

518. The relations of origin and position, so far as the organs of the plant are concerned, are discussed in the first volume; the relations of origin and position of the component parts of their structure have occupied the earlier portion of the present volume. From a review of the facts there presented, it appears that any given part may subserve different ends; for instance, a leaf may carry on its proper work, namely, that of assimilation, and at the same time may aid as a tendril, and, in the case of Nepenthes, as a stomach for digestion. On the other hand, it is equally clear that the same kind of work may frequently be performed by different parts. For instance, the proper work of the leaf can be carried on by any green tissue; not merely in proper leaves, but in the cortex of young stems, and even in the outer tissues of young roots of certain aerial plants. It is therefore sometimes advantageous in Vegetable Physiology to distinguish between systems of tissues having different offices, rather than between organs which are often masses of heterogeneous tissues.

519. Among the systems of classifications of tissues chiefly upon a physiological basis is that of Haberlandt, which is as follows: —

A. The Protective System.
  1. Of the surface (Epidermis, cork, and bark).
  2. Of the skeleton (Bast-fibres, libriform cells, collenchyma, and sclerotic parenchyma).

B. The Nutritive System.
  1. Absorbing system (Epithelium of roots and the root-hairs; absorbing tissue of haustoria, etc.).
  2. Assimilating system (Chlorophyll parenchyma, both palisade and spongy).
  3. Conducting system (Conducting parenchyma, vascular bundles, latex cells and tubes).
  4. Storing system (Reserve-tissues of seeds, bulbs, and tubers; water-tissue, etc.).
  5. Aerating system (Aeriferous intercellular spaces, together with their external openings, stomata and lenticels).
  6. Receptacles for secretions and excretions (Glands, oil, resin, and mucus canals, crystal-sacs, etc.).

To these might be added the groups of tissues concerned in reproduction.

MECHANICS OF TISSUES.

520. In Haberlandt's classification[1] the tissues having a mechanical office to fill are brought into one group, which is then subdivided into (1) those tissues which protect the softer tissues of the interior from the harm which would result from exposure, and (2) those which hold the soft tissues in place. An examination of the work performed by tissues may accompany an investigation of the work by organs themselves; in the examination of the work of organs in Part II. the necessary facts relative to their structure will be presented.

521. Those tissues which serve simply to impart strength to the plant belong almost as much to lifeless as to living parts, and can best be examined before the subjects of physiology are taken up. The present division has for its object the consideration of that which in Haberlandt's classification is called the skeleton, and which is known to serve chiefly mechanical ends.

522. In the case of a water-plant, for instance an alga, which has about the same specific gravity as the water in which it is borne, no special mechanical support is demanded. Its own buoyancy suffices to keep the structure as a whole in place; while the different parts of the simple organism have a degree of stability which enables them to resist the action of the waves. As might be expected, such an organism can attain a very great size: for instance, Macrocystis pyrifera of the Southern Pacific Ocean has been known to measure nearly one thousand feet, and less trustworthy measurements have been recorded which far exceed this. In this and other water-plants the medium which buoys the plant up takes the place practically of any internal framework.

523. A land-plant, existing in a far lighter medium than the water-plant, must have a definite mechanical support. Those species of Calamus which furnish the "rattan" of commerce possess a terminal shoot from which are unfolded in rapid succession strong leaves armed with recurved hooks. Having reached the thickly clustering tops of a tropical forest, the terminal bud develops its leaves, and these cling with tenacity to the branches upon which they rest, so that the mechanical support is afforded in this case by the vegetation beneath. Thus supported, the extension of the shoot is indefinite, so that examples of Calamus

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[1] Physiologische Pflanzenanatomie (Leipzig, 1884).

with a length of 300 feet are not uncommon, and some figures much higher than this are noted.

524. In both the above cases the extraordinary size has been attained with very little expenditure of material for mere mechanical support. The same is true, although in a less striking because a more familiar manner, in our ordinary twining and climbing plants; other plants or outside supports of some kind being necessary to bring their stems and leaves into the best relations to their surroundings. But what tissues serve to keep erect or in position the larger plants which are not water-plants or climbers? What tissues serve mainly mechanical ends?

525. The subject was extensively investigated, so far as monocotyledonous plants are concerned, by Schwendener,[1] in 1874, since which time some important additions have been made. According to Schwendener, the mechanical elements in the plant are (1) bast-fibres, (2) libriform cells and fibres, (3) collenchyma cells. That these are the chief elements of strength, especially in monocotyledonous plants, appears from his instructive experiments, which have been repeated by others. Strips, 150 to 400 mm. in length and about 2 to 5 mm. wide, were carefully taken from stems or leaves and immediately fastened in a vise at one end, the other end being firmly grasped by strong pincers to which weights could be attached at will. Behind a strip, vertically suspended from the vise, a measuring-bar was placed, so that any elongation of the strip under tension could be accurately measured. After the apparatus was properly adjusted, a small weight was attached to the pincers, the elongation of the strip observed, and the weight then removed in order to see whether the strip recovered its original length. Up to a certain point the recovery was found to be complete: beyond this point the elasticity was lost, and not again regained.

526. Strips from the middle part of the leaf of Phormium tenax, 390 mm. long and 1.5 to 2 mm. wide, were placed in the apparatus and subjected to the action of a weight of 10 kilograms. They became 5 mm. longer, but on removal of the weight were found to recover their original length; in other words, they remained perfectly elastic under this weight. A weight of 15 kilograms broke the strips into two parts. These strips contained only five fibro-vascular bundles, with an amount of bast which was believed to be about half a square millimeter in cross-

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[1] Das mechanische Princip im anatomischen Bau der Monocotylen (Leipzig, 1874).

section. From this experiment Schwendener places the strength of the bast of Phormium tenax at 20 kilograms per square millimeter.[1]

527. The tables in the notes show that good bast equals good iron in its tensile strength within the limits of elasticity, while in its breaking-weight it is greatly exceeded by the latter. Schwendener well remarks that Nature has given her whole care to providing that these mechanical elements should be strong within the limits of elasticity, and with good reason; for beyond those limits the plant gains nothing by greater strength. Attention is called also to the great difference between bast and the metals with regard to their elongation under weight.

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[1] The results of experiments made with the bast of various plants in the manner described are given below. Most of the cases cited are from Schwendener; others are from Haberlandt (Physiologische Pflanzenanatomie, p. 105). The determinations for metals are from Weisbach.

Name.	Elongation in 1000 parts.	Tensile strength in kilograms per sq. mm. (within limits of elasticity).	Breaking-weight in kilograms per sq. mm.
Phormium tenax	13.	20.	25.
" "	14.	16.	
Fritillaria imperialis	12.	. . .	
Lilium auratum	7.6	19.	
Jubæa spectabilis	12.6	20.	
Dasylirion longifolium	13.3	17.8	21.6
Dracæna indivisa	17.	17.	21.8
Hyacinthus orientalis	. . . .	12.3	16.3
Allium Porrum	. . . .	14.7	17.6
Polytrichum juniperinum (stem)	. . . .	. . . .	7.5
" " (seta)	. . . .	. . . .	11.5
Papyrus antiquorum	15.2	20.	
Molinia cœrulea	11.	22.	
Pincenectia recurvata	14.5	25.	
Dianthus capitatus	7.5	14.3	
Secale cereale	4.4	15 to 20	

These should be compared with the results of determinations made with other materials: —

Name.	Elongation in 1000 parts.	Tensile strength per sq. mm.	Breaking-weight in kilograms
Malleable iron in rods	.67	13.13	40.9
" " in wire	1.00	21.9	
" " in plate	.80	14.6	
Hammered German steel	1.20	24.6	82.
Brass	.75	4.85	
Brass wire	1 35	13.3	
Cast zinc	.24	2.3	
Copper wire	1.00	12.1	
Silver	. . .	11.	29.

528. The strength of other tissues besides bast has been measured; thus Ambronn assigns to collenchyma a breaking-weight of 12 kilograms per square millimeter, and these cells become permanently elongated under a weight of from 1.5 to 2 kilograms.

Haberlandt found that the breaking-weight of the internal "thread" of the common graybeard lichen, Usnea barbata, is 1.7 kilograms per square millimeter, but that this thread could be stretched to double its length before breaking. The breaking-weight of cotton fibre is calculated to be between 18 and 20 kilograms per square millimeter, and that of the seed-hair of Asclepias Syriaca not far from 40 kilograms.

529. Examination of any of the figures of fibro-vascular bundles given in Part I. shows how well their elements are distributed in order to secure the greatest strength with economy of material. To the elements which impart strength to a bundle Schwendener has given the name *stereom;* to the other parts of the bundle, *mestom;* thus the fibres are stereom elements, the ducts are mestom elements.

530. The striking adaptations[1] of the fibro-vascular bundles to serve as light and very strong building materials in the plant

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[1] The following table from Schwendener, with a few illustrative examples, is given to serve as a guide to the student in tracing out a few of these adaptations: —

DISTRIBUTION OF MECHANICAL ELEMENTS IN MONOCOTYLEDONS.

I. In cylindrical organs.
  1. System of subepidermal nerves of bast. Simple fascicles of bast lie under the epidermis.
    First type. Arum, Arisæma.
    Second type. Petioles of Colocasia and Alocasia.
  2. System of compound peripheral girders. Subepidermal fascicles of bast unite with those which lie more deeply to form girders in which the "web" or binding-tissue is partly mestom, partly parenchyma.
    Third type. Stems of Scirpus cæspitosus and Eriophorum alpinum.
    Fourth type. Stems (above ground) of Cyperus alternifolius.
    Fifth type. Stems of Schœnus nigricans.
    Sixth type. Stems of Juncus effusus.
    Seventh type. Carex lupulina.
    Eighth type. Scirpus lacustris.
    Ninth type. Isolepis pauciflora.
    Tenth type. Cladium Mariscus.
  3. System characterized by a nerved hollow cylinder, the nerves of which are united with those at the epidermis.
    Eleventh type. Many grasses; *e. g.*, Alopecurus pratensis.
    Twelfth type. Panicum Crus-galli.
  4. System of peripheral bast-fascicles strengthened by mestom.
    Thirteenth type. Zea Mais.

are seen plainly when the distribution of the bundles in the stems of monocotyledons is examined in cross-section. In many cases the shape of the section of the bundle is nearly that of the well-known "I" or "H" beam or girder. In the most clearly marked instances the stereom portion is well developed on both sides of the mestom, and thus forms the "flanges" or "plates," while the mestom is the "web;" the stereom has therefore to bear either compression or tension, according to the bending of the part. It will further be observed that in all cases the beam is placed with respect to the rest of the stem, so as to insure the greatest efficiency of the stereom portion.

But it is only upon a careful examination of the many methods of arrangement of the stereom and mestom in the bundles of diverse forms of dicotyledonous stems, together with an examination of the arrangement of the bundles themselves with respect to the surrounding tissues, that the adaptations of the various elements to strength can be fully appreciated.

The modes of distribution of the stereom and mestom met with in monocotyledons are so numerous that they cannot be reduced to a few types; their diversity is so great that they can only with difficulty be brought into any system of classification.

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5. System of subcortical fibro-vascular bundles with strongly marked bast development.
    Fourteenth type. Bambusa species.
    Fifteenth type. Palms.
    Sixteenth type. Yucca.
    Seventeenth type. Musa.
    Eighteenth type. Maranta.
6. System of subcortical fibro-vascular bundles united tangentially.
    Nineteenth type. Juncus Gerardi.
7. System characterized by a simple hollow cylinder with imbedded or attached fascicles of Mestom.
    Twentieth type. Commelynaceæ.

II. In bilateral organs.
1. System of subepidermal girders.
    First type. Leaves of Cyperus.
    Second type. Middle part of leaves of Zea.
    Third type. Leaves of Musa.
    Fourth type. Leaves of Tradescantia.
    Fifth type. Leaves of Pardanthus.
2. System of internal girders.
    Sixth type. Leaves of Cypripedium.
    Seventh type. Petiole of Aspidistra.
3. System of complex girders: subepidermal nerves of bast combined with interior girders.
    Eighth type. Petioles of many palms.

531. The distribution of material in the skeleton of a ligneous dicotyledonous plant is somewhat different from that in a monocotyledon.[1] More of the mechanical work falls on the proper wood, but even here in some cases the bast serves an important purpose.

532. The data for calculating the strength of the woody stem and branches of a dicotyledonous plant are to be found in various works on mechanical engineering; but it is to be borne in mind that the figures given for timber are usually based on experiments with dry heart-wood.

533. The trunk is to be regarded as a column bearing the weight of the whole crown of branches, each of these being a tapering beam supported at one extremity. The crushing-weight the crown exerts upon this column is far within the limits of safety, even when the liability of the trunk to be much bent and twisted by high winds is taken into account. The branches at their point of union with the trunk form different angles in different plants,[2] and this angle must be taken into consideration

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[1] DISTRIBUTION OF MECHANICAL ELEMENTS IN DICOTYLEDONS.

1. With bast in the bark.
   First group. Axial organs when young have an unbroken ring of bast; in much older stems this is interrupted or cast off. Aristolochia.
   Second group. Axial organs with a layer of bast-bundles which is thrown off later. The bast-bundles form the first mechanical system, which is soon replaced by the ring of wood. Nerium Oleander.
   Third group. With simple ring of bast-bundles in first year, later with isolated bast-fibres. Æsculus Hippocastanum.
   Fourth group. With strong bast, even when far advanced. Tilia.
   Fifth group. With subepidermal bast-nerves. Russelia.
2. With transition to an intra-cambium ring of libriform cells.
   Sixth group. The cambium of the bundles lies partly outside, partly inside the mechanical ring, or is imbedded therein. Gaillardia.
   Seventh group. Isolated vascular bundles. Silphium perfoliatum.
3. Intra-cambium libriform ring without medullary rays.
   Eighth group. Without bast on the outer side of the cambium or cambiform layer. Impatiens Nolitangere.
   Ninth group. With larger or smaller amounts of bast on the outer side of the cambriform. Urtica dioica.
   Tenth group. In the libriform elements all shades of transitions to ducts. Mirabilis Jalapa.
4. Intra-cambium libriform ring with parenchyma rays.
   Eleventh group. Rays formed of elongated cells. Vinca major.
   Twelfth group. Typical dicotyledons with medullary rays.

[2] McCosh has given the angles in a large number of plants, a few of which are here cited: Ash, 60°; horse-chestnut, 50° – 55°; alder, 50°; elm, 50°; oak, large branches, 50°, small branches, 65° – 70°; beech, 45°; linden, 40°. He calls attention to the fact that in these and many other cases the angle at which the

in determining the actual force exerted upon the fibres at the base of the branch.[1]

534. The part which sclerotic parenchyma and thickened epidermal and hypodermal cells play in affording strength to plants need only be alluded to (see 211). In a few cases, especially in some succulents, a considerable share of the mechanical support of the plant is afforded by the more superficial parts.[2]

535. The veining of leaves and the structure of leaf-margins present some interesting problems. Comparative investigations[3] have shown that strength at the edge of the leaf is obtained in very different ways, even in closely allied plants. The resistance to tearing which is exhibited by some of the larger leaves of dicotyledons is remarkable.

The distribution of the strong ribs in the leaves of the greater water lilies (for instance, Victoria regia), and to a less striking extent that in the smaller water lilies of cold climates, secures great strength with the utmost economy of material.

The trunks of many tropical trees are provided with lateral projections (buttresses) which strengthen the stem very materially.[4]

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veinlets come off from the midrib is the same as that formed by the branch and the trunk. The angles in the above cases are those formed above the points where the branches arise (British Assoc. Report, 1852, part ii. p. 68).

[1] Very instructive illustrations of the different capacity of different trees to resist the action of high winds are given in the Reports of the Signal Service.

[2] Full and interesting accounts of the adaptations of the framework to the external conditions of plants are to be found in the works of Schwendener and Haberlandt.

[3] Westermaier: Monatsber. der k. Akad. d. Wissenschaften Berlin, 1881.

[4] "All are tall and upright columns, but they differ from each other more than do the columns of Gothic, Greek, and Egyptian temples. Some are almost cylindrical, rising up out of the ground as if their bases were concealed by accumulations of the soil; others get much thicker near the ground like our spreading oaks; others again, and these are very characteristic, send out towards the base flat and wing-like projections. These projections are thin slabs radiating from the main trunk, from which they stand out like the buttresses of a Gothic cathedral. They rise to various heights on the tree, from five or six to twenty or thirty feet; they often divide as they approach the ground, and sometimes twist and curve along the surface for a considerable distance, forming elevated and greatly compressed roots. These buttresses are sometimes so large that the spaces between them if roofed over would form huts capable of containing several persons. Their use is evidently to give the tree an extended base, and so assist the subterranean roots in maintaining in an erect position so lofty a column, crowned by a broad and massive head of branches and foliage" (Wallace: Tropical Nature, 1878, p. 30).

PART II.

CHAPTER VI.

PROTOPLASM AND ITS RELATIONS TO ITS SURROUNDINGS.

536. UPON the framework which imparts strength to the plant the active, living cells are distributed. In old ligneous dicotyledonous plants the living parts are relatively so superficial that they have been said to form a mere film of living tissue held in place by a dead skeleton.[1]

537. The living cells are those which contain protoplasm. Each of these cells has definite relations to the neighboring cells, most of which relations have been presented in Part I. But each of these cells has also definite relations to the external world, which it is the province of Physiology to investigate. Such an investigation naturally begins with a consideration of the character of protoplasm.

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[1] "The living parts of a tree or shrub, of the exogenous kind, are obviously only these: 1st, The summit of the stem and branches, with the buds which continue them upwards, and annually develop the foliage. 2d, The fresh roots and rootlets annually developed at the opposite extremity. 3d, The newest strata of wood and bark, and especially the interposed cambium-layer, which, annually renewed, maintain a living communication between the rootlets on the one hand and the buds and foliage on the other, however distant they at length may be. These are all that are concerned in the life and growth of the tree; and these are annually renewed. . . . The plant is a composite being, or community, lasting, in the case of a tree, through an indefinite and often immense number of generations. These are successively produced, enjoy a term of existence, and perish in their turn. Life passes onward continually from the older to the newer parts, and death follows, with equal step, at a narrow interval. No portion of the tree is now living that was alive a few years ago; the leaves die annually and are cast off, while the internodes or joints of the stem that bore them, as to their wood at least, buried deep in the trunk under the wood of succeeding generations, are converted into lifeless heart-wood, or perchance decayed, and the bark that belonged to them is thrown off from the surface. It is the aggregate, the blended mass alone, that long survives" (Gray's Structural Botany, pp. 83, 84.)

538. **Protoplasm,** the living matter of the plant, can be examined to advantage, either as it exists without a cell-wall in some of the lower organisms (Myxomycetes), or confined within a transparent cell-wall, as in young plant-hairs.

539. The Myxomycetes live in the interstices of moist porous substances; for instance, decaying leaves and stems, spent tan, etc. Passing over all details regarding their fructification, — a subject to be looked for in the volume on "Cryptogamic Botany," — their present examination can begin with the period when the germinating spores of these plants rupture their walls, and become confluent as masses of naked protoplasm known as plasmodia.

540. The plasmodium of Æthalium septicum is not difficult to procure, as it occurs in summer upon heaps of moist tan in the open air, and even during the winter in moist places in greenhouses where tan is used as a stratum for flower-pots. It is a soft, gelatinous mass of yellowish color, sometimes measuring several inches in diameter. Removal of any portion of this mass to a glass slide is apt to break up the plasmodium so much as to render it useless for observation; therefore the following explicit directions given by Strasburger for obtaining small portions to examine will be found useful. A tumbler is to be filled with water up to the brim, and from the brim a strip of moist filtering-paper, somewhat less than an inch in width and one or two inches in length, is to be stretched to the top of a glass slide placed in a vertical position (or, better, leaning a little outwards); the lower end of the slide being placed in sand to catch the water which will soon begin to flow slowly over its surface. Next, a piece of bark with the plasmodium upon it is to be placed at the foot of the slide, the whole covered with a bell-jar and a dark cover of pasteboard, and from time to time the water in the tumbler replenished. In the course of ten or twelve hours some of the protoplasmic mass will climb up the slide in the form of delicate threads, which branch more or less and constitute a sort of network. The slide is then transferred to the stage of the microscope, care being taken (1) to use only a little light, and (2) to avoid any pressure by the cover-glass. The latter may be prevented by fragments of glass placed under the corners of the cover-glass; or, better still, the cover-glass may be fastened on the slide by means of four minute drops of cement, leaving its side exposed, and then the slide, thus furnished with a cover, placed in the nearly vertical position already advised, when the plasmodium will creep under the cover,

and be all ready for examination, with no disturbance whatever. If the plasmodium is allowed to creep over the face of a slide placed horizontally, it is apt to be too thick for a demonstration of some of the points which are now to be referred to.

541. **Chemical and physical properties of protoplasm.** When the plasmodia of Æthalium septicum collect in large masses on the surface of spent tan, they afford good material for the examination of some of the chemical and physical characters of protoplasm; but there is, of course, the serious objection that it is impossible to obtain the protoplasm in a state of absolute purity. Upon such material, however, Reinke and Rodewald[1] have conducted some instructive experiments, the principal results of which are detailed in the following paragraphs.

542. The organic substance of the protoplasm of Æthalium proved to have the following elementary composition:[2] —

		Per cent, air-dried substance.	Per cent, dry substance.
First analysis.	*C.*	38.56	40.52
	H.	5.82	6.10
	N.	5.63	5.91
Second analysis.	*C.*	38.61	40.47
	H.	5.99	6.29
	N.	5.39	5.65
In both analyses oxygen is a fourth constituent.			

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[1] Studien über das Protoplasma, Berlin, 1881.

[2] The composition of the air-dried substance is approximately as follows: —

Water	4.80
Pepsin and Myosin	1.00
Vitellin	5.00
Plastin	27.40
Guanin Xanthin Sarkin	.01
Ammonic carbonate	.10
Asparagin and other amides	1.00
Pepton and Peptonoid	4.00
Lecithin	.20
Glycogen	4.73
Æthalium sugar	3.00
Calcic compounds of higher fatty acids	5.33
Calcic formate Calcic acetate	.42
Calcic carbonate	27.70
Sodic chloride	.10
Hydropotassic phosphate (PO_4K_2H)	1.21
Iron phosphate (PO_4Fe ?)	.07

543. One hundred and seventy-nine grams of fresh protoplasm of a soft consistence were placed in closely woven linen cloth and subjected to pressure by the hand; 58 grams of a turbid fluid were expressed; the mass was then placed under a pressure of 4,000 kilograms, by which 62 grams more were forced out, leaving a dry cake behind. Thus 66.7 per cent of the mass was pressed out. The fluid thus expressed has a specific gravity of 1.209. That this fluid is intimately incorporated with the more solid portion of the protoplasm, appears from the fact that it cannot be forced from the protoplasm by centrifugal force alone. To it the name *enchylema* has been given; to the solid matter, the name *stroma* is applicable. The amount of water contained in fresh protoplasm of Æthalium septicum is approximately 71.6 per cent.

The reaction of protoplasm is alkaline.

544. In young cells the protoplasm exhibits essentially the same characteristics as those presented by the naked protoplasm of the Myxomycetes already alluded to. The phenomena in cells can be most satisfactorily seen in thin-walled plant-hairs. These should be transferred to a glass slide with as little injury as possible, covered immediately with pure water, and examined under a cover-glass which is prevented by bits of wax or thin glass from pressing on the delicate object. The stamen-hairs of Tradescantia Virginica, pilosa, or zebrina are the best, for in these the cells are sufficiently large to be managed without difficulty, and the walls are perfectly transparent. The cells in the thin leaves of many water-plants answer very well, but they generally contain so much chlorophyll that the protoplasm is obscured. The hairs of the flowers and of the young leaves of plants of the Gourd family and those of the nettle[1] are also excellent objects for the study of protoplasm; and in general it may be said that almost any plant-hair, if it is young enough and has a thin wall, will serve very well (see Fig. 175).

545. Protoplasm in cells exists as a nearly colorless mass

Ammonio-magnesic phosphate	1.44
Tricalcic phosphate	.91
Calcic oxalate	.10
Chlolesterin	1.40
Fatty acids extracted by ether	4.00
Resinous matter	1.00
Glycerin, coloring-matter, etc.	.18
Undetermined matters	5.00

[1] Huxley: Protoplasm (Half Hours with Modern Scientists, 1871).

lining the walls and extending irregularly from side to side in slender threads. At some one part the mass appears a little denser than at others, and if the outline of this firmer mass is at all well defined it is easily recognized as the nucleus (see Fig. 2).

546. **Circulation of protoplasm in cells.** Under a power of 300 diameters the delicate threads of protoplasm can be clearly seen to have imbedded in them minute granules which are slowly moving. It happens sometimes that a slight warming is required before any motion is apparent. When the current is fully established, its different changes can be watched for a long time without other disturbance of the specimen than that resulting from the addition of water to replace that lost by evaporation.

Two features of the motion require special notice: (1) the granules do not pass from one cell to the contiguous one, but remain confined in one; (2) the threads in which the granules move gradually change their shape and direction, growing wider in one place and becoming narrower in another, while at the points of contact with the lining of the wall the threads seem to slip or glide very slowly, and accumulations of the protoplasm here and there take place. The movement of the granules from place to place in a steady current is called the circulation of protoplasm; the sluggish changes of the threads as they alternately increase and diminish in size resemble the amœboid movements (see 555 and Fig. 175).

547. In some examinations it is instructive to add a very little glycerin or sugar to the water on the slide, in order to cause a slight contraction of the protoplasm; its whole mass then appears as a shrunken sac, in the interior of which the circulation can be detected.

548. In a good specimen of the stamen-hair of Tradescantia the protoplasmic currents are seen to course in slender threads with a considerable degree of regularity. In some of the threads or bands the currents go in one direction, in others in another; and it occasionally happens, as Hofmeister has pointed out, that two opposite currents may pass in a single narrow channel.

549. There is more or less accumulation of protoplasmic matter in the immediate vicinity of the nucleus, and there are generally some slight projections into the interior of the cell. The rate of circulation appears to be greater at the middle of the threads than at the sides or ends of the cell.

550. If these movements in a cell are compared with the

movements exhibited by naked protoplasm, no substantial difference can be seen beyond that which depends upon the confinement of the mass in one case within practically rigid walls. The naked protoplasm moves slowly from place to place, by thrusting out an irregular projection which soon enlarges, and in its turn gives out new projections, while the mass behind is slowly moving up. This movement is identical with that observed in the amœba. In the substance of a mass of naked protoplasm granules can be seen to move in varying channels; and this corresponds strictly to the movement known as the circulation. Moreover, in the naked protoplasm larger or smaller vacuoles (see 120) are observed to increase and diminish in size, their limiting walls answering essentially to the threads before described.

551. **Rotation of protoplasm in cells.** The film of protoplasm in contact with the cell-wall does not generally share in the movement of the softer part which it encloses, but usually remains entirely stationary, or else very slowly shifts its position on the wall. In some cases, however, the whole mass of protoplasm slowly revolves on its own axis, carrying with it all imbedded matters. This movement should be called *rotation;* but the term is often employed interchangeably with *circulation.*

552. **Rate of protoplasmic movements.** In the cells of the shaft of any Chara which has transparent walls — for instance, Nitella — the rapid movement can be very clearly seen to be confined to the interior of the protoplasm, the outer part in which chlorophyll-granules are imbedded not moving to any great extent, if indeed at all. At its interior the protoplasm moves with what seems under the microscope to be a very rapid rate; it is, however, absolutely very slow; being only about one and a half millimeters per minute, at a temperature of 15° C.

553. The rate differs considerably in different plants; for instance, according to several observers, the distance traversed in one minute at a temperature of 15° C. is as follows: —

Name of plant.	mm.	Observer.
Potamogeton crispus, leaf-cell	.009	Hofmeister.
Ceratophyllum demersum, leaf-cell	.094	Mohl.
Tradescantia Virginica, stamen-hair	.137	
Sagittaria sagittæfolia	.174	Mohl.
Vallisneria spiralis	.225–1.086	Mohl.
Hydrocharis Morsus-ranæ, root-hair	.543	
Nitella flexilis, cells of the shaft	1.500–1.600	Nägeli.

In the naked protoplasm of Myxomycetes the rates of movement of the currents are much greater, as Hofmeister shows by the following examples: —

	mm. per minute.
Didymium Serpula	10.
Physarum species	5.4

554. The above rates are not constant even in the same specimen; after having been uniform for a few minutes, the rate may slowly diminish for a time, the temperature and other conditions remaining apparently unchanged, and then as slowly increase until the maximum is again reached. Again, the rate is subject to sudden changes. In general, however, it is nearly the same for the same part of a given plant.

555. **The amœboid movement** in naked protoplasm is rather more sluggish than the circulation, as the following figures from Hofmeister show: —

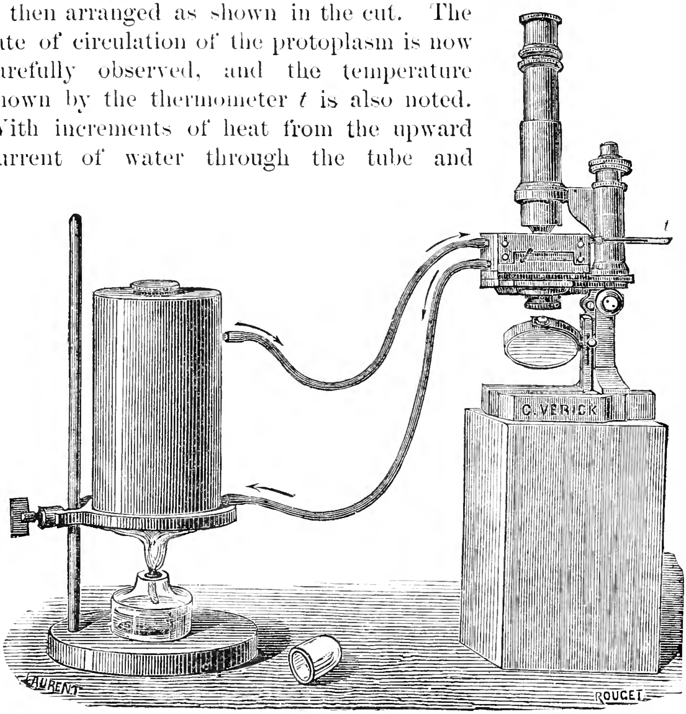
	mm. per minute.
Didymium Serpula	0.4
Physarum sp.	0.29
Stemonitis fusca	0.15

The far more rapid movement of ciliated protoplasmic bodies will be described under "Movements."

556. The effects upon protoplasm of various agents — for instance, heat, light, electricity, etc. — can be studied in the same cells in which the movements are observed; in fact, their effects upon the movements themselves are among the most striking phenomena noticed. It must be remembered, however, that in experimenting upon the protoplasm in cells which are furnished with a cell-wall and provided with cell-sap, other factors are present than those which must be taken into account in dealing with the naked protoplasm of plasmodia. And hence it is proper in most cases, in interpreting the results obtained in experiments upon the protoplasm of cells, to speak of the effects of the agents upon the cells themselves.

557. **Relations of protoplasm to heat.** In experimenting upon the effect of heat on protoplasm, the apparatus generally employed is the so-called warm chamber. In its simplest form this consists of a hollow-walled box, having a slit in which a slide can be placed, and at the centre of the upper and lower walls holes of the same size as the largest diaphragm of the microscope, so as to allow light to pass from the mirror directly through the slide and thence to the objective. Connected with the box are two tubes to which pieces of rubber tubing may

be attached; these pieces run to a small reservoir of water which can be heated at pleasure by means of a spirit-lamp, as shown in the figure. Suppose a slide to have upon it a good specimen of a stamen-hair of Tradescantia, furnished with sufficient water and properly covered. It is placed in the aperture *f* of the hollow box, and the rest of the apparatus is then arranged as shown in the cut. The rate of circulation of the protoplasm is now carefully observed, and the temperature shown by the thermometer *t* is also noted. With increments of heat from the upward current of water through the tube and through the box the rate of the protoplasmic circulation is increased. The amount of heat applied can be easily regulated by the height of the reservoir. If it is desirable to observe the effects of cold, the reservoir can be placed in a vessel of ice and raised above the stage of the microscope, so that a current of cold water can flow down through the box.



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558. Experiments upon the effect of heat can also be conveniently conducted by means of a less expensive apparatus which consists of a double-walled box of zinc placed on firm supports at the height of a few inches above the table, and large

enough to receive the body of the microscope. Through a hole in the top of the box the tube of the microscope projects for a short distance, and the front of the box is furnished with a glass window, which affords enough light for the mirror. The space between the walls of the box having been filled with water, and the object placed on the stage of the microscope, a lamp under the box is lighted, and the effects of the increase of temperature noted. It is best in this case to have the thermometer in the closest proximity to the slide. It is essential in the use of both these instruments to note the temperature at short intervals, and it is only by the greatest care in the use of the thermometer that any trustworthy results can be obtained (see Fig. 170).

559. As might be expected from the nature of heat as a mode of molecular motion, the rate of protoplasmic movement is accelerated by increase of temperature up to a given point (the optimum); with increase beyond this point the movement may continue, but with diminished rapidity, until an upper limit of temperature (the maximum) is reached, above which no movement is observable. At or very near this limit structural changes take place, and death of the protoplasm speedily ensues.

560. The optimum temperature for protoplasmic movement is different for different plants, but is not far from 37°.5 C.

Name of plant.	Optimum temperature.	Observer.
Nitella syncarpa	37°	Nägeli.[1]
Chara fœtida	38°.1	Velten.[2]
Vallisneria spiralis	38°.75	" [2]
" "	40°	Sachs.[3]
Anacharis Canadensis	36°.25	Velten.[2]

561. The maximum temperature beyond which no movement is seen, is also different for different plants, but may be given as not higher than 50° C.

Name of plant.	Maximum.	Observer
Chara fœtida	42°.81	Velten.[2]
Vallisneria spiralis	45°	" [2]
" "	50°	Sachs.[3]

Sachs[4] states that when the hairs of Cucurbita Pepo are immersed in water of 46° or 47° C. the protoplasmic movements are arrested within two minutes; but that the hairs can bear

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[1] Beiträge z. wiss. Botanik, 1860, ii. p. 77.

[2] Flora, 1876, p. 177 *et seq.*

[3] Flora, 1864, p. 5 *et seq.*

[4] Lehrbuch der Botanik, 1874, p. 700.

exposure for ten minutes to a temperature of 49° – 50° in the air before arrest of movement takes place. In Tradescantia hairs the current stops within three minutes upon exposure in air of a temperature of 49°, beginning again when the temperature falls.

562. The lower limit (minimum) of temperature at which motion takes place may be stated at 0° C., although —2° has been observed[1] in a single plant, — Nitella syncarpa.

Until a temperature of at least 15° C. is attained, the movement is sluggish.

563. Sudden changes of temperature have been said by some writers to cause a temporary arrest of the protoplasmic movement. Thus de Vries[2] observed that in the root-hairs of Hydrocharis Morsus-ranæ the protoplasmic current at 21°.7 C. was so rapid that it passed through one millimeter in 205 seconds; but upon sudden elevation of temperature to 33° C., 240 seconds were required for it to traverse the same distance. And Hofmeister[3] found that the rapid movement in Nitella flexilis was arrested in two minutes when the specimen was taken from a room at 18°.5 to one at 5°. But, on the other hand, Velten[4] failed to detect such an effect.

564. At or near the maximum temperature remarkable changes take place in the form of the protoplasmic threads and films. They become more or less rounded, although very irregularly, and may be completely disintegrated. Such changes have been noted by Max Schultze[5] at a temperature of about 40° C. in the hairs of Urtica, the stamen-hairs of Tradescantia, and the leaf-cells of Vallisneria. According to Kühne,[6] such changes take place within two minutes in the plasmodium of Æthalium septicum (see 540) at a temperature of 39° C.; the plasmodium of Didymium serpula was affected in the same way at a considerably lower point, namely, 30° C.

565. When subjected to a temperature lower than the minimum for movement, the protoplasmic mass may become disintegrated, the solid part separating from a watery portion, which latter may freeze.[7] If, now, very gradual increments of heat

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[1] Botan. Zeitung, 1871, p. 723 (Cohn).

[2] Archiv. Néerlandaises, v., 1870, p. 385.

[3] Die Lehre von der Pflanzenzelle, 1867, p. 53.

[4] Flora, 1876, p. 213.

[5] Das Protoplasma d. Rhizopoden und Pflanzenzellen, 1863, p. 48.

[6] Untersuchungen über das Protoplasma, 1864, p. 87.

[7] Untersuchungen über das Protoplasma, 1864, p. 101.

are applied, the disorganized parts may become reunited, and after a while the movement may begin again. No such recovery, however, is possible when the protoplasmic mass has become disintegrated by a high temperature; the change thus produced is practically coagulation.[1]

566. The temperature of certain hot springs in which living algæ have been found shows that protoplasm can bear without injury a greater degree of heat than is indicated by the figures in 561. Thus algæ have been seen in the following thermal waters: —

	Temperature.	Observer.
Carlsbad	53°.7 C.	Cohn.[2]
Lip Islands	53°.	Hoppe-Seyler.[3]
Dax	57°.	Serres.[4]
California Geysers . .	93°	Brewer.[5]

Hoppe-Seyler found algæ growing on the edge of a fumarole where they were subjected to a temperature (from the escaping vapor) of 60°.[6]

567. That the protoplasm of many kinds of seeds and spores can preserve its vitality during exposure to dry air at a temperature above that of boiling water has been shown by many experimenters;[7] but unless the precaution is taken to remove all water from the seeds by very careful and slow drying, any temperature above 100° C. is injurious. Seeds thus cautiously freed from moisture have been heated to 110°, and even for a short time to 120°, without losing their power of germination (see also "Germination"). Nor does there seem to be any essential difference between the seeds which contain oils and those which contain starch in their capacity to endure high temperatures. Hoffmann[8] and Pasteur[9] have shown that the vitality of perfectly dry seeds and spores may in some cases be retained until a temperature of 130° C. is reached.

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[1] Pfeffer: Pflanzenphysiologie, 1881, ii. p. 386.

[2] Flora, 1862, p. 538.

[3] Pflüger's Archiv., 1875, p. 118.

[4] Botan. Centralblatt, 1880. p. 257.

[5] Am. Journ. Sc. and Arts, 2d series, xli. 391.

[6] Pflüger's Archiv., 1875, p. 118.

A much higher temperature is noted by Humboldt; namely, 85° C. for the hot spring of Trinchera, Caraccas, in which he found the roots of certain plants growing.

[7] Milne Edwards and Colin: Ann. des Sc. nat., sér. 2, tome i., 1834, p. 264; Sachs's Handbuch der Experimental-Physiologie, 1865, p. 65 *et seq.*; Just, in Cohn's Beiträge zur Biologie der Pflanzen, 1877, p. 311.

[8] Pringsheim's Jahrb., 1860, p. 324.

[9] Ann. d. Chimie et de Physique, 1862, p. 90.

568. On the other hand, the protoplasm of dry seeds can be subjected to extremely low temperatures without suffering any injury (see "Germination").

569. **The relations of protoplasm to light** are best examined in the plasmodia of the myxomycetes and the hairs of Tradescantia, for here they are not complicated by the presence of chlorophyll (which, as will be seen later, exerts a marked influence). According to Hofmeister, plasmodia thrust forth longer and more numerous processes in darkness than in light. In Æthalium septicum the processes developed in light are short and compressed, while those grown in darkness are long, slender, and thin.[1] This is especially noticeable when the light falls only on one side of the mass. In some of Baranetzky's experiments,[2] in which the incident rays of light were parallel to the substratum (wet filtering-paper) on which the plasmodium was placed, the change of form resulting from diminished extension on the lighted side and increased extension on the other was very marked after fifteen minutes' exposure to bright sunlight, while in diffused light half an hour was required for a similar change. These results should be compared with those obtained by Schleicher,[3] who observed that young plasmodia move towards light of low intensity, and that older plasmodia may move even towards strong light. The movement into bright light appears to just precede the formation of the spores.

570. The more refrangible rays of light — that is, the violet and indigo — appear to be more efficient in influencing movement than are the less refrangible, — the red and yellow.

571. The "circulation" of protoplasm in plant-hairs goes on not only in darkness, but even when the hairs are developed on plants blanched by absence of light.[4] No marked effect upon the rate of such movement appears to be caused by presence or absence of light, except so far as the concomitant action of heat comes into play. Hofmeister states that he saw the protoplasmic

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[1] Die Lehre von der Pflanzenzelle, 1867, p. 21.

[2] Mémoires de la soc. des sciences nat. de Cherbourg, 1875, p. 340. It is, however, well known that plasmodia often emerge slowly from their substratum; for instance, tan, if the surface is only very faintly lighted.

[3] Jenaische Zeitschrift, 1878, p. 620.

[4] Sachs: Botan. Zeit., 1863, Supplement. Reinke: ibid., 1871, p. 797. Kraus: ibid., 1876, p. 504. Few observations have been recorded upon the effect upon protoplasmic movements of sudden changes of illumination. In the case of an amœba (Pelomyxa palustris) Engelmann found that light, and not its sudden withdrawal, appeared to exert a stimulant effect (Pfeffer: Pflanzenphysiologie, ii. p. 387).

movement as distinctly in hairs which had been developed in darkness, and had remained without light for thirty hours, as in any which had grown in the open daylight. According to Dutrochet, it requires a withdrawal of the light for about twenty days to cause an entire cessation of the movement in Chara.

The effect of very intense light, and the influence exerted by it upon protoplasm containing chlorophyll, will be examined under "Assimilation."

572. **Relations of protoplasm to electricity.** Chemical changes within the plant result in the production of electrical currents in protoplasm; at this point it is proper to examine briefly the effect produced upon protoplasm by continued and induced currents.

When the plasmodium of a myxomycete is placed between platinum electrodes on a glass slide under the microscope, and a current sent through the mass from one small Grove element, very little if any effect is observable; but if the current from a few elements is employed, there is at once more or less rounding of the branched mass, and there may also be a reversal of the course of the circulation. When more elements are used, the protoplasm may be killed. If the protoplasm in cells be experimented upon, nearly similar phenomena are noticed. Protoplasm is not a good conductor of electricity. Jürgensen made some experiments on the action of a current from small Grove elements upon the leaf-cells of Vallisneria spiralis. A continued current from one element did not cause any appreciable change in the protoplasmic movement; but when two, three, or four were employed, the current retarded the movement, and after a while completely arrested it. In those cases where the movement had been simply checked, it was re-established in full intensity shortly after cutting off the current of electricity; but in those where it had been entirely stopped, it did not begin again.

573. The effect of an interrupted current of electricity is essentially the same as that produced by mechanical shock. The protoplasm generally contracts at certain points forming small roundish masses in the lines of the slender threads, and the movements are arrested.

574. Hofmeister states that a constant current is practically without any influence upon the circulatory movement in the cells of Chara, but that the interruption of the current produces nearly the same effect as a sudden mechanical shock or a sharp change of temperature. He observed essentially the same phenomena in the hairs of the nettle, although in these there was

also more or less of the aggregation into rounded masses alluded to in 564.

575. **The effect of mechanical irritation upon protoplasm** in plants can be easily examined in cells or in plasmodia. When a cell of Nitella which exhibits rapid circulation of protoplasm is held somewhat firmly by pressure on the cover-glass, the movement is arrested instantly, but after a short time it is resumed. Even in those cases where the pressure has been sufficient to disturb the arrangement of the chlorophyll granules, the arrested motions are soon to be seen again. For experiments upon the effect of pressure and shock, the stamen-hairs of Tradescantia are even better than cells of Nitella or Chara, for pressure brings about an apparent disintegration of the threads, and all motion is suspended for several minutes; but if the injury has not been too severe, it soon begins again. How far such injuries can be carried without affecting the vitality of the protoplasm, may be seen from the following observations.

According to Gozzi,[1] if a cell of Chara is ligated firmly, the circulation is checked for a short time, and then begins in each half of the cell. It is stated by Hofmeister that when a root-hair of Hydrocharis Morsus-ranæ is severed, the protoplasm in the cell remains motionless for a short time, during which the cut surface of the cell is being closed by a portion of the protoplasmic mass. When the surface is completely closed, the circulation begins again within the healed cell.

576. Rosanoff's observation,[2] which has been repeated many times, is of much interest in connection with this subject. When a cell from the endosperm of Ceratophyllum demersum, having rapid circulation of protoplasm, is placed under the microscope, and a slight pressure is exerted on the cover-glass for a moment, the circulation stops at once, the thick axile threads of protoplasm begin to round at one or more places, and from the aggregations slight processes, somewhat like tentacles, appear. After a while these are retracted, and the normal circulation is resumed. But sometimes it happens that these tentacles become separated from the threads to which they belong, for a time lie without movement near them, and then become again confluent with them.

Mechanical shock[3] causes the active plasmodia of the myxo-

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[1] Quoted by Hofmeister in Die Lehre von der Pflanzenzelle, 1867, p. 50.

[2] Die Lehre von der Pflanzenzelle, p. 51.

[3] Hofmeister: Pflanzenzelle, p. 26.

mycetes to become rounded into the form of somewhat flattened drops, from which slender branches protrude after a short time. If pressure is now made upon those portions of the branched plasmodium in which circulation is to be seen, the movement stops at once, and is not resumed for two or three minutes; but after that period of rest it goes on as before. When a plasmodium is cut in halves, the circulation is to be seen after a while in the separated portions.[1]

577. **Relations of protoplasm to gravitation.** Concerning the influence of gravitation on the form assumed by protoplasm, it need only be said here that the less dense plasmodia appear sometimes to yield to this force. But Pfeffer[2] found that in a saturated atmosphere the plasmodium of Æthalium moved in the dark with equal freedom whether the moist bibulous paper on which it rested was held horizontally or vertically; Strasburger[3] also has noted the same fact. If one part of the paper is more moist than another, it is to the very wet spot that the plasmodium wanders.

578. **Relations of protoplasm to moisture.** The relations of water to the activity of protoplasm are not yet thoroughly understood. It has been seen (577) that there is a tendency of plasmodia to move to the points where there is the most moisture; and in general it may be said that a large amount of water is favorable to all protoplasmic movements. Thus Dehnecke[4] found that the protoplasm in the cells of the collenchyma of Balsamina exhibited no circulation until the section had been placed in water; and the same phenomena can be shown in sections of many active plants.

On the other hand, Velten has shown that in some cases the protoplasmic movement stops when a plant-hair is placed or kept for a time in water, but is resumed if it is transferred to a dilute solution of gum-arabic, although the protoplasm was furnished with a greater supply of water in the former than in the latter case.

579. Some harmless plasmolytic agents (see p. 27), for instance a dilute solution of sugar, added to the water in which the

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[1] Pfeffer: Pflanzenphysiologie, ii. 390.

[2] Pfeffer: Pflanzenphysiologie, ii. 388.

[3] Wirkung des Lichtes auf Schwärmsporen, 1878, p. 71. Dehnecke (Ueber nicht assimilirende Chlorophyllkörper, 1880) has shown that the various bodies which occur in protoplasm of cells — for instance, chlorophyll granules, starch-grains, and the like — have a marked tendency to sink to that part of the cellulose wall which is lowest. The change of position takes place sometimes in a few minutes, sometimes only after several hours.

[4] Flora, 1881, p. 8.

protoplasm of the cells of Tradescantia stamen-hairs is exhibiting rapid circulation, cause an increase in the rate of movement. This fact has been considered to show, in connection with the cases mentioned, that for the most rapid circulation of protoplasm there must be a definite amount of water, — the optimum.

580. When any of these plasmolytic agents are used in too concentrated a solution they may exert a much more marked effect upon the protoplasmic contents of a cell; not only does all movement cease, but the mass shrinks into small bulk, and does not afterwards recover its former shape and size. As a result of their action, two other phenomena are presented: (1) the protoplasm of one cell can be seen in some cases to be connected through the cell-wall with the protoplasm in the adjoining cell; (2) a change takes place in the firmness or turgor of the cell-wall. Both of these phenomena must receive attention at a later stage. When a cell containing living protoplasm is placed in a harmless and dilute solution of any coloring-matter, for instance logwood, its wall becomes more or less tinged by the dye, but the protoplasm retains for a while at least its power of movement, and does not take up any of the dye. If, however, the protoplasmic mass is injured or dead, it absorbs the coloring-matter with great avidity.

581. **Relations of protoplasm to various gases.** Experiments upon the effects of gases on the behavior of protoplasm can be best conducted by means of the simple gas-chamber shown in Fig. 195. A current of the gas employed is drawn through the tube *a* by means of any simple aspirator; and in a few seconds the specimen previously placed upon the glass at *b*, and protected by a cover-glass, is thoroughly surrounded by it. By the use of this apparatus it has been found that the presence of free oxygen is essential to protoplasmic movements. Hofmeister and Kühne have shown that when this gas is no longer supplied to the protoplasmic mass or to the cells in which the protoplasm is contained, all movements cease. Thus Hofmeister[1] found that the circulation of Nitella was completely arrested in thirteen minutes after the air was wholly removed. Kühne[2] replaced by hydrogen the air in which the hairs of Tradescantia had shown rapid movement, and after several hours all motion was arrested.

582. Corti,[3] the discoverer of the circulation in Nitella, placed

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[1] Die Lehre von der Pflanzenzelle, p. 49.

[2] Untersuchungen über das Protoplasma, 1864, p. 107.

[3] Meyen: Pflanzenphysiologie, ii. 224.

cells in which the movements were plainly seen, in olive-oil, in order to exclude the air. A short time after this was done the movement stopped. In Hofmeister's[1] repetition of Corti's experiment the arrest of the protoplasmic movement occurred in five minutes in olive-oil; after the oil had been carefully poured off, the movements recommenced in thirty minutes.

583. Kühne experimented also upon the replacement of the oxygen needful for protoplasmic movements by carbonic acid, and found this gas much better than oil for excluding air. Upon removal of the plant-hairs from oil, it is difficult to take away the last trace of adherent oil.

584. The ordinary anæsthetics, chloroform and ether, arrest the movements of protoplasm.[2]

585. **The structure of protoplasm.** Having thus briefly examined some of the more striking phenomena of protoplasmic movement, the question must now be asked, What is the structure of a substance which exhibits these phenomena?

By the highest power of the microscope it appears as a homogeneous hyaline mass holding in its substance, but apparently as foreign bodies, very minute granules. But when the protoplasmic matter is stained by the skilful use of pigments, its homogeneous character disappears.

586. Schmitz has confirmed and extended the observations of Frommann, which show that in some cases at least the protoplasmic body is a reticulated framework of extremely delicate fibrils, between the meshes of which is a homogeneous liquid. There is unobstructed communication between the different meshes, so that the whole of the liquid may be regarded as practically one mass. The network of fibrils does not possess any rigidity, but is constantly mobile under favorable conditions, and undergoes manifold changes of form. The reticulated structure is most clearly seen in the parietal protoplasm, and the larger bands of cells which contain relatively considerable sap.

When, after hardening, protoplasm is carefully stained with hæmatoxylin, the whole mass appears to be equally and evenly colored; but it is in reality only the network which takes up the color, the liquid in the meshes remaining uncolored.

Imbedded in the protoplasm, especially in the inner portions, there are generally minute granules which have a high degree of refringency, and which stain very deeply with the dye; these are the microsomata of Hanstein.

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[1] Die Lehre von der Pflanzenzelle, p. 49.

[2] Claude Bernard: Leçons sur les Phénomènes de la Vie, 1879.

587. Up to the present time the microscope has not revealed more than these facts respecting the intimate structure of protoplasm, and from these alone no clear conception can be formed of the mechanics[1] of protoplasmic movements.

588. It is just at this stage of the inquiry respecting the structure of protoplasm that many have sought to apply an hypothesis known as Nägeli's; namely, that all organized bodies consist of structural particles (termed *micellæ*), each of which is individually enveloped by a film of water holding various substances in solution. According to Nägeli's view, as originally given, the micellæ are never spherical, but possess a true crystalline character, as shown by the relations of organized bodies to polarized light.[2] These micellæ are believed to obey

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[1] Hofmeister regarded protoplasmic movements as directly dependent upon changes in the capacity of living protoplasm for absorbing water, shown by pulsating vacuoles (see 120). In the mass of a plasmodium, or in the free spores of some algæ, there are generally to be detected easily under the microscope minute spherical cavities filled with watery sap which are constantly changing in size. Their rhythm of change, or pulsation, as it is called, is different for different plants, varying from a few seconds to as many hours. Their increase in size is usually gradual until the maximum is reached, when suddenly the cavity or vacuole contracts even to the point of vanishing, and then it slowly begins to form again at the same place in the mass. The rhythm of the pulsations can be made to vary with changes in the surroundings; for instance, with changes of temperature, or by the application of dilute solutions, or by any agent which modifies the absorptive power of protoplasm for water. But these agents are also efficient in controlling the rate of protoplasmic movement. The spontaneously pulsating vacuoles appear to indicate that the absorptive power of protoplasm changes spontaneously, and is different successively in different parts of the mass, thus disturbing the equilibrium of the soft mass sufficiently to force some portions from place to place. But Hofmeister gave no explanation of the cause of variations in the imbibition power of protoplasm.

[2] In his earliest work on the subject (Die Stärkekörner, 1858) Nägeli applied the word *molecule* (which had not then obtained such general acceptance in chemistry and physics, with a different signification) to what he now calls the micella. His hypothesis has undergone sundry changes from time to time, one of his last important publications (Theorie der Gärung, 1879) containing some modifications.

The terminology now proposed by Nägeli applies the word *pleon* to those aggregates of molecules which cannot be increased or diminished without changing their chemical nature; for instance, crystals which contain water of crystallization would be called pleons, for the molecule H_2O has a definite numerical relation to the molecules of the salts, and examples of similar pleons are afforded by such compound salts as the alums.

Compare with this the following statement: —

"It has also been a question among chemists whether molecular combination was possible; in other words, whether it is possible for molecules of different the following attractions: (1) that of cohesion, by which each individual micella is an aggregate of molecules; (2) that which tends to bring adjacent micellæ together; (3) that of adhesion, by which the surfaces of the micellæ retain their films of water.

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kinds to combine chemically, each preserving its integrity in the compound. . . . Any antecedent improbability on theoretical grounds is far more than outweighed by the evidence of a large number of compounds whose constitution is most simply explained on the hypothesis of molecular combination. For example, in the crystalline salts it is impossible to doubt that the water exists as such, not as a part of the salt molecule, but combined with it as a whole. So also there are a number of double salts whose constitution is most simply explained on a similar hypothesis" (Cooke's Chemical Philosophy, 1882, p. 137).

The word *micella* is applied by Nägeli to those aggregates of molecules which (like crystals) can increase or diminish in size without changing their chemical nature. The micella is assumed to be much larger than the pleon. "The internal structure of the micella is crystalline, while the exterior may assume any shape." The micellæ unite to form micellar aggregates; of such the crystalline protein granules afford a good example. Thus, according to Nägeli, five terms must be recognized, — the atom, the molecule, the pleon, the micella, and the micellar aggregate. Pfeffer applies a general term, *Tagma*, to all aggregates of molecules, thus bringing under one head the pleon, micella, and micellar aggregate; and he applies the name *Syntagma* to all bodies made up of tagmata. The subject will be again referred to under "Osmosis."

To make clearer the conception of a micella, it may be well to examine briefly two terms in common use; namely, atom and molecule.

When a solid body, for instance a crystal of sodic chloride (common salt), is mechanically separated into the smallest possible fragments, each particle still possesses all the properties of salt. Beyond this mechanical limit of separation the process of subdivision may be carried still further by solution: the minutest fragments of the salt can be broken up and diffused through the solvent, and yet not lose their essential character as salt; in fact, they can be again recovered without change from the solution. But it is impossible to go beyond this latter limit of separation without altering the essential properties of the substance. In other words, by this subdivision the physical limit has been reached; namely, the molecule.

A *molecule* is understood to be the smallest amount of any substance which can exist as such in the free state. Hence the molecule is the physical unit.

If, however, the salt is subdivided by chemical means, — for instance, by the action of strong sulphuric acid, — its identity is destroyed, and its component parts enter into new relations, and cannot be restored to their original relations except by an exceedingly complicated process. In other words, the physical limit has been overpassed and the chemical limit reached; namely, the atom.

Atom is generally defined as "the smallest amount of a given substance which can exist in combination," or "the smallest mass of an element that exists in any molecule." The atom is the chemical unit.

Atoms are variously combined to form molecules: molecules are variously aggregated to form masses.

Contiguous micellæ in any organized substance, for instance cell-wall or starch, frequently possess different chemical characters, as is shown by the fact that from such a substance one portion can be taken without materially disturbing the external form.

589. By means of the changes which go on in the formation of new micellæ, and in their reconstruction, it is sought to account for the nutrition, growth, and movements of organized substances. This is essentially the basis on which Engelmann[1] founds his explanation of the movements of protoplasm.[2]

590. **Continuity of protoplasm.** It was supposed until recently that the protoplasm in one young cell is completely shut off from that in contiguous cells by an imperforate cell-wall, and that even in the cases where the wall is perforate there is no communication of protoplasm through the pores. There is abundant evidence to show the incorrectness of this view. In some cases the protoplasm in one cell is practically continuous with that in

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[1] Hermann's Handbuch der Physiologie, i. 1879, p. 374.

[2] The application of this hypothesis by Sachs is given somewhat fully in the following extract (Text-book of Botany, 2d Eng. ed., 1882, p. 666): "Chemical compounds of the most various kinds meet between the micellæ of an organized body, so that they act upon and decompose one another. It is certain that all growth continues only so long as the growing parts of the cell are exposed to atmospheric air; the oxygen of the air has an oxidizing effect on the chemical compounds contained in the organized structure; with every act of growth carbon dioxide is produced and evolved. The equilibrium of the chemical forces is also continually disturbed by the necessary production of heat; and this may also be accompanied by electrical action. The movements of the atoms and molecules within a growing organized body represent a definite amount of work, and the equivalent forces are set free by chemical changes. The essence of organization and life lies in this: — that organized structures are capable of a constant internal change; and that, as long as they are in contact with water and with oxygenated air, only a portion of their forces remains in equilibrium even in their interior, and determines the form or framework of the whole; while new forces are constantly being set free by chemical changes between and in the molecules, which forces in their turn occasion further changes. This depends essentially on the peculiarity of micellar structure, which permits dissolved and gaseous (absorbed) substances to penetrate from without into every point of the interior, and to be again conveyed outwards. Neither the chemical nor the molecular forces are ever in equilibrium in the protoplasm; the most various elementary substances are present in it in the most various combinations; fresh impulses to the disturbance of the internal equilibrium are constantly being given by the chemical action of the oxygen of the air; and energy is continually being set free at the expense of the protoplasm itself, which must lead to the most complex actions in a substance of so complicated a structure. Every impulse from without, even when imperceptible, must call forth a complicated play of internal movements, of which we are able to perceive only the ultimate effect in an external change of form."

the next, by means of delicate threads which pass through pores in the intervening cell-wall. Doubtful instances afforded by the cribrose-cells have been already alluded to (see 279). The endosperm cells of seeds of Strychnos Nux-vomica afford a well-marked example of the cases of communication between cells of seeds. Tangl[1] advises that very thin sections parallel to the flat surface of the seed be shaken with dilute tincture of iodine or with a solution of iodine in iodide of potassium for about five minutes, and then thoroughly washed with pure water. The protoplasmic and other contents of the uninjured cells will then appear as a contracted ball having somewhat the shape of the cell. From the mass in one cell minute threads run through pores or canals in the wall to the masses in the adjoining cells, and there is no break in their continuity. In the endosperm of the allied species, Strychnos potatorum, Tangl did not detect canals of the character found in S. Nux-vomica.

Gardiner[2] has demonstrated the existence of communication between the protoplasmic masses in contiguous cells of the pulvini of the leaves of some plants having the power of motion. When sections of these leaves are placed in a solution of a salt which causes contraction of the protoplasm, the shrunken mass is seen to be connected with the cell-wall by extremely delicate threads of protoplasm. The threads can be traced to pits in the wall, and there it can be seen that they are exactly opposite the threads on the other side of the wall. If the solution of the salt used is too strong, some of the threads may be ruptured, and then one free end of each thread will retract to the main mass while its other part goes to the cell-wall. If fresh sections are treated with strong picric acid, and then, after washing in alcohol, are stained with anilin blue, the continuity of the protoplasm in uninjured cells becomes apparent. Mimosa affords excellent material for this purpose.

Hillhouse[3] reports similar continuity of protoplasm in the cortex of the stem of Laburnum, and in the petiole of several leaves. The fresh material is to be placed for a few days in absolute alcohol, and the thin sections made from it are to be treated with dilute alcohol. The sections are then to be placed in concentrated sulphuric acid, and after the acid has removed the cell-wall, its excess is to be withdrawn by means of a pipette,

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[1] Pringsheim's Jahrbücher, 1880, p. 170.

[2] Philosophical Transactions Royal Society, 1883, clxxiv. 817.

[3] Botanisches Centralblatt, 1883, xiv. 89, 121.

and the preparation very carefully washed. The application of strong glycerin completes the treatment. The specimen must not be removed from the slide during the whole series of operations. If the manipulation has been careful throughout, the minute threads can be seen passing from one mass of protoplasm to the next.

591. The directions given by Strasburger for demonstrating the continuity of protoplasm are as follows: From the stem of a dicotyledonous shrub or tree (the diameter of which should be at least a centimeter) the periderm is removed by a knife, and very thin tangential longitudinal sections are then made through the soft green bark. The parenchyma cells which are intermingled with the liber contain more or less chlorophyll, and may have pits, the very smallest of which are not bordered (see 268). If the first sections have shown in any case that these cells are furnished with pits, others are then prepared and placed at once in a drop of a solution of iodine (that of iodine in an aqueous solution of potassic iodide is best). The excess of the solution is at once removed and the preparation covered with a glass cover. At the edge of the cover-glass there is placed a drop of concentrated sulphuric acid, and by the side of this a couple of drops of dilute sulphuric acid; when these are mingled the mixture is allowed to flow under the cover-glass, while a bit of filtering-paper on the other edge of the glass draws it through. The specimen becomes dark blue. If the color is deep, the cover-glass is cautiously lifted and the preparation is then thoroughly but carefully washed in water. After this washing, a drop of a solution of anilin blue is added, whereby the object becomes stained; then, after washing again, a little glycerin[1] is added, and the cover-glass is fastened down with some cement. For the examination of the specimen the strongest objectives — preferably the so-called "homogeneous immersion," employed with cedar-oil — are indispensable.

Under a sufficiently high power the middle lamella of the wall is seen to be somewhat swollen, while the contents of the cells are contracted and colored. The periphery of the individual protoplasmic masses in the cells of the cortical parenchyma is smooth on that face which was in contact with the cell-wall having very small pits; but it has minute protrusions on that face which was next the bordered pits. Moreover, the protrusions in contiguous cells are exactly opposite each other. Between

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[1] Strasburger advises the addition of a little anilin blue to the glycerin.

the protrusions at the bordered pits there extend extremely delicate threads of protoplasm which have a granular character. The threads are somewhat curved (especially the outer ones), and are slightly swollen in the middle. In peculiarly good preparations it has been shown that there is an apparent interruption at the middle of their course, but that at this break there are still minute filaments which serve to connect them. From these and kindred observations Strasburger and some others have adopted the view that there is such a degree of continuity between the protoplasmic masses in the cells that they form throughout the plant an unbroken whole.[1]

592. That protoplasm may perhaps occur in intercellular spaces appears from the observations of Russow[2] and of Berthold.[3] To demonstrate this, one-year-old twigs of Ligustrum vulgare are hardened for a few days in absolute alcohol, longitudinal sections of the primary cortex placed in dilute iodine solution (see 30), the excess of iodine removed, and dilute sulphuric acid added. The contents of the cells and of the intercellular spaces will then appear as yellowish-brown masses.

593. That protoplasm can in some cases pass through an imperforate cell-wall appears from the observation of Cornu,[4] that in the formation of the macroconidia of a certain Nectria all the protoplasm of the five or six cells of the spore emerges to form the macroconidium, which arises as an outgrowth of one of the cells of the spore. The four or five partition-walls through which the protoplasm must pass are, however, neither dissolved nor perforated.

It is probable that a striking phenomenon of fertilization in phænogams, namely, the complete emptying of the pollen-tube of its protoplasm (see "Fertilization") without apparent break in the continuity of the wall, must be referred to the same penetrative power of protoplasm.

The withdrawal of the principal part of the protoplasmic matters from deciduous leaves before the fall of the leaf may be perhaps explained in the same way.

Strasburger cites as an illustration of this penetrative power the well-known case of the removal of protoplasmic matters

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[1] Das botanische Practicum, 1884, p. 617. Strasburger: Bau und Wachsthum der Zellhaüte, 1882, p. 246. Frommann: Beobachtungen über Structur des Protoplasma der Pflanzenzellen, 1880.

[2] Sitz. der Dorpater Naturforscher-Gesellschaft, 1882, p. 19.

[3] Berichte der deutschen botanischen Gesellschaft, ii. 20.

[4] Comptes Rendus, 1877, tome lxxxiv. p. 133.

from the cells around the buds which form on the incised leaves of Begonia.[1]

594. **The relations of the cell-wall to protoplasm** are not yet fully understood; and in regard to some of them there exists among botanists considerable diversity of opinion. The two principal views are the following: 1. The cell-wall is formed by the solidification upon the exterior of a protoplasmic mass, of matters previously dissolved in it. The pellicle thus produced is regarded as a sort of excretion (since in most cases it is not again to be dissolved and employed by the organism) or as a secretion (because in a few instances it can be dissolved and utilized a second time by the plant). The substance capable of thus solidifying upon the surface of protoplasm consists of cellulose combined with water and a small amount of incombustible matters, but it is not positively known in what condition these were previously combined in the protoplasm. 2. The cell-wall may be regarded as directly produced by a conversion of the outer film of protoplasm into cellulose with which some other matters are intermingled.[2]

595. The young cell-wall [3] is practically a homogeneous film of cellulose, which speedily undergoes changes both in its chemical and physical character. In many of the lower plants the wall differs in some particulars from that found in the higher plants (see p. 29), but the differences need not enter into the present description.

596. Two views are held respecting **the mode of growth of the cell-wall.** The first may be regarded as based upon the hypothesis of Nägeli spoken of in 588. From some of the materials held dissolved in the adherent film of water around each micella new micellæ of cellulose are supposed to be produced,

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[1] "That protoplasm can pass through closed cell-walls is beyond doubt" (Vines, note to second edition of Sachs's Text-book, p. 946).

[2] The view that cellulose is a kind of secretion is stated at great length in Hofmeister's Pflanzenzelle, and in several communications by Sachs in Botanische Zeitung. The second view is given by Schmitz, Sitz. der niederrheinischen Gesellschaft für Natur- und Heilkunde, Bonn, 1880. He bases his opinion largely upon the fact that in some cases the cells gradually become emptied of protoplasm as the amount of cell-wall increases, and upon the phenomena which attend the increase of the cell-wall in thickness.

[3] It was believed by some of the earlier phytotomists that the cell-wall was a close, firm network of extremely fine fibres, while others held it to be composed of minute granules. In these explanations of structure it was confessed that the ultimate fibres, or ultimate granules, lie quite beyond the reach of the highest powers of the microscope.

which are interpolated between the old. This is the intussusception theory. It has gradually displaced an older theory, namely, that of growth by apposition. As the older theory was usually held, it presented two modifications,[1] — one that the growth of a cell-wall in thickness takes place on the exterior of the wall, so that in a stratified wall all the outermost portions are the newer; the other, that all the new matter is laid down upon the interior of the old.

The apposition theory has recently attracted much attention from the studies of Schmitz, and from its adoption and advocacy by Strasburger.[2] As now held by these authors, the view is this: stratified and other cell-walls grow in thickness by the deposition of new particles upon the inner face of the cell, much as a crystal adds new particles to itself; growth in surface is the result of a simple stretching of the wall by the pressure of the contents upon it.

Any solution which causes a shrinking of the contents of the cell, and thus diminishes the pressure on the wall, may cause a diminution of the size of the cell itself. The bearing of this upon the turgescence of the cell will be again adverted to under "Properties of New Cells and Tissues."

To the physical characters of cellulose already mentioned (see 129), may now be added that property which is possessed also by many other organized substances; namely, that of swelling greatly when placed in water. The wall of a living and active cell is of course moist, and its increase in size on the addition of more water is seldom marked; but under certain circumstances the amount of water in the cell-wall even of an active cell may fall below its usual amount, and then the application of water will cause an appreciable change of bulk. Such change in the amount of water may take place with great rapidity upon slight external disturbances, such as shock: in these cases, the amount of water in the protoplasm in contact is correspondingly modified.

597. **Historical note regarding protoplasm.** The word *protoplasm* appears first in a memoir by Mohl, in 1846, "On the Movement of Sap in the Interior of Cells," which deals, however,

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[1] For an account of the two modifications of the apposition theory, the student is referred to Harting's paper, translated in Linnæa, 1846, and Mohl's, in Botanische Zeitung, 1846. A fair statement of the first modification is presented in Mulder's Physiological Chemistry.

[2] Strasburger: Bau und Wachsthum der Zellhaüte, 1882.

not so much with the movement of what would to-day be called cell-sap, as with the general behavior of all the motile contents of active vegetable cells. After showing that his predecessors had not clearly understood the important part played in the life of the cell by the viscous matter known vaguely up to that time as *schleim*, or mucus, Mohl points out the essential identity of the nucleus, primordial utricle, and the basic substance filling all but the sap-cavities of the cell. For the substance which is essential to the formation of every new cell and to the development of newly formed cells he proposed, upon physiological grounds, the significant name *protoplasma*.

For convenience of reference, the paragraph in which the word is first employed is here given: —

> "Da wie schon bemerkt diese zähe Flüssigkeit überall, wo Zellen entstehen sollen, den ersten, die künftigen Zellen andeutenden festen Bildungen vorausgeht, da wir ferner annehmen müssen, dass dieselbe das Material für die Bildung des Nucleus und des Primordialschlauches liefert, indem diese nicht nur in der nächsten räumlichen Verbindung mit derselben stehen, sondern auch auf Jod auf analoge Weise reagiren, dass also ihre Organisation der Process ist, welcher die Entstehung der neuen Zelle einleitet, so mag es wohl gerechtfertigt sein, wenn ich zur Bezeichnung dieser Substanz eine auf diese physiologische Function sich beziehende Benennung in dem Worte *Protoplasma* vorschlage." [1]

In 1835 Dujardin described a contractile substance capable of spontaneous movement in certain of the lower animals, to which he gave the name *Sarcode*. The identity of sarcode with that substance which forms the essential body of animal cells and with the protoplasm of vegetable cells was suggested by several investigators and finally demonstrated by Max Schultze in 1861.[2]

Schwann, even as early as 1839, pointed out various analogies and homologies between animal and vegetable cells, and enunciated the following proposition: animal cells are completely analogous to vegetable cells, and are quite as independent in their mode of growth. The bearing of Schultze's demonstration upon the foregoing proposition is obvious. Schwann instituted also certain comparisons between the mode of formation of cells and that of crystals ("Microscopical Researches into the Accordance in the Structure and Growth of Animals and Plants," translated by Henry Smith for the Sydenham Society, 1847).

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[1] Botanische Zeitung, 1846, p. 75.

[2] Archiv für Anatomie, Physiologie, und wiss. Medicin, 1861, pp. 1–27, and Das Protoplasma der Rhizopoden und der Pflanzenzellen, Leipzig, 1863.

CHAPTER VII.

DIFFUSION, OSMOSIS, AND ABSORPTION OF LIQUIDS.

DIFFUSION AND OSMOSIS.

598. When two liquids which are not miscible — for instance, oil and water — are shaken together, and then left at rest, they will separate sooner or later, according to their specific gravity. But if two miscible liquids are shaken together, they remain as a homogeneous mixture no matter what their specific gravity may be. Also when two miscible liquids are left in contact, without any agitation they become thoroughly commingled, and constitute a uniform mixture; this uniform commingling of two or more miscible fluids is termed *diffusion*.[1]

599. Furthermore, if two miscible liquids are separated by a membrane which can be moistened by them, they will diffuse through it and make a uniform mixture. This latter kind of diffusion, in which the contact between the two liquids is not direct, but takes place through a septum of some substance, is known as *osmosis*. In the plant and in its surroundings the two kinds of diffusion play such an important part that they must receive special attention.

600. **Diffusion of liquids.** The rate of diffusion varies with the nature of the liquids and the temperature. The statements in the following paragraphs are substantially as given by Graham.[2]

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[1] Pfaundler applies this term to the commingling whether it is or is not brought about by agitation (Müller's Lehrbuch, 1877, i. 162).

[2] They are based upon two series of experiments conducted with very simple apparatus. In the first series a small, wide-mouthed vial containing one liquid was placed in a jar holding the other liquid, allowed to stand a few days, withdrawn, and the amount of diffusion noted. In the second series Graham pursued the plan of placing in a cylindrical glass jar, 152 mm. high and 87 mm. wide, seven tenths of a liter of pure water, and then carefully carrying to the bottom of the jar, by means of a fine pipette, one tenth of a liter of the liquid to be diffused. The jar was then left at rest in an apartment where the temperature was nearly constant, and after a certain time its contents were drawn off carefully in portions of fifty cubic centimeters, each portion evaporated separately, and the residue remaining after evaporation weighed.

601. Different salts in solutions of equal strength diffuse in unequal times. Thus potassic hydrate diffuses with double the rate of potassic sulphate, and the latter with double the rate of crystallized sugar. But these substances have a comparatively high rate of diffusion. A solution of caramel (sugar heated till it becomes brown) diffuses very slowly; the sugar in this case has been so changed in its character that its rate of diffusion has been reduced from a high to a very low one. Gelatin may be taken as the representative of the almost "fixed" or slowly diffusible class of substances; most crystalline substances, as representatives of the highly diffusible class. The former are collectively known as colloids (κόλλα, glue), the latter as crystalloids. It must be noted that Graham's use of this word "crystalloid" is different from that in which it has been employed in speaking of the protein bodies (177).

602. With each salt the rate of diffusion increases at a slightly higher rate than the temperature of the solution.

603. The members of certain chemical groups are equally diffusible. Thus hydrochloric, hydrobromic, and hydriodic acids; the chlorides, bromides, and iodides of the alkaline metals, etc., have equal rates of diffusion into pure water.

604. The diffusion of a solution of a salt into the dilute solution of another salt takes place nearly as rapidly as into pure water;

The difference in the rates of diffusion of ten per cent solutions of different substances experimented upon in the manner described on the preceding page is clearly shown by the annexed table.

Number of stratum from above downwards.	Sodic Chloride.	Sugar.	Gum.	Tannin.
1	.104	.005	.003	.003
2	.129	.008	.003	.003
3	.162	.012	.003	.004
4	.198	.016	.004	.003
5	.267	.030	.003	.005
6	.340	.059	.004	.007
7	.429	.102	.006	.017
8	.535	.180	.031	.031
9	.654	.305	.097	.069
10	.766	.495	.215	.145
11	.881	.740	407	.288
12	.991	1.075	.734	.556
13	1.090	1.435	1.157	1.050
14	1.187	1.758	1.731	1.719
15, 16	2.266	3.783	5.601	6.097
	9.999	10.003	9.999	9.997

The first series of experiments are described in Philosophical Transactions, 1850; the second, in 1861.

but if the second solution contains some of the salt, like that in the first solution, the rate of diffusion is retarded.

605. The rate with which a salt passes from a stronger into a more dilute solution is nearly proportional to the degree of concentration. The approximate times required for the diffusion of equal weights of various substances into water are given in the following table: —

Hydrochloric acid	1.
Sodic chloride	2.33
Magnesic sulphate	7.
Cane-sugar	7.
Albumin	49.
Caramel	98.

606. Of the colloids, Graham says:[1] "Low diffusibility is not the only property which the bodies last enumerated possess in common. . . . Although often largely soluble in water, they

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[1] Philosophical Transactions, 1861.

Graham says further: "Although chemically inert in the ordinary sense, colloids possess a compensating activity of their own arising out of their physical properties. While the rigidity of the crystalline structure shuts out external impressions, the softness of the gelatinous colloid partakes of fluidity, and enables the colloid to become a medium for liquid diffusion, like water itself. The same penetrability appears to take the form of cementation in such colloids as can exist at a high temperature. Hence a wide sensibility on the part of colloids to external agents. Another and eminently characteristic quality of colloids is their mutability. Their existence is a continued metastasis. A colloid may be compared in this respect to water while existing liquid at a temperature under its usual freezing point, or to a supersaturated saline solution. Fluid colloids appear to have always a pectous modification (πηκτός, curdled), as fibrin, casein, albumin. But certain liquid colloid substances are capable of forming a jelly, and yet still remain liquefiable by heat and soluble in water. Such is gelatin itself, which is not pectous in the condition of animal jelly, but may be so as it exists in the gelatiferous tissues. Colloids often pass under the slightest influences from the first into the second condition. The solution of hydrated silicic acid, for instance, is easily obtained in a state of purity, but it cannot be preserved. It may remain fluid for days or weeks in a sealed tube, but is sure to gelatinize and become insoluble at last. Nor does the change of this colloid appear to stop at that point. For the mineral forms of silicic acid, deposited from water, such as flint, are often found to have passed during the geological ages of their existence, from the vitreous or colloidal into the crystalline condition (H. Rose). The colloidal is, in fact, a dynamical state of matter; the crystalloidal being the statical condition. The colloid possesses energia. It may be looked upon as the probable primary source of the force appearing in the phenomena of vitality. To the gradual manner in which colloidal changes take place (for they always demand time as an element), may the characteristic protraction of chemico-organic changes also be referred."

are held in solution by a most feeble force. They appear singularly inert in the capacity of acids and bases, and in all the ordinary chemical relations. But, on the other hand, their peculiar physical aggregation with the chemical indifference referred to, appears to be required in substances that can intervene in the organic processes of life. The plastic elements of the animal body are found in this class."

607. **Osmose, or Osmosis.** Diffusion of liquids through membranes. The interposition of a permeable septum between miscible liquids does not prevent diffusion. Thus if a solution of sodic chloride is separated from pure water by an intervening membrane, as one of bladder or of vegetable parchment (see page 32), diffusion takes place in about the same time as if no membrane were present.

608. For most experiments in osmosis the simple apparatus known as an osmometer answers very well. It consists of a small reservoir furnished with a membrane bottom, and a graduated tube at its upper part. A very good osmometer can be prepared from a short-necked bottle from which the bottom has been carefully removed. After the edges at the bottom have been made smooth, a piece of wet parchment paper is tightly fastened on by waxed thread. Great care must be taken to select parchment or parchment paper which is free from perforations,[1] and the tube at the neck must be well fitted to a velvet cork, so that no escape of liquid can take place in any way. A film of ordinary unsized paper evenly covered with a solution of warm gelatin, which cools to form a firm mass upon its surface, makes a good substitute for parchment in this apparatus. A thin film of white of egg coagulated by heat will also serve well for a covering.

609. The osmometer, filled to a certain point on the tube with the liquid to be experimented upon, is suspended in pure water so that the liquid in the apparatus is on exactly the same level as the water. It will be seen by the experiment that not only does diffusion take place, but that there is a change in the level of the liquid in the tube.

610. When any of the more diffusible substances are placed in a state of solution in the reservoir, a small amount of the crystalloid passes outwards, while a much larger amount of

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[1] The existence of actual perforations in good parchment can be demonstrated by subjecting the apparatus to pressure, or even by repeatedly wiping the exposed surface of the parchment with filtering-paper.

water passes inwards. The change of level caused is of course accompanied by an immediate change in the hydrostatic pressure, and hence water should be added to or removed from the outer vessel, to balance inequalities of height as fast as they occur.

611. The proportional amounts of the substances interchanged have been determined by various observers. Jolly,[1] by an ingenious modification of the osmometer, obtained the following results; the figures representing the weight of water which replaced in osmosis one part by weight of the substance:

Sodic chloride	4.3
Sugar	7.1
Sodic sulphate	11.6
Magnesic sulphate	11.6
Potassic sulphate	12.
Potassic hydrate	215.7

612. These figures are known as the *osmotic equivalents* of the respective substances, but they are by no means constant; since, as Ludwig[2] has shown, they depend partly on the degree of concentration of the solution used, the duration of the experiment, and the character of the membrane.

613. If, however, a colloidal body is placed in the reservoir, very little comparatively passes outwards, and in the case of some colloids nothing. "Indeed, an insoluble colloid, such as gum-tragacanth, placed in powder within the osmometer, was found to indicate the rapid entrance of water, to convert the gum into a bulky gelatinous hydrate. Here, no outward or double movement is possible."[3] This very important fact must be borne in mind in the application of the phenomena of osmose to those of absorption of liquids by the colloids in active vegetable cells.

614. **Precipitation-membranes.** Traube[4] (in 1867) discovered that when a drop of a solution of copper-sulphate is placed in a solution of potassic ferrocyanide, there is produced over its whole surface a coherent membrane (of precipitated cupric ferrocyanide), known as a "precipitation-membrane." This at once begins to increase in size, but somewhat irregularly, as if breaks occurred at the upper part through which a portion of the liquid

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[1] Zeitschrift für rationelle Medicin, 1849, vii. p. 83.

[2] Poggendorff: Annalen der Physik und Chemie, lxxviii. p. 307.

[3] Graham: Journ. Chem. Soc., 1862, p. 269.

[4] Archiv für Anat. u. Physiol. du Bois-Reymond u. Reichert, 1867, p. 87.

within flowed out only to meet the exterior liquid, and there formed instantly a precipitate cohering with the edges of the rupture. If a fragment of chloride of copper is placed in a test-tube containing a strong solution of potassic ferrocyanide, the action is more rapid than with copper-sulphate. The fragment dissolves at once, and forms a green globule at the bottom of the tube. If it now be carefully watched, it will be seen that a delicate transparent film (the precipitate of cupric ferrocyanide, which in a flocculent state is brown) is produced over the globule, and the sphere begins at once to grow into a cylindrical body. The liquid in the upper part of the closed cylinder is almost colorless; that at the bottom is deep green. The intermittent growth in height appears to admit of only one explanation: namely, that the membrane is torn by the great pressure within, and the solution of copper chloride which flows through is immediately covered by a newly formed film. By careful management, such growths of cylindrical form can be produced several inches long.

Traube also discovered that when a drop of β gelatin (gelatin which has been boiled continuously for about three days, thereby losing its power of coagulation) is placed in a solution of tannin, a film forms at once, which begins to grow into a spherical cell, but without the appearance of irregular and intermittent rupture. Such an artificial cell is best prepared by placing a glass tube having a drop of β gelatin on the tip into a solution of tannin. Its growth is even and uninterrupted, and unless the apparatus is disturbed, no appearance of rupture is observed. A further discovery was made by Traube; namely, that a coherent film may be formed even by the contact of pure water. The coagulum produced when gelatin is acted on by tannin (the so-called tannate of gelatin) is soluble in a concentrated solution of tannin, but is insoluble in a dilute solution. If a drop of a solution of tannate of gelatin thus prepared is placed in pure water, a coherent film forms at the surface which can increase up to a certain size.[1]

615. Pfeffer has employed the precipitation-membranes discovered by Traube, in an ingenious apparatus by which the pressure developed in the so-called artificial cell can be accurately measured. The apparatus consists of a porous porcelain

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[1] At this point should be mentioned the observation of Nägeli, that whenever cell-contents rich in protein matters come in contact with watery media, a membranous film is formed over the surface (Pflanzenphysiologische Untersuchungen, 1855, pp. 9, 10).

or clay cell, like those which are used in the Bunsen battery, connected by means of a glass collar with a suitable manometer. Within the clay cell a precipitation film is formed;[1] the cell is

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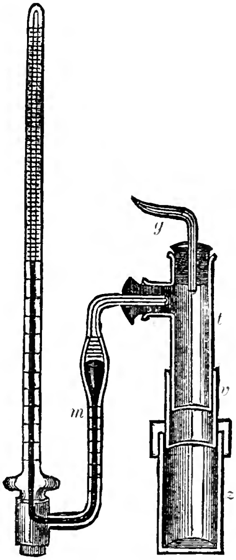
[1] The following account of details essential to success in these experiments of Prof. Pfeffer has been prepared by one of his students, Dr. W. P. Wilson.

The principal portion of the apparatus is a porous porcelain cell, *z*, 46 mm. high and 16 mm. in diameter, with walls 1½ mm. in thickness. This cell is cemented on to a piece of glass tubing, *v*. A second piece of tubing, *t*, with lateral tube, is cemented into the first piece. The lateral opening is for the manometer *m*, the one at *g* is for the convenience of filling and sealing the cell.



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One of the two fluids used in forming the membrane for experimentation is allowed to penetrate the porous cell from without. When this has thoroughly taken place, the second fluid is poured into the interior. The contact of the two fluids takes place, therefore, on the inner surface of the porous cell, and here the precipitate is formed which is termed the *pellicle-membrane* or precipitation-membrane. Substances which by their mutual contact give rise to such precipitation-membranes are termed *membranogenic*. It will readily be seen that during any internal pressure the porous porcelain cell acts as a support for the membrane. If the exterior solution is copper-sulphate, the interior solution potassic ferrocyanide, then the precipitated membrane will be cupric ferrocyanide. After the membrane has been formed, then any solution not chemically incompatible with it may be employed in the cell; namely, syrup from cane-sugar, a solution of saltpetre, or a still stronger solution of potassic ferrocyanide than was used in the preparation of the cell.

As the successful working of the apparatus depends upon the exact carrying out of quite a number of minor details, the following description of the methods of putting the parts together may be found useful: —

In order to insure absolute freedom from any foreign substance, the porcelain cell must be successively washed in dilute solutions of potassic hydrate and hydrochloric acid, and then thoroughly dried. Warm a piece of sealing-wax in the spirit-lamp and draw it to a point. Slowly heat the open end of the cell in the alcoholic flame. When hot enough to very readily melt the wax, apply the point; and while the cell is continually rotating, cover evenly a space to the depth of 15 mm. with wax in the interior. It should be about 2 mm. in thickness. Pick up the short piece of tubing, *v*, which has been previously waxed on one end, and rotate it over the flame. When both porcelain cell and glass tube are as warm as they can be made and yet the wax kept smooth then filled with any diffusible liquid, — for instance, a dilute solution of sugar, — the manometer is attached, and the whole apparatus is placed in pure water or any aqueous solution.

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and even on all sides, place them quickly together, lapping about 15 mm., and continue the rotary motion until cool. Take a scalpel with a point bent at right angles to the blade, heat it, and, inserting it in the glass tube, cut away the wax at its inner end, thus exposing a shoulder of the thickness of the glass. Roll out in the form of a pencil about 2 mm. in diameter a piece of sealing-wax which has been made a little soft by the addition of a drop or two of turpentine. A piece of this, equal in length to the inner circumference of the glass tube, in a long coil, should be placed on the point of the scalpel, carried in to the shoulder and pressed into it. A little heat very cautiously applied from without, with proper turning of the cell, will easily cause this softer wax to flow and fill the shoulder with perfect smoothness. The use of the softer sealing-wax makes a joint which will not crack under strong pressure. Now cement the tube *t* very firmly into *v*, with the same precautions as above. Unless a pressure of more than three atmospheres is desired, the soft wax need not here be used.

The cell is now ready to be prepared for filling. In order to saturate the porous porcelain with any given solution, the air must first be wholly removed. Place the apparatus in a beaker of water which has been freed from air by boiling, and set the whole under the bell-jar of an air-pump. Exhaust and admit the air into the bell-jar repeatedly until bubbles can no longer be seen to rise from the porcelain. Transfer the cell to a three per cent solution of copper-sulphate, and exhaust the air again. Four or five hours will be required for this solution to thoroughly penetrate the porous cell. At the end of this time remove it from the copper-sulphate, empty it, and with some long twisted strips of bibulous paper quickly dry up all moisture from its inner surface. If at any time the exterior surface of the cell begins to appear dry before the moisture from within has been wholly removed, dip it at once in the solution from whence it came. At the moment when the moisture is properly removed, fill the cell to the second joint with a three per cent solution of potassic ferrocyanide and replace it in the copper-sulphate, taking care that the surfaces of the two fluids are in the same plane. An interim of at least twelve hours must now elapse in order that the membrane may be properly formed. At the end of this time the cell is ready to be used, either with the solution which it already contains or with some other. If some other solution is to be employed, then carefully empty out the potassic ferrocyanide, and after washing the cell with a little distilled water, fill it with the fluid to be used.

The cell must be so filled and sealed as to leave absolutely no air within, otherwise the pressure cannot be accurately measured. Insert a perforated rubber cork at *g*. Fill the manometer from the quicksilver to the extremity of the tube with potassic ferrocyanide, or whatever other solution is to be used in its place, and push it into position in the cork. Fill the cell completely full, and press firmly into place the second perforated cork, taking great care, first, that no bubble of air remains at its base; and second, that not a particle of potassic ferrocyanide comes in contact with the outside of the cell.

A bent glass tube, drawn to a capillary point at one end, should now be filled with potassic ferrocyanide and slowly pushed into the cork. If this is

In certain experiments by Pfeffer, made with a single cell, in which was a solution of cane-sugar containing a trace of one of the membranogenic substances, while the water outside contained a trace of the other, the following pressures were indicated: —

Percentage of sugar in the solution, by weight.	Temperature.	Mercurial pressure.
1	13°.7 C.	53.8 cm.
1	13.6	53.2 "
2	14.	101.6 "
4	13.8	208.2 "
6	14.7	307.5 "
1	14.6	53.5 "

With a 3.3 per cent solution of potassic nitrate in the cell, Pfeffer obtained a mercurial pressure of 436.8 cm.

616. An active vegetable cell is an osmotic apparatus. The chief agent in its work of absorption is the peripheral film of the colloidal protoplasmic mass, and this receives mechanical support from the wall of cellulose in which it is held. It was formerly believed that in osmosis there is always an exchange of materials, one current passing inwards (endosmose), the other outwards (exosmose); and there are numerous cases in which this is true, and in which the osmotic equivalent can be calculated (see 612). But Pfeffer's experiments show how great a force may be exerted by osmosis in cases in which there is little or no substance passing out to replace the liquid absorbed. In the series of experiments in which a solution of sugar was employed in his osmotic apparatus, no trace of this

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properly done, any small quantity of air which may be in the upper part of the cork will rise during insertion to the capillary point. Gradually and cautiously warm the tube, beginning close to the cork. This will expand the fluid and drive the air wholly out. At the moment when the solution completely fills the tube, fuse the capillary point in the spirit-lamp. The cell is now entirely free from air and hermetically sealed. During the time of inserting the manometer, corking, and sealing, the porcelain part of the cell must not be allowed to become dry, but must be frequently dipped into the solution from which it was taken. With unannealed brass wire secure both corks after the fashion of champagne-bottles.

Now suspend the cell in the solution of copper sulphate so that the porcelain shall be wholly submerged but shall not touch the sides of the vessel containing the solution. Note the position of the mercury in the manometer, and see that the temperature remains constant in the room. If the cell is perfect, a certain degree of pressure will be indicated in less than an hour.

substance could afterwards be discovered in the water on the outside. The apparatus lined with its colloidal film, containing a small amount of saccharine solution, and surrounded by a very dilute aqueous solution of mineral matters, is an instructive imitation of a vegetable cell.

ABSORPTION OF LIQUIDS THROUGH ROOTS.

617. Submerged aquatics may absorb with their whole surface. They are bathed in dilute saline solutions containing the gases essential to vegetative activity, and the materials for their food can be taken from the medium surrounding them, perhaps quite as well by one of their parts as by another. This fact is well illustrated by the larger algæ, in which the organs popularly called roots are merely mechanical hold-fasts, and the work of absorption can proceed at any part of the frond. The simplest differentiation of organs for absorption is met with in the rhizoids or complex root-hairs of mosses, and in the filaments of fungi which bury themselves in a nutrient substratum. Above the mosses the differentiation of organs into roots for absorption, and stems for the support of the assimilative tissue, is very plain. For our present purpose it is best to begin an examination of the absorption of liquids by plants with a study of the structure and the office of the root.

618. It has been shown in Part I. that the younger parts of the root are clothed with extremely delicate epidermal cells, which, with the slender trichomes associated with them, constitute the absorbing apparatus of the plant. (These epidermal cells of the root, taken collectively, have been called the Epiblema.[1])

619. The root-tip with its protective cap does not share to any great extent, if indeed at all, in the work of absorption; and yet to the soft, spongy, rounded mass of tissue forming the root-tip was formerly given the name of spongiole, on account of its spongy nature, and its supposed office of sucking up nutrient matters from the soil.[2]

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[1] This term, early introduced, was retained by Schleiden: Principles of Scientific Botany, 1849, pp. 68, 218.

[2] Thus De Candolle, in his Physiologie Végétale, 1832, p. 41, says: "La succion des racines s'exécute par des points spéciaux qu'on nomme spongioles, qui sont composés d'un tissu cellulaire très-fin et toujours nouveau, puisque les racines s'alongent sans cesse par leur extrémité. Le liquide de la terre tend à entrer dans les méats de ce tissu: I. par la force de capillarité; II. par

620. **Root-hairs.** It was shown experimentally by Ohlert[1] in 1837, that the tip of the root is not the absorbing part. By careful excision of the tip, and the use of a harmless water-proof varnish to cover the wound caused, he obtained full absorption of liquids through the sides, and not the end of a young root. He further demonstrated the very general occurrence of delicate hairs upon the sides of young roots, and expressed the opinion that these were the efficient agents in root absorption.

621. That the abundance of the hairs on new roots is dependent largely on the amount of moisture to which they are exposed, appears from experiments on the roots of some of the more common cultivated plants, — Allium Cepa, Cucurbita Pepo, Zea Mais, etc. In all these cases the plant can almost be said to regulate the amount of its absorbing surface by the amount of moisture within its reach, and it is thought by some that all the epidermal cells of a young and developing root have the power of extending into hairs. The number of hairs to the square millimeter on a root of Zea Mais grown in a moist place was found by Schwarz to be 425; and on a root of Pisum sativum, 232.

622. Root-hairs are, as has been shown in Part I., cylindrical protuberances from the external wall of the epidermal cells. They vary in length from .1 mm. to 8 mm. The former length occurs in a few grasses, the latter in some water plants. Schwarz gives the following measurements of length: root-hairs of Potamogeton, 5 mm.; of Anacharis, 4 mm.; of Brassica Napus in moist air, 3 mm.; of Pisum sativum and Avena sativa, 2.5 mm.; of Vicia Faba, 8 mm.

623. When root-hairs are developed in contact with soil, they become much distorted (see Fig. 89), and generally dwarfed; they curve more or less irregularly around the particles of soil, and frequently are enlarged at the immediate place of contact. Moreover, the character of the cell-wall is somewhat changed at the place of contact with the particles; in many instances the wall undergoes a sort of mucilaginous modification, and becomes so firmly united to the particles that these cannot be removed

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l'hygroscopicité. Ces deux propriétés de tissu peuvent bien expliquer l'énorme quantité d'eau qui pénètre dans la plante vivante, les variations de cette quantité selon les espèces, les saisons, etc. Il souffit d'admettre que les cellules des spongioles douées de contractions alternatives, augmentent et diminuent alternativement les méats intercellulaires, et tendent ainsi à absorber de l'eau en quantité proportionnée à la force et à la rapidité de leurs contractions vitales."

[1] Linnæa, 1837.

without laceration of the delicate cells. Notwithstanding the extreme tenuity of the cell-wall, it is thought by some to play an important mechanical part in fastening the roots in the soil.[1]

624. That the hairs upon the root vastly increase its absorbing surface is self-evident. Schwarz has shown that in Indian corn grown in moist air the surface presented by the velvety hairs which cover the young roots is 5.5 times greater than that of the part of the root on which the hairs occur; while the ratio of these surfaces in the roots of peas is as 12.4 to 1; and in the aerial roots of Scindapsus pinnatus, as 18.7 to 1. But all these figures, which are at best only approximate, appear to be very low.

625. **Extent of Root-systems.** In extending, the root, by growth at its protected extremity, can insinuate itself between particles of soil which could not be easily displaced by simple thrust. The branches from the main root extend exactly as does the main root itself, — by continual additions just behind the tip, — and the area covered by a root-system finally becomes very large. One of the earliest recorded measurements is that by Hales,[2] who estimated that the roots of a sunflower (3½ ft. high), taken together, were no less than 1,448 feet in length. The plant had "eight main roots reaching fifteen inches deep, and sideways from the stem; it had, besides, a very thick bush of lateral roots, which extended every way in a hemisphere about nine inches from the stem and main roots."

626. Nobbe has shown that in year-old plants of certain closely allied gymnosperms the root-systems differ remarkably in the number of the rootlets and the total length of the roots.[3] In three species the determinations of the total length were as follows: —

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[1] Haberlandt: Physiologische Pflanzenanatomie, 1884, p. 152.

[2] Hales gives as the entire surface of these roots 2,286 square inches, or 15.8 square feet (Vegetable Statics, 1731, p. 6).

[3] The plants examined were grown from May to October. Two of Nobbe's tables (Die landwirthschaftlichen Versuchs-Stationen, xviii., 1875, p. 279) are here given: —

a. Number of Rootlets.

	Norway Spruce.	Silver Fir.	Scotch Pine.
Roots of the 1st order.	1	1	1
" " 2d "	85	48	404
" " 3d "	162	85	1,955
" " 4th "	5	0	749
" " 5th "	0	0	26

Silver Fir	1 meter.
Norway Spruce	2 meters.
Scotch Pine	12 meters.

All the plants upon which these averages are based were grown under the same conditions.

627. When any plant is lifted, even with great care, from the soil in which it has grown, many of its more delicate rootlets are torn off and left behind. Hence it is difficult to ascertain the total amount of roots belonging to a plant. Even the best plan yet devised for cleaning the root previous to measuring it — that of allowing a stream of water to wash away all the earth which it will detach — usually causes a few of the finer rootlets to be carried off. It has been shown, however, that the roots of peas, beans, and the common cereals are abundantly branched to a depth of more than a meter, and that many of them penetrate considerably further. Schubart states that the amount, by weight, of roots in peas and wheat, compared with that

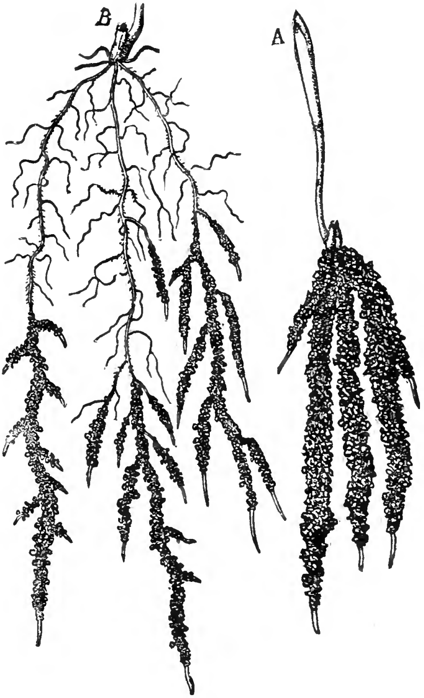

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FIG. 144. Roots of seedlings of Triticum vulgare. *B*, plant four weeks older than *A*. The soil clings in each case to the *younger* parts. (Sachs.)

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b. LENGTH IN MILLIMETERS.

	Norway Spruce	Silver Fir.	Scotch Pine.
Roots of the 1st order.	290	300	873
" " 2d "	1,333	636	4,438
" " 3d "	312	56	5,491
" " 4th "	5	—	1,143
" " 5th "	—	—	41

of the whole plant (all being dried), is less than fifty per cent.[1] By comparison of the weights and lengths of average pieces of the roots of barley, it has been found that the whole root-system in a vigorous plant is not far from thirty-seven meters in length; and that all this could be packed in a small volume of fine soil (about $\frac{1}{40}$ of a cubic foot).[2]

628. The nature of the soil, and especially the amount of moisture and of nutritive matters which it contains, have a marked influence upon the development of the root-system of a plant. Other things being equal, fertility of the soil favors compact branching, as is shown by experiments by Nobbe.[3]

Indian corn was grown for a time in several cylinders containing clay soil; then the earth was carefully washed away and the roots were compared. In the first cylinder the soil had

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[1] Amounts as given in Chemische Ackersmann, i. p. 193.

Roots of winter wheat (in April)	40 per cent.
" peas (four weeks after planting) . . .	44 "
" " (at flowering)	24 "

[2] Hellriegel: Hoffmann's Jahresbericht, 1864.

Nobbe (Versuchs-Stationen, 1875, p. 279) has given some instructive figures, showing the ratio of the surface above ground to that below in yearling plants of some common species of Conifers grown under similar conditions. Some of his figures are here given.

a. SURFACE OF ROOTLETS.

	Square millimeters.
Silver Fir	2,452.
Norway Spruce	4,139.
Scotch Pine	20,515.

b. SURFACE OF THE GREEN PARTS OF THE PLANTS.

	Square millimeters.
Silver Fir	1,451.
Norway Spruce	1,551.
Scotch Pine	4,304.

c. RATIO OF PARTS IN THE PLANTS EXAMINED.

	Silver Fir.		Norway Spruce		Scotch Pine
Parts above ground . . .	100	:	107	:	297
Parts below ground . . .	100	:	168	:	837

d. RATIO OF THE PARTS ABOVE GROUND TO THOSE BELOW.

Silver Fir	100 : 169
Norway Spruce	100 : 267
Scotch Pine	100 : 477

[3] Versuchs-Stationen, iv., 1862, pp. 220, 221.

been uniformly mixed with a fertilizing substance, and in this soil the roots had developed in a normal manner. In the second cylinder a layer of the fertilizing material had been placed three to four centimeters below the surface, and in the soil at this plane the roots had branched very abundantly. In the third cylinder a similar layer of the fertilizing matter had been placed half-way down the cylinder, and here the root-branches were far more numerous than elsewhere. In other cases the fertilizing substance had been placed at the bottom, around the sides, or in the middle of the cylinder, and in these places respectively the root-branches were most abundant. Substantially the same thing is observed in earth where the roots of plants meet with buried bones: the finer root-branches are developed around and afterwards in the substance of the decomposing animal matter, often forming dense mats.[1]

629. In some cases roots extend to very great distances; thus those of an elm have been known to fill up drains fifty yards distant from the tree.[2] It may be said, in general, that the roots of the common forest and shade trees reach to and beyond the eaves of the roof made by the leafy branches. "There is a constant relation between the horizontal extension of the branches and the lateral spreading of the roots. It is not by watering a tree close to the trunk that it will be kept in vigor, but by applying the water on the soil at the part corresponding to the ends of the branches. The rain which falls on a tree drops from the branches on that part of the soil which is situated immediately above the absorbing fibrils of the roots." [3]

630. The root-system of a plant, ever extending by its innumerable subdivisions into new soil, and clothed near the extremities of the rootlets with delicate epidermal cells, is a complex apparatus for osmosis placed under the most favorable conditions for absorption.

631. The course of the water after it has found its way into a plant through the epidermal cells of the newer portions of the roots, and the pressure which at times the watery liquids in roots exert, can be more conveniently examined at a later stage (see Chapter IX., "Transfer of Water through the Plant").

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[1] See also a paper by Detmer: Versuchs-Stationen, 1872, p. 107.

[2] Journal Royal Agricultural Society, vol. i. p. 364, contains some interesting cases of great length of roots.

[3] Balfour: Class Book of Botany, 1854, p. 427.

CHAPTER VIII.

SOILS, ASH CONSTITUENTS, AND WATER-CULTURE.

632. WHEN a plant is carefully dried at a temperature slightly exceeding that of boiling water until it ceases to lose weight, there remains behind a brittle combustible residue. The difference between the weight of the plant and that of the residue represents the amount of water previously contained in the plant. This differs widely, according to the kind of plant and its age. The following table gives the proportion of water contained in a few of the most common plants: —

Red Clover, before flowering	83	per cent.
" " in full flower	78	"
Oats, before flowering	82	"
" in flower	77	"
Turnip (root)	91	"
Beech (leaves), in summer	75	"
" " in autumn	55	"
Dry grains	14 to 15	"
Dry woods	15	"

633. If the brittle residue left after complete expulsion of the water is burned in the open air, there remains behind a small amount of gray ash; all the rest is wholly consumed. The amount of ash also varies widely, according to the kind of plant and its age. In the following table[1] are given the proportions for a few common plants: —

	Per cent of ash in fresh material.	Per cent of ash in dry material.
Red Clover	1.5	5.6
Sugar Beet (root)	.8	4.3
Indian Corn	1.1	5.5
" " (grain)	2.1	1.5
Beech (leaves), in summer . . .	1.3	—
" " in autumn . . .	3.	—

634. In a general way it may be said that the combustible matters are derived chiefly from the atmosphere, while all the

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[1] The student is referred, for detailed accounts of analyses from which these figures have been chiefly taken, to Johnson's "How Crops Grow," 1868.

water and the incombustible ash come from the soil. In the case of aquatics this general statement would not appear to hold, for they obtain all their substance from the water in which they live; but, as will be seen later, this source is essentially the same. We have examined in the previous chapter one of the means by which plants obtain their supply of water and ash materials, and it will be best to consider now the source from which this supply comes, before approaching the study of the combustible substance of plants.

SOILS.

635. **Formation of soils.** Soils are produced by the disintegration of rocks. This may be mechanical, as that caused by crushing, attrition, and the action of frost; or it may be and generally is associated with more or less chemical change. In soils, some of the products of the decomposition of organic substances are usually intermingled with purely mineral matters aggregated in various degrees of fineness. Soils exposed to atmospheric influences constantly change both in their physical properties and chemical composition, the changes being brought about chiefly by the combined action of moisture, carbonic acid, and oxygen.

636. Water not only wears away solid rocks by its mechanical action, but after it has insinuated itself into the crevices of rocks it accomplishes the work of disintegration far more rapidly by its expansion during freezing.[1]

When rocks become loosened by running water, or by the slow movement of glaciers, the crushing and grinding of the pieces which come into contact are sufficient to pulverize the hardest of the more common ones.

Water, especially when it holds carbonic acid in solution, is a very important agent in changing the characters of rocks: sometimes it does this by dissolving out portions of the rocks, sometimes by bringing about new combinations of their constituents. Moreover, rain-water contains a minute quantity of other matters besides carbonic acid, and these exert a powerful effect in disintegrating and dissolving certain rocks.

637. The free oxygen of the atmosphere is also an efficient agent in the changes by which rocks are broken down to form

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[1] The amount of expansion is usually given as approximately one fifteenth of the volume.

soils. Many rocks contain ferrous oxide, which readily undergoes further oxidation; certain sulphides in rocks are oxidizable under the ordinary conditions found in a moist atmosphere, and in such cases the chemical action results in rendering the rocks brittle.

638. Water can easily transport the finer particles of soil from where they were formed by disintegration of the rocks to points at distances from their source, varying with their weight. For this reason the particles accumulate in different degrees of fineness at different points along water-courses.

639. It is believed that during the Glacial period, when large portions of the northern hemisphere were covered deeply with sheets of moving ice, immense amounts of coarse and fine soils were carried far from the places where they were formed, and were heaped up more or less irregularly in the masses which now form gravelly hills and ridges. The glacial action now going on in the Alps shows how vast must have been the soil-making and soil-carrying power of the glaciers which once covered so much of our continent.

640. Soils which have not been carried by water or ice from the place where they were formed by some of the agencies mentioned above are not generally of great depth, and their nature can usually be made out by examination of the contiguous rocks.

641. **Classification of soils.** For our present purpose soils may be classified as gravelly, sandy, clayey, calcareous, loamy, and peaty. *Gravelly* soils differ widely in their chemical character, since the pebbles which compose them may be either chiefly quartz and fragments of rocks in which quartz predominates, or there may be also a good proportion of limestone, or of feldspathic rocks. With the coarse pebbles is intermingled a certain proportion of finer soil. *Sandy* soils are usually made up of fine quartz with which some other matters are associated, such as some compound of iron, grains of feldspathic minerals, micaceous particles, etc. In a few cases, however, the sandy soils differ widely from this composition; for instance, the green sand of New Jersey contains a large proportion (more than fifty per cent) of green grains of a silicate of iron and potassium. *Clayey* soils are generally derived from the disintegration of various feldspathic rocks, and are mixtures of hydrated aluminic silicate with many other matters. Such soils are generally adhesive, are retentive of water, and dry into a hard mass; these characters which belong to true clay are

found also in some soils which are not clays, and hence the term *clayey* is sometimes loosely applied. *Calcareous* or lime soils contain calcic carbonate in large amount. To calcareous clay, when the ingredients are in a state of rather fine subdivision, the name *marl* is frequently applied. *Peaty* or humus soils are those which contain a considerable proportion of partially decayed vegetable matter; when such matter decays under water it becomes peat, or muck; when it decays without much water it is generally known as mould.

642. By mechanical analysis, as by simple washing and sifting, it is possible to separate a soil into its mechanical ingredients, which are: (1) Gravel; (2) coarse sand; (3) fine sand; (4) clayey sand; (5) clayey substance, or fine clay.

The mechanical subdivision of soils has an important bearing upon their physical properties and upon their adaptability to the growth of roots and the sustenance of plants.[1]

From interesting studies by Darwin,[2] it is plain that in some localities earth-worms have exerted, by their burrowing and tunnelling, a vast influence in changing the physical character of the soils in which they thrive.

643. **Physical properties of soils.** Of these, the most important to be considered here are those which affect the relations of soils to liquids, to gases, and to heat; for all of these directly affect the growth and indirectly the nutrition of plants.

644. **Absorption and retention of moisture by soils.** It is convenient to examine the relations of soils both to liquid water and to aqueous vapor. Soils can absorb from the atmosphere and condense upon the surface of their particles, or in their interstices, a certain amount of the vapor of water. This property of absorption, known as that of **hygroscopicity,** is different in different soils, as shown by the following table from Schübeler.[3]

Five hundred centigrams of each soil carefully dried were spread over a surface of thirty-six thousand square millimeters, and exposed for varying periods to an atmosphere saturated with watery vapor; the amounts of waters absorbed (in centigrams) were as follows: —

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[1] The reader should examine a paper by J. D. Whitney (Plain, Prairie, and Forest), in which is discussed the probable influence of the extreme fineness of prairie soils upon the absence of forests. See American Naturalist, October and November, 1876.

[2] Darwin: The Formation of Vegetable Mould through the Action of Worms.

[3] Knop's Lehrbuch der Agricultur-Chemie, 1868, vol. ii. pp. 13, 14.

	12 hours.	24 hours.	48 hours.	72 hours.
Quartz sand . .	0.0	0.0	0.0	0.0
Calcareous sand	1.0	1.5	1.5	1.5
Clayey soils . .	10.5 to 15.	13 to 18.	14 to 20.	14 to 20.5
Clay	18.5	21.0	24.0	24.5
Garden earth .	17.5	22.5	25.0	26.0
Humus . . .	40.0	48.5	55.0	60.0

From these figures it appears (1) that the greater part of the vapor is condensed before the expiration of a single day, (2) that humus is by far the most hygroscopic, but (3) that clay can absorb a large quantity of vapor.

Temperature exerts a marked influence upon the capacity of soils to absorb aqueous vapor, as is shown by Knop's examination[1] of a sandy and of a rich earth; the amount of vapor absorbed diminishes with elevation of temperature.

645. The amount of liquid water which soils can absorb and retain is very different for different kinds of earth. In the following determinations by Schübeler dry soils were saturated with water upon a funnel, and the increase of weight was noted after all the excess of water had dripped away. The first column gives the percentage of increase in weight of soil; the second, the number of volumes of water that one hundred volumes of soil can take up; the third, the percentage of this water which evaporates from the soil in four hours when it is spread over a given surface.[2]

	1.	2.	3.
Quartz sand	25	37.9	88.4
Calcareous sand	29	44.1	75.9
Clay soil (60 % clay) . .	40	51.4	52
Clay soil (76 % clay) . .	50	57.3	—
Heavy clay (89 % clay) . .	61	62.9	34.9
Pure clay	70	66.2	31.9
Humus[3]	190	69.2	25.5

646. The degree of fineness exerts also some influence upon the absorptive power; but while pulverization increases that

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[1] Versuchs-Stationen, vi., 1864, p. 281, where are found also some interesting results recorded by Knop, in regard to the absorption of aqueous vapor by various organic substances.

[2] Knop's Lehrbuch, 1868, vol. ii. p. 26. The third column is cited from Johnson's "How Crops Feed," 1870, p. 180.

[3] Samples of peat have been known to absorb from 300 to more than 500 per cent of water.

power in some kinds of soil it diminishes it in others. Thus Zenger has shown that fine quartz sand absorbs about twice as much water as that which is coarse; on the other hand, fine brick-clay is not so absorbent as coarse.

647. Admixture of heterogeneous matters with soil generally lowers the absorptive and retentive power both of the soil and of the added substances. Treutler examined certain soil mixtures in the following manner: fifty grams of the soil were placed in one hundred cubic centimeters of water for twenty-four hours, the excess of water was allowed to drip away, and the amount then retained noted. The following are among his results: —

Soils.	Cubic centimeters of water retained.	Mixtures.	Cubic centimeters of water retained.
Fine earth	34.2	40 grm. fine earth and 10 grm. caustic lime	44.
Quartz sand	14.	40 grm. quartz sand and 10 grm. caustic lime	19.
Caustic lime	61.	40 grm. quartz sand and 10 grm. bone-dust	16.5
Bone-dust	46.	30 grm. quartz sand and 20 grm. bone-dust	9.

From Treutler's tables it appears that the absorptive and retentive capacity of a mixture of two substances *may* equal that of the constituents, but that generally it becomes lower.

648. A soil may be so fine and compact that rain will not readily penetrate it; or on the other hand it may be so porous as to allow the water which falls on it to pass rapidly down through it. A soil of proper texture will receive the rains, and, as has been shown by the foregoing paragraphs, retain a certain amount in its pores, the excess draining away.

649. Evaporation of water goes on continually from the surface of moist soil, unless the atmosphere is saturated, and the amount of evaporation depends largely upon the amount of moisture present in the state of vapor in the atmosphere at any given time. But the retentive power spoken of above (which is plainly opposed to evaporation) is very different in different soils; for this reason about three times as much water evaporates from quartz sand as from the same amount of humus equally exposed for a given time. When by evaporation the soil becomes dry at the surface, a draft is made upon the supply of water retained in it at a greater depth, and this water then rises by capillarity to the drier layers. It is therefore said that there is a constant movement of water in the soil.

650. A distinction may be properly made between (1) that water which remains as a copious supply beneath the surface of the ground, existing there plainly as a liquid, (2) that which adheres to the particles of soil imparting to them a moist appearance, (3) that which adheres to the particles of an air-dry soil and which does not affect at all the appearance of the particles. The first has been called *hydrostatic*, the second, *capillary*, the third, *hygroscopic* water. It is from the two latter that the roots of plants other than aquatics usually obtain their supply of moisture.[1]

651. The relations which evaporation and drainage bear to the total rain-fall upon the soil have been examined during a series of nineteen years at Rothamsted, in England. The following figures are based on the results during ten years (September, 1870, to August, 1880).

Rain-fall	30.68	inches.
Drainage from soil		
at 20 inches depth	13.21	"
at 40 " "	13.94	"
at 60 " "	12.17	"
Amount of water retained by soil, or evaporated		
at 20 inches depth	17.47	"
at 40 " "	16.74	"
at 60 " "	18.51	"
Percentage of rain-fall lost by drainage		
at 20 inches depth	43.1	"
at 40 " "	45.4	"
at 60 " "	39.7	"
Percentage of rain-fall retained by soil, or lost by evaporation		
at 20 inches depth	56.9	"
at 40 " "	54.6	"
at 60 " "	60.3	"

652. Soils are not only acted upon by the solvent power of water, as shown in 636, but many soils possess the remarkable property of removing saline matters from aqueous solutions.

The interesting fact that impure water can be freed from some of its foreign matter by being filtered through earth has long been known, but its significance in the nutrition of plants does not appear to have received attention until 1819. Gazzeri[2] at

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[1] For a full discussion of this subject, which is most important in its bearings upon the cultivation of plants, the student should study Johnson's "How Crops Feed," p. 199.

[2] From a note by Orth: Versuchs-Stationen, xvi., 1873, p. 57. The discovery is generally ascribed to Bronner, 1836. The fullest treatment was by Way: Journal Royal Agricultural Society, 1850, and later.

that date says: "Earth, especially clay, seizes upon the soluble matters intrusted to it, and holds them back, in order that it may gradually furnish them to plants according to their needs."

653. When dilute solutions of a salt are slowly filtered through sand which contains a good admixture of clay, the water passes out for a time without more than a trace of the salt, and in some cases all the salt is retained by the soil. Even sewage liquids can by this method be freed from their offensive ingredients. This phenomenon of filtration is due to adhesion (that is, the attraction which the surface of one kind of matter has for another kind of matter). The substances which are removed by the particles of soil are so fastened to them that even when the soil is washed in pure water only traces of them are removed.

654. **Chemical absorption by soils.** Besides this physical adhesion, there are exhibited by many soils certain chemical phenomena also, which have been collectively termed *chemical absorption.* If a solution of potassic nitrate is filtered through a well-pulverized clay soil containing an admixture of insoluble compounds of magnesium and calcium, such as are met with in almost any ordinary soil, the water which drains off will contain very little if indeed any potassium; but it will have, instead, magnesium and calcic nitrate in appreciable amount. But this absorptive power of a soil is soon satisfied; for after a certain amount of potassium has been removed no more is taken up.

The strength of the saline solution affects the amount of absorption, more of the base being absorbed from strong solutions. Different substances are absorbed by the soil in different amounts; thus in the experiments by Peters the bases were absorbed in the following order: (1) Potassa, (2) Ammonia, (3) Soda, (4) Magnesia, (5) Lime. Different soils absorb the same substance in different amounts, depending upon the physical condition of the soil, but chiefly, it is believed, upon the mode in which the substance is combined; thus, more potassa is absorbed from the phosphate than from the carbonate, and more from the latter than from the sulphate.

In general it may be said that the salts of the alkalies and the alkaline earths are so absorbed by rich soils that the bases are retained in new combinations, while the acids pass off, having also, of course, formed new combinations. The phosphates and silicates are retained undecomposed. The case of the latter compounds may be regarded as the ordinary physical absorption, that of the former as the so-called chemical absorption.

655. The matters absorbed by the soil may be released after a time and pass into solution again, or they may be displaced from the soil-particles by the filtration of new solutions. When it is remembered that rain-water exerts a powerful solvent action upon some portions of the soil, and that, on the other hand, the soil can remove from aqueous solutions some of the matters therein dissolved, the complicated nature of the problem which presents itself is at once apparent. Examination of the waters which drain through soil, and which may fairly represent the resultant of the solvent action of the water and the absorptive power of the soil, shows that from thirteen to fifty parts of solid matters may remain dissolved in 100,000 parts of water. (The question of nitrogen compounds in drainage-water will be examined in a subsequent chapter.)

656. **Condensation of gases by soils.** Soils have the power of condensing in their pores certain amounts of different gases. These condensed gases are released when the soils are subjected to a high temperature, say 140° C., and their amounts can then be measured. The figures below give the results of the measurements in several instances, 100 grams of soil being taken in each case.

Soil.	Cubic centimeters of gas yielded.
Peat	162
Clay	30
Moist garden soil	14

It is found that in the soil there is present a smaller amount of oxygen and a larger amount of nitrogen than in the atmosphere. The percentage of carbonic acid in the soil is also somewhat larger than that in the atmosphere; especially in soils which contain much organic matter.

657. **Root-absorption of saline matters from soils.** Having seen that the soil, the principal medium in which roots extend, possesses the power of absorbing and retaining water, saline matters, and gases, attention must next be directed to the conditions under which the root-hairs can abstract from it the matters requisite for the plant. These conditions are (1) presence of free oxygen, (2) a certain temperature, (3) the presence of saline matters in an available form in the soil.

658. Free oxygen is necessary to all protoplasmic activity,

and the plant will speedily show when the amount required for the absorptive activity of its roots is not furnished. Different plants, however, require different amounts: thus aquatics and marsh-plants do not need so much oxygen for their roots as do plants which ordinarily grow in a porous soil. Partial exclusion of oxygen from the roots of the latter by keeping the soil saturated with water usually injures the plants in a short time.

It has been shown by Sachs and others that seedlings of many plants normally growing in dryish soil will develop if treated as aquatics; better results are obtained, however, if air is occasionally passed through the water.

659. The temperature needed for the absorptive activity of roots varies with different plants. It may be said, however, that for any given plant the absorptive power increases with increase of temperature.

660. Different soils have very different relations to temperature. Leaving out of account the small amount of warmth derived from the chemical changes going on in the soil by which heat is evolved, it may be said that the heat of the soil is derived from the sun's rays. The angle at which these rays strike the soil must have a great influence upon its temperature. Again, there are various local causes, such as protecting or reflecting walls, which may considerably modify the temperature in any given case. The soil itself exerts a marked influence upon the amount of heat which it can receive and retain. Dark soils absorb heat most readily; but it has been shown that black soils are less absorbent of heat-rays than are those which are dark gray. The radiating power of a soil depends upon the character of its surface, being much greater in the case of fine mould than in that of coarse, gravelly soils.

661. It must be noted, however, that the heat-rays which fall upon a given soil may have different degrees of intensity. Some bodies (*e. g.* lampblack), can absorb and give off by radiation heat of high as well as that of low intensity; while other bodies (*e. g.* snow), absorb heat of low intensity only. Heat of high intensity is converted into that of low intensity by the interposition of a black covering of any kind which can absorb it and give it out below as heat of low intensity.

662. At the depth of fifty feet the temperature of the soil in the temperate zone varies within the limits of one degree, and at a depth somewhat below this it is constant. The stationary temperature at such a depth is the same as that of the mean

annual temperature of the atmosphere in temperate regions.[1] Moisture exerts a very great effect in equalizing the capacities of different soils for absorbing and retaining heat.

663. That the saline matters in the soil must be in a form in which the plant can make use of them, appears from what has been said about osmosis. It should be specially noticed, however, that younger roots may exert a solvent action upon soil-particles.

Root-hairs, as Sachs[2] has shown, evolve small amounts of acid, which exert a distinctly corrosive effect upon certain mineral matters with which they come in contact. Hence there is a continual unlocking of the nutritive mineral materials fastened in the soil; the release being at the very points where the root-hairs are present to absorb them.

ASH CONSTITUENTS OF PLANTS.

664. These occur in all parts of plants. It has been shown (p. 39) how frequently cell-walls are impregnated or incrusted by mineral matters, which after careful calcination may be left as a distinct skeleton of the tissues of which they formed a part. But the matters within cells, both the protoplasmic substance and the cell-sap, also contain a certain amount of incombustible material. The total amount of ash constituents varies greatly in different plants, in different parts of the same plant, and also

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[1] Penhallow, Soil Temperatures (Houghton Farm Experiment Department), 1884. See also Knop, Agricultur-Chemie, i., 1868, p. 469.

[2] Moldenhawer (Beyträge), in 1812, expressed the view that roots probably set free certain matters which can unloose nutritive materials. De Candolle (Physiologie, 1832) described the corrosive action of lichens on underlying rocks; and Liebig, in 1839, studied the action of roots on the color of litmus solutions.

Sachs's experiment (1860) is well adapted to class demonstration. A polished plate of marble is covered with moist saw-dust, and in this a few seeds are planted. After the seedlings have grown for a time the saw-dust is removed, when the marks left upon the stone by the corroding rootlets can be plainly seen. If the corroded marble is rubbed slightly with a little vermilion, the traces made by the root-hairs will be very distinct. In the early publication of Sachs, the secretion by which the corrosion is effected was said to be carbonic acid; but he does not appear to hold this view now. Whether the action is due to acetic acid, as Oudemann and Rauwenhoff suggest, or to different acids varying with plants or times, as intimated by Pfeffer, it is certainly highly corrosive in some cases. In an experiment by Schulz, the rootlets of germinating Leguminosæ and Gramineæ exhibited a faint alkaline reaction (Journal für Praktische Chemie, lxxxvii., 1862, p. 135).

in many cases with the age of the plant. The following table[1] indicates the per cent of ash in a few instances: —

Turnip (fresh)	.7
Sugar beet (fresh)	.8
Potatoes (fresh)	.9
Red clover (fresh)	1.3
Red clover (dry)	5.6
Birch-wood (dry)	.2
Apple-tree wood (dry)	1.1
Walnut-wood (dry)	2.5
Birch-bark	1.1
Mulberry leaves (fresh)	1.1
Horse-chestnut leaves (spring)	2.1
Horse-chestnut leaves (autumn)	3.0
Apples (fresh)	.3
Pears (fresh)	.4
Flax-seed	3.2
Clover-seed	3.6
Hemp-seed	4.8
Beech-nuts	2.7
Wheat-grains	1.7
Hemp (entire plant)	2.8

665. **Composition of the ash of plants.** Examination of trustworthy analyses of the ash of flowering plants shows that certain elements are always present in it. These are *potassium*, *calcium*, *magnesium*, and *phosphorus*. Besides these, which always appear in appreciable amount, there are others which are nearly or quite as constant in occurrence, although in some reports of analyses they are not given, because existing in such small proportion. They are *iron*, *chlorine*, *sulphur*, and *sodium*. The elements mentioned are usually recorded in analyses in the following combinations: potassa, phosphoric acid, lime, magnesia, sulphuric acid, soda, and ferric oxide. But it is to be observed that the combinations stated in the tabulation of analyses are by no means designed to exhibit all those in which the elements occur in the plant; for instance, the sodium and potassium are presumably combined with the chlorine. Again, it must be noticed that upon combustion the mineral matters in the plant are commingled with a larger or smaller amount of carbonates, the

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[1] E. Wolff, Die Mittlere Zusammensetzung der Asche, 1865, p. 77 *et seq.* See also an excellent revised translation of Wolff's tables in the Appendix of Johnson's "How Crops Grow" (1868). For the percentage of ash in trees and woody plants, as well as the amounts of phosphoric acid and potash found in such ash, see a very valuable table by Storer (Bulletin Bussey Institution, 1874, pp. 207–245).

amount depending somewhat "upon the temperature at which the ash is prepared." In the following short table a few of the many analyses collated by Johnson[1] have been brought together to exhibit the proportions of the ash constituents.

Name of plant.	Potassa.	Phosphoric acid.	Lime.	Magnesia.	Sulphuric acid.	Soda.	Ferric Oxide.	Silica.	Chlorine.
Root of sugar beet .	48.	14.4	6.4	9.5	4.7	10.4	1.	3.8	2.3
Potato tubers . .	60.9	18.3	2.4	4.6	7.	1.7	.9	1.9	2.7
Stalks of Indian corn	36.3	8.3	10.8	5.7	5.2	1.25	2.4	28.8	
Wheat-grain . .	31.3	46.1	3.2	12.3		3.2		1.9	

666. The foregoing table indicates that wide diversity exists in the amounts of the ordinary ash constituents of common plants. But comparison of a large number of analyses shows that the following general statements may be made: —

1. Plants which closely resemble each other in structural characters have substantially the same proportions of ash constituents.

2. The proportions of the ash constituents in any part of a plant may vary within certain limits; and these limits may differ at different periods of growth.

3. The proportions may vary widely for different parts of the same plant.

667. Not only are the elements enumerated in the first list in 665 always present in the ash of flowering plants, but they are shown by experiment to be indispensable to their full development; and there is a reasonable certainty that iron, sulphur, and probably chlorine, should be placed in the same category of indispensable elements.

According to Nägeli,[2] some of the flowerless plants, notably the moulds and the schizomycetes, can attain full development with fewer elements.

WATER-CULTURE.

668. **Apparatus.** While chemical analysis of the ash of plants reveals the character of the mineral matters which they absorb from water and soil, it cannot materially aid the investigator in

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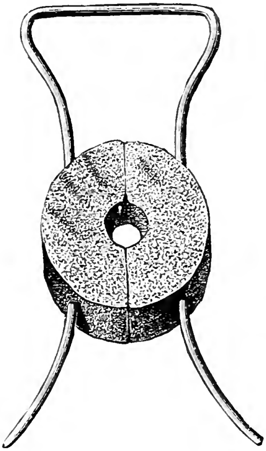
[1] How Crops Grow, 1868, p. 150.

[2] Sitzungsb. d. bayer. Akad., 1879, p. 340.

learning the office of each constituent. This is more satisfactorily accomplished by water-culture, which, reduced to its simplest terms, consists in furnishing to the plant under proper conditions different mineral matters in aqueous solution, and noting their effects upon it. It has been long known that plants can be grown to a considerable size in ordinary river-water, or water holding in solution certain mineral salts.[1] But it was not until 1858 that the method of water-culture was systematically applied by Sachs, Knop, and Nobbe to the investigation of the relative value and the office of the different mineral constituents in the nutrition of plants. It has since been widely employed in the examination both of flowering and flowerless plants.

669. The method adopted for ordinary flowering plants is essentially as follows: seeds are made to germinate upon some clean support, for instance moist sponge or cotton, horse-hair cloth, or perforated parchment-paper, and when the root of the seedling is a few centimeters long and the plumule is somewhat developed, the plantlet is secured to a firm support at the surface of a cylindrical glass vessel, in such a manner as to allow the roots to dip into the nutrient liquid which it contains, while the body of the seed is not immersed. One of the simplest supports for the plantlet is shown in Fig. 145. A perforated cork is cut in halves, and the two parts are held together by a spring. The pressure exerted by the spring is sufficient to keep the plantlet in place, and not enough to injure it in any way. When the plant has attained the height of a few inches, it is well to provide a firm rod at the side of the cork, so that the stem can be held in place. Certain precautions have been found advantageous: (1) the roots in the liquid should be kept darkened; (2) the solution should be frequently renewed.



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When skilfully managed, this method of culture gives very

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[1] Woodward (Philosophical Transactions, 1699) and Duhamel (Traité des Arbres, 1765) have given accounts of their cultivation of various plants in this way.

satisfactory results; in many cases plants have been carried safely throughout their whole development from seed to seed. The principal difficulties arise from the invasion of moulds, and from the continual changes which the nutrient solution undergoes.

670. In Tharandt,[1] where the method has been very successfully applied in numerous series of cultures, the following outfit suffices: (1) small glass vessels covered with gauze, upon which the seeds swollen by twelve hours' immersion in water, and subsequently sprouted on filtering-paper, are placed for further development; (2) wide-mouthed vessels of the capacity, respectively, of one, two, and three liters, each of which is provided with the spring and cork already described.

671. By the careful use of these simple appliances the rôle which each of the ash constituents plays in the life and growth of plants has been ascertained. But although there is a substantial agreement among experimenters as to the more important points, there are a few unsettled questions.[2]

672. **Normal nutrient solution.** It is plain that an aqueous solution of the salts necessary for the most active and complete development of the plant should have these salts in the right proportion. The solution advised for ordinary use in the above experiments is generally known as the Tharandt normal-culture solution. Nobbe[3] gives the proportions as follows: —

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[1] Success in water-culture demands the closest attention to all the external conditions of the plant. The amount of light and heat must be carefully regulated, and the plants must be kept free from any insects and parasitic fungi. The latter is one of the most difficult and discouraging tasks connected with the method of experimenting. In order to secure the best surroundings for the cultivation of plants in water, a heavy table moving with wheels on rails has been employed at the experiment-station at Tharandt; upon this the glass vessels can be carried with the least liability to jarring, from the open air in the daytime to a suitable protection at night or during wet weather.

[2] Moreover it is to be borne in mind that the conditions of water-culture are very unlike those of ordinary culture in respect to the surroundings of the roots themselves, and it is believed that to this difference of conditions may be ascribed some of the unsettled questions. The root-hairs developed in contact with moist particles of soil are not the same as those grown in water alone. To avoid this possible source of error, various finely divided substances have been suggested as a proper support for the roots and rootlets; for instance, the charcoal from sugar, powdered quartz, etc. When these are employed, the roots of the plant are made to grow directly in the artificial soil which is watered with the experimental solutions.

[3] By the use of this solution buckwheat plants can be carried through their entire development, as is shown by Nobbe, in Versuchs-Stationen, 1868, p. 4. He arranged nine plants in five vessels, each of three litres capacity, in such

4 Equivalents of	Potassic chloride
4 Equivalents of	Calcic nitrate
1 Equivalent of	Magnesic sulphate (crystallized)

One part of the mixture of these salts is to be dissolved in one thousand parts pure water, and then a trace of ferric phosphate is to be added, and at times during any culture a trace also of potassic phosphate. The proportions of the above salts to a liter of water are given as follows by Bretfeld:[1] —

	Gram.
Potassic chloride	.207
Calcic nitrate	.456
Magnesic sulphate	.171

673. Pfeffer recommends the formula suggested by Knop:[2] —

Calcic nitrate	4 parts by weight
Potassic nitrate	1 part by weight
Magnesic sulphate (crystallized)	1 part by weight
Potassic phosphate	1 part by weight

These salts are to be thoroughly mixed and the mixture used in the proportions of $\frac{1}{2000}$, $\frac{1}{1000}$, $\frac{1}{500}$ parts of water. To the solutions, when ready for use, a drop or two of a solution of some iron salt, or a decigram of ferric phosphate, must be added.

674. According to Knop, the first of the solutions mentioned above (one half pro mille) is as dilute as can be useful; and on the other hand, a five pro mille solution is as strong as can be employed with safety. But the stronger solution should be used as the plant comes into flower. The slight turbidity which is frequently noticed in these solutions may be disregarded.

If the solutions become alkaline while in contact with the roots, as they are very apt to do, a trace of dilute nitric acid may be added with advantage. But it must not be forgotten that it is best in every case to renew the solutions frequently, and as a rule to employ them in tolerably large amounts. Moreover, it is advantageous to pass a current of air occasionally through the solutions in which the roots are placed, for the purpose of supplying more oxygen to them.[3]

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a manner that 1 and 2 contained one plant each, 3 and 4 two plants each, and 5 three plants.

[1] Das Versuchswesen auf dem Gebiete der Pflanzenphysiologie, 1884, p. 120.

[2] Lehrbuch der Agricultur-Chemie, i. 1868, p. 605.

[3] For solutions for the cultivation of fungi various formulas have been proposed, only a few of which can be here referred to: (1) 3 to 8 grams of sugar

675. The constituents may be taken up by the roots in larger proportion than the needs of the plant demand. The excess may (1) remain in solution in the sap of the plant, (2) may escape to a slight extent through superficial parts,[1] (3) may form insoluble incrustations or concretions upon or in the plant.[2]

676. **The office of the different ash constituents.** *Potassium.* The most conclusive evidence in regard to the importance of this element is afforded by experiments by Nobbe, Schroeder, and Erdmann.[3] Plants of Japanese buckwheat were grown in a nutrient solution free from any trace of a potassium salt. Examination after a few weeks showed that all the organs of the plants were free from starch, and that although the points of growth remained sound, all growth had practically ceased. Even in the chlorophyll-granules not more than a trace of starch could be detected. As soon as a salt of potassium was added to the water, the plants began to grow again, and thenceforth the development was normal. From the same series of experiments it appeared that the chloride was the best form in which potassium could be given to these plants, and the nitrate the next best; while on the other hand the phosphate and the sulphate appeared to exert a less favorable effect. After use of a solution of the latter salt the leaves were fleshy, more or less rolled up, and it was evident that the starch formed in them was not transferred to the other organs of the plant. Nobbe's statement follows: "The production of starch in the leaves is not dependent upon the form in which potassium is afforded to the plant, but this

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in 100 cubic centimeters of water, to which $\frac{1}{2}$ to 3 pro mille of the above salts (see 673) may be added, and also a trace of ammonic tartrate (Pfeffer, Pflanzenphysiologie, i. p. 254); (2) Pasteur (Ann. de Chimie et de Physique, 1862, p. 106) recommends the addition to 100 c.cm. of water, of 10 grams of cane-sugar, .5 gram of ammonic tartrate, and .1 gram of the ash of yeast; (3) Nägeli (Sitzungsb. d. bayer. Akad., 1879) has the following: 100 cm. water, 3 grams cane-sugar, 1 gram ammonic tartrate, 4 grams phosphoric acid neutralized by the ash of peas or wheat; (4) Nägeli suggests also, for the cultivation of Schizomycetes, 100 c.cm. water, .1035 gram hydro-potassic phosphate, .016 gram magnesic sulphate, .013 gram potassic sulphate, .0055 gram calcic chloride.

[1] Sachs (Botanische Zeitung, 1862, p. 264) states that drops of water placed on the leaves of Tropæolum and Cucurbita are found after a time to be alkaline. Saussure (Recherches chimiques, 1805, p. 263) asserts that if leaves of fresh plants are washed with water, the ash which they yield on combustion is found to be poorer in alkaline salts than that of leaves which have not been so treated.

[2] Cystoliths and the like, the incrustations upon certain species of Saxifrage, are cited as examples of the latter.

[3] Versuchs-Stationen, xiii., 1870, p. 357.

element must be present in order to have any starch formed. The transport of the starch from the leaves to other parts is, however, dependent upon the form in which the potassium is presented to the plant, and for this purpose the chloride is most efficient."

677. *Calcium and magnesium.* These elements cannot replace one another in the plant, though it is not clear what office they perform. Pfeffer regards it as possible that calcium may play an important part in the formation of the cell-wall, inasmuch as it can always be detected there. Melnikoff is quoted by Pfeffer[1] as stating that in the cell-wall calcium generally exists as the carbonate. It is suggested by Sachs that this element may enter into combination with cellulose, as it does with some other carbohydrates.

When seedlings are grown in pure water their development after a short time becomes completely checked, and the addition of all necessary substances except calcium salts fails to stimulate a normal growth; but after the addition of a small amount of any calcium salt the normal processes of the plant recommence at once.[2] Regarding the almost universal occurrence of calcic oxalate in plants, Sachs says: "The importance of calcium must therefore be sought partly in its serving as a vehicle for sulphuric and phosphoric acid in the absorption of food-material, and partly in its fixing the oxalic acid, which is poisonous to the plant, and rendering it harmless."[3]

678. *Phosphorus.* The principal and perhaps the only combination of this element available for plants is phosphoric acid (the phosphates). The experiments by Ville upon the absorption by plants of calcic phosphite and hypophosphite, although not conclusive, make it appear probable that these salts cannot replace the phosphate in absorption.

It is not clear what the office of phosphorus is in the plant, but in some of its compounds it is so often associated with the soluble albuminoids that it is believed to assist in the transfer of these matters. Schumacher holds that the chief work of the alkaline phosphates is the acceleration of the diffusion of these difficultly diffusible substances (the albuminoids).[4] (See 957.)

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[1] Pflanzenphysiologie, i., 1881, p. 259.

[2] Boehm: Sitzungsb. d. Wien. Akad. Band lxxi. Abth. i., 1875, p. 481.

[3] Text-book, 2d ed., 1882, p. 699.

[4] "If these [alkaline phosphates] substances are mixed with a solution of albumin, or if a solution of them is permitted to diffuse against one of albumin, a much greater amount of the latter will pass through the membrane than

679. *Iron.*[1] When a plant is provided with a nutrient solution containing all essential elements except iron, its chlorophyll-granules fail to attain complete development. They remain in an imperfect condition, and do not have the characteristic green color. Upon the addition of a mere trace of a salt of iron to the solution a change is observable at once, the granules assuming their proper shape and color. Plants grown in a solution without iron have a pale and even blanched look, which at once disappears when iron is added; moreover, a local effect is produced when a solution of a salt of iron is placed on the surface of the blanched leaves of such plants, — a green color is given wherever it touches. But it must not be supposed that the failure of some leaves to produce chlorophyll at certain points or spots is always due to absence of iron.

It is not clear that iron, which is so necessary to the production of chlorophyll, enters into the composition of either the granule or the pigment; but according to Pfeffer there is a strong probability that in the latter it exists in the form of some organic compound. Iron has been found in the cell-walls of certain algæ[2] (as an incrustation), and also in the fruit of Trapa natans, the frond of Lemna trisulca, and sparingly in other plants, as shown by the analyses collated by Wolff.

680. *Chlorine.* This element appears, from experiments by Nobbe[3] and Beyer,[4] to be indispensable to the full development of some plants (*e. g.*, buckwheat), but it is not required for many others (*e. g.*, Indian corn).[5] Nobbe concludes, from his experi-

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would otherwise be the case. In the life of the plant this work of the alkaline phosphates plays a very important rôle" (Physik der Pflanze, 1867, p. 129).

[1] That iron is indispensable to the full vigor of plants was shown by Eusèbe Gris in 1843, and the subject was further studied by Arthur Gris in 1857. Salm-Horstmar (in 1856), Sachs, and others have added much to the knowledge of the subject, showing that no other element can replace iron in producing the changes noted above.

[2] Cohn: Beiträge zur Biologie der Pflanzen, 1870, p. 119.

[3] Versuchs-Stationen, vii., 1865, p. 371; xiii., 1870, p. 394.

[4] Versuchs-Stationen, xi., 1869, p. 262.

[5] Knop: quoted by Pfeffer, Pflanzenphysiologie, i., p. 259.

The conclusions reached by Johnson in 1868 appear to need little modification at the present date. "1. Chlorine is never totally absent. 2. If indispensable, but a minute amount is requisite in the case of the cereals and clover. 3. Buckwheat, vetches, and perhaps peas, require a not inconsiderable amount of chlorine for full development. 4. The foliage and succulent parts may include a considerable quantity of chlorine that is not indispensable to the life of the plant" (How Crops Grow, p. 182).

ments, that it is required for the transfer of starch. Associating this view with what is known regarding the office of potassium, it is easy to see why potassic chloride should be so useful a salt.[1]

681. *Sulphur* is absorbed by plants in the form of the soluble sulphates. These are believed to undergo immediate decomposition in the plant; for example, calcic sulphate is decomposed at once by oxalic acid, and calcic oxalate is formed. The sulphuric acid thus set free is reduced, the sulphur entering into the constitution of the albuminoids[2] (see 884).

682. *Sodium* salts cannot wholly replace potassium salts in the plant; nevertheless, for a portion of the potassium needed by the plant an equivalent amount of sodium can in some cases be substituted. It has been found possible to cultivate successfully some maritime plants which normally contain a certain amount of sodium salts, when potassium has replaced sodium in the water furnished to the plant.

683. **Rarer constituents.** Besides the ash constituents always detected in plants, there are certain elements which are only occasionally met with in greater or less amount, and these will be next considered.

684. Silicium. This element is so abundant in the ash of many grasses, Equisetaceæ, etc., that it almost claims a place in the list of indispensable elements; but experiments have shown abundantly that in grasses at least, the proportion of it present can be reduced to a very low point without materially affecting the vigor of the plant or the strength of the culms. Thus Sachs[3] showed, in 1862, that the amount of silicic acid in the ash of Indian corn could be reduced from 18 per cent to .7 per cent. without injurious effect on the plant.

685. Zinc has been detected in many plants grown on soil containing it in considerable amounts; for instance, that at Altenberg[4] (near Aix). Freytag[5] found that all plants experimented upon were able to absorb more or less zinc when it

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[1] Bretfeld: Das Versuchswesen, 1884, p. 134.

[2] Holzner: Flora, 1867. An interesting paper by Hilgers (Pringsh. Jahrb., vi., 1867, p. 285) gives an account of the formation of crystals of calcic oxalate in various parts of plants, and presents certain speculations as to their origin.

[3] Flora, 1862, p. 53. Further experiments are recorded by Knop (Versuchs-Stationen, iv., 1862, p. 176), Rautenberg and Kühn (Versuchs-Stationen, vi., 1864, p. 359), Birner and Lucanus (Versuchs-Stationen, viii., 1866, p. 141).

[4] Sachs: Handbuch der Experimental-physiologie, 1865, p. 153.

[5] Chemisches Central-blatt, 1870, p. 517.

was offered in large amount; nevertheless, Gorup-Besanez[1] could detect none in peas and buckwheat cultivated in a soil containing a fair amount of zinc carbonate. It is sometimes said that Viola tricolor and Silene inflata grown on zinc soil take up an appreciable amount of this element; and further, that certain plants are directly affected in shape by the presence of zinc in the soil; in fact, varieties based upon this supposed relation have been described. The experiments of Hoffmann,[2] however, throw much doubt upon the relation of the zinc to a change of form, except in the single case of Viola lutea.

Aluminium[3] occurs in traces in many plants, while in species of Lycopodium (*e. g.* complanatum) it is present in large amount.

Manganese[4] is abundant in the ash of Trapa natans, Quercus Robur, and Castanea vesca.

Cæsium and Rubidium[5] have been detected by the spectroscope in minute amounts in many plants.

Fluorine[6] has been found in the ash of Lycopodium clavatum, and traces of it in other plants. Iodine and Bromine[7] are found in marine algæ, in much smaller proportions in aquatics growing in estuaries (for example, Zostera), and in minute amount in some plants grown far from the sea.

Barium, Strontium, and Silver have been found in the ash of Fucus. Mercury, Lead, Copper, Cobalt, Nickel, Tin, Thallium, Selenium, Titanium, and Boron have all been found by analysts in the ash of certain plants, but always in the merest traces. Arsenic[8] has also been detected in a few instances.

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[1] Annalen der Chemie und Pharmacie, cxxvii., 1863, p. 243. This paper contains an account of the relations of agricultural plants to metallic poisons.

[2] Botanische Zeitung, 1875, p. 628.

[3] Knop: Lehrbuch, p. 263; Rochleder: Phytochemie, 1854, p. 237.

[4] Wolff's Die Mittlere Zusammensetzung der Asche.

[5] Laspeyres: Annalen der Chemie und Pharmacie, cxxxviii., 1866, p. 126.

[6] Salm-Horstmar: Annalen der Physik und Chemie, cxi., 1860, p. 339.

[7] Chatin, in Comptes Rendus, lxxxii., 1876, p. 128.

[8] Numerous references to the literature of this subject will be found in Sachs's Experimental-physiologie, and in Mayer's Lehrbuch der Agrikulturchemie.

CHAPTER IX.

TRANSFER OF WATER THROUGH THE PLANT.

686. WATER is a constituent of all active cells. The protoplasmic body of the cell possesses a marked affinity for it, and up to a given point can abstract it from the ordinary surroundings, but under certain conditions releases it again. If a water-plant in full activity is removed from water and exposed to the air, it speedily loses by evaporation a considerable part of its constituent water, and shows the effect of this loss by a collapsing of its cell-walls and by a withering of all its parts. But if only a small portion of the plant is lifted above the surface of the water, the loss which takes place will be partially supplied by transfer through the cells remaining submerged. Two points are made clear by this simple experiment: (1) evaporation goes on with great rapidity from the exposed surface of the plant; (2) only a part of the loss of water can be made good by transference from submerged portions.

687. Comparison of the structure of a water-plant with that of an ordinary plant adapted to growth in the air shows that the surface of the latter is such as to prevent very rapid evaporation, and also that the loss caused by the evaporation can be made good if the lower part of the plant remains in contact with water. In other words, the plant (1) has a surface which protects it against too great loss of water; and (2) is provided with a system by which the needed supply of water can be replenished.

688. But it is not alone by evaporation from the surface that water is consumed by the plant. Wherever growth goes on or work is done, water is consumed, and a fresh supply is required. The question of the transfer of water is therefore a general one.

SOME OF THE RELATIONS OF WATER TO TISSUES.

689. The cell-wall which separates the cavity of one cell from that of its neighbor is a permeable membrane. According to the hypothesis of Nägeli (see 588), it is composed of solid particles (micellæ), each of which is enveloped in an adherent film

of water, and thus prevented from coming in contact with those around it. According to this hypothesis, all the water in a cell-wall is practically continuous, and can flow freely between the micellæ; therefore, if a cell contains its maximum amount of water, and the cell-wall is tense, the water is in a state of equilibrium. Likewise in a tissue containing its maximum amount of water this is in equilibrium. But the balance can be easily disturbed in a plant by evaporation from the surface, or by other causes before mentioned. If, however, a sufficient part of the absorbing surface of the plant is in contact with water, the balance can be restored, since the water in the cell-walls is practically continuous with that in the surroundings. The equilibrium is restored by the transfer of the water outside the cell-wall to the cell-wall itself, and thence to the parts within. The tendency to the restoration of the equilibrium of water in a plant is so great that root-hairs can abstract even the firmly adherent hygroscopic water from particles of soil (see 644). From the roots or other absorbing organs the water passes sooner or later to the place of consumption.

690. In most cellular plants and in masses of cellular tissue all the cell-walls have substantially the same capacity for transfer of water; but in all plants which possess a fibro-vascular system the transfer takes place chiefly by means of the lignified cell-walls; and even in cellular plants like mosses, it is in those cells which are elongated and otherwise differentiated to form an imperfectly developed framework that the rapid transfer is made.

691. **Transfer of water in woody plants.** In ligneous plants the water is transferred most rapidly through the woody tissues. This is experimentally proved by "girdling" their stems; that is, removing a ring of bark without injuring the wood. For a time the leaves remain fresh, and the plants appear to suffer only slightly, if indeed at all. An early experiment in regard to the transfer of water is that by Hales (in 1731), who says:[1] "I cut off the bark, for one inch length, quite round a like branch of the same oak; eighteen days after the leaves were as green as any on the same tree." Further experiments have shown that the rapid transfer is made chiefly in the younger wood of the stem, and not in the heart-wood; and, also, that the water is transferred most rapidly in the portions of new wood having the coarser texture known as spring wood[2] (see 395).

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[1] Statical Essays, i., 1731, p. 130.

[2] Sachs: Vorlesungen über Pflanzenphysiologie, 1882, p. 275.

692. The converse of Hales's experiment is equally conclusive. If the continuity of the wood of a stem is interrupted by the removal of a short truncheon without at the same time much injuring the bark, the leaves wither in a short time. Cotta[1] asserts that upon a shoot of willow which still maintains its connection with the plant through the bark, but has had a section of wood removed, the leaves will wither as quickly as they would upon a shoot wholly severed from the parent plant.

693. That water can be conveyed through the stem in a direction opposite to its normal course is shown in an experiment by Hales: "I took a large branch of an apple-tree, and cemented up the transverse cut at the great end, and tied a wet bladder over it; I then cut off the main top branch where it was $\frac{6}{8}$ inch diameter, and set it thus inverted into a bottle of water. In three days and two nights it imbibed and perspired four pounds two ounces and one half of water, and the leaves continued green; the leaves of a bough cut off the same tree at the same time with this, and not set in water, had been withered forty hours before."[2]

694. **Determination of path and rate of transfer.** Two modes of experimenting have been employed in order to ascertain exactly the path and the rate by which water is transferred through ligneous plants. The first of these consists in using a colored solution, which, when taken into the plant, tinges all the tissues with which it comes directly in contact. The stem or branch used in the experiment is cut sharply off and its end is plunged at once into a colored solution, for instance, of some aniline dye or some colored vegetable juice. As the liquid ascends the stem, certain portions of the tissues become more or less deeply tinged, and its course and rate of ascent can be traced by sections made at any given time, at different distances above the cut end. A similar method has been also employed by plunging in colored water the uninjured roots of the plant to be examined.[3]

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[1] Quoted by Pfeffer: Pflanzenphysiologie, i. 123.

[2] Statical Essays, i., 1731, p. 131.

[3] "Quel que soit le liquide employé et les variations de l'expérience, les résultats généraux ont peu varié, savoir : que l'eau colorée ne pénètre ni par l'écorce ni par la moelle, mais toujours au travers du corps ligneux, tantôt dans toute son étendue, quelquefois dans sa partie la plus jeune, savoir, l'extérieur du corps ligneux des exogènes, et l'intérieur des endogènes. On obtient ce même résultat général, soit qu'on plonge les plantes munies de toutes leurs racines, soit qu'on emploie des branches coupées" (De Candolle's Physiologie végétale, p. 83).

695. The two objections to the first method are: (1) that the protoplasmic body of the cell resists the entrance of nearly all coloring-matters, therefore with many dyes it is necessary to experiment with cut stems and branches, allowing the dye to enter at the cut surface; but, as will be shown later, a cut surface which has been exposed to the air, even for an instant, loses part of its power of absorbing water; (2) it is by no means certain that the dye passes through the stem as rapidly as the water in which it is dissolved. That it does not, seems more than probable from the simple experiment of suspending one end of a strip of filter-paper in a solution of any dye; the water will rise faster than the dye, and form a moist space above that part of the paper which becomes colored.

696. The second method of experimenting is based upon the ease with which certain chemical substances foreign to the plant can be detected in it if once they can be introduced into and carried through its tissues. Dilute solutions of salts of lithium, for instance the citrate, serve best for this method, and Pfitzer suggests that they be applied to the roots of a plant which has been allowed to wilt somewhat from drought.

697. The two objections which may be urged against the second method, are: (1) the chemical used may cause more or less disturbance in the plant, and may even excite disordered processes, and it is plain that no correct conclusions relative to the rapidity of transfer in a healthy plant can be drawn from one which is in a state of disease; (2) the presence of a diffusible salt, for instance one of lithium, may change the osmotic relations of the tissues with which the salt comes in contact. But in spite of these serious difficulties, these methods are of considerable use when cautiously employed.

698. The above methods indicate that the most rapid transfer of water is through the lignified cell-walls of the framework of the plant. The source of supply at the root furnishes the needful amount of water to the ligneous tissues of the fibrils, and these convey it to the converging bundles which constitute the framework of the plant. In the leaves the framework divides and subdivides to form the network of the leaf blade, and here the ligneous cells and ducts are in intimate contact with the parenchyma cells which make up the pulp of the leaf. That water finds its way by preference through the fibro-vascular bundles even in the more delicate parts, is shown by placing the cut peduncle of a white tulip, or other large white flower, in a harmless dye, and then again cutting off its end in order to bring a

fresh surface in contact with the solution, when after a short time the dye will mount through the flower-stalk and tinge the parts of the perianth according to the course of the bundles.

699. **Rate of ascent.** The following are some of the discordant results obtained by the methods mentioned in 694 : —

Name of plant	Rate of ascent per hour.	Observer.
Prunus Laurocerasus	42–100 cm.	McNab.
Salix fragilis	85 "	Sachs.
Vitis vinifera	98 "	"
Nicotiana Tabacum	118 "	"
Helianthus	2200 "	Pfitzer.

700. But little is known as to the reason of the high conducting power of ligneous tissues. That it is not wholly due to capillarity (as has been suggested on account of the abundance of ducts of small calibre in most wood), is shown by the structure of the wood of coniferous plants in which no ducts are present. Again, at the very time when the evaporation from leaves of plants is most rapid, and the transfer of water to supply the loss must be greatest, the cavities of the ducts are not wholly filled with liquid, but contain a considerable amount of air; whereas according to the theory of capillarity they should contain only liquid. By a very ingenious series of experiments Sachs has determined the relative amount of space occupied by the cell-walls, water, and cavities in several fresh woods. In the case of fresh coniferous wood he found the following ratios in 100 cubic centimeters of wood: —

Cell-wall, reckoned as dry	24.81
Water, in the cell-wall and in the cavities	58.63
Air-spaces	16.56

But, as Sachs says, since neither intercellular spaces nor ducts are present in this wood, the 16.56 per cent of air must be contained in the cavities of the wood-cells; and further, since the cell-walls can take up only about half their volume of water (say 12.4 cubic centimeters), the remainder (46.23 c.c.) must exist in the cell-cavities.

701. The method of determining the amount of water held by the cell-walls of dry wood is the following: —

A thin cross-section of fresh wood is hung up in dry air until it ceases to lose weight. During drying a crack appears, running from the centre to the circumference. After ascertaining the weight of the disc thoroughly dried (at 100° C.), the wood is suspended in a saturated atmosphere until enough water is absorbed to cause a swelling of the tissues and a closing of the crack. In this condition it is safe to assume that the cell-walls themselves are saturated, but that there is no liquid water in the cavity of the cells. The difference between the weight of the dry and that of the saturated disc gives the weight of the water taken up and held; this, converted into volume, is found to be approximately one half that of the space occupied by the cell-wall itself.

702. The water which is taken up in relatively small amount and held in the micellar interstices of lignified cell-wall is in the state of equilibrium previously described. When, however, this equilibrium is disturbed by evaporation at any point, there is an immediate transfer of the imbibed water to that point, and the loss from this transfer must be made good at once by the reception of more water. This interstitial transfer may take place through any length of woody tissue, provided there is a consumption of the water at one extremity and an adequate supply at the other. When the consumption of water is only that which is due to the opening of growing buds, or to some chemical process, a slow transfer of water to the point of consumption[1] must take place. When, however, it is due to evaporation from the leaves, the transfer is exceedingly rapid.

703. Boehm[2] considers the ascent of water in ligneous tissue[3] to be "a phenomenon of filtration caused by differences in pres-

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[1] A similar transfer can be demonstrated to take place in porous inorganic matter, for instance powdered hydrated gypsum. If a long tube be filled with this material and well saturated with water, one end being placed in water and the other exposed to a dry atmosphere, the continual loss by evaporation above will be made good by water brought up from below.

Jamin's apparatus for demonstrating the pressure exerted by the imbibition of water by a porous substance consists of a cylinder, in the mouth of which can be placed a tightly fitting plug of wood, through which passes a manometer tube. The pulverulent substance, for instance zinc oxide, is closely packed in the interior of the cylinder, around the open end of the manometer, and the whole apparatus is then placed in water. With zinc oxide the manometer shows a pressure of five atmospheres; with powdered starch, more than six atmospheres. If a manometer is similarly placed in a block of dry chalk, and the chalk is then submerged, a pressure of three to four atmospheres is indicated (Leçons professées devant la Société chimique, Séance du 8 mars, 1861, quoted by Dehérain: Cours de Chimie Agricole, 1873, p. 165).

[2] Ann. des Sc. nat., sér. 6, tome vi., 1878, p. 236.

[3] As might be expected, woody tissues never conduct water so readily in a transverse as in a longitudinal direction. Experiments with regard to this have been conducted by Wiesner (Sitzungsb. d. Wien Akad., Bd. lxxii. 1 Abth., 1875) upon cubes of wood. Four sides of these were protected by varnish

sure in contiguous cells. . . . In parenchymatous tissues filled with sap the movement of water caused by evaporation is a function of the elasticity of the cell-walls and of atmospheric pressure."

Herbert Spencer has shown that when a cut stem is quickly bent backwards and forwards there is a marked increase in the rapidity with which colored fluids ascend through it. "To ascertain the amount of this propulsive action, I took from the same tree, a Laurel, two equal shoots, and, placing them in the same dye, subjected them to conditions that were alike in all respects save that of motion: while one remained at rest, the other was bent backwards and forwards, now by switching and now by straining with the fingers. After the lapse of an hour I found that the dye had ascended the oscillating shoot three times as far as it had ascended the stationary shoot, this result being an average from several trials. Similar trials brought out similar effects in other structures."[1]

704. **Effect upon transfer of exposing a cut surface to the air.** One of the most interesting characteristics of the woody tissues in relation to the transfer of water is the immediate change which the cut surface of a stem undergoes upon exposure to air, unfitting it for its full conductive work. De Vries[2] has shown that when a shoot of a vigorous plant, for instance a Helianthus, is bent down under water, care being taken not to break it even in the slightest degree, a clean sharp cut will give a surface which will retain the power of absorbing water for a long time; while a similar shoot cut in the open air, even if the end is instantly plunged under water, will wither much sooner than the first. Shoots cut in the manner first described remain turgescent for several days. If a cut shoot placed in water has begun to

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against the entrance and exit of water, and one of the two surfaces remaining uncovered was placed in water, the other exposed to air, when the transfer of water through the wood was found to be more rapid in a longitudinal than in a transverse, and in a radial than in a tangential direction.

Another method of experimenting was also employed by him: five sides of a cube of wood were surrounded by separated portions of dry calcic chloride, and the remaining side was placed in contact with water; the difference in rate of transfer ascertained by comparing the weights of the portions of calcic chloride after a fixed time was found to be essentially that given by the other method.

Experiments by Sachs (Arbeiten des botan. Instituts in Würzburg, 1879, p. 298), in which water was forced in different directions through the wood of coniferous stems, showed, however, that under pressure water passes through wood more readily in a tangential than in a radial direction.

[1] Transactions of Linnæan Society, xxv., 1866, p. 405.

[2] Arbeiten des botan. Inst. in Würzburg, i., 1874, p. 292.

wilt, cutting off the stem a little higher up will cause it to regain in part the power of absorption which it lost upon exposure.

705. Although osmosis can have very little to do directly with the rapid transfer of water through the stem, branches, and leaves, it plays, as has been seen, a very important part in the introduction of water into the plant, and in supplying the requisite amount of it to cells which lie, so to speak, away from the main channel of transfer.

706. **Pressure and "bleeding."** If, before its leaves unfold, a grape-vine be cut off near the root, or a little higher up on the stem, the cut surfaces will bleed copiously. The part connected with the roots will continue to yield a supply of watery sap for a considerable time. The flow is plainly regulated to a very great degree by the surroundings of the plant, being accelerated by heat and checked by cold. It is not merely passive; the application of a suitable pressure-gauge shows that the escaping liquid exerts much force.

One of the early experiments on this subject was made by Hales,[1] who found the pressure in the case of the grape-vine to be equal to thirty-eight inches (105 cm.) of mercury, or more than forty-three feet of water. Other experimenters have reported higher figures; for example, Clark[2] found in Betula lenta a pressure of eighty-five feet of water.

707. Pitra[3] has shown that a certain amount of pressure is exerted by sap, even in stems which have been severed from the parent plant, the lower extremity being placed in water. In some of his experiments he found that it was not exerted at once, but only after the lapse of a considerable time. He further shows that a considerable pressure is exerted by the sap which flows out of a cut stem the leaves and twigs of which are submerged.

708. There are considerable individual differences in plants as to the force with which the sap flows from wounds. Wilson found that while one specimen of Ampelopsis quinquefolia gave

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[1] Statical Essays, i., 1731, p. 114.

[2] The apparatus for demonstrating the pressure can be easily used. Reduced to its simplest terms, it consists of a mercurial pressure-gauge, which can be securely attached to the wounded part of the plant. To the stump of the plant the gauge must be fastened by means of stout rubber tubing, which has been made to fit tightly around both plant and tube, and then wired firmly to prevent the escape of any liquid. Dahlia variabilis, Vitis vinifera, and Helianthus annuus are good plants for purposes of demonstration.

[3] Pringsheim's Jahrb., xi., 1878, p. 437.

no pressure for the root-system, another showed a pressure of twenty centimeters of mercury.

709. Bleeding is not by any means of universal occurrence in wounded plants. Horvath found none in the following cases: Humulus Lupulus, Hedera Helix, Syringa vulgaris, and Sambucus nigra. In some cases there appears to be bleeding only from the cut root, none occurring from the stem.

710. The bleeding from a plant may be greatest immediately after the wound is made, or it may in a few cases not reach a maximum for some hours or even days, after which it gradually declines until it ceases. It may recommence after the wound is reopened. According to Hartig,[1] bleeding may continue in some cases for a month.

711. The amount of sap which escapes during bleeding is variable even in the same species. The following cases show that the loss is very large: —

Betula papyracea, 24 hours, 63¼ lbs. (Clark).
Agave Americana, 24 hours, 375 cubic inches (Humboldt).

712. Hofmeister has given the following example, to show how large is the relative amount of sap which can flow from certain plants. From a specimen of Urtica urens (stinging nettle), whose root-system had a volume of 1,450 cubic centimeters, there escaped in 2½ days 11,260 cubic centimeters of sap.

713. The pressure at the cut surface of a plant varies widely in any given case, according to the surroundings. The following details of an experiment by Clark[2] will indicate the variations in pressure noted during a comparatively short time.

"A gauge was attached to a sugar-maple March 31st, three days after the maximum flow of sap for this species. . . . The mercury [in the gauge] was subject to constant and singular oscillations, standing usually in the morning below [its] zero, so that there was indicated a powerful suction into the tree, and rising rapidly with the sun until the force indicated was sufficient to sustain a column of water many feet in height. Thus at 6 A. M., April 21st, there was a suction into the tree sufficient to raise a column of water 25.95 feet. As soon as the morning sun shone upon the tree the mercury suddenly began to rise, so that at 8.15 A. M. the pressure outward was enough to

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[1] Botanische Zeitung, 1862, p. 89.

[2] Report of the Secretary of the Massachusetts Board of Agriculture for 1873, p. 187.

sustain a column of water 18.47 feet in height, a change represented by more than 44 feet of water."

714. The pressure of the sap rises and falls with the temperature. The greatest pressure in ligneous plants is found when a cold night is followed by a warm morning. This has been explained by the expansion of the air contained in the wood-cells and ducts. Detmer observed the greatest outflow of sap in the case of the herbaceous plants Begonia and Cucurbita to be at a temperature of from 25° to 27° C., and that the outflow ceased at 32° for Begonia, at 43° for Cucurbita.[1]

715. Besides the variations both in bleeding and in pressure of sap due to external influences there are some periodical changes which are not yet satisfactorily explained. Baranetzky found that the greatest extravasation of sap from the crown of the root took place in Ricinus between 8 and 10 o'clock A. M., in Helianthus annuus between 12 M. and 2 P. M., and in Helianthus tuberosus between 4 and 6 P. M., the plants being under essentially the same conditions.

716. The great pressure exerted by sap under certain conditions is thus explained by Sachs. From the root-hairs, into which the water comes by osmosis, it passes by osmosis into the parenchymatous cells of the cortex. "But a difficulty occurs in answering the question why the turgescent cortical cells of the root expel their water only inwards into the woody tissues, and not also through their outer walls. We may, however, here be helped by the supposition that the micellar structure of the cell-walls is different on the outer and inner sides of the cells, and that those facing the exterior of the root are best adapted for permitting filtration under high endosmotic pressure." [2]

Among the recorded experiments which show a great root-pressure is one by Clark, described by him thus: "A gauge was attached to the root of a black birch-tree as follows. The tree stood in moist ground at the foot of a south slope of a ravine, in such a situation that the earth around it was shaded by the

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[1] A full and satisfactory treatment of this subject in detail will be found in the following works: —

Schröder: Beitrag zur Kenntniss der Frühjahrsperiode des Ahorn (Pringsh. Jahrb., vii., 1869). In this, the spring phenomena of the maple are clearly given.

Baranetzky: Untersuchungen über die Periodicität des Blutens (Abhandl. des naturforschende Gesellschaft zu Halle, 1873). In this memoir the experiments cover a wide range.

[2] Text-book of Botany, 2d English edition, 1882, p. 688.

overhanging bank from the sun. The root was then followed from the trunk to the distance of ten feet, where it was carefully cut off one foot below the surface, and a piece removed from between the cut and the tree. The end of the root was entirely detached from the tree and lying in an horizontal position at the depth of one foot in the cold, damp earth, unreached by the sunshine, and for the most part unaffected by the temperature of the atmosphere, measured about one inch in diameter. To this was carefully adjusted a mercurial gauge April 26th. The pressure at once became evident, and rose constantly with very slight fluctuations, until at noon on the 30th of April it had attained the unequalled height of 85.80 feet of water."[1]

717. Pfeffer[2] attributes the tendency of water to pass only inwards into the woody tissues wholly to the fact that upon that side of the cells which faces the interior of the root the osmotic capacity is greater. Within the plant the cell-walls are never saturated with pure water; but the imbibed liquid is different on different sides, and hence the plasma membrane in contact with the sides must have different capacities for osmosis.

718. In midwinter or in earliest spring some of the tissues of ligneous plants are stored to a large extent with starch and other solid products manufactured during the previous season. At the coming of warmer weather chemical changes take place, largely following the absorption of water, by which these solid substances are transformed into a liquid state, occupy a greater space than before, and of course exert much greater pressure. The saccharine sap of the maple represents that which during the early winter existed in the tissues as starchy matter. This conversion of material will be further discussed under "Metastasis."

719. **Exudation of water from uninjured parts of plants.** Under certain circumstances water can exude in a liquid form from uninjured parts; for instance, through chinks or rifts in the leaf-tips of many monocotyledonous plants, and through water-pores of dicotyledons, especially when these are young. Musset[3] reports eighty-five drops of liquid falling in one minute from the tip of a leaf of Colocasia esculenta. Duchartre[4] gives the following figures: Twenty-five drops fell in one minute from

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[1] Report of the Secretary of the Mass. Board of Agriculture for 1873, p. 189.

[2] Pflanzenphysiologie, i., 1881, p. 170.

[3] Comptes Rendus, lxi., 1865, p. 683.

[4] Ann. des Sc. nat. bot., sér. 4, tome xii., pp. 247, 250.

the tip of a leaf of Colocasia antiquorum, and 22.6 grams of liquid were collected in one night. From the young leaves of certain Aroids water is sometimes ejected in a fine jet to a distance of a few inches.[1] In these and the previous cases the liquid escapes through rifts.

TRANSPIRATION.

720. The evaporation of water from the surface of the younger parts of plants exposed to the air makes, as has now been seen, a continual draught upon the sources of water-supply. But while evaporation from the free surface of water or from any dead membrane ceases in an atmosphere saturated with moisture, there is some experimental evidence to show that, under certain conditions of radiation, evaporation from the living plant may continue to take place even when the atmosphere is completely saturated. This difference between evaporation from a free surface and that from a plant, although not fully established, renders it advisable to employ for the latter phenomenon the term *transpiration*. This term is sometimes employed in Physics with another signification; but its prior use in Vegetable Physiology should prevent any confusion.

721. **Stomata.** Neither through the cutinized cell-walls of the epidermis, nor through the suberized cell-walls of cork, can transpiration take place to any extent;[2] but at myriads of points in the epidermis of leaves and young stems there are minute orifices which permit the air outside the plant to come into communication with the air within. It has been shown in Part I. that these openings, the stomata, possess definite relations as regards position to the intercellular spaces below them,

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[1] Musset: Comptes Rendus, 1865.

Muntingh (1672), according to a reference in Flora (1837, p. 717), noted the projection of a small jet of water from the leaf of an Aroid, as from a fountain.

[2] "It is of the highest significance that those plants which are submerged, or those parts of plants which grow in the ground and therefore cannot lose water by transpiration, possess a cuticle which permits water and dissolved matters to pass through with comparative facility; while the parts growing in the air have a cuticle of a different quality, through which water passes only with difficulty, and thus they are protected from too great a loss of water" (Pfeffer: Pflanzenphysiologie, i., 1881, p. 139).

The amount of aqueous vapor which can escape through cuticle is very small. According to Boussingault, .005 gram of water may evaporate in one hour from one square centimeter of the rind of an apple, while from the surface of a peeled apple fifty-five times as much is lost (Agronomie, vi., 1878, p. 349).

so that they may be fairly regarded as a part of the system for aerating the plant.

722. By reference to the structure of the more common kinds of leaves (see Chapter III.), it will be seen that the terminations of the delicate fibrils of the framework approach very closely to the aeriferous spaces, and thus by the uninterrupted communication between the minute fibrils in the root-system, the stem-system, and the leaf-system of the plant, water which has been absorbed by the roots is brought finally to the parenchyma cells which surround the spaces under the stomata. If it evaporates from the outer side of the wall of these cells into the intercellular spaces, the water may make its escape through the stomata.

723. Stomata are not mere epidermal rifts having an aperture of unvarying width. The guardian cells of a stoma are so arranged with respect to each other and the proper epidermal cells contiguous to them, that the width of the opening between them can be increased or diminished upon certain changes in the surrounding conditions.

724. **Mechanism of Stomata.** In examining the mechanism of stomata it is necessary to distinguish between their three parts which are shown in a vertical section; namely, (1) the anterior groove, (2) the cleft, and (3) the posterior groove, which is usually continuous with an intercellular space. It is plain that a stoma is most widely open when the edges of the cleft are farthest apart and the rim of the cup not closed. Hence an inspection of the anterior face of a stoma is not sufficient to show whether the stoma is most widely open; the width of the cleft itself must be ascertained.

725. In distinction from proper epidermal cells, the guardian cells contain chlorophyll, and hence under the influence of light can produce carbohydrates (see "Assimilation"). As might be expected, the osmotic tension is different in these two groups of cells.

726. The following account, condensed from Strasburger, shows the relations which the guardian cells sustain to those around the stoma as regards the thickness of the walls. The guardian cells are strongly thickened on the upper and under angles of the walls of their opposed faces, while elsewhere their walls are relatively thin. At the cleft there are opposing projections forming its edges. The opening and closing of a stoma depend upon the difference in the thickness of the parts of the walls. When the turgescence of the guardian cells

increases, they curve more strongly, and the cleft widens; but when their turgescence diminishes, the cleft becomes straighter and narrower, it being clear that with increasing turgescence the guardian cells must become more convex on the side of least resistance, and more concave upon the side of greatest resistance.

727. **Relations of stomata to external influences.** In a classical series of experiments upon the relations of stomata to their surroundings, Mohl[1] has shown that when the uninjured leaves of certain orchids, lilies, etc., are wet with water, the clefts of the stomata open; but these plants form exceptions to the general rule, for it was found that in the greater number of cases studied the cleft closes when the stoma is brought in contact with water. In Amaryllis and the grasses, this closing takes place with great rapidity.

728. When a thin film of epidermis with its stomata is detached, and examined under the microscope, the behavior is the reverse of that above. In a detached film the guardian cells of the stoma are partially freed from the action of the contiguous proper epidermal cells, and as a result the cleft widens when water is applied, the turgescence being increased; but if a solution of sugar in water is employed, the cleft grows narrower, since the turgescence of the cells is at once diminished by osmosis.

According to Mohl, in a wilted leaf the clefts of the stomata are partially or wholly closed, but the application of water causes them to open. If kept wet, they soon close again.

729. The cleft of a stoma opens more widely in the light than in darkness; thus leaves of Lilium which have been kept in the dark in a saturated atmosphere for some days have the stomata closed, and when wet the cleft opens only slightly. Upon exposure to sunlight, the cleft gradually opens.

730. According to Van Tieghem,[2] stomata are always open in sunlight and closed in darkness. In order to cause open stomata to close, it is merely necessary to suddenly change the amount of light. This closing of the stomata takes place in half an hour when a bright light is replaced by diffused light.

It has been found that heat has no marked effect upon the opening and closing of stomata; thus when a plant is kept in darkness at a temperature of from 15° to 17° C., they are closed,

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[1] Botanische Zeitung, 1856.

[2] Traité de Botanique, 1884, p. 636.

and will not open when the plant, still kept in darkness, is subjected to a higher temperature, say from 27° to 30° C.

731. From the foregoing, it appears (1) that stomata are delicately balanced valves, which are exceedingly sensitive to external influences; (2) that in wilted leaves they are partially closed; (3) that in most cases, on the application of liquid water, stomata which are open close; (4) that strong light causes stomata to open widely; (5) that a sudden shock causes them to close.

732. **Amount of water given off in transpiration.**[1] This is determined chiefly by the balance.

In the oft-cited experiment of Hales,[2] in 1724, the amount

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[1] The earliest experiments upon this subject appear to have been those by Woodward in 1699 (Philosophical Transactions). They were made from July to October, and gave the following results (here reduced for convenience to grams): —

Name of plant and kind of water furnished.	First weight of the plant.	Final weight of the plant.	Total amount of water evaporated.
Mint in rain water . . .	1.79	2.88	192.3
Mint in spring water . .	1.72	2 68	163.6
Mint in Thames water . .	1.79	3.45	159.5
Pea in spring water . . .	6.27	6.46	160.

Woodward's most interesting observations relate to the ratio of growth to evaporation when plants are cultivated in different kinds of water. Thus when mint was grown in water mixed with garden earth, the ratio of growth to evaporation was 1:52; but when it was grown in distilled water, 1:214.

[2] "July 3, 1724, in order to find out the quantity imbibed and perspired by the Sun-Flower, I took a garden-pot with a large *Sun-Flower*, 3 feet + ½ high, which was purposely planted in it when young; it was of the large annual kind.

"I covered the pot with a plate of thin milled lead, and cemented all the joints fast, so as no vapour could pass, but only air, thro' a small glass tube nine inches long, which was fixed purposely near the stem of the plant, to make a free communication with the outward air, and that under the leaden plate.

"I cemented also another short glass tube into the plate, two inches long and one inch in diameter. Thro' this tube I watered the plant, and then stopped it up with a cork; I stopped up also the holes at the bottom of the pot with corks.

"I weighed this pot and plant morning and evening, for fifteen several days, from July 3, to Aug. 8, after which I cut off the plant close to the leaden plate, and then covered the stump well with cement; and upon weighing found there perspired thro' the unglazed porous pot two ounces every twelve transpired from a vigorous sunflower, three feet and a half high, during twelve hours of a very warm day, was one pound fourteen ounces, and, on an average, one pound four ounces was transpired every twelve hours. Any evaporation from the surface of the soil in the flower-pot in which the plant was growing was prevented by a lead cover.

A still simpler method of preventing evaporation is to envelop the flower-pot with a thin rubber membrane, and tie this tightly around the stem of the plant. A fresh supply of water can be given to the plant at any time by means of a tube close to the stem. In experiments upon transpiration the plant should be weighed frequently, care being taken to note all the external conditions, such as light, moisture of the atmosphere, etc. For weighing, an open balance with large pans should be used. The form known as the box scale will answer all ordinary purposes; but for delicate weighings one of special construction, having a long beam, is preferable.

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hours day, which being allowed in the daily weighing of the plant and pot, I found the greatest perspiration of twelve hours in a very warm dry day, to be one pound fourteen ounces; the middle rate of perspiration one pound four ounces. The perspiration of a dry warm night, without any sensible dew, was about three ounces; but when any sensible, tho' small dew, then the perspiration was nothing; and when a large dew, or some little rain in the night, the plant and pot was increased in weight two or three ounces. N. B. *The weights I made use of were* Avoirdupoise *weights.*

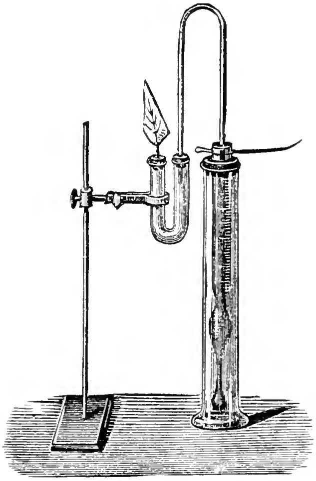
"I cut off all the leaves of this plant, and laid them in five several parcels, according to their several sizes, and then measured the surface of a leaf of each parcel, by laying over it a large lattice made with threads, in which the little squares were $\frac{1}{4}$ of an inch each; by numbering of which I had the surface of the leaves in square inches, which multiplied by the number of the leaves in the corresponding parcels, gave me the area of all the leaves; by which means I found the surface of the whole plant, above ground, to be equal to 5616 square inches, or 39 square feet.

"I dug up another Sun-Flower, nearly of the same size, which had eight main roots, reaching fifteen inches deep and sideways from the stem: It had besides a very thick bush of lateral roots, from the eight main roots, which extended every way in a Hemisphere, about nine inches from the stem and main roots.

"In order to get an estimate of the length of all the roots, I took one of the main roots, with its laterals, and measured and weighed them, and then weighed the other seven roots, with their laterals, by which means I found the sum of the length of all the roots to be no less than 1448 feet.

"And supposing the periphery of these roots at a medium, to be $\frac{10}{76}$ of an inch, then their surface will be 2286 square inches, or 15.8 square feet; that is, equal to $\frac{3}{8}$ of the surface of the plant above ground" (Vegetable Staticks, 2d ed., 1731, vol. i. p. 4).

733. Vesque has devised an automatic apparatus[1] by which the disturbance of the equilibrium of the balance as the water evaporates can be recorded upon a revolving drum. In this apparatus, as soon as the needle records the moment of descent of the beam, an electrical current releases a valve so as to permit the passage of a sufficient quantity of mercury to the losing side of the balance to restore the equilibrium.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734. The registering apparatus of Krutizky[2] is simple, but unfortunately can be used only with cut stems or branches. It consists of a U-tube filled with water, in one end of which a leaf or stem (cut off under water) is inserted, through a tightly fitting cork. Through a cork in the other end extends the short leg of a siphon. In a jar of water there floats a tube balanced to keep it erect. This is somewhat like an hydrometer (but open at the top), and contains a certain amount of water into which comes the long leg of the siphon. When by evaporation from the plant water is drawn up through the siphon out of the floating tube, the tube (called a "swimmer") of course becomes lighter and rises in the jar. If an index is attached to the swimmer, as in the figure, it can be used to record upon a revolving drum the rise of the swimmer as the plant transpires. To prevent evaporation from the water in the jar and in the swimmer, its surface is covered by a film of oil.[3]

735. When a transpiring plant is placed under a bell-jar, a certain amount of the transpired water will collect upon the inside of the jar, — often a sufficient quantity to appear as large

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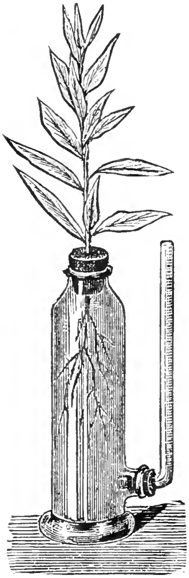
[1] For a full account of its construction see Annales des Sc. nat., sér. 6, tome vi., 1878, p. 186.

[2] Botanische Zeitung, 1878, p. 161.

[3] A simpler piece of apparatus arranged by Pfeffer answers well for class demonstration. It is easily understood from Fig. 147. The fall of water in the small lateral tube is very marked, but attention should be called to the varying pressure caused by the constantly changing level of the water in the tube.

FIG. 146. Krutizky's apparatus.

drops. This method of demonstrating transpiration has been used, when somewhat modified, by many investigators, notably Dehérain.[1] It is well adapted to class experiments, since very simple appliances[2] can be used: for instance, a leafy stem can be inserted in a piece of pasteboard, and the cut end of the stem placed in a tumbler of water; another tumbler, inverted over the stem, rests on the pasteboard. The water in the lower tumbler is prevented from evaporating into the upper one. The amount of water which collects on the inside of the upper tumbler comes wholly from the transpiration of the plant, and will be found to vary according to the surroundings (see page 275 *et seq*).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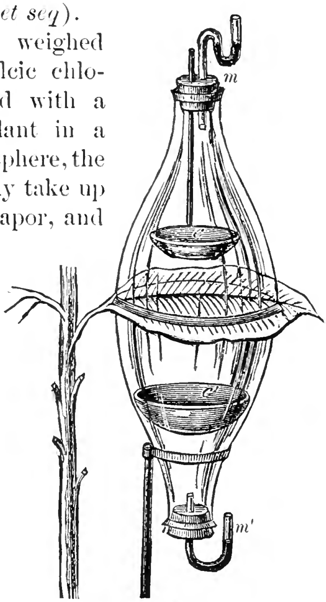
736. If a weighed amount of calcic chloride is placed with a transpiring plant in a confined atmosphere, the salt will readily take up the aqueous vapor, and its increase in weight gives the amount of water exhaled by the plant. This method of measuring the amount of transpiration has been employed by several experimenters, who have obtained results substantially in accord. It must be noted, however, that in this method the air to which the plant is exposed is rendered abnormally dry by the presence of the salt, and the plant is therefore subjected to an unusual draft upon its water-supply.



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737. Garreau's method of comparing the relative amounts of transpiration on opposite sides of a leaf is based on that last

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[1] Cours de Chimie Agricole, 1873, p. 180 *et seq.*

[2] Henslow. See Oliver's Botany (1864), p. 15.

FIG. 147. Apparatus for demonstration of transpiration.
FIG. 148. Garreau's apparatus.

mentioned, and is of easy application. Two tubulated bell-jars, each furnished with a mercury trap (*m* and *m'*), are secured firmly with soft wax to opposite sides of any large leaf. In each bell-jar is a small capsule (*c* and *c'*) containing dry calcic chloride of known weight. After a given time the salt placed in each bell-jar is weighed, and the excess over its original weight shows the amount of water transpired. The following are some of Garreau's results: —

(1) The quantity of water exhaled by the upper face of a leaf is to that exhaled by the lower as 1 : 1, 1 : 3, or sometimes as 1 : 5.

(2) There are marked but not exact relations between the quantity of water exhaled and the number of stomata.[1]

738. **Transpiration compared with evaporation proper.** The evaporation from a given surface of water is between three and six times as great as that from an equal surface of green leaves similarly exposed. Unger[2] found that leaves of Digitalis purpurea with a surface of five thousand square millimeters transpired from 3.232 to 1.232 grams in a given time; while from an equal surface of water from 4.532 to 8.459 grams evaporated. Sachs[3] found that from a surface of sunflower stem and leaf measuring 4,920 centimeters enough water transpired to form a layer 2.23 mm. thick over the same surface; while from an equal surface of water enough evaporated to lower the level 5.3 mm.

Sachs also found that the evaporation from an animal membrane is greater than that from an equal surface of free water. When a surface of water is covered by a moist layer of vegetable parchment, evaporation is somewhat retarded;[4] but even then it is greater than that from an equal surface of leaves.

But the area of a leaf does not express its evaporating surface, since the latter consists of intercellular spaces which have been estimated to bear the ratio of ten to one to the cuticularized exterior. In the intercellular spaces the air is saturated with moisture, hence the slowness of the rate of transpiration.[5]

739. **Effect of moisture in the air upon transpiration.** All experiments show that with increase in the amount of aqueous vapor contained in the air the amount of water transpired from

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[1] Ann. des. Sc. nat., sér. 3, tome xiii., 1849, p. 321. Bonnet's early experiments are interesting.

[2] Sitzungsb. d. Wiener Akad., Bd. xliv., Abth. 2, 1861, p. 206.

[3] Handbuch der Experimental-physiologie, 1865, p. 231.

[4] Baranetzky: Botanische Zeitung, 1872, p. 65.

[5] American Naturalist, 1881, p. 385.

a plant exposed to it diminishes.[1] When the air is completely saturated, a slight amount of transpiration can take place,[2] which, as Sachs has pointed out,[3] is probably due to the fact that the temperature of the plant is higher than that of the surrounding air.

740. Instructive experiments upon the exhalation of moisture by some of the more common desert plants in the dry air of the Western plains have been made by Sereno Watson,[4] from which it appears that in about four hours young shoots furnished with about fifty per cent of leaves lost, when severed from the stem, water amounting to nearly half their weight.

741. **Effect of the soil upon transpiration.** The physical properties of the soil have an influence upon transpiration. Sachs[5] cultivated plants of tobacco in clay and in sandy soil, and observed the amount of water transpired by them under like conditions. Although his experiments are not conclusive, they indicate that transpiration is more uniform from the foliage of the plants grown in clay than from the plants grown in sand; the former soil is much more retentive of moisture, and thus the supply of hygroscopic water is given up more gradually to the roots of the plant.

The chemical properties of soils affect transpiration to a certain extent. Senebier, in 1800, stated that acids increase the rate of transpiration, and he ascribed the same effect also to

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[1] The relations between humidity of the air and transpiration are shown by the results obtained by Unger with two plants of Ricinus, one of which was in the open air, the other under a bell-jar. (The leaf surface of one plant was 190, and that of the other 160 square centimeters; but in the table a correction has been made so that equal surfaces are compared).

Duration of the Experiment.	Loss of water, open air.	Loss of water, bell-jar.	Temperature of the air in C°.
July 19 to 20	11.60 cc.	1.60 cc.	16.
" 20 to 21	17.05 "	1.14 "	13.6
" 21 to 22	16.77 "	1.55 "	15.4
Total	45.42 cc.	4.35 cc.	

The total losses bear a ratio of 10.44 : 1.

[2] Handbuch der Experimental-physiologie, 1865, p. 227. Dehérain in Comptes Rendus, lxix. p. 381.

[3] Sitzungsber. d. Wiener Akad., Bd. xxvi., 1857, p. 326.

[4] Report of the Geological Exploration of the Fortieth Parallel, Botany (1871), p. l.

[5] Versuchs-Stationen, 1859, p. 232.

alkalies. But as Sachs[1] showed in 1859, even a very little free acid in water hastens, while an alkali retards, transpiration.

Burgerstein[2] in a long series of experiments showed that while a single salt added to water in less amount than .5 per cent hastens transpiration, any per cent above this produces a marked retardation. When a solution of nutrient salts is used, even if its concentration is as low as .05 of solid matter, there is a retardation, and this is greater when the solution is more concentrated.

In the experiments, the results of which are given below, four plants of Indian corn were employed. The temperature varied between 16.7°, and 18° C., and the observations continued through one hundred and three hours. The amounts transpired are given in percentages of the weight of the fresh plants.

Nutrient solution	247.4
Distilled water	264.17
Potassic nitrate	283.2
Ammonic nitrate	334.2

742. **Temperature and transpiration.** Rise of temperature increases the rate of transpiration not only by affecting evaporation in general, but indirectly also by augmenting the absorption of water and heightening the turgescence of the cells. Burgerstein shows that leafy twigs of yew can transpire even at a temperature of —10.7° C., while the leafless shoots of horse-chestnut are said by Wiesner to transpire at —13° C.[3]

Sudden changes of temperature greatly influence transpiration, since the "atmosphere and the plant cannot follow the course of temperature with equal rapidity, and a rarefication of the air saturated with moisture within the plant must favor its release."[4]

743. **Effect of light upon transpiration.** Transpiration goes on more rapidly in light than in darkness, even when the temperature in darkness is somewhat higher. But differences in the intensity of diffused light do not produce very marked differences in the amount of transpiration. When, however, diffused light

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[1] Versuchs-Stationen, i., 1859, p. 223.

Sachs met with some anomalies in his experiments, in one case finding a noticeable retardation of transpiration upon the addition of an acid.

[2] Sitzungsb. d. Wiener Akad., 1876 and 1878.

[3] Quoted by Pfeffer: Pflanzenphysiologie, i., 1881, p. 148.

[4] Pfeffer: Pflanzenphysiologie, i., 1881, p. 148.

is replaced by direct sunlight, the increase in transpiration is striking.[1]

744. **Effects of different rays upon transpiration.** Wiesner's conclusions,[2] based on a study of transpiration in different rays of the spectrum, are as follows: (1) the presence of chlorophyll appreciably increases the action of light upon transpiration; (2) it is the rays corresponding to the absorption-bands of chlorophyll, and not the most luminous rays, which cause transpiration; (3) rays which have passed through a solution of chlorophyll have only a feeble effect upon the process; (4) the non-luminous heat-rays act as do the luminous rays, but in a less marked manner, the ultra-violet chemical rays have substantially no effect; (5) whatever the rays are, they always act by elevating the temperature of the tissues.

745. **Effect of shock upon transpiration.**[3] According to Baranetzky,[4] shaking a plant for a short time increases transpiration

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[1] As shown by the following experiments by Wiesner: —

Name of plant.	In darkness.	In diffused daylight.	In sunlight.
Zea Mais, etiolated . . .	106 mg.	112 mg.	290 mg.
Zea Mais, green	97 "	114 "	785 "
Spartium junceum (flowers)	64 "	69 "	174 "
Malva arborea (flowers) . .	23 "	28 "	70 "

The amounts of water are calculated for a surface of 100 square centimeters, and for one hour. But it is not perfectly clear to what the special action of light can be due. The increased size of the cleft of stomata under light cannot account for all cases; for according to Wiesner young maize plants, in which the transpiration is large, have their stomata closed.

[2] Annales des Sc. nat., sér 6, tome iv., 1877, in which may be found also a note upon the same subject by Dehérain.

[3] See also Herbert Spencer's Experiments, on page 263.

[4] Botanische Zeitung, 1872, p. 89.

The following example will show the results of Baranetzky's experiment upon a leafy stem of Inula Helenium.

Time (morning)	State of plant.	Transpiration in grams.	Air temperature C°.	Atmospheric moisture.
7.40	quiet.	—	—	—
8.10	"	.50	22.1	76 per cent
8.40	shaken.	.52	22.2	76 "
9.10	quiet.	.68	22.4	76 "
9.40	"	.47	22.5	76 "
10.10	"	.55	22.7	77 "
10.40	"	.54	22.9	76 "
11.10	shaken.	.59	23 1	76 "
11.40	quiet.	.45	23.3	75 "
12.10	"	.52	23.4	76 "

appreciably; if the plant is then kept at rest, the rate falls below that previous to the shaking, after which it gradually rises to its normal point. Even a sharp single shock is enough to produce some effect upon transpiration, but the shaking must continue at least a second in order to change the rate very much.

If, however, the shaking is long continued, or short shakings are often repeated, there is a noticeable diminution in the rate. Baranetzky attributes the heightening of the rate by a sudden shock to the correspondingly sudden compression of the intercellular spaces and the consequent renewal of the air therein contained; while the diminished rate which follows continued shaking is due to a partial closing of the stomata (see also 731).

746. **Relation of age of leaves to transpiration.** According to Dehérain[1] and Höhnel,[2] young leaves exhale more water than older leaves. Experiments were made by the former upon the upper, middle, and lower leaves of rye. From the newly developed leaves more water was exhaled than from the middle, and more from the latter than from those farther down the stem. Sachs[3] states that young leaves exhale less than those which are fully developed, but that there is some diminution in the case of old leaves.

747. Under external conditions which are as nearly uniform as can be secured there are variations in the rate of transpiration not yet understood; these are generally referred to variations in the tension of tissues (see 1025).

748. **Relation of transpiration to absorption.** It is plain that transpiration from leaves is the chief cause of absorption by the roots; but it has been shown by Vesque[4] that these two functions are not necessarily proportional. According to him it is only when a plant is subjected to uniform conditions of diffused light, and a moderate amount of moisture in the air, that they are about equal. In a very dry air, transpiration in the case of most plants far exceeds absorption until wilting comes on. When, on the other hand, a plant is withdrawn from a moderately moist air and placed in an atmosphere saturated with moisture, absorption goes on for a time more rapidly than transpiration, but both become soon arrested.

The dependence of the rate of absorption upon temperature

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[1] Cours de Chimie Agricole, 1873, p. 178.

[2] Forschungen auf d. Geb. d. Agrikulturphysik, 1878.

[3] Handbuch der Experimental-physiologie, 1865, p. 226.

[4] Annales des Sc. nat., sér. 6, tome vi., 1878, p. 222.

has been shown by many investigators, notably by Sachs,[1] who found that well-rooted and full-leaved plants of gourd and tobacco wilted when the temperature of the air and soil ranged from 3.7° to 5° C., although the ground was plentifully supplied with water. When the temperature of the soil became higher, the leaves became again turgescent.

Another cause which may disturb the relation between absorption and transpiration is found in the diminished conductivity of woody tissue at low temperatures.[2]

749. **Checks upon transpiration.** Among the more obvious adaptations of plants to dry climates are: (1) reduction of foliage to a minimum, as in the case of condensed stems (see Vol. I. p. 64); (2) a coriaceous or even denser texture of leaves or of branches resembling leaves, such as phyllocladia (Vol. I. p. 65); (3) vertically placed leaves or their analogues, phyllodia, in many if not most of which the structure of the parenchyma and of the epidermis with its stomata is the same on both sides; hence the sides have substantially the same exposure to air, and, in the compass leaves, to light as well (see 448). Another adaptation has been pointed out by Pfitzer[3] and by Westermaier;[4] namely, the possession of an epidermal or subepidermal "water tissue," or "water-storing tissue" (see 209).

Leaves provided with water-storing tissue show the effect of drought first in the partial collapse of these cells, their radial walls becoming somewhat undulate, while the assimilating cells remain full and unchanged in form. These water-storing cells lose comparatively little water by transpiration; the water which they contain is given up as required to the assimilating parenchyma. When a fresh supply of water is afforded to the collapsed water-storing tissue, the recovery of turgescence is immediate. Examples are found in the following among many other plants: Peperomia, Tradescantia discolor, Ficus elastica.

In numerous succulents the vacuoles of the assimilating cells frequently contain a thin mucus, from which water evaporates only slowly, and this is believed to play an important part in the storage of water.[5]

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[1] Botanische Zeitung, 1860, p. 124.

[2] Beiträge zur Theorie des Wurzeldruckes, 1877, p. 38, quoted by Pfeffer, Pflanzenphysiologie.

[3] Ueber die mehrschichtige Epidermis, Pringsheim's Jahrb., viii., 1872, p. 16.

[4] Ueber Bau und Function des pflanzlichen Hautgewebesystems, *ibid.*, xiv.

[5] Plants which are peculiarly adapted to dry climates are termed by De Candolle *Xerophilous.* Among them are found many Compositæ, notable

750. **The chief effects of transpiration upon the plant** are: (1) the transfer of dilute solutions of mineral matters to the cells where assimilation, or the production of organic matter, takes place; (2) the concentration of these dilute solutions by evaporation. The extent to which such concentration must take place can be easily inferred from the large amounts of water which are exhaled from some common plants under ordinary conditions of culture. According to Haberlandt,[1] the total amount of water exhaled from a plant of Indian corn during 173 days of growth was 14 kilograms; of hemp during 140 days, 27 kilograms; and of sunflower during the same period, 66 kilograms. Höhnel[2] estimates the amount of aqueous vapor given off between June 1st and December 1st, by a hectar of beech forest (the trees averaging rather more than one hundred years in age), to be between 2,400,000 and 3,500,000 kilograms. That the leaves in autumn contain more ash constituents than in spring, appears from numerous analyses, of which a few are here given from Storer's compilation.

Name of Plant.	Time.	Condition of Dryness.	Per cent of Ash.	Analyst.
Oak	May	Fresh.	1.30	Saussure.
"	Sept.	"	2.40	"
Mulberry . . .	April	"	2.15	Pupils of Fresenius.
" . . .	Aug.	"	4.90	" "
Beech	May	Dried at 100° C.	4.67	Rissmüller.
"	Nov.	" "	11.42	"

751. **Influence of transpiration upon the air.** Ebermeyer[3] has shown that in the course of the year the absolute humidity in the

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proportions of Labiatæ, Liliaceæ, Palmaceæ, Myrtaceæ, and Euphorbiaceæ; but the most characteristic orders are Zygophyllaceæ, Cactaceæ, Mesembryanthemaceæ, Cycadaceæ, and Proteaceæ (Constitution dans le règne végétal de groupes physiologiques, Arch. Bibliothèque universelle, l., 1874).

[1] Wissensch.-prakt. Untersuchungen, 1877, Bd. ii., p. 158.

[2] Ueber die Transpirationsgrösse d. forstl. Holzgewächse, 1879, p. 42. Both this and the preceding citation are from Pfeffer's Pflanzenphysiologie, i. p. 153.

"Some of Haberlandt's figures for crops are obviously too high, probably from overlooking the diminution in the rate of transpiration which attends crowding plants together. Thus he makes the total amount of water exhaled from an hectar of oats during the period of vegetation to be 2,277,760 kg.; of barley, 1,236,710 kg."

[3] Die physikalischen Einwirkungen des Waldes auf Luft und Boden, 1873, p. 148.

air of a forest is scarcely greater than that in air over open ground. But the relative humidity in the former case is about six per cent greater than that in the latter.

752. It has been held by many that forests have a direct effect in increasing the amount of rain-fall, presumably by bringing, through transpiration, the amount of moisture in the atmosphere of a wooded place nearer the point of precipitation. But the weight of evidence now available is against this view.[1]

753. On account of the shelter which they afford, the trees of a forest play an important part in the storage of a water-supply. Under their branches small plants can thrive, and by their hold upon the ground impart to even very porous soil a good degree of stability.

Soil covered with mosses and other humble plants which live in the shade not only holds back a large part of any given rain, so that the water drains off more slowly, but it is not likely to be itself washed down to lower levels. Upon a treeless slope, however, the rains which fall sweep down at once.

754. There is, furthermore, less evaporation from a soil covered by a growth of trees than from open ground. Observations during the summer months recorded by Ebermeyer[2] show that the evaporation of water from the soil of a forest, when the surface is not covered by grass, is only sixty-two per cent of that which takes place from open ground. But if the soil under the shade of a forest is covered with grass, the evaporation is eighty-five per cent of that in the open ground.

Von Mathieu found that the evaporation from open ground from April to October was about five times as much as from wooded soil; but he does not state whether the soil in the latter case had grass upon it or not.

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[1] "Forests increase the annual relative moisture of the air, but this influence is much more noticeable at high elevations than at low elevations. The precipitation of moisture (dew, cloud, rain, snow) takes place more readily on this account in wooded than in treeless regions, and the frequency and intensity of these precipitations increase with elevation above the surface of the sea. Moisture descends more readily and frequently upon a wooded than upon a treeless mountain of the same height. Forests affect rain-fall only so far as they increase the relative amount of water held in the air, and thus bring the relative amount nearer the point of saturation ; thus with the fall of temperature in the forest, a part of the moisture is easily precipitated. . . . Forests make the climate of a country moister, and especially so in summer" (Ebermeyer : Die physikalischen Einwirkungen des Waldes auf Luft und Boden, 1873, p. 151).

[2] Die physikalischen Einwirkungen des Waldes, p. 175.

755. **Effect of transpiration upon the soil.** The amount of water taken from the soil by the trees of a forest and passed into the air by transpiration is not as large as that accumulated in the soil by the diminished evaporation under the branches. Hence there is an accumulation of water in the shade of forests which is released slowly by drainage. But if the trees are so scattered as not materially to reduce evaporation from the ground, the effect of transpiration in diminishing the moisture of the soil is readily shown. It is noted especially in case of large plants having a great extent of exhaling surface, such, for instance, as the common sunflower. Among the plants which have been successfully employed in the drainage of marshy soil by transpiration probably the species of Eucalyptus[1] (notably E. globulus) are most efficient.

756. **Do leaves absorb aqueous vapor?** It is everywhere known that leaves which wilt during the daytime from slight dryness of the soil may recover their turgescence during the night, for then transpiration is reduced to a minimum, and the demand for water is very slight, so that there is a speedy readjustment of the equilibrium which was disturbed during the day. It is still a disputed point whether wilted leaves can absorb any appreciable amount of water from the dew which falls upon them. Experiments by Duchartre[2] indicate that the amount must be very small, if indeed any at all. That leafy branches detached from the plant can absorb water through the leaves is well known, and has been already alluded to.

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[1] See a very interesting account by Mueller in Eucalyptographia, 1881. Also an article by H. N. Draper in Chambers's Journal, lviii. 193, reprinted in Littell's Living Age, cxlix. 376.

[2] Ann. des Sc. nat., sér. 4, tome xv., 1861, p. 109.

CHAPTER X.

ASSIMILATION IN ITS WIDEST SENSE, APPROPRIATION OF CARBON, NITROGEN, SULPHUR, AND ORGANIC MATTERS.

757. THE term *assimilation*, as generally understood in Vegetable Physiology, means the conversion by the plant, through the agency of chlorophyll, of certain inorganic matters into organic substance.

Some authors, however, give to the word assimilation a wider signification, namely, the conversion into utilizable substance of all matters whatsoever brought into the organism. Such[1] regard chlorophyll assimilation as only a special case under a general class which comprises the appropriation of (1) carbon, (2) nitrogen, (3) sulphur, so far as this is a constituent of protoplasm, (4) certain organic matters.

758. It will presently be seen that with the appropriation of carbon by the plant, there is always associated the appropriation of the elements of water, namely, hydrogen and oxygen; but the mere entrance, transfer, and exit of water, which is known to undergo no chemical change in the organism, have already been examined in Chapters VII. and IX., and do not strictly belong to the process of assimilation. There are sundry mineral matters which, though absolutely essential to the well-being of the plant, are conveniently examined without special reference to assimilation, even in its widest sense. Some of them, like the salts of potassium, are indispensable to the process of assimilation; but they do not become at any period an *indispensable* part of the substance of the plant. In the case of sulphur, however, a small amount of the element is appropriated by the plant and constitutes a component part of its protoplasmic matter. The matters which by their temporary presence in the plant contribute to its activities, have been likened to the absolutely necessary lubricants without which machinery cannot run easily or perhaps at all.

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[1] See Pfeffer's Pflanzenphysiologie, i. 186.

APPROPRIATION OF CARBON, OR ASSIMILATION PROPER.

759. The appropriation of carbon, and its combination with the elements of water, is by far the most striking of the kinds of assimilation; and since it underlies to a certain extent the formation of the matter with which nitrogen and sulphur are incorporated to constitute the living substance, it may well lay claim to be considered assimilation proper. It was employed in this sense by Asa Gray in 1850, in the second edition of the Text-book.

For brevity, therefore, the term *assimilation* in the present section will be made to refer to the appropriation of carbon.

760. With some exceptions, to be mentioned later, the following statement holds good for all plants: *assimilation is essentially a process of reduction* in which the inorganic matters are (1) water taken from the soil, and (2) carbonic acid[1] taken from the air; and the organic substance produced from these is some carbohydrate which contains less oxygen than the two together. Hence in assimilation there is, with the evolution of oxygen, a partial reduction of the inorganic matters employed in the process.

761. Assimilation takes place only under the following conditions: (1) The assimilating organ must contain living chlorophyll or its equivalent; (2) water and carbonic acid must be furnished in proper amount; (3) rays of light of a certain character must act upon the organ; (4) it must be kept at a certain temperature, there being a minimum degree of heat below which, and a maximum degree above which, no assimilation can occur; (5) a minute amount of certain inorganic matters other than those named, notably some compound of potassium, must be within reach.

762. **The assimilating system of the plant.** All cells which contain chlorophyll or its equivalent, and which admit of exposure to the sun's rays, constitute the assimilating system of the plant; but it must not be understood that they perform only assimilative work. In the simplest vegetable organisms (unicellular or filamentous algæ) and even in some water plants of the higher grade (Anacharis) these cells are at one and the same time members of an absorbing, a storing, and an assimilative system. In land plants, and in some water plants, however, certain cells have the office of assimilation as their special and dominant

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[1] In general throughout this work, the term *carbonic acid* will be employed, instead of carbon dioxide, to denote CO_2.

function. These cells are found chiefly in expansions upon or of the axis; of course, most commonly in ordinary leaves. But in many cases the primary axis itself and the secondary and other axes (branches) may have a considerable share of the proper assimilating tissue of the plant. In some instances, for example, in solid-stemmed and fleshy plants (as Cactaceæ), the whole assimilative apparatus is to be found on the surface of axial instead of foliar organs; and the same is true of certain ligneous plants specially adapted to desert conditions (*e. g.*, Colletia).

763. The development of the assimilative system in land plants appears to have been controlled by two opposed factors; namely, (1) the advantage to be derived from exposure to air and light, and (2) the disadvantage consequent upon too great loss of moisture by evaporation. Even the most superficial examination of the tropical plants cultivated in our hot-houses reveals the striking manner in which a balance has been struck between these conflicting influences: the plants of warm jungles (*e. g.*, Scitamineæ) having broad and long leaves suited to a humid atmosphere, while the plants of parched sands (Cactaceæ and the like) are characterized by some protection against excessive evaporation. In both these extreme cases the provision for a certain amount of evaporation is, on the whole, seen to be tributary to the essential work of all green tissue, namely, assimilation.

764. Proper exposure of the assimilating apparatus of a plant to light is secured (1) by the shape and position of the assimilating organ, whether it be axis or leaf, and (2) by the arrangement in the organs of the cells themselves. Concerning the first, see Volume I.; in regard to the second, see this volume, page 159.

765. **Chlorophyll**[1] (χλωρός, *green*, and φύλλον, *leaf*). The term chlorophyll, originally applied to the pigment rather than to the substance which contains it, is now used indifferently to denote the coloring-matter and the portions of protoplasmic mass which are tinged by it. It is better, however, to designate the former chlorophyll pigment, the latter, chlorophyll granules, or grains.

766. In regard to the genesis of the chlorophyll granules which are the essential constituent of the assimilative cells, the

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[1] "Nous n'avons aucun droit pour nommer une substance connue depuis longtemps, et à l'histoire de laquelle nous n'avons ajouté que quelques faits; cependant nous proposerons, sans y mettre aucune importance, le nom de *chlorophyle*, de *chloros*, couleur, et φύλλον, feuille; ce nom indiquerait le rôle qu'elle joue dans la nature" (Pelletier and Caventou: Journ. de Pharmacie, iii., 1817, 490).

following view[1] appears to be most in consonance with recent investigations. Imbedded in the protoplasm at every growing point there are peculiar bodies (plastids) which have substantially the same characters and structure as the protoplasm, and are more or less clearly differentiated from it even at an early period. As the cells which develop from the growing point assume the different characters which fit them for special service, for example, those in certain tubers and roots for storehouses, those in leaves for assimilation, and those in some flowers and fruits for color, their plastids may likewise assume special characters. Those which are destined for the storehouses become leucoplastids, or starch-formers; those in green tissue, chloroplastids or chlorophyll granules; and those in colored flowers and fruits, chromoplastids. As might be expected from their common origin, the plastids which under one set of conditions might become leucoplastids, may, under another set, become chloroplastids, etc.

767. The recognition of this view regarding the origin of chlorophyll grains, etc., although it is as yet partly hypothetical, will enable the student to explain some of the extraordinary intermediate forms met with; for instance, those where the

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[1] Meyer (Das Chlorophyllkorn, 1883, and Botanisches Centralblatt, 1882) has reached substantially the same results as those obtained by Schimper, which in the account above given have been presented with Schimper's nomenclature. Meyer employs, however, the somewhat different terminology given below.

	Older Nomenclature.	Schimper.	Meyer.	Van Tieghem.
General term.		Plastid.	Trophoplast.	Leucite.
Special terms.	Colorless protoplasmic granule.	Leucoplastid.	Anaplast.	Leucite proper.
	Chlorophyll granule.	Chloroplastid.	Autoplast.	Chloroleucite.
	Color-granule.	Chromoplastid.	Chromoplast.	Chromoleucite

For a fuller account of the views of Meyer and Schimper, the student must consult the original memoirs in Botanische Zeitung, 1883, or an excellent abstract by Bower (Quarterly Journal of Microscopical Science, 1884).

Schmitz (Die Chromatophoren der Algen, 1882) has described at great length certain structures analogous to chlorophyll, occurring in some of the lower plants. These granular bodies, called chromatophores, possess considerable diversity of form, but all agree in consisting of a matrix or basis permeated by coloring-matter. In most green algæ there are also found one or more minute, rounded, granular, colorless bodies embedded in the chromatophore, known as pyrenoids. These are frequently associated with granules of starch. Chromatophores are believed by Schmitz to increase only by the process of division, but the pyrenoids either by division or by fresh formation.

plastids of one sort can for a time undertake the office of the plastids of another sort. It explains, partially at least, the intrusion of chlorophyll grains into parts of the plant where they do not seem to properly belong, and accounts for some of the apparent changes which they may subsequently undergo.

768. According to the early investigations of the subject, the chlorophyll granules were regarded as differentiations, at an early stage in the embryo and seedling, from a mass of homogeneous protoplasm: according to the present view they are derivatives by division from pre-existing plastids.[1] When developed in darkness, they are pale yellowish, or even devoid of color. Plants grown in the dark (compare 788) become green upon exposure to the light, provided they are not at the same time kept too cold. The minimum temperature at which they turn green is different for different plants, but may be said to be in general not far from 6° to 10° C.

Certain Gymnosperms, notably seedlings of Abies and Pinus, develop a bright green color in the deepest darkness, provided, as before stated, the temperature is not below a certain point.

769. **Occurrence of the chlorophyll granules.** The granules are found only very sparingly in epidermis, being chiefly confined to the guardian cells of stomata. They occur principally in parenchyma cells, immediately below the epidermis, and seldom out of reach of the light. But they occur also in a few deep-seated structures, for instance, in the thick cortex of some ligneous plants, and in the tissues of not a few embryos.

770. That chlorophyll granules are found in the interior of some of the lower animals appears reasonably certain, but the green matter does not always present the same characters. According to recent authorities, it assumes in most cases, for instance in Spongilla and Hydra, the form of minute granules. The pigment agrees in some of its essential properties with that of ordinary chlorophyll.[2] In some cases it must still be considered an open question whether the granules may not be (or at least represent) independent organisms dwelling in certain cavities of

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[1] The views of Gris (Ann. des Sc. nat. bot., 1857) may be summarized as follows: The granules arise by differentiation of the protoplasm in certain young cells into two portions; one of these assumes the form of roundish or lenticular bodies (the proper granules), which under the influence of light become colored green, while the other remains as a matrix in which they are embedded.

[2] For an interesting treatment of this subject, consult Geddes: Nature, 1882, and Lankester, Journal of the Royal Microscopical Society, 1882, p. 241.

these lower animals. These cases of possible symbiosis deserve and are receiving careful investigation.

771. Many species of plants derive all or a part of the organic matter required for their growth and proper activities either from other plants (when they are called parasites), or from decaying organic matters, such as vegetable mould (when they are called saprophytes). In the tissues of a few such plants minute traces of chlorophyll may sometimes be detected.

772. **Structure of chlorophyll granules.** Under a moderately high power of the microscope the granules appear as spheroidal[1] or polyhedral bodies, apparently homogeneous in structure, having neither vacuoles nor granular matter. By the action of certain solvents it is possible to remove from the granule the pigment which has imparted to it its characteristic color, when the mass remains without any change of form. Hence it is proper to distinguish between the chlorophyll pigment and the chlorophyll granule, each of which will now be considered. A method recently discovered makes it possible to demonstrate the peculiar structure of the granules without complete removal of the pigment. This method, known as Pringsheim's,[2] depends upon the action of dilute hydrochloric acid on the green parts of plants. When a thin green tissue,

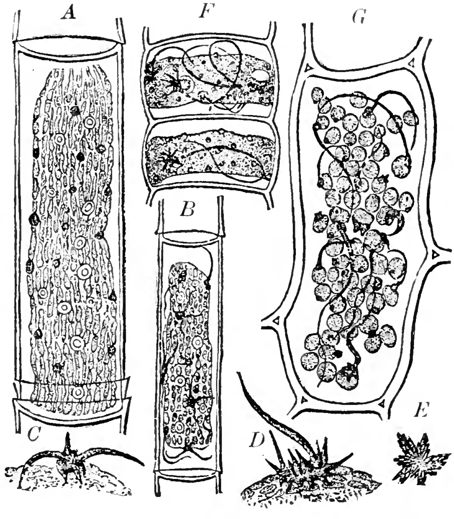

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FIG. 149. Hypochlorin. *A*, a cell of Œdogonium treated with hydrochloric acid for a few hours; *B*, the same after some days; *C*, *D*, *E*, needle-like forms; *F*, two cells of Draparnaldia kept in hydrochloric acid one month; *G*, cell of Anacharis in hydrochloric acid after five months' treatment. (Pringsheim.)

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[1] In some of the Thallophytes, the whole or nearly the whole of the protoplasmic mass seems to be evenly colored, presenting the appearance of colored spirals, lamellæ, stellate forms, etc.; and such colored masses are strictly chlorophyll bodies (Die Chromatophoren der Algen. Fr. Schmitz. Bonn, 1882).

[2] Pringsheim's Jahrb., xii., 1879, p. 289.

for instance a leaf of Vallisneria or of Anacharis, is treated with a solution of one part of concentrated hydrochloric acid in four parts of water, the first change observed is merely a fading of the green color of the granules to a yellowish or brown. After a few hours, however, upon the periphery of each granule there appears a small rounded mass of a deep brown color, generally keeping much the shape of the granule from which it has been extruded. Often more than one of these masses can be detected, and they sometimes assume needle-like or staff-like shapes. But, whatever their form may be, they carry out of the granule all of the coloring-matter, and leave it as a honey-combed mass of its original shape. Similar extrusion of a colored mass can be effected by the action of the vapor of boiling water, or even by immersion in boiling water; but here the change is produced in a single hour, or even less (in some cases, in five minutes). When much starch is present in the chlorophyll granules there is generally considerable change of outline of the whole mass, and more or less breaking down of their internal structure. The nature of the vehicle which, under the action of hydrochloric acid or moist heat, carries out of the granule all of the coloring-matter, will be referred to later, under the name given it by Pringsheim, namely, *Hypochlorin.*

773. The mass of the granule is left by this removal of its coloring-matter, as a spongy body of about the original shape of the granule. This spongy stroma, or "trabecular mass," is plainly different from the granule which is decolorized by the action of solvents, for example, alcohol, ether, etc.; for in the latter case the mass appears to be with an unbroken contour, and has a solid structure.

774. **The chlorophyll pigment** can be extracted, although with various associated waxy and fatty matters, by alcohol and other solvents. To prepare a solution of the pigment for a study of its most striking properties, fresh leaves should be bruised, acted on for a few hours in the dark by warm, strong alcohol, and then, without exposure to bright light, the liquid should be carefully decanted. It is not difficult to separate the dark green solution into two distinct colors by means of the following methods: —

(1) *Fremy's process.* One volume of the alcoholic solution is shaken with a mixture of two volumes of ether and one of concentrated hydrochloric acid; after standing for a time, its upper, or *ether layer*, is yellow (phylloxanthin or xanthophyll), while its lower, or *acid layer*, is blue or greenish blue (phyllo-

cyanin). If considerable alcohol is now added, and the mixture shaken, the liquid again becomes thoroughly mixed and of a clear green color. Fremy's later researches have led him to regard the so-called phyllocyanin as really an acid (phyllocyanic), which is probably combined with potassium, and the salt thus formed mixed with phylloxanthin to form the green coloring-matter of chlorophyll.

(2) *Kraus's process.* This method of separating the two coloring-matters is based on the action of benzol. The alcoholic solution prepared as directed on page 290, or, much better, with alcohol of 65 %, is shaken with about twice its volume of benzol, or, according to R. Sachsse, with benzin (sp. gr. .714). After a while the turbid liquid separates into a benzol layer above, having a bluish-green color, and an alcohol layer below, tinged yellow. The yellowish pigment is called by Kraus, xanthophyll, the bluish-green, kyanophyll. According to Wiesner, kyanophyll is nearly pure chlorophyll freed from its associated yellow pigment xanthophyll. It is believed by many that the yellow pigment separated by this process is identical with that found in plants blanched (etiolated) in darkness, and which has been called etiolin.

Different methods (some of which are noticed briefly in the foot-notes [1]) have been employed for the isolation of the pure

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[1] (1) Berzelius evaporates the alcoholic extract to dryness, and after treatment with hydrochloric acid (sp. gr. 1.14), again dissolves it in alcohol. He then precipitates with water, redissolves the precipitate after filtration, and lastly, by acetic acid, precipitates the nearly pure pigment (Annalen der Chemie und Pharmacie, xxi., 1837, p. 257 ; xxvii., 1838, p. 296.) (2) Fremy throws down from its alcoholic solution, by use of either aluminic or magnesic hydrate, all coloring-matter ; and after thoroughly washing the precipitate dissolves it in alcohol (Comptes Rendus, l., 1860, p. 405 ; lxi., 1865, p. 188). (3) Hoppe-Seyler first extracts all waxy matters from green leaves by repeatedly washing them with cold ether, and then treats the leaves with boiling absolute alcohol. After the alcoholic solution has been cooled, again heated, and allowed to stand, reddish crystals (erythrophyll) separate from it. These are red in transmitted, but green or whitish in reflected light. After their separation the residue of the solution is evaporated to dryness and again dissolved in ether; from the ether solution, upon slow evaporation, granules are thrown down, which are brown in transmitted and green in reflected light. These granules may be obtained, by repeated solution and by spontaneous evaporation of the solution, in the form of crystals of a high degree of purity, which are called by Hoppe-Seyler chlorophyllan (Zeitschr. phys. Chem., iii. 1879, p. 339). (4) In Gautier's process, bruised leaves are mixed with sodic hydrate and pressed. After this the residue of the leaves is treated with alcohol at 55° C., again pressed, and then treated with cold 83 per cent alcohol, all waxy matters being left by the process undissolved. The alcoholic solution is mixed with animal charcoal and

coloring-matters of leaves: crystalline substances have been obtained, one of which, marked by its blue or bluish-green color, contains about five per cent of nitrogen.[1]

775. **Spectrum of chlorophyll.** When a ray of white light which has passed through a coloring-matter, for instance, a solution of one of the coal-tar dyes, red wine, or a solution of chlorophyll, is examined by means of a spectroscope, certain dark bands, known as the absorption-bands, are observed at definite places in its spectrum.

776. For convenience in examining the spectra of small amounts of coloring-matters, a direct-vision spectroscope attached to the tube of a microscope is employed, and the coloring-matter in question is placed in a flat-walled bottle or a glass cell on the stage of the microscope. The ray of light which is reflected from the mirror under the stage passes first through the colored matter, next through the objective, and lastly through the prisms which compose the microspectroscopic attachment to the tube.

777. In order to compare the spectra of different substances, a second prism or set of prisms is often used, by which the spectrum of a second liquid can be projected by the side of that of

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allowed to stand for five days; all the chlorophyll pigment is thus removed by the charcoal. Alcohol of 65 per cent strength extracts from the coal a yellow crystallizable substance, while ether or benzine dissolves out matter which, upon evaporation of the solution, yields pure chlorophyll pigment (Comptes Rendus, lxxxix., 1879, p. 861). By the action of sodium on a benzine solution of the coloring-matter of Primula or of Allium, R. Sachsse has obtained two colored masses. One of these is green, solid at ordinary temperatures, insoluble in pure water, soluble in a dilute alkali, and also in alcohol and ether; the other, yellow, brittle, crumbling into an orange mass, soluble in the same liquids as the first. Besides these two coloring substances he found also a glucoside (that is, a body which under certain conditions can be split into some one of the sugars and another substance which is capable of further changes). Both of the colored masses can be readily broken up into several different coloring-matters. The matters obtained by this process from the green mass differ from those obtained from the yellow, in containing about three to five per cent of nitrogen, while those from the yellow contain none at all.

[1] The green crystals obtained by the evaporation of a purified solution of chlorophyll in alcohol are called chlorophyllan by Hoppe-Seyler, and chlorophyll by Gautier. Their analysis reveals the following composition: —

	Hoppe-Seyler.	Gautier.
C.	73.345	73.97
H.	9.725	9.80
O.	9.525	10.33
N.	5.685	4.15
Ash	1.73	1.75

the first. The spectra of chlorophyll solutions from two different sources can thus be at once compared. One of the combinations can also be employed to project the solar spectrum (unchanged by passing through any color whatever), and its constant lines (Fraunhofer's lines) can be used for the determination of position of the bands seen in the spectrum of the liquid by its side.

778. The spectra of many substances, among which chlorophyll occupies a prominent place, have absorption-bands of such constancy in position and appearance that they are justly regarded as characteristic.

779. The spectrum of an alcoholic solution of chlorophyll has been shown to be essentially the same as that of the chlorophyll granule itself. In order, however, to obtain all the absorption-bands characteristic of chlorophyll, it is necessary to examine successively solutions of different degrees of strength, some of the bands appearing only in dilute and others only in strong solutions. For comparison, absorption spectra obtained from different sources are here given.

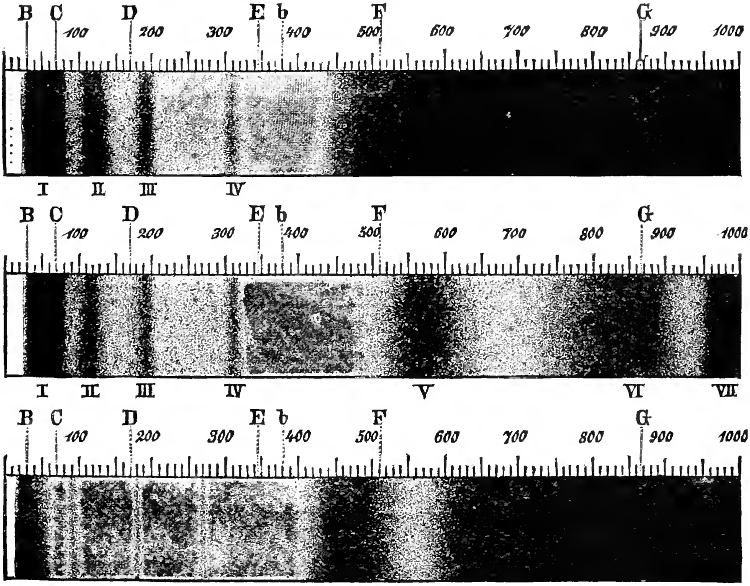

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FIG. 150. Spectra of chlorophyll. The upper figure shows the spectrum of an alcoholic solution of medium concentration, while the middle figure gives all the absorption-bands of chlorophyll; those on the right as shown only in dilute solutions. The lowest figure exhibits the spectrum of a living leaf of Deutzia scabra. (Kraus.)

780. **The fluorescence of chlorophyll pigment** is best shown by allowing rays of light, made convergent by passing through a double convex lens, to fall upon the surface or side of a strong alcoholic solution of chlorophyll. The color at the focus of the lens will then appear blood-red, but by transmitted light the same solution will appear dark green. By fluorescence is meant the property possessed by certain substances of diminishing the refrangibility of some rays of light; in the case of chlorophyll all the rays towards the violet end of the spectrum are made to conform in refrangibility to those near the red. A bright solar spectrum[1] cast upon the side of a flat vessel containing a solution of chlorophyll appears much like a stripe of dull red; in this red stripe are bands corresponding in their position to the absorption-bands of chlorophyll. If the blood-red color produced by a strong light falling on the surface of a concentrated solution of chlorophyll is examined through a spectroscope, only red rays having the same degree of refrangibility as those of the deep absorption-band of the chlorophyll spectrum come to the eye.

781. **Plants without chlorophyll.** If whole plants (certain parasites and saprophytes, for example, Monotropa) are either white or slightly tawny throughout, it is owing to a complete or partial absence of chlorophyll; but in some instances such plants may impart to alcohol, in which they are immersed, a decided tinge, frequently blue.

782. **"Colored" plants.** When leaves or stems have some color other than green, they are said to be colored: if two or more different colors are intermingled the parts are variegated.

783. In the case of healthy leaves exposed to light, white spots, streaks, etc., are generally, if not always, characterized by an absence of chlorophyll. Such spots have relations to their surroundings which are different from those of the contiguous green parts; they do not have the power of assimilating inorganic matters.

784. In plants, the paleness of colors verging upon green or blue (for example, those in many kinds of cabbage) sometimes depends wholly on the existence upon the surface of the part, of a great amount of the waxy matters known collectively as bloom (see 226). The tissues beneath the surface may be vivid green.

785. Red and yellow colors of healthy and vigorous leaves are usually due to the presence in the cells (often merely those of

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[1] Hagenbach: Annalen der Physik und Chemie, cxli., 1870, p. 245.

the epidermis) of colored cell-sap. This is sometimes in such large amount as to mask completely the green granules which are contained in the same cells.

786. In the Florideæ (rose-red marine algæ) the chlorophyll is masked by the presence of a reddish coloring-matter which is easily extracted by pure water. This reddish pigment is called phycoërythrine. In solution it is carmine-red by transmitted, and orange by reflected light. Analogous pigments extracted by water from algæ of colors other than red have received the following names, — phycophæine (brownish), phycocyanine (bluish), phycoxanthine (yellowish-brown).

When these coloring-matters have been extracted by cold water, the chlorophyll is left unchanged in the plant, and it then imparts to the thallus its characteristic green color. Owing to the nearly complete insolubility of these reddish pigments in alcohol, and the complete solubility of the chlorophyll pigment in that liquid, a green color is given at once to alcohol when an alga is immersed therein.

787. Colored bodies, not readily, if indeed at all, distinguishable from ordinary crystalloids (see 177), are found in many algæ. In some cases these colored granules of crystalline form occur normally in the living plant; in others they arise from changes produced by the action of reagents upon the matters of the cells. The name rhodospermin, given by Cramer to the granules having the latter origin, has been adopted by Klein in an extended memoir.

788. **Etiolation.** Green plants placed in darkness soon turn pale and become blanched or *etiolated*. The chlorophyll granules change their color, and finally appear to become merged, with more or less change of form, in the protoplasmic mass, from which they are then no longer easily distinguishable. Etiolated plants when exposed to light recover their color only when the temperature is above a certain point. The action of light in restoring color is, moreover, local, being confined to the part of the plant which is exposed to its influence. It may be here noted that some plants are not etiolated until after long exposure to darkness; thus the older parts of Cactus speciosus, kept in the dark, remained green for three months, but the new shoots were etiolated. Selaginella remained green from four to five months.[1]

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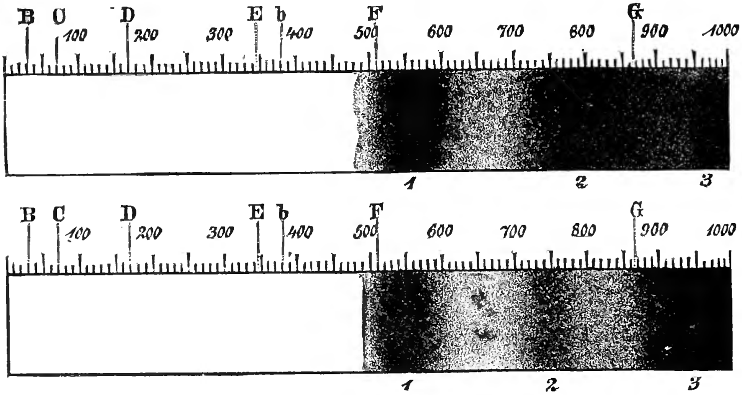
[1] Sachs: Handbuch der Experimental-physiologie, 1865; also Botanische Zeitung, 1864, and Flora, 1863.

The instructive similarity between the spectrum of the yellow coloring-matter of chlorophyll and that of the so-called *etiolin*, or yellow coloring-matter which can be extracted from blanched leaves, is shown in the two figures here given.



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789. An alcoholic solution of chlorophyll undergoes very little if any change when kept in the dark; but even a short exposure to strong light destroys its green color, and leaves the liquid pale brown, or nearly colorless. When, however, strong sunlight passes through a solution of chlorophyll before it reaches a second receptacle filled with the same liquid, the first solution *protects* the second for a considerable time; and only after the first has lost a portion of its green color can the second be also acted upon.

790. Sachs[1] has pointed out the interesting fact that green leaves, especially those of delicate texture, become paler when exposed to a very bright light, and resume their deep green color when again subjected to a less intense light. If one leaf is partially shaded by another, the shaded leaf preserves its normal deep green color, while the leaf exposed to the light grows distinctly paler. This effect, due probably to a change of position of the chlorophyll grains, can be shown experimentally in the following manner: Fasten closely to a green leaf, still

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[1] Ber. über die Verhandlungen (Math. Phys. Classe) der Sächsischen Gesellsch. xi., 1859, 226; and also in Experimental-physiologie, 1865.

FIG. 151. The upper spectrum is that of the yellow constituent of chlorophyll from Deutzia scabra; the lower, that of the coloring-matter of etiolated barley, in dilute solution. (Kraus.)

connected to its plant, a narrow strip of flexible lead or tin foil, and expose the leaf to bright sunlight. After a quarter or half an hour remove the strip, and the spot which has been kept shaded by it will be seen to be distinctly deeper in color than the part which has been exposed to the sun's rays.

791. **Chlorosis,** or blanching of plants from lack of iron. Although iron has not been detected as a constant component of the pure pigment of chlorophyll, this element has been shown in many ways, especially by water-culture, to be essential to the green color and even to the normal formation of the granules. When a seedling of Indian corn is grown with its roots abundantly supplied with a nutrient solution from which all salts of iron are absent, and it has all other conditions favorable to rapid and healthy development, the leaves are pale yellow, or even whitish, and the whole plant sooner or later appears sickly and ill-nourished. When, however, a salt of iron is supplied to the nutrient liquid, a normal green color is at once imparted to the leaves and the plant becomes healthy and vigorous. The effect of the local application of a salt of iron is thus described: When a weak solution of ferric chloride, ferric nitrate, or ferrous sulphate is applied to a leaf blanched by want of iron, the part moistened assumes a normal green color in a few days, and sometimes in a much shorter period. Neither cobalt nor nickel salts have similar relations to chlorophyll.[1]

792. **Autumnal changes in color.** The leaves of many deciduous plants undergo changes of color at some period before they fall. In not a few instances these changes occur early in the season after full development of the leaf; for example, during the first days of summer it is not unusual to find on the swamp maple bright red and yellow leaves. The colors, however, become most striking in temperate climates at the approach of autumn.

The change of color in autumn leaves is due to changes which take place in the chlorophyll pigment. This breaks up into various matters of unknown composition, but classed in a general way with the erythrophyll (the reddish coloring-matter) and xanthophyll (the yellowish), obtainable artificially from chlorophyll. Comparison of the spectra of these substances exhibits certain very striking features of similarity.

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[1] Eusèbe Gris, 1844, and Arthur Gris, in Ann. des Sc. nat., sér. 4, tome vii., 1857, p. 179.

793. These autumnal changes have been compared, not inaptly, to those belonging to the ripening process in colored fruits; but this general statement of similarity must not disguise the fact that in the ripening of fruits special chromoplastids play the chief part, whereas in the leaf before its fall there is a breaking up of the protoplasmic basis of the granules of chlorophyll,[1] preparatory to the withdrawal from the leaves into the plant of the useful products of disintegration.

The changes during disintegration may involve (1) both color and form of the granules at one and the same time, or (2) the change in color may precede that in form, or (3) the latter may occur first.

794. In general, the reddish coloring-matters are found in the cell-sap of the colored leaves, the yellow in the substance of the disintegrating grain, and, finally, the brown in the modified character of the cell-wall itself.

795. That frost is not essential to the production of the leaf-colors of autumn is plain from the widely known fact that many leaves undergo precisely these changes of color long before any frosts appear. It is generally believed, however, that freezing may somewhat hasten the process of chlorophyll disintegration which underlies all the changes.

The fact is generally recognized that the autumnal colors, crimson and scarlet, are more brilliant in the cooler portions of America than those which characterize the foliage in Europe, and it has even been remarked that the leaves of American trees cultivated in Europe do not undergo such marked changes of color as individuals of the same species do in their native habitat. This has been accounted for on the ground that there is less humidity in the atmosphere of eastern America; but this explanation is not satisfactory, and exact observations regarding the relative brilliancy of color are wholly wanting.

796. **Chlorophyll in evergreen leaves.** At the approach of cold weather the leaves of evergreens undergo, according to Mohl,[2] certain changes of color. Kraus[3] recognizes two types of change: (1) the leaves become greenish brown, as in most Conifers, or (2) they take on a red color on the upper side, as in Mahonia and some species of Sedum. According to him, in leaves of the first type the chlorophyll granules become disinte-

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[1] Sachs: Die Entleerung der Blätter im Herbst, Flora, 1863, p. 200.

[2] Vermischte Schriften, 1845.

[3] Sitzungsb. der phys.-med. Societät zu Erlangen, 1871, 1872.

grated and impart a brown color to the protoplasmic mass of the cells: but in the leaves of the second type the color is due to a highly refractive reddish or yellow mass (supposed to be tannin), concealing from a surface view the clustered chlorophyll granules within, which retain their vivid hue. In all cases of evergreen leaves the granules of chlorophyll, at the beginning of the cold season, pass from the walls to the centre of the cells, and are there aggregated in compact clusters. Their normal condition is restored in the warm days of early spring.

797. Kraus has examined the changes in autumn in the chlorophyll of Ruscus aculeatus. He finds that in this plant some of the more superficial cells under the epidermis contain minute granular masses of a brownish color, but no chlorophyll granules are to be distinctly seen, and that the subjacent cells have more or less broken-down granules which are yellowish or brownish green. In the cells making up the more spongy tissues there are a few chlorophyll granules quite intact, but there are indications that some others have been completely destroyed and their coloring-matter taken up by the surrounding protoplasm, apparently in a state of solution.

798. It was thought by Kraus that the winter change in the character of the chlorophyll was due to the lower temperature. He based his views largely upon experiments with a branch of Buxus (Box); but it has been shown by Batalin[1] and Askenasy[2] that light has a more important influence upon the chlorophyll than changes of temperature.

799. **The raw materials required for assimilation, and their reception by the assimilating organs.** These are (1) water and (2) carbonic acid. In earlier chapters it has been shown in what manner and to what extent water and small traces of mineral matters are brought from the soil into the plant. It is now necessary to ascertain in what way carbonic acid enters the organism and is appropriated by it.

800. **Absorption of carbonic acid by water plants.** These can absorb carbonic acid substantially as they absorb mineral salts, directly from the water in which they live. The amount of carbonic acid found in rain and other waters is variable, ranging, according to the best authorities, from about one per cent to considerably less than one tenth of one per cent. The amount existing in the free state in natural waters in which plants thrive

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[1] Botanische Zeitung, 1874.

[2] Botanische Zeitung, 1875.

is shown in the following table (taken from the comprehensive synopsis in Watts's dictionary): —

	Cubic centimeters in each liter of water.
Loch Katrine (Scotland)	.3
Bala Lake (Wales)	1.1
Rhine at Strasburg	7.6
Rhone at Geneva	8.4
Thames at Kew	50.3

All the free carbonic acid dissolved in water can be expelled by boiling.[1]

801. **Absorption of carbonic acid by land plants.** These, with their foliage exposed to the air, obtain from that source all their supply of carbonic acid. No carbonic acid is taken up by their roots:[2] the supply enters the plant through the younger epidermal tissues, chiefly, of course, that of the leaves. By the process of respiration within the plant (see Chapter XI.) a small but appreciable amount of carbonic acid is produced, and a part of this is doubtless appropriated directly by the plant for the process of assimilation.

802. Carbonic acid and other gases found in the atmosphere sustain to vegetable membranes certain relations which must

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[1] According to Bunsen (Jahresb. der Chemie, 1853, p. 317), one volume of water absorbs at 760 mm. barometric pressure, and at the temperatures noted, the following amounts of various gases: —

	3°.2 C.	19°.6 C.
Nitrogen	.02189 vol.	.01515 vol.
Oxygen	.04553 "	.03253 "
Carbonic acid	1.5184 "	.8545 "

According to the same authority, these gases occur in rain-water in the following relative proportions: —

	0° C.	10° C.	20° C.
Nitrogen	63.20	63.49	63.69
Oxygen	33.88	34.05	34.17
Carbonic acid	2.92	2.46	2.14

[2] This appears to be settled by the results of experiments made by Moll: (1) when carbonic acid is afforded, even in excess, to shoots, whose leaves are kept in an atmosphere free from carbonic acid, no formation of starch takes place; (2) if such leaves are in the open air, the formation of starch is not increased above its normal rate; (3) when carbonic acid is supplied to roots of plants whose leaves and shoots are kept in an atmosphere free from carbonic acid, no formation of starch takes place. If the leaves and shoots of such plants are in the open air, there is no increase of starch above the normal amount (Arbeiten des bot. Inst. in Würzburg, 1878, p. 113).

now be presented in a general manner; and some introductory reference must be here made to the well-known physical properties of gases.[1]

803. **Diffusion of gases.** When two or more gases are brought into contact, spontaneous intermixture takes place. This process of diffusion, as it is called, goes on even when the gases are very different in specific gravity, and when they are kept externally at perfect rest. Thus if a jar of carbonic acid be placed in connection with a jar of oxygen, the two gases, after a while, will become uniformly commingled.

Similar commingling of gases also takes place through permeable substances, such as thin plates of unglazed porcelain, graphite, films of membrane, etc.

804. Different gases diffuse through a given membrane in different times. The rates of diffusion of different gases at the same temperature and barometric pressure have been shown by Graham to differ nearly in the inverse ratio of the square roots of their densities, thus: —

Name of gas.	Rate of diffusion (air being taken as unity).	$\frac{1}{\sqrt{\text{Density}}}$.
Hydrogen	3.83	3.78 nearly
Carbonic oxide	1.01 nearly	1.01 "
Nitrogen	1.01 "	1.01 "
Oxygen	.95 "	.95 "
Carbonic acid	.81 "	.81 "

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[1] Graham, who made a careful study of the laws which govern gaseous diffusion, has given the following clear account of the physical hypothesis, which is now generally received: "A gas is represented as consisting of solid and perfectly elastic spherical particles which move in all directions, and are animated with different degrees of velocity in different gases. Confined in a vessel, the moving particles are constantly impinging against its sides and occasionally against each other, and this contact takes place without any loss of motion owing to the perfect elasticity of the particles. If the containing vessel be porous, then gas is projected through the open channels, by the motion described, and escapes. Simultaneously the external air is carried inwards in the same manner and takes the place of the gas which leaves the vessel. To this molecular movement is due the elastic force, with the power to resist compression, possessed by gases. The molecular movement is accelerated by heat and retarded by cold, the tension of the gas being increased in the first instance and diminished in the second. Even when the same gas is present both without and within the vessel, or is in contact with both sides of our porous plate, the movement is sustained without abatement — molecules continuing to enter and leave the vessel in equal number, although nothing of the kind is indicated by change of volume or otherwise. If the gases in communication be different, but possess sensibly the same specific gravity and molecular velocity as nitrogen and carbonic oxide do, an interchange of

805. The movements of gases within the plant are of two kinds, (1) molecular (see note on the previous page), and (2) "the movement of the whole mass depending exclusively on expansive force." These are generally conjoined in the passage of gases through the plant.

806. **Passage of gases through epidermis free from stomata.** The assimilating apparatus in ordinary land plants consists of parenchyma cells frequently so loosely conjoined as to have very conspicuous intercellular passages, which communicate with stomata either directly or indirectly. All of these parenchyma cells have walls of cellulose generally without any impregnation of foreign matter. But the peripheral cells which bound the whole as epidermis proper are cutinized on their external aspect, and must possess relations to gases different from those presented by common parenchyma with uninfiltrated walls.

807. Through ordinary cell-walls, that is, those which are composed of nearly pure cellulose, water passes and gases diffuse with facility. But as cutinized cell-walls, like those of the epidermis of leaves, are nearly impervious to water and to aqueous vapor, it would at first sight appear unlikely that gases could make their way through them; such, however, is not the case. Experiments upon epidermal tissues free from stomata show that under ordinary circumstances gases can diffuse through cutinized walls.

Thus N. J. C. Müller[1] used the epidermis of the leaves of Hæmanthus puniceus in three series of experiments upon the diffusion of different gases. The membrane employed was, in the first series, two films of epidermis with a layer of water between them; in the second, two moist films without any layer of water; in the third, two films joined together and then carefully dried in an exsiccator at 40° C. The method used by Müller is open in some of its details to criticism, but in a general way the results are instructive. The following are the mean ratios indicating the rate of diffusion obtained: —

	Series I.	Series II.	Series III.
Hydrogen	100	100	100
Oxygen	502	55	37
Nitrogen	471	73	30
Carbonic acid	687	48	45

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molecules also takes place without any change in volume. With gases opposed of unequal density and molecular velocity, the permeation ceases, of course, to be equal in both directions" (Philosophical Transactions, 1863).

[1] Pringsheim's Jahrb., 1869, p. 169.

808. Experiments by a wholly different method were conducted by Boussingault,[1] upon leaves of Oleander. By a leaf having an upper surface of 37.2 square centimeters free from stomata, and completely closed on the under side by tallow, 17.5 cubic centimeters of carbonic acid were absorbed in a given time.

In another series of experiments Boussingault fastened the under surfaces of two leaves closely together by means of paste, so that only the upper surfaces (free from stomata) were exposed to the air; with these leaves nearly the same results were obtained as in the first series.

809. **Passage of gases through stomata.** Stomata (see Figs. 52 and 54) are practically minute apertures in thin plates, and under ordinary circumstances there is no obstruction to the ready passage of gases through them from the surroundings into the interior of the plant. The changing pressure caused by agitation of the foliage exerts, as it does in aqueous transpiration, an important influence in facilitating this passage.

810. Merget[2] holds that it is chiefly through stomata that the interchange of gases with the outer air takes place in the plant; but, on the other hand, it is claimed by Barthelemy[3] that they play only a very subordinate part. There can be little doubt that the earlier view advanced and illustrated by Dutrochet,[4] and further by Garreau,[5] is substantially correct; namely, that gases enter and escape from the plant freely both by diffusion through the cuticularized cell-walls of the epidermis and by passage through the stomata.

811. **Atmospheric air** is chiefly a mixture of two gases, oxygen and nitrogen. The proportions in which these substances and others, occurring in much smaller amounts, are found in dry air are usually stated as follows: —

	Proportions by volume.	Proportions by weight.
Nitrogen	79.01984	76.8399
Oxygen	20.94000	23.1000
Carbonic acid	.04000	.0600
Ammonia	.00016	.0001
	100.	100.

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[1] Agronomie, iv., 1868, p. 374.

[2] Comptes Rendus, lxxxiv., 1877, p. 376.

Ann. des Sc. nat. bot., sér. 5, tome xix., 1874, p. 131.

[4] Ann. des Sc. nat., tome xxv., 1832, p. 242.

[5] Ann. des Sc. nat. bot., sér. 3, tomes xv., xvi.

The first two substances occur in very nearly the same proportions in free atmospheric air wherever found,[1] but the amounts of the last two vary within narrow limits.

Besides the foregoing substances, the following are also mentioned as having been found in dry air in minute traces: Nitric acid, nitrous acid, ozone, marsh gas, carbonic oxide, sulphurous, sulphydric, and hydrochloric acids, and hydrogen.

812. Under ordinary circumstances the proportion of carbonic acid in the atmosphere does not increase much beyond the amount stated above, namely, four one-hundredths, or one twenty-fifth of one per cent.[2] Pettenkofer assigns one twentieth of one per cent as the amount in the air of Munich (1,690 feet above the level of the sea).

In confined spaces, however, the accumulation of carbonic acid (once known by the significant term *fixed air*) may become so great as to render the air irrespirable. It was the consideration of the question how such air could be again rendered fit for respiration that led to the first successful[3] investigation of the action of plants upon the atmosphere.

813. The amount of carbonic acid found in ordinary water which has been exposed for a time to the air is sufficient for the supply of this gas to water plants. The percentage of the gas in the atmosphere under ordinary conditions is ample for all the needs of land plants. The consideration of the effect of supplying a larger amount than usual of this gas to water and land plants, in order thereby to influence the activity of the assimilative process, must be deferred until all the conditions essential to assimilation have been considered; but it may be said, in passing, that any large excess of carbonic acid over the supply furnished to plants in nature diminishes assimilative activity.

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[1] For a very instructive summary of results of the examination of the air in different localities, the reader should consult "Air and Rain, the Beginnings of a Chemical Climatology," by R. Angus Smith (London, 1872).

[2] Angus Smith gives the following results of his examination in 1864 of the air of Manchester, England: —

	Per cent of CO_2 in atmosphere.
In the streets, usual weather	.0403
During fogs	.0679
Where the fields begin	.0369
In close buildings	.1604
Minimum amount found in suburbs	.0291

See also Ann. de Chimie et de Physique, 1883, for reports on the amount of CO_2 in the atmosphere of different localities.

[3] See the historical sketch, pp. 323, 324.

814. **Practical study of assimilation.** Before examining the remaining conditions of assimilation, a simple experiment is here described by which the reader can study in their proper relations all the essential conditions of the process, and thus obtain a clearer idea of the means by which the activity of assimilation is measured and the indispensable character of the conditions established.

Fill a five-inch test-tube, provided with a foot, with fresh drinking water. In this place a sprig of one of the following water plants, — Anacharis Canadensis, Myriophyllum spicatum, M. verticillatum, or any leafy Myriophyllum (in fact, any small-leaved water plant with rather crowded foliage). This sprig should be prepared as follows: Cut the stem squarely off, four inches or so from the tip, dry the cut surface quickly with blotting-paper, then cover the end of the stem with a quickly drying varnish, for instance asphalt-varnish (see 115), and let it dry perfectly, keeping the rest of the stem if possible moist by means of a wet cloth. When the varnish is dry, puncture it by a needle, and immerse the stem in the water in the test-tube, keeping the varnished larger end uppermost. If the submerged plant be now exposed to the strong rays of the sun, bubbles of oxygen gas will begin to pass off at an even and rapid rate, but not too fast to be easily counted. If the simple apparatus has begun to give off a regular succession of small bubbles, the following experiments can be at once conducted.

(1) Substitute for the fresh water some which has been boiled a few minutes before, and then allowed to completely cool: by the boiling, all the carbonic acid has been expelled. If the plant is immersed in this water and exposed to the sun's rays, no bubbles will be evolved; there is no carbonic acid within reach of the plant for the assimilative process. But,

(2) If breath from the lungs be passed by means of a slender glass tube through the water, a part of the carbonic acid exhaled from the lungs will be dissolved in it, and with this supply of the gas the plant begins the work of assimilation immediately.

(3) If the light be shut off, the evolution of bubbles will presently cease, being resumed soon after light again has access to the plant.

(4) If glass of different colors be interposed in the path of the sun's rays, it will be shortly seen that orange light differs from violet light in its effects upon the rate of the evolution of the bubbles.

(5) Place around the base of the test-tube a few fragments of

ice, in order to appreciably lower the temperature of the water. At a certain point it will be observed that no bubbles are given off, and their evolution does not begin again until the water becomes warm.

(6) Examine, at the close of the series of simple experiments, some of the leaves with iodine solution, for the detection of starch. Even with no precaution the chlorophyll granules will reveal the presence of a considerable amount of the first visible product of assimilation, namely, starch. Lastly, keep a second uninjured spray of the same plant in the light for a time, and then in darkness for a day or two, after which examine it for starch; probably after this lapse of time no starch can be detected, for although it has been made in the light, in darkness it has been consumed in the various activities of the plant.

815. According to the accepted theory, light consists of waves which are set in motion in a tenuous elastic medium termed *the ether*. The existence of this medium is made known to us only by the phenomena which light itself presents; but, having assumed its existence, the phenomena of light can be explained. The tenuity of this medium, which fills all space, far exceeds that of any known gas, and its elasticity is far higher than that of any known elastic solid. In it a luminous body sets in motion undulations which produce upon the retina the sensation of light; upon differences in the amplitude and the duration[1] of these undulations depend differences in the intensity and the color of the light which reaches the eye.[2]

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[1] The terms just employed, namely, amplitude and duration, seem hardly applicable to waves of such incredible minuteness and velocity as those named in the following table: —

Color of light.	Number of waves of light in one second of time.	Length of each wave.
Red	477 millions of millions.	650 millionths of a millimeter.
Orange . . .	506 " " "	609 " " "
Yellow . . .	535 " " "	576 " " "
Green . . .	577 " " "	536 " " "
Blue	622 " " "	498 " " "
Indigo . . .	630 " " "	470 " " "
Violet . . .	699 " " "	442 " " "

[2] "The intensity of the luminous impression must depend upon the force of the atomic blows which are transmitted to the optic nerves, and it is also evident that this force must be proportional to the square of the velocity of the oscillating atoms, or, what amounts to the same thing, to the square of the amplitude of the oscillation; assuming, of course, that the oscillations are isochronous. The connection of color with the time of oscillation is not so

816. **Light and assimilation proper.** Energy has been defined as the power of doing work. Of this there are two types: the energy of actual motion (sometimes termed *kinetic*), and the energy of position (known as *potential*). The illustration of their difference is usually given as follows: A ball thrown upwards has the power of overcoming the force of gravity tending to pull it down, and possesses energy of motion; suppose the ball at the end of its course is lodged upon some projecting shelf, then its energy of motion disappears, and it now possesses energy of position. Whenever it is dislodged, it will fall with the same power which was required for its ascent. From this and similar examples it is plain that one form of energy can be changed into another; when one seems to disappear, it has in fact merely been converted into some other.

817. These types of energy are to be found in molecules as well as in masses of matter. It is held that all molecules of all matter are in a state of motion, invisible, but none the less real. One form of such invisible kinetic energy is heat, and another is radiant light, where the energy of motion is embodied in the vibrations or undulations of the ethereal medium. A third form is that of electrical separation; and still another, with which Physiology deals especially, is known as chemical separation, of which a familiar illustration may be given: An atom of oxygen has so strong an attraction for one of carbon, that if the two are united, it is difficult to separate them, the force required to do this being comparable to that demanded to raise a weight to a certain height. As in the latter case the weight held in its raised position represents by that position the force which was employed to raise it, so the separated atoms represent energy of position ready to be again converted into energy of motion.[1]

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obvious; and why it is that the waves of ether beating with greater or less rapidity on the retina should produce such sensations as those of violet, blue, yellow, or red, the physiologist is wholly unable to explain. We have, however, an analogous phenomenon in sound, for musical notes are simply the effects of waves of air beating in a similar way on the auditory nerves; and, as is well known, the greater the frequency of the beats, or, in other words, the more rapid the oscillations of the aerial molecules, the higher is the pitch of the note. Red color corresponds to low, and violet to high notes of music, and the gradations of color between these extremes, passing through various shades of yellow, green, blue, and indigo, correspond to the well-known gradations of musical pitch" (Cooke: Chemical Philosophy, 1882, p. 189).

[1] It is seldom that one of these forms of molecular energy when exhibited in the phenomena of living beings is not associated with some other form. Thus

818. The conversion of the energy of the motion of the ethereal medium (in radiant light) into chemical separation of oxygen from the carbon of carbonic acid, and the production of this treasured energy under other forms, is the chief office of the plant.

819. Attention has already been called (see page 306) to the well-known fact that a beam of sunlight is composed of rays or lines of undulations differing both in respect to their amplitude and velocity. Hence it is to be expected that in their action on the plant these rays, which are in fact vehicles of kinetic energy, must have diverse effects.

820. **Classification of the rays of the spectrum.** When a beam of sunlight is transmitted through a triangular prism, it is broken up into its constituent rays, which, falling upon a screen, form what is known as a spectrum. The colors of the spectrum grade from red at one end, through orange, yellow, green, blue, and indigo, to violet. The violet rays are bent further from their course by the prism than any of the others above spoken of, and hence are termed the most refrangible; experiment has also shown that these highly refrangible rays are most efficient in producing the chemical changes long known to be attributable to light: for this reason they have been denominated chemical (or sometimes actinic) rays. The red rays are bent far less from their course than any of the others above mentioned, and hence they are termed the least refrangible. It is at the red end of the visible spectrum that the greatest amount of heat is found. The rays which constitute yellow and orange light are of medium refrangibility; they are the most distinctly luminous. It is proper, therefore, for convenience, to distinguish rays of the solar spectrum as chemical, luminous, and heat rays, according to the dominant effect which they produce. But it should be stated that each of these three groups may share some of the work specially belonging to the others; and further, that beyond the visible spectrum are rays which are efficient in accomplishing certain kinds of work. These latter are known respectively as the ultra-violet and the ultra-red rays.

Before examining the action of these different rays of light upon the assimilative activity of chlorophyll granules, inquiry must be made as to

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absorption, which is essentially a process of molecular adhesion, is accompanied, as is capillary attraction, by electrical disturbances. In no case is energy lost: one form disappears only to reappear in some other.

821. **The depth to which light can penetrate green tissues.** This can be ascertained approximately by a simple apparatus suggested by Sachs.[1] A pasteboard tube, a foot or so in length and about an inch in diameter, is cut at one end so as to fit around the eye very closely and allow no rays to enter except through the other end of the tube. If a thin leaf be placed over the distal end of the tube, and it be held towards a bright light, a large portion of the light will be received by the eye. If leaf after leaf be placed over the first, the green color soon gives way to a dull red, and finally is excluded altogether. The same apparatus shows to what depth light can penetrate superposed layers of green cells taken from a stem or from thick leaves.[2]

822. **The quality of the light which penetrates a leaf,** or which has passed through one layer of cells containing chlorophyll, is shown by means of the spectroscope. From what has been shown (p. 296), it is clear that the light which acts on the cells below the first layer exposed to the sun's rays must be different from the incident rays themselves. The light which reaches the deeper tissues of a leaf has passed through more than one film of green tissue.

823. The degree of intensity of white (that is, uncolored) light most favorable to assimilation has not been determined with certainty. The lowest limit at which any assimilation has been observed is considerably above that at which etiolated chlorophyll turns green.[3]

824. It has been shown[4] that very intense white light, even after it has been deprived of nearly all of its heat rays, can destroy the vitality of vegetable cells. Considerably before the death of the cells from this cause, the chlorophyll granules in them lose all their coloring-matter, even when they preserve their general form, and having once lost their green color, do not afterwards regain it.

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[1] Handbuch der Experimental-physiologie, 1865, p. 5.

[2] But it has been shown by Hankel that the angle at which a beam of light strikes a plate of glass makes a noticeable difference in the amount of the chemical rays which can pass through it; thus while at a vertical angle 81 per cent of the rays are transmitted, the rest being absorbed, at an angle of 60° the amount transmitted is reduced to 71 per cent, and at 80° to 33 per cent. The subject as relating to plants has not received the attention it deserves (Berichte über die Verhandlungen der Sächsischen Gesellschaft der Wissenschaften).

[3] Sachs: Experimental-physiologie, 1865, p. 8.

[4] Pringsheim: Monatsberichte der Berlin Akademie, 1879.

825. **Colored light and assimilation.** Daubeny, in 1835, was the first[1] to experiment systematically upon this subject. His method[2] of investigation was as follows: "A certain number of fresh leaves, which presented in each case an extent of surface as nearly as possible equal, and had been previously ascertained to give out equal quantities of oxygen, were introduced severally into jars filled with water impregnated with carbonic acid gas, placed on the surface of a pneumatic trough, and exposed for a certain time to the influence of the solar rays. The jars in which the leaves thus selected stood, were severally covered over by a wooden screen which intercepted all light from the included jar," excepting in front, where a frame was fitted, into which (1) colored glass or (2) flat bottles filled with differently colored liquids could be fastened, so that the light reaching the leaves could be variously modified. The amount and character of the gas escaping into the upper part of each jar were carefully determined. The leaves used were those of Brassica oleracea, Salicornia, Fucus, Tussilago, Cochlearia Armoracia, and Mentha viridis. Besides plain glass, the following colored varieties were employed: orange, red, blue, purple, green; while the liquids used were, for blue, ammonio-sulphate of copper, and for red, port wine.

In all cases Daubeny determined the amount of gas given off by the leaves, and afterwards analyzed it in order to ascertain the percentage of oxygen. He concluded from his experiments,[3] "that the effect of light upon plants corresponds with its illuminating rather than with its chemical, or its calorific influence."

826. J. W. Draper, in 1844, published an account of his experiments upon the relations of green plants to light, as regards the amount of assimilative activity indicated by the oxygen given

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[1] Senebier and others had already conducted some inconclusive experiments in nearly the same field.

[2] On the Action of Light upon Plants, and of Plants upon the Atmosphere (Philosophical Transactions, 1836, p. 149).

The activity of assimilation proper, as will be seen later, can be measured with a very close approximation to accuracy, by the amount of oxygen gas which is set free from the assimilating tissues, or, what amounts to substantially the same thing, by the amount of carbonic acid decomposed by them. For the sake of uniformity, the word *assimilation* is to be used in the following paragraphs, even where the authorities cited refer to the process under the terms *decomposition of carbonic acid*, *evolution of oxygen*, etc. The term assimilation, in its restricted sense, was adopted by Sachs (1863).

[3] Philosophical Transactions, 1836, p. 151.

off during exposure to different rays of the solar spectrum. From his results it appears that "the rays which cause the decomposition of carbonic acid gas have the same place in the spectrum as the orange, the yellow, and the green; the extreme red, the blue, the indigo, and the violet exerting no perceptible effect."[1]

Draper lays great stress upon the interesting fact previously noticed by Daubeny, that the chemical rays appear to have no effect upon the work of assimilation. He does not, however, offer any explanation of the curious fact that the chemical activity of the plant is dependent upon other rays than the chemical for its excitation.

827. The principal results obtained with submerged water plants by Cloëz and Gratiolet,[2] who exposed Potamogeton and

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[1] A Treatise on the Forces which produce the Organization of Plants, 1844, p. 177. The method of experimenting is detailed by Draper as follows: "Having, by long boiling and subsequent cooling, obtained water free from dissolved air, I saturated it with carbonic acid gas. Some grass leaves, the surfaces of which were carefully freed from any adherent bubbles or films of air by having been kept beneath carbonated water for three or four days, were provided. Seven glass tubes, each half an inch in diameter and six inches long, were filled with carbonated water, and into the upper part of each the same number of blades of grass were placed, care being taken to have all as near as could be alike. The tubes were inserted side by side in a small pneumatic trough of porcelain. It is to be particularly remarked that the blades were of a pure green aspect, as seen in the water; no glistening air-film, such as is always on freshly gathered leaves, nor any air bubbles, were attached to them. Great care was taken to secure this perfect freedom from air at the outset of the experiments.

"The little trough was now placed in such a position that a solar spectrum, kept motionless by a heliostat and dispersed by a flint-glass prism in a horizontal direction, fell upon the tubes. By bringing the trough nearer to the prism or moving it farther off, the different colored spaces could be made to fall at pleasure on the inverted tubes. The beam of light was about three fourths of an inch in diameter. In a few minutes after the commencement of the experiment the tubes on which the orange, yellow, and green light fell commenced giving off minute gas bubbles; and in about an hour and a half a quantity was collected sufficient for accurate measurement.

"The gas thus collected in each tube having been transferred to another vessel and its quantity determined, the little trough, with all its tubes, was freely exposed to the sunshine. All the tubes now commenced actively evolving gas, which, when collected and measured, served to show the capacity of each tube for carrying on the process. If the leaves in one were more sluggish, or exposed a smaller surface than the others, the quantity of gas evolved in that tube was correspondingly less. As may be readily supposed, I never could get tubes so arranged as to act *precisely* alike; but after a little practice I brought them sufficiently near to equality. And in no instance was this testing-process of the power of each tube for evolving gas omitted after the experiment in the spectrum was over."

[2] Annales de Chimie et de Physique, sér. 3, tome xxxii., 1851, p. 67.

Myriophyllum to the action of light colored by passing through glass, may be stated as follows: The activity of the plant in decomposing carbonic acid diminishes with glasses used in the order given: (1) uncolored "ground" glass, (2) yellow, (3) uncolored transparent glass, (4) red, (5) green, (6) blue. By all the experimenters now referred to, the evolved gas was collected and examined.

828. **Measurement of the amount of assimilation.** Sachs, in 1864, appears to have been the first to employ the now well-known method of measuring the activity of the assimilative process by counting the bubbles of gas which are given off by a submerged water plant (see 814). Since the gas given off by the plant is not pure oxygen, but is variable in composition,[1] the method cannot be regarded as sufficiently precise for very accurate experiment; but as it admits of such rapid change in all external conditions, it answers for all practical purposes.

829. The effect of colored light upon the assimilative activity of plants not submerged, as in the above experiments, but in the air, was first examined by Cailletet,[2] in 1867. He placed the plant under bell-jars containing air with eighteen, twenty-

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[1] For remarks upon the possible errors which may attend the use of this method, consult Müller (Pringsheim's Jahrb. vi., 1868, p. 478).

[2] L. Cailletet placed leaves in jars filled with air containing from 18 to 30 per cent of carbonic acid, and then exposed these to light which had passed through colored glass. In one case the light was transmitted through a solution of iodine in carbon bisulphide. After an exposure of from eight to ten hours, the amount of carbonic acid remaining undecomposed by the action of the leaves was found to be as follows: —

Medium.	Per cent of carbonic acid in the air.			Remarks as to chemical activity of light.
	18 p. c.	21 p. c.	30 p. c.	
Iodine in CS_2	18	21	30	Photographic paper not blackened.
Green glass	20	30	37	Argentic chloride slowly discolored.
Violet glass	18	19	28	Sensitive paper blackened rapidly.
Blue glass	17	16.50	27	" " "
Red glass	7	5.50	23	No blackening of argentic chloride or sensitized paper.
Yellow glass	5	1	18	Paper not blackened.
Ground glass	0	0	2	Paper discolored rapidly.

Two points must be specially noticed: (1) the striking effect of the large amount of carbonic acid in the third series; (2) the anomaly presented by the green glass, which is quite unexplained. It is to be regretted that no fuller account of the character of the glasses used is given (Comptes Rendus, lxv., 1867, p. 322).

one, or thirty per cent of carbonic acid, and made of red, yellow, green, blue, violet, and colorless glass. His results agree in general with those obtained by the other methods.

830. In 1870 further investigations in the same subject were made by Pfeffer.[1] The following is a *résumé* of the results of his experiments with the leaves of five different plants exposed to colored light: Only the visible rays of the spectrum cause decomposition of carbonic acid; and in this process the brightest, that is, the yellow rays, are as efficient as all the others taken together, while the most refrangible rays, those which act most energetically upon chloride of silver, have only very slight influence upon the work of assimilation.

Every color of the spectrum may be said to possess a specific quantitative influence upon assimilation. This influence remains unchanged whether the color is isolated, combined with one, or with all the other colors of the spectrum when it acts upon a part of a plant containing chlorophyll.

831. Examination of the spectrum of chlorophyll (779) shows that the part of the spectrum which absorbs most of the rays is that which is pre-eminently its chemical end; but by all the observers whose results have been cited in the text, it is held that the chemical end is that which is least efficient in assimilation. With the exception of the narrow though strong absorption-band in the red, all the deep absorption-bands of chlorophyll and its solutions belong at the violet or chemical end of the spectrum. Müller and Timiriazeff, cited in the notes, have endeavored to investigate this anomaly.

832. Timiriazeff,[2] in a series of researches in 1877, experimented upon the slender leaves of Bamboo, which he placed in tubes of small calibre containing air of known composition,

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[1] Arbeiten des botan. Inst. in Würzburg, 1871, p. 1.

The following works may also be cited: —

A. von Wolkoff, Einige Untersuchungen über die Wirkung des Lichtes von verschiedener Intensität auf die Ausscheidung der Gase durch Wasserpflanzen. Pringsh. Jahrb., v., 1866, p. 1.

Adolf Mayer, Production von organischer Pflanzen-Substanz bei Ausschluss der chemischen Lichtstrahlen, Versuchs-Stationen, ix., 1867, p. 396.

N. J. C. Müller, Untersuchungen über die Diffusion der atmosphärischen Gase in der Pflanze und die Gasausscheidung unter verschiedenen Beleuchtungsbedingungen, Pringsh. Jahrb., vi., 1867, 478; and vii., 1869, 145.

Timiriazeff, Botanische Zeitung, 1869, p. 169.

Prillieux, Ann. des Sc. nat., sér. 5, tome x., 1869, p. 305.

Baranetzky, Botanische Zeitung, 1871, p. 193.

[2] Annales de Chimie et de Physique, sér. 5, tome xii., 1877, p. 355.

and exposed to different parts of a large spectrum formed by a hollow prism filled with carbon bisulphide. By employing a narrower slit for the light than that used by previous experimenters, he obtained an exposure of the leaves to a very limited portion of the spectrum: and to this difference in his apparatus he chiefly attributes his results, which are at variance with those of his predecessors. Assuming that the results of his analysis of the evolved gas are accurate, they indicate that the amount of carbonic acid decomposed by leaves is proportional to the distribution of *effective* calorific energy in the spectrum.

Timiriazeff[1] in his earlier paper did not himself attempt to apply his results to an explanation of the peculiar relations of the rays of the spectrum to assimilation; but Van Tieghem, who substantially adopts the results of Timiriazeff, gives the following application of them to the associated phenomena. He calls attention to the fact that the maximum of decomposition of carbonic acid, under the conditions of Timiriazeff's experiments, takes place at the deep absorption-band of chlorophyll, between B and C; and therefore concludes that the decomposition of carbonic acid by leaves exposed to solar radiation depends on two elements: (1) the elective absorption of the chlorophyll, and (2) the calorific energy of the absorbed radiations. According to this view, the most efficient radiations must be those which, being best absorbed by the chlorophyll, possess at the same time the greatest calorific energy. Hence, (1) the extreme red and the dark heat-rays, in spite of their extraordinary calorific energy, have no effect, because they pass through chlorophyll without visible absorption; and (2) the blue rays, which are very strongly absorbed, exert scarcely any effect, owing to their feeble calorific energy.[2]

833. Timiriazeff's results should be compared with those of Engelmann, who finds that for green cells the absolute maximum of assimilative activity lies in the red, between the lines B and C, at the point of the first and most pronounced absorption-band of chlorophyll, and that there is also more or less activity in the blue at F. If the cells are not of a green color, the maximum of activity is in some other point; thus in the case of bluish-green cells it is in the yellow, and in that of red cells in the green.

Engelmann's method is based upon the extraordinary sensi-

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[1] Ann. de Chimie et de Physique, sér. 5, tome xii., 1877, p. 394, and Ann. des Sc. nat., sér. 7, tome ii., p. 99.

[2] Traité de Botanique, 1884, p. 149.

tiveness[1] of certain bacteria to the presence of free oxygen. By an ingenious device, simple in its application, it is possible to determine the parts of the spectrum in which an assimilating cell or filament gives off oxygen most copiously. Under the stage of the microscope is placed a microspectroscope, which throws a clear spectrum upon any object on the glass slide in its place on the stage, for instance a filament of an alga. The alga is placed upon the slide in water which contains numbers of the common Bacterium (B. Termo), easily procured from putrescent matters. If it is kept from the light, or is exposed to only very faint light, all assimilative activity is suspended, and the bacteria after a time are quiescent. But when light in sufficient amount is permitted to pass through the specimen, assimilative activity is at once manifested, and the evolution of oxygen from the filament brings the bacteria into rapid movement. If, instead of white light, the rays from the spectroscope are passed through the specimen, the activity of the bacteria is equally manifest, but it is confined to a comparatively small part of the spectrum; the bacteria collecting chiefly at the points which are known to coincide with the absorption-bands of chlorophyll.[2] When a somewhat thick cell is employed, there is a noticeable difference between the amount of activity on its upper and under side. The figures show the ratio of activity of assimilation between the under side first exposed, and the upper side which receives light that has first passed through a green film.

	B-C.	D.	D½E.	E-b.	F.	F½G.
Lower	100.	48.5	37.	24.	36.5	10.
Upper	36.5	94.	100.	52.	22.	12.

It is to be noted that Engelmann did not in any case find any assimilation in uncolored chlorophyll, even when the light was tempered by the interposition of a colored medium (compare 850).[3] He has proved that assimilation proper takes place only in

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[1] According to Engelmann, the sensitiveness of bacteria is so great that by their reaction the trillionth part of a milligram of oxygen can be detected (Botanische Zeitung, 1883, p. 4). Clerk Maxwell's estimate of the weight of a molecule of oxygen was one thirteen trillionth of a milligram (Philosophical Magazine, 1873, p. 453).

[2] It is interesting to compare these determinations of the point of greatest assimilative efficiency in the spectrum with the results of Langley's researches upon the distribution of energy in the spectrum (American Journal of Science, xxv., 1883, p. 169).

[3] Botanische Zeitung, 1882, p. 419; 1883, p. 17.

protoplasm which contains coloring-mater, as for instance the chlorophyll granules, the colored granules in algæ, etc.

834. **Artificial light and assimilation.** De Candolle[1] exposed the submerged leaves of several species of plants to the light emitted by six Argand lamps, and failed to obtain thereby any evolution of gas. He estimated that the lamps had about five sixths of the intensity of sunlight. In this experiment the light, though insufficient to cause the evolution of gas, restored etiolated plants to their original green color.

835. When, however, a submerged water plant is exposed to the rays from a calcium light[2] (as that of an ordinary projecting lantern), there is a copious evolution of gas from its leaves. The light from burning magnesium wire is also sufficient to cause the decomposition of carbonic acid and the evolution of oxygen.[3]

836. The influence of the **electric light** upon assimilation has been investigated by numerous observers. Dehérain, who experimented in the Palais de l'Industrie, in Paris, found that the total assimilation produced in the leaves of Anacharis Canadensis, during an exposure for five days, was not equal to that which followed exposure to sunlight for a single hour.[4] Siemens has shown that (1) many plants do not require any period of rest during the day, but thrive under continued illumination by electric light and sun-light; (2) electric light, properly regulated, accelerates growth, and produces upon plants effects comparable to those produced by sun-light.[5]

837. **Temperature and assimilation proper.** In certain cases the *minimum* temperature at which assimilation can take place is only slightly above the freezing-point of water. Boussingault[6] found that the leaves of the larch decompose carbonic acid at a temperature of from 0°.5 – 2°.5 C.; while Kraus[7] gives the

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[1] Mem. prés. par divers Savans, à l'Institut des Sciences, tome i., 1806, p. 333, and Physiologie végétale, 1832, p. 131.

Biot, in 1840 (Froriep's Notizen, xiii. 10), when measuring, in Spain, the length of a degree of latitude, found that the light from the powerful signalling apparatus used was not sufficient to cause any evolution of gas from submerged plants of Agave Americana.

[2] Prillieux: Comptes Rendus, lxix., 1869, p. 408.

[3] Heinrich: Versuchs-Stationen, xiii., 1871, p. 153.

[4] Annales Agronomiques, tome vii., 1881, p. 385.

[5] Proceedings of the Royal Society, xxx., pp. 210, 295, and Report of the British Association for the Advancement of Science, 1881, p. 474.

[6] Ann. des Sc. nat., sér. 5, tome x., 1868, p. 336.

[7] Kraus (Pringsh. Jahrb., vii., p. 522) placed seedlings of Lepidium sativum in the dim light of the back of a room, where after six days the cotyledons

minimum temperature for assimilation by Anacharis, Lepidium, and Betula as 3°–5° C.; and Heinrich[1] gives it as 2°.5–4°.5 C. for Hottonia.

The *maximum* temperature at which assimilation can occur in Anacharis[2] is between 45° and 50° C.; in Hottonia,[3] just below 56° C.

The *optimum*[4] temperature for Hottonia appears to be not far from 31° C.

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showed no trace of starch. The plants were then distributed in three rooms of the temperatures mentioned in the annexed table, and with the results there detailed: —

After	12°.8-13°.7 C.	5°.9-6°.5 C.	0°.3-0°.5 C.
2 hours.	The first starch granules appear in the chlorophyll cells on the margin of the leaves.	No starch.	No starch
3 hours.	Starch in the whole tip, margins, and petiole.	Some traces of starch at margins of the leaves.	"
5 hours.	Starch in the whole upper half of the leaf.	Tip and narrow edge with starch.	"
13 hours.	The whole leaf contained starch.	Margin with much, surface with little starch.	"

[1] Versuchs-Stationen, xiii., 1871, p. 136.

[2] Schutzenberger and Quinquaud: Comptes Rendus, lxxvii., 1873, p. 272.

[3] Heinrich: Versuchs-Stationen, xiii., 1871, p. 136.

[4] Heinrich's figures are so instructive that they are here presented in the following table, which gives the number of bubbles of gas passing off from the cut surface of single leaves of Hottonia during the space of five minutes: —

Temp. C.°	No. of bubbles.
11	145–160
12	180–190
13	215–
15	245–255
17	255–265
21	325–360
22	375–
25	390–450
31	547–580
37	420–517
43	225–255
50	110–220
56	0

The student must be reminded that the amount of gas which comes off in this experiment with submerged plants is not an *exact* measure of the assimilation.

838. **The amount of carbonic acid unfavorable to assimilation.** Experiments made by Saussure[1] at the beginning of this century proved beyond question that plants are not tolerant of an atmosphere containing a large proportion of carbonic acid. In carbonic acid alone, or even in an atmosphere containing 66 per cent of this gas, vegetation was speedily destroyed. It was shown, however, that if the plants were exposed to full light, they could sustain 8 per cent of carbonic acid without injury. Saussure thought that the presence of free oxygen is necessary to the assimilative work of the leaf.

839. In 1849, Daubeny[2] carried on an extensive series of researches, chiefly upon plants allied to the dominant vegetation of the Carboniferous period, namely, ferns and their allies, from which it appeared that even for these plants an amount of carbonic acid above 10 per cent is injurious. Five species were placed in a receptacle containing about 46 liters of air, and to this air was added one per cent of carbonic acid, and also one per cent daily thereafter, until the amount present reached 20 per cent. This proportion was kept for twenty days, small amounts being added, as occasion required, to make up for loss by leakage. On the thirteenth day a sensible impairment of the plants was noticed; and at the end of thirty days all of them had been more or less damaged, most having lost their fronds.

840. Boussingault,[3] in 1864, conducted a series of experiments in order to ascertain whether the presence of free oxygen in an atmosphere containing carbonic acid is necessary to the work of assimilation. The results of his researches are given as follows: —

(1) Leaves exposed to sunlight, in pure carbonic acid, do not decompose this gas, or if at all, very slowly.

(2) Leaves exposed to sunlight in an atmosphere containing a mixture of common air and carbonic acid decompose the latter gas rapidly; but the oxygen of the air has no part in this operation, since,

(3) Leaves exposed to sunlight rapidly decompose carbonic acid gas when this gas is mixed with nitrogen, hydrogen, carbonic oxide, or carburetted hydrogen.

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[1] Saussure: Recherches chimiques sur la végétation (Paris, 1804), p. 29. An earlier experiment was made by Percival.

[2] Report of British Association, 1849, p. 56; and 1850, p. 159.

[3] Agronomie, iv., 1868, p. 301.

841. **The amount of carbonic acid most favorable to assimilation.** The results of the most exhaustive study of the amount of carbonic acid most favorable to assimilation have been given by their recorder as follows: —

(1) Increase in the amount of carbonic acid in the air, up to a certain limit (the optimum), favors the evolution of oxygen by plants; beyond this it is more or less injurious.

(2) The optimum of carbonic acid is different for different plants: for Glyceria spectabilis on clear days it is between 8 and 10 per cent; for Typha latifolia, between 5 and 7 per cent; for Oleander, somewhat less.

(3) Any given increase in the amount of carbonic acid below the optimum favors the evolution of oxygen far more than a similar increase above the optimum hinders it.

(4) The stronger the intensity of the light the more the evolution of oxygen is favored by increase in the amount of carbonic acid up to the optimum; and when this limit is passed the evolution is checked so much the less.

(5) From (4) it follows that the influence of the intensity of the light on the evolution of oxygen is greater in proportion to the amount of carbonic acid in the air.

842. **Ratio of the oxygen evolved by plants to the carbonic acid decomposed.** The volume of oxygen evolved by plants during assimilation proper is very nearly that of the carbonic acid decomposed.[1]

Numerous experiments by Boussingault exhibit this relation in a very striking manner. In forty-one experiments the volume of carbonic acid was to that of the oxygen set free as 100 : 98.7.

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[1] Saussure (Recherches chimiques sur la végétation, 1804, pp. 40, 59) is regarded as the first to indicate this. He arrived at this conclusion by experimenting upon a number of plants under different conditions. His first recorded experiment consisted in surrounding seven plants of Vinca (Periwinkle) with an atmosphere containing a known quantity of carbonic acid gas. The plants were exposed to sunlight from five to eleven o'clock in the morning for six days, after which the air in the bell-jar was examined.

	Air in the jar before the experiment.	Air in the jar after the experiment.
Nitrogen	4199 cubic cent.	4338 cubic cent.
Oxygen	1116 "	1408 "
Carbonic acid	431 "	0 "
Total volume	5746 "	5746 "

Saussure's conclusion is that plants, in decomposing carbonic acid, assimilate a part of the oxygen gas therein contained, and, further, that the amount of carbon retained by the plant bears a definite relation to the amount of CO_2 taken up by it.

The following table by Boussingault[1] is very instructive, as it shows the relation of volume between the amount of carbonic acid consumed and the oxygen evolved in assimilation; and also the decomposing power of various kinds of plants under different conditions.[2]

Plants.	CO_2 disappearing.	Oxygen appearing.	Time of exposure to light.	Surface of leaves.	CO_2 decomposed per square decimeter each hour.	Constitution of atmosphere.
	c. c.	c. c.	h. m.	cm. sq.	c. c.	
Cherry laurel	5.2	5.9	4 0	134	.8	CO_2
"	23.2	22.9	4 0	124	4.7	CO_2 + air.
"	4.	4.5	4 0	90	1.0	CO_2
"	19.6	19.9	4 0	90	5.5	CO_2 + air.
Pine	13.0	13.0	7 0	204	.9	CO_2
"	18.1	17.8	7 0	204	1.3	CO_2 + air.
Oak	4.9	4.0	4 0	224	.5	CO_2
"	25.	24.7	4 0	224	2.8	CO_2 + air.
Holly	5.1	4.9	5 30	52	1.8	"
Mistletoe	9.9	9.9	5 0	100	2.	"

843. The gas emitted during the process of assimilation proper is not pure oxygen. Both Daubeny[3] and Draper[4] found variable amounts of nitrogen in all the cases examined by them.

844. **What are the products of assimilation proper?** It has now been shown under what conditions the green tissues of a plant decompose carbonic acid and evolve oxygen.[5] As the chief result of this decomposition and its associated processes, there is formed within the cells which contain chlorophyll a carbohydrate of some kind. This carbohydrate contains the same elements as the carbonic acid and the water from which it was produced, but it contains less oxygen than the total amount found in those substances taken together. Hence the process of assimilation is essentially one of reduction. There is, however, no substantial agreement as to the nature or constitution of the primary carbohydrate formed by it.

The difficulty which attends the investigation of assimilation

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[1] Agronomie, iv., 1868, p. 286.

[2] A well-known relation of volume between oxygen and carbonic acid may here be pointed out; namely, that "free oxygen occupies the same bulk as the carbonic acid produced by uniting it with carbon."

[3] Philosophical Transactions, 1836.

[4] "In every instance which I have examined, the gas evolved from leaves is not pure oxygen, but a variable mixture of oxygen and nitrogen. This result is of uniform occurrence" (Chemistry of Plants, 1844, p. 182).

[5] For an account of the transient evolution of oxygen under exceptional circumstances where carbonic acid is not present, see Müller's Handbuch der Botanik, 1880.

is apparent at a glance. The raw materials, the apparatus, and the ultimate products of manufacture are known; but the intermediate processes by which chlorophyll granules under the influence of certain rays of light can cause the dissociation of carbon from the oxygen with which it is combined in carbonic acid, and bring about the synthesis of an organic substance from materials wholly inorganic, are not at present known.

845. The wide field which the synthesis of organic from inorganic matter opens to conjecture has not been left unoccupied. It is generally admitted that in assimilation there is first formed some *ternary* substance, namely, one which contains the three elements, carbon, hydrogen, and oxygen; and further, that this contains less oxygen than the two inorganic matters, carbonic acid and water, from which it is produced, taken together. Exactly what the ternary substance is, or how the dissociation or reduction is carried on in the chlorophyll granule, is still left in doubt.

846. **Starch** ($C_6H_{10}O_5$) is the first *visible* product of assimilation, as was first pointed out by Sachs in 1862.[1] Although Sachs appears to have held at one time that it is the first product, his later expressions are more guarded, and simply state the fact universally admitted, namely, that starch is the first product which the microscope can detect. When a seedling has been kept for a time in a dimly lighted room, its cotyledons and other leaves grow pale or etiolated, and if they are examined for starch, no trace of it will be found. But upon a very short exposure of the plant to the direct rays of the sun, provided the other conditions are favorable, a certain amount of starch will appear in the chlorophyll granules of the cells at the margin of the leaves. If the plant is again withdrawn from the light, its scanty store of starch is speedily consumed, but on renewed insolation the loss is made good; this process can be repeated many times. From the constant appearance of starch in the chlorophyll granules under the above circumstances it has been generally recognized as the first visible product of assimilation proper. But it has obviously such a complex molecular structure that chemists are unwilling to believe that its formation in the plant is not preceded by the production of some simpler substance. Furthermore, there are a few cases in which oil replaces starch as the first visible product, thus indicating that there may be some earlier product possibly common to both.

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[1] Botanische Zeitung, 1862; Flora, 1862.

847. **Glucose.** It is held by some that this product is glucose ($C_6H_{12}O_6$) or some substance having the same atomic proportions of these elements. Early and not well-defined views in regard to glucose may be replaced by the following statement of a theory widely taught.

848. **Formic aldehyde hypothesis.** According to Gautier,[1] chlorophyll exists in two conditions, *white chlorophyll*, rich in hydrogen, and *green chlorophyll*, poorer in this element. By his hypothesis the yellow ray absorbed by the assimilating tissues furnishes a certain amount of energy which is partially converted into heat, and promotes evaporation of water (transpiration); and at the same time it permits the chlorophyll granule to decompose the water with which the protoplasmic mass is saturated. In the presence of CO_2 and H_2O the reducing process gives rise to formic acid (CH_2O_2), which in its turn is reduced to formic (or methylic) aldehyde, CH_2O. The latter has the same atomic proportions as glucose ($C_6H_{12}O_6$).

849. Whether, in assimilation, the ternary substance be formic aldehyde, or glucose, or starch, it is certainly a substance capable of undergoing further oxidation, and hence, chemically speaking, an unsaturated compound. When this unsaturated compound is oxidized,[2] a definite amount of energy of motion is set free, and this is manifested to us under one of its many phases, namely: (1) movements of the whole plant, as in some of the lowest organisms; (2) movements of liquids within the plant, as in the transfer of matter to points of consumption; (3) heat; (4) electrical disturbances, and all the proper vital activities correlated with these. The energy of motion in solar radiance is treasured for a time in the ternary and derivative products, thence to be released as occasion requires.

850. It is proper to refer at this point to a novel view in regard to the product of assimilation which has received much adverse criticism; namely, that of Pringsheim.[3] Attention has already been called to the interesting observations by this botanist on the constitution of chlorophyll granules. In prosecuting his investigations he became convinced that the peculiar colored substance which is extruded from the granules under the influence of certain agents is a product of assimilation. To this product he gave the name *hypochlorin*. According to him, when

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[1] La Chimie des Plantes. Revue Scientifique, Feb. 10, 1877, p. 767.

[2] Compare Claude Bernard, Leçons sur les Phénomènes de la Vie, 1878.

[3] Jahrb., xii., 1879–1881, p. 288.

any active cells containing chlorophyll granules are subjected to conditions favorable to assimilation, hypochlorin is formed in considerable amount; but when the conditions for assimilation are not present, only traces of it are produced. Pringsheim used an entirely novel method of experimenting; namely, that of subjecting the chlorophyll granules to the action of intense light from which the heat rays had been extracted as perfectly as possible; and under these conditions he failed to detect any hypochlorin, but observed a marked increase in the amount of CO_2 given off as in ordinary respiration (see Chapter XI.). Hence he arrived at the conclusion that assimilation proper is the characteristic office of chlorophyll granules solely on account of their pigment, which *tempers* the light reaching them. According to him, the pigment, by its absorption of the so-called chemical rays, serves as a *regulatory* screen governing the amount of light, and so controlling the amount of respiration and assimilation proper.

851. **Outline of the early history of assimilation.** The following extracts from the works of early experimenters upon the relations of green leaves to the atmosphere show the manner in which the problem of assimilation was first attacked.

852. Priestley[1] discovered in 1771[2] that air in which candles can no longer burn, and which is irrespirable, can be restored to its original condition by the presence in it, for a time, of vigorous plants. The account below is given in his own words:

"Finding that candles would burn very well in air in which plants had grown a long time, and having had some reason to think, that there was something attending vegetation which restored air that had been injured by respiration, I thought it was possible that the same

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[1] Experiments and Observations on Different Kinds of Air (3d edition, 1781), p. 51.

[2] In 1754 Bonnet published his observations upon the behavior of leaves in water. It is well known that when green leaves are immersed in water and exposed to sunlight for a time, bubbles of air appear on their surface. Bonnet believed that the leaves drew common air from the water and this swelled into conspicuous bubbles under the heat of the sun. He was confirmed in this belief upon ascertaining that bubbles did not appear on green leaves exposed in water which has been boiled to expel the air (Recherches sur l'usage des Feuilles dans les Plantes, p. 26). If we consider the state of chemical science at the time of Bonnet's researches, his error is in no wise surprising. It is now known that the bubbles which Bonnet took to be air are nearly pure oxygen which escapes as a by-product of assimilation. But from water which has been boiled, all the carbonic acid essential to assimilation has been expelled.

process might also restore the air that had been injured by the burning of candles.

"Accordingly on the 17th of August, 1771, I put a sprig of mint into a quantity of air, in which a wax candle had burned out, and found that, on the 27th of the same month, another candle burned perfectly well in it. This experiment I repeated, without the least variation in the event, not less than eight or ten times in the remainder of the summer.[1]

"Several times I divided the quantity of air in which the candle had burned out, into two parts, and putting the plant into one of them, left the other in the same exposure, contained also in a glass vessel immersed in water, but without any plant; and never failed to find that a candle would burn in the former, but not in the latter. I generally found that five or six days were sufficient to restore this air, when the plant was in its vigour; whereas I have kept this kind of air in glass vessels immersed in water many months without being able to perceive that the least alteration had been made in it."

853. **Ingenhousz** in 1779 showed that light is necessary to assimilation. He proved experimentally that the purification of air does not go on in darkness, but that light is essential. His statements are here given: —

"Plants not only have a faculty to correct bad air in six or ten days, by growing in it, as the experiments of Dr. Priestley indicate, but they perform this important office in a complete manner in a few hours. This wonderful operation is by no means owing to the vegetation of the plant, but to the influence of the light of the sun upon the plant. . . . This operation of plants diminishes towards the close of the day, and ceases entirely at sunset, except in a few plants which continue this duty somewhat longer than others. This office is not performed by the whole plant, but only by the leaves and the green stalks that support them. Acrid, ill-scented, and even the most poisonous plants perform this office in common with the mildest and the most salutary."[2]

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[1] Priestley thought that this effect upon the air is due to the *growth* of the plant, an idea which will be shown in Chapter XII. to be wholly erroneous. On pages 50 and 52 of the volume quoted above are the following statements: "One might have imagined that since common air is necessary to vegetable, as well as to animal life, both plants and animals had affected it in the same manner; and I own I had that expectation when I first put a sprig of mint into a glass jar standing inverted in a vessel of water: but when it had continued growing there for some months I found that the air would neither extinguish a candle nor was it at all inconvenient to a mouse which I put into it. . . . This restoration of the air, I found, depended upon the *vegetating state* of the plant; for though I kept a great number of the fresh leaves of mint in a small quantity of air in which candles had burned out, and changed them frequently, for a long space of time, I could perceive no melioration in the state of the air."

[2] Experiments upon Vegetables, discovering their great Power of purifying the Common Air in the Sun-shine, 1779, p. xxxiii.

854. **Senebier**[1] first demonstrated that plants obtain all their carbon from carbonic acid gas.

855. That definite quantitative relations exist between the amounts of carbonic acid decomposed, carbon retained, and oxygen evolved by the plant, was first pointed out by **Saussure.**[2]

APPROPRIATION OF NITROGEN.

856. It has been shown that all land and many water plants contain a variable amount of air in their tissues, chiefly in the intercellular spaces and older modified cells (tracheïds, tracheæ, etc.). When there is an active interchange of gases by any plant, a portion of the nitrogen contained in its included air is very likely to be eliminated. A trace of nitrogen is so generally found with the oxygen evolved during assimilation proper, that this has been regarded by some as a constant accompaniment of the assimilative process.

857. **Amount of nitrogen in the plant.** Besides the free nitrogen which constitutes a part of the included air of the plant, there is a certain amount of combined nitrogen always present in active cells as an essential component of their living matter. The protoplasmic matters in plants contain about 15 per cent of nitrogen in combination. For all practical purposes they may be regarded as having chemically a common albuminous[3] basis (roughly comparable to the white of egg), with which (as has

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[1] Mémoires Physico-chymiques, 1782.

Many of Senebier's observations are almost identical with those of Ingenhousz (as given in his "Nutrition of Plants"), and it has been thought by some that the priority of the above discovery belongs rightfully to the latter. It is to be remembered that at the date at which both of these experimenters were working, chemists were just beginning to acquire, through the studies of Lavoisier, clear notions in regard to the important part which oxygen plays, and that in the early part of this transition period an obscure nomenclature renders it difficult to apportion to each of these observers his proper share of credit.

[2] Recherches chimiques sur la végétation, 1804.

Some of the relations of light to the process of decomposition of carbonic acid by green parts of plants were first indicated by Daubeny, and further examined by Draper. The subsequent history of assimilation, to which Sachs, Pfeffer, Engelmann, and many others have contributed, has been referred to in the text and in citations in the notes.

[3] Attention may again be called to the various expressions employed to designate the compounds in the plant which resemble albumin, and which have been collectively termed albuminoids. Authors have made a distinction

been seen on page 197) there is always intermingled an inconstant amount of carbohydrates, or proper food-materials, etc. At different stages in the life of a cell its protoplasmic matters may pass through considerable changes of form and structure, as indicated in an examination of a ripening seed; but under all these varying conditions nitrogen in combination is never absent from the living substance of the plant.

858. For the formation of new protoplasmic matters in the plant, supplies of nitrogen in an available form must be furnished; for healthful growth, these supplies must be adequate in amount.

859. Dissolved albuminous matters of various kinds are met with in the sap of some cells. This in many cases appears to be, as will be shown later, a form in which their transport from one part of the plant to another is secured. A small number of these albuminous substances have been shown to be *ferments*, which play a very important part in the nutrition of the plant.

860. Although by far the greater part of the combined nitrogen of the plant exists in one or more of the combinations mentioned in Chapter XI., there is often to be detected a small and variable amount as a nitrate[1] (generally potassic), and even as a salt of ammonia.

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between certain groups of these bodies as they are represented in the animal kingdom, dividing them into (1) albuminous matters and (2) their derivatives or albuminoids (see Gorup-Besanez, Lehrbuch der Chemie, iii., 1874, p. 115). Although the latter term, without the restriction here noted, is in common use in vegetable physiology to designate these bodies, an objection can justly be urged against its employment, on account of the more common use in botany of the word *albumen* with an entirely different signification (see Volume I. p. 14).

In 1838 Mulder published the theory that all these bodies are practically derivatives from one substance, termed by him proteine (from πρωτεύω, to be first); but it was soon shown that this theory was erroneous, and it has been generally abandoned. The term introduced by Mulder to designate the hypothetical compound common to all these bodies has, however, been since employed to conveniently denote the whole class. In using the convenient term protein bodies, or *proteids*, to designate the members of this group, it must not be understood that the abandoned theory of Mulder is taken into account at all.

[1] For the detection of nitrates the following test may be employed: To a drop of the sap under examination add a drop of a solution of brucine, mix, and then add a few drops of concentrated sulphuric acid, when, if a nitrate is present, a red color will appear. Sprengel's reaction may also be used: One part of phenol is dissolved in four parts of concentrated sulphuric acid, and two parts of water are added. If a drop of this solution is added to a solid nitrate, a reddish color is produced. On adding strong ammonia, the color turns green and afterwards yellow.

861. There can be found in a large number of plants a small amount of certain matters termed alkaloids, which contain a definite percentage of nitrogen. Such are *morphia* in the poppy, *quinia* in Peruvian bark, *caffeine* in coffee, etc. (see 961).

862. In most analyses the combined nitrogen of the plant is usually rendered as "albuminoid." The percentages in a few cases are here given:[1]—

Red clover, full blossom	3.7
Sugar beets	.8 to 1.0
Carrot root	1.5
Carrot leaves	3.2
Cabbage	1.5
Winter wheat	13.0
Beans (field)	25.5
Apples	.22 to .52

Of these amounts about 16 per cent may be roughly estimated as the content of nitrogen. Therefore in such a case as the carrot root above mentioned, the total amount of nitrogen is really very small (0.24 per cent); but the presence of this small percentage is absolutely essential to the life as well as to the health of the plant.

863. Reserving for a later chapter all consideration of the numerous chemical transformations which nitrogenous matters may undergo in the plant, it is necessary to ask now, (1) whence can the plant obtain adequate supplies of available nitrogen, and (2) how can the plant appropriate, or, to use an equivalent term. assimilate them.

864. **Sources of nitrogen for the plant.** It must first be shown whence nitrogen is *not* supplied. The *free nitrogen* of the atmosphere does not appear to be directly available for plants. Although most of the higher plants possess an aerating system (see p. 300), through which atmospheric air can easily enter and traverse the plant and be brought into contact with the tissues, the nitrogen which forms so large a part of the atmosphere is not utilized. This is the interpretation of experiments in culture in which every kind of combined nitrogen is carefully excluded from the plants while they have, at the same time the free nitrogen of the atmosphere in an unlimited supply.

865. The earliest[2] systematic investigations relative to the

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[1] For other cases the student should consult the tables in the Appendix to Johnson's "How Crops Grow," 1868, pp. 385–392.

[2] The following citations refer to earlier observations, none of which, however, can be considered as having fixed any important points relative to the use of atmospheric nitrogen by plants: —

above subject were made by Boussingault in 1837,[1] who employed the following method: In calcined soil, supplied with distilled water, and having free access of air, clover was cultivated for two and for three months, and at the end of that time it was found that there was a very slight gain in nitrogen over the amount which had been present in the seed sown. In two parallel experiments with wheat no gain was observed. One year later, peas, clover, and oats were experimented on; both the peas and clover gained a little nitrogen, but there was no gain whatever in the case of the oats. Boussingault's conclusions from this series have been stated as follows: Under several conditions certain plants seemed adapted to take up the nitrogen in the atmosphere, but it is still a question under what circumstances and in what state the nitrogen is fixed in the plants.

866. It was not, however, until 1851 that the subject received any further attention from Boussingault. In that and the two subsequent years his experiments were conducted with certain precautions, by which the plants were confined in limited volumes of air; and in no case was an unequivocal gain in nitrogen to be detected. In 1854 he placed plants in a suitable receptacle where they could be supplied with a current of air washed to free it from all traces of combined nitrogen. The atmosphere within the receptacle was furnished with from two to three per cent of carbonic acid. In all of the experiments, part of which were upon leguminous plants, there was a slight loss of nitrogen.

867. During the progress of the experiments now alluded to others were conducted in the following manner: Plants were placed in a case from which nearly all dust could be excluded, but which would allow of a free circulation of the external air; and under these circumstances there was the very slight gain in nitrogen equal to about one twelfth of that contained in the seed sown. Boussingault attributed this almost inappreciable gain

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Priestley: Experiments and Observations on Different Kinds of Airs, iii., 1772.

Saussure: Recherches chimiques sur la végétation, 1804, p. 205. In this will be found a short account of the results of the previous observers and also of Saussure's own conclusions, which are, — that plants do not appropriate any appreciable amount of nitrogen furnished to them as it exists in the atmosphere in the free state.

[1] For a short but excellent abstract in English of Boussingault's researches, referred to in the text, the student may consult Philosophical Transactions of the Royal Society for 1861, p. 447. The original communications are in Annales de Chimie et de Physique, sér. 2, tomes lxvii. and lxix., 1838.

to the ammonia in the atmosphere, and also to organic matters in small amount which may have entered the case in the form of very fine dust; but, taking into consideration all the conditions of the experiment, he was not inclined to the belief that any nitrogen had been received by the plants from the free nitrogen of the atmosphere.

868. In 1855 and 1858 the same chemist experimented upon certain plants which were supplied with a known amount of combined nitrogen in some available form. The results of his experiments have been formulated as follows: (1) There was no appropriation of free nitrogen; (2) There was a slight loss of the nitrogen which had been supplied to the plant; (3) The amount of assimilation of carbon bore a close relation to the amount of nitrogen taken up by the plant.

869. From 1849 to 1854 Georges Ville, of Paris, conducted experiments which were interpreted as showing that plants can take from the nitrogen of the atmosphere a certain part of that which they require. In the autumn of 1854 he carried on a series of researches at the Jardin des Plantes, under the supervision of a committee appointed by the French Academy. Towards the close of the work an element of error crept into it which could not then be eliminated; but as to the result of the investigation the committee reported,[1] — that the experiment made at the Museum d'Histoire Naturelle by M. Ville is consistent with the conclusions which he has drawn from his previous labors.

870. In 1861 Lawes, Gilbert, and Pugh,[2] of England, pub-

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[1] The report by Chevreul will be found in Comptes Rendus, xli. p. 757. Results so directly in conflict as those of the two experimenters referred to in the text led others to investigate this subject, and in 1857–1859 an exhaustive series of investigations was carried on at Rothamsted, England, by Lawes, Gilbert, and Pugh.

Mène, in 1851, concluded from his experiments that plants do not appropriate the free nitrogen of the air.

Roy interpreted the results of his own experiments as showing that free nitrogen dissolved in water can be taken up by plants.

Luca (1856) suggested that the air surrounding plants may be ozonized, and thus the nitrogen in it converted into nitric acid and made available for the plants.

Harting (1855) concluded that the free nitrogen of the air is not proved to serve directly for the nutrition of the plant.

[2] Philosophical Transactions, 1861, p. 431. For an excellent description and drawing of the complicated apparatus employed in this capital investigation the student may consult Johnson's "How Crops Feed," p. 30.

lished the results of a series of experiments upon the subject of the appropriation of nitrogen by plants. These experiments were designed to settle the disputed question. Every conceivable precaution was taken to avoid any error, and the plants were grown under conditions as little unlike their ordinary surroundings as possible. Under these conditions to insure healthy growth, they were deprived of all access to nitrogen except as it existed in the free state in the atmosphere or dissolved in the water supplied to them. It was found that no plants appeared to make use of the free nitrogen of the atmosphere or of the nitrogen dissolved in water supplied to their roots. But in certain cases, especially of leguminous plants cultivated in the open air, there is an apparent gain in the amount of nitrogenous products in the plant over and above that which is directly attributable to the combined nitrogen furnished to it.[1]

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[1] The following extracts from the paper by Lawes, Gilbert, and Pugh will convey a clear idea of the cautious manner in which their important results are reported: —

"The results obtained with Graminaceæ in 1858 . . . point without exception to the fact that under the circumstances of growth to which the plants were subjected, no assimilation of free nitrogen has taken place. The regular process of cell-formation has gone on; carbonic acid has been decomposed, and carbon and the elements of water have been transformed into cellulose; the plants have drawn the nitrogenous compounds from the older cells to perform the mysterious office of the formation of new cells; those parts have been developed which required the smallest amount of nitrogen, and all the stages of growth have been passed through to the formation of glumes, pales, and awns for the seed. In fact, the plants have performed all the functions that it is possible for a plant to perform when deprived of a sufficient supply of combined nitrogen. They have gone on thus increasing their organic constituents with one constant amount of combined nitrogen until the percentage of that element in the vegetable matter is far below the ordinary amount of it, — that is, until the composition indicates that further development had ceased for want of a supply of available nitrogen. Throughout all these phases, water saturated with free nitrogen has been passing through the plant; nitrogen dissolved in the fluid of the cells has constantly been in the most intimate contact with the contents of the cells and with the cell-walls" (p. 523).

Of leguminous plants the investigators say, "In those cases in which we have succeeded in getting leguminous plants to grow pretty healthily for a considerable length of time, the results, so far as they go, confirm those obtained with Graminaceæ, not showing in their case, any more than with the latter, an assimilation of free nitrogen" (p. 526).

Further, they say, "From the results of various investigations, as well as from other considerations, we think it may be concluded that under the circumstances of our experiments, on the question of the assimilation of free nitrogen by plants, there would not be any supply to them of an unaccounted quantity of combined nitrogen due either to the formation of oxygen com-

871. **Nitrogen compounds in the atmosphere.** The atmosphere contains minute amounts[1] of combined nitrogen in the form of ammonia, nitric acid, and nitrous acid. The ammonia is believed to exist (except where from local causes there is an escape of free ammonia from some source) combined with either carbonic or nitric acid.

872. **Nitrogen in rain-water.** The nitrogen compounds are more or less perfectly removable from the air by rain, and in solution can be made available to plants through the soil. It is now necessary to examine the results of analyses of rain-water in order to ascertain the amount of nitrogen contained in it.

The following data are taken from the careful experiments at Rothamsted, under the direction of Lawes, Gilbert, and Warington. The nitrogen existing as nitric acid and ammonia in the rainfall of one year is not far from 3.3 pounds per acre. The proportion of this calculated as ammonia is between 2.3 and 2.6 pounds per acre, the residue being given as nitric acid. Besides the foregoing substances, there is also a small amount of nitrogenous organic matter in the air which appears in the analyses of rain-water, and amounts, according to Frankland, to .19 parts per million parts of water. Taking a somewhat lower estimate than this, Lawes, Gilbert, and Warington give the quantity of nitrogen in the form of organic matter annually

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pounds of it under the influence of ozone, or to that of ammonia under the influence of nascent hydrogen" (p. 540).

But, as shown by Lawes, Gilbert, and Pugh, as well as by many other experimenters, leguminous crops appropriate from some source considerably more nitrogen than do grasses; for instance, under apparently similar circumstances of supply of combined nitrogen.

For an excellent treatment of the whole matter of appropriation of nitrogen, the student should consult memoirs by Atwater, "On the Acquisition of Atmospheric Nitrogen by Plants" (American Chem. Journ., vol. vi., 1885, no. 6).

[1] The following figures serve simply to indicate the wide range in results obtained by different observers who have investigated the amount of ammonia in the atmosphere. The data are from Proceedings of Am. Assoc. for Advancement of Science, 1857, p. 152.

Observer.	Station.	Amount of ammonia in one million cubic meters atmosphere.
Fresenius	Wiesbaden (during the day)	127.27 gr.
"	" (at night)	219.47 "
Kemp	Ireland	4423.00 "
Ville	Paris	27.39 "
Horsford	Boston (in July)	640.70 "

contributed in the rain as 1.08 pounds per acre. "We may probably take 4.5 pounds per acre as the best estimate we can at present give of the total combined nitrogen annually supplied in the Rothamsted rainfall. This is only about two thirds as much as the earlier results indicated as due to ammonia and nitric acid alone. . . . In addition to the combined nitrogen carried down from the atmosphere in rain, we have to consider any gain to the soil or to the crop by direct absorption of ammonia or nitric acid from the air. As far as any gain from the atmosphere to the plant itself is concerned, there is very little direct experimental evidence on the point, but such as is available would lead to the conclusion that its amount is practically immaterial. As to the amount of gain by absorption by the soil, there is unfortunately no direct or satisfactory evidence at command. From such evidence as does exist, we are disposed to conclude that with some soils the amount will probably be greater and with others less than that supplied by the rainfall."[1]

873. **Direct absorption of ammonia by leaves.** Under certain circumstances ammonia can be absorbed directly by leaves. This will be further adverted to under "Appropriation of Organic Matters."

874. **How the nitrogen compounds of the atmosphere are formed.** It is a familiar fact that under certain circumstances the free nitrogen of the atmosphere can be made to unite with oxygen for the production of nitric acid; for instance, by the passage of a spark of electricity through a confined atmosphere a small amount of combined nitric acid may be formed. The bearing of this fact upon the existence of nitrogen compounds in the atmosphere is very obvious. Schlœsing,[2] in an interesting study of the nitrogen compounds of the air and soil, attributes to the atmosphere a very important office in forming and distributing nitrogen compounds. According to him, the nitric acid contained in rainwaters on escaping from the soil, where it is only lightly held, finds its way to the sea, where under various agencies (notably that of vegetable organisms of the lowest grade) it becomes, sooner or later, changed into ammonia. This readily escapes into the air, and is carried in the atmospheric currents to all parts of the world, becoming thereby available to land plants.

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[1] Journal Royal Agricultural Society, vol. xix., part 2, 1883.

[2] Comptes Rendus, tome lxxxi., 1875. The same idea has been more or less treated by others.

875. **Available nitrogen in the soil.** When animal matters rich in nitrogen undergo rapid putrefaction,[1] they give rise to numerous compounds, prominent among which are those of ammonia. Under certain conditions, notably the presence (1) of free oxygen in large amount, or (2) of an alkali, or an alkaline carbonate, such animal matters are also slowly broken up, and nitrates are formed. The process by which various compounds of nitrogen are converted into nitrates is termed nitrification.[2]

876. Vegetable matters which contain nitrogenous substance in the usual amount may likewise undergo decomposition; but owing to the presence in such matters of a large proportion of carbohydrates, for instance the cellulose of the cell-walls, the process of decomposition is more complex than in animal matters and its products more diverse. Some of the products are probably identical with those formed from the decomposition of albuminous matters of animal origin; namely, ammonia,[3] or ammonia compounds, and nitrates; but the larger number of them are compounds which are nearly or quite insoluble and have been thought to be inert.[4] But experiments have shown that under certain conditions these less available compounds of nitrogen

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[1] For a discussion of the various phases and conditions of decomposition the student is referred to the third volume of this series, in which the different forms of fermentation and putrefaction are to be treated. It is enough now to note that these processes are essentially due to the presence and activity of minute organisms, — the lowest fungi.

[2] The student will find in Johnson's "How Crops Feed," p. 289, an excellent account of this most important topic. He is referred also to Boussingault's "Agronomie," 1860, and various articles in Versuchs-Stationen.

[3] The following data indicate the amounts of nitrogen in certain soils, as determined by Boussingault (Agronomie, ii., 1861, pp. 14, 18). The reductions to pounds per acre are from Johnson's "How Crops Feed," p. 276.

Source of the Soil.	Ammonia.		Nitrogen in organic combination.	
	per cent.	lbs per acre.	per cent.	lbs. per acre.
Liebfrauenberg (light garden soil)	0.0020	100	.259	12,970
Bechelbronn (wheat-field clay)	0.0009	45	.139	6,985
Argentan (rich pasture)	0.0060	300	.513	25,650
Rio Cupari, S. A. (rich leaf-mould)	0 0525	2,875	.685	34,250

[4] Experiments by Boussingault (Agronomie, i. 1860) can hardly be interpreted in any other way. One reason for his results has been sought in the fact that he employed only very small amounts of vegetable matter in his admixtures of soil; but all of his experiments are regarded as models of accuracy

in the soil can be turned to a very important account by the plant.

877. **Nitrogen used by wild and cultivated plants.** From the sources described, wild plants obtain a sufficient supply of available nitrogen. In some localities, notably in portions of the tropics and along the rich alluvial deposits of rivers, the stores of available nitrogen are so abundant that all vegetation flourishes with great vigor, and even cultivated plants, which appear to be more exacting than wild plants in their demands for nitrogen, can obtain an adequate supply. Further, it has been abundantly shown by the long-continued experiments at Rothamsted, that the same soil, unenriched by additions of manures, can yield even after twenty-five years enough nitrogen for the needs of fair or moderate crops.

878. In the ordinary cultivation of plants it is profitable to augment in some way the supply of nitrogen in most soils. Under some circumstances this augmentation can be accomplished to a certain extent by mere tillage or by the exposure of fresh portions of soil to the action of the atmosphere. But it is usually effected by the employment of natural or artificial manures. The former consist of the excrementitious matters of animals or of the waste products from plants. These excrementitious matters represent a large part of what the animals have consumed, and must have come either directly or indirectly from the vegetable kingdom; hence they only restore to the soil that which plants had at some time removed therefrom.

In the preparation of artificial fertilizers an effort is made to provide for the plant the mineral and nitrogenous matters which it requires. A large proportion of these fertilizers are composed

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throughout, and can leave no doubt that, under the conditions of his trials, there was practically no utilization of the soil nitrogen by the plants.

On the other hand, experiments by Wolff (Chemisch.-Pharmaceut. Central-Blatt, 1852, p. 657), Johnson (Peat and its Uses, 1866, p. 79), and Storer show that under certain conditions the plant can avail itself of the nitrogen organically combined in the soil. The works of the above authors, which are only a few of those bearing on this important matter, will place the student in possession of the methods of experimenting.

Storer's interesting communication in the Bulletin of the Bussey Institution (vol. i., 1874, p. 252), "On the Importance as Plant-food of the Nitrogen in Vegetable Mould," gives not only an account of his experiments but also a forcible presentation of the principal arguments in favor of the belief that the "soil-nitrogen" (that is, the nitrogen in vegetable mould) is by no means inert.

of a certain amount of available calcic phosphate together with a salt of potassa and some available nitrogenous matter.[1]

It has been shown (p. 248) that some plants require more of one kind of food than others; and hence the attempt has been often made to prepare exactly the special fertilizer which a given crop may require.

879. **Nitric acid and the nitrates.** Experiments with water-culture have shown that plants can derive all the combined nitrogen needed for their growth from nitric acid and the nitrates. But it has also been clearly shown that there are striking differences in the capacity which plants possess for appropriating nitrogen from these compounds. Even in the common agricultural plants there are some differences in this respect.

880. A large number of nitrogen compounds, such as asparagin, urea, albumin, etc., have been employed in experiments upon plants, but most of the results possess little interest. It may be said, in general, that the so-called alkaloids (which contain nitrogen) cannot be utilized even by the very plants from which they were made.[2]

881. **Synthesis of albuminous matters in the plant.** A distinction is made between the newly formed or first-formed albuminous substances in the plant and those which have undergone chemical changes in the organism, as for instance the changes in germination. Two views have been held respecting the place where the formation of the new protein matters occurs in the

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[1] The following analyses, taken from the Report of the Connecticut Agricultural Experiment Station for 1883, indicate the composition of a few such substances: —

	Nitrogen of nitrates.	Nitrogen of ammonia salts.	Nitrogen of organic matter.	Phosphoric acid.		Potash.
				soluble.	reverted.	
Tobacco manure (No. 972).	1.20	2.90	1.21	7.52	2.08	4.35
" " (No. 965).	.10	4.15	.60	3.41	1 52	9.03
Forage crop " (No. 976).	.21	.17	2.91	6.48	.77	4.06
Potato " (No. 905).		2.59	.67	6.87	.67	9.76

For an account of the commercial prices of the available nitrogen compounds for 1883–1884, see Report of Connecticut Agricultural Experiment Station, 1885.

[2] For a short account of the bibliography of this subject the student should consult Pfeffer's Pflanzenphysiologie, i., 1881, p. 242.

higher plants; namely, (1) that in favor of the chlorophyll cells, (2) that in favor of the conductive tissues of the petiole and stem. So far as analogy drawn from the lower plants is concerned, one of these views is as tenable as the other; for while in a simple alga all the formation of new protein matters must go on in a cell where there is chlorophyll or its equivalent, in the case of a fungus, nourished as in the experiments of Pasteur upon a simple ternary body and a nitrate, the process must of necessity take place in cells where no chlorophyll is present.

882. Exact observations upon the subject of the formation of albuminous matters in the plant are not abundant. Reference will be made here chiefly to those by Emmerling, who carried on an extended series of investigations with Vicia Faba. He examined all parts of the plant with respect to the inorganic nitrogen compounds furnished, and then sought for the protein compounds resulting therefrom. His results are interpreted as showing that the nitric acid which is absorbed from the soil, and can be detected in all parts of the roots and stems, disappears very rapidly in the leaves and all parts which are actively growing, so that there is found only a mere trace in them. According to him, it is in green leaves that the transformation of nitrogenous matters takes place. The first product of this transformation is not at present certainly known; but there is good reason to regard it as a member of the group of carbamides.[1] Those parts of the plant which are rapidly growing are much richer in amides than the older and more fully developed portions. This fact is shown by Kellner[2] to be true of pasture grass, in which the amides are more abundant in the young than in the old parts.

APPROPRIATION OF SULPHUR.

883. The amount of sulphur which exists as an essential part of the albuminous matters of the plant is quite small, being not far from one per cent.[3]

884. As already shown (681), sulphur is taken into the plant in the form of sulphates, chiefly calcic. The calcic sulphate[4] is probably decomposed by the oxalic acid produced by the plant, and thus an insoluble calcic oxalate is formed; then

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[1] Versuchs-Stationen, xxiv., 1880, p. 113.

[2] Centralbl. f. Agric.-Chem., 1879, p. 271.

[3] Ranging, according to Ebermayer, from .4 to 1.8 per cent (Physiologische Chemie der Pflanzen, 1882, p. 616).

[4] Holzner: Flora, 1867.

by a process of reduction the sulphur is set free to unite with the albuminous matters already described.

The abundant occurrence, in conducting tissues of stems and petioles, of calcic oxalate resulting from the changes described has been held to indicate the probable seat of albuminous synthesis.[1]

885. The general statements which have now been made respecting the appropriation of carbon, nitrogen, and sulphur hold good for all ordinary land and water plants. There are a few plants, however, concerning which they must be somewhat modified, and these are here for convenience treated of together; as humus-plants, parasites, insectivorous plants, and epiphytes. It must be remembered that in all these apparently exceptional cases the mechanism of nutrition is not radically different from that which other plants possess at some period of their lives or in some slight degree.

APPROPRIATION OF ORGANIC MATTERS.

886. **Humus-plants,[2] or Saprophytes.** Among the higher plants there are some (for example, Epipogium [3]) which derive all their

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[1] Sachs: Text-book, 2d Eng. ed., 1882, p. 711.

[2] As a matter chiefly of historical interest, the "humus theory" must be referred to. As stated in the words of Liebig, its author, it is briefly as follows: —

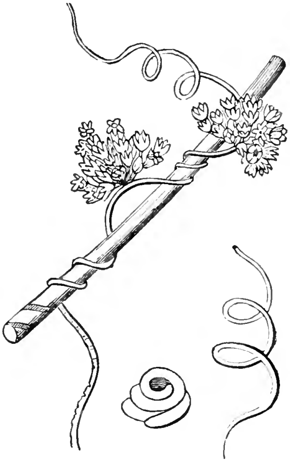
"Woody fibre in a state of decay is the substance called *humus*. . . . Humus acts in the same manner in a soil permeable to air as the air itself; it is a continued source of carbonic acid, which it emits very slowly. An atmosphere of carbonic acid, formed at the expense of the oxygen of the air, surrounds every particle of decaying humus. The cultivation of land by tilling and loosening the soil, causes a free and unobstructed access of air. An atmosphere of carbonic acid is therefore contained in every fertile soil, and is the first and most important food for the young plants which grow in it. . . . The roots perform the functions of the leaves from the first moment of their formation: they extract from the soil their proper nutriment, namely, the carbonic acid generated by the humus. . . . When a plant is quite matured, and when the organs, by which it obtains food from the atmosphere, are formed, the carbonic acid of the soil is no further required. . . . Humus does not nourish plants by being assimilated in its unaltered state, but by presenting a slow and lasting source of carbonic acid, which is absorbed by the roots" (Chemistry in its Application to Agriculture, American edition, 1842, pp. 65 *et seq*).

It has been shown by the investigations referred to in the text that plants can be grown with vigor and carried to complete maturity without the supply of carbonic acid to the roots, and hence the "humus theory" is emptied of all its value; but, as will be shown later, the decaying vegetable matter in soils has important functions.

[3] Pfeffer's Pflanzenphysiologie, i., 1881, p. 226.

nutriment from the decaying or decayed remains of other plants; while others, like Monotropa uniflora and the Orobanchaceæ, obtain part of their food from living plants. True parasites obtain their nourishment from living organisms, whereas humus-plants, or saprophytes, live upon the structures of dead ones. From the decaying vegetable mould they procure all the ternary substances needed for their own fabric, and also the nitrogenous substances needed for their own protoplasmic matters. It is not known exactly how saprophytes turn to account the comparatively inert nitrogenous matters of vegetable mould, but the process is thought to depend upon the action of a solvent, unorganized ferment, somewhat similar to that which effects changes in the food within reach of the embryo of the seed.

887. **Parasites** obtain a large part of their food from living organisms. In some cases they appear to be able thus to procure all the food they require; but most of them can be shown to elaborate, by means of the small amount of chlorophyll which they possess, a small part of their food. The haustoria, by means of which they abstract from other plants the assimilated matters, have been described in 351. After the parasite has fairly fastened itself upon the host-plant, it acts with respect to the tissues of the latter much as if it were an offshoot of the host. It appropriates the assimilated matters as they are needed, and consumes them in substantially the same way that an embryo consumes the food stored in the endosperm.[1]



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888. **Insectivorous or carnivorous plants,** as already explained in Volume I. page 110, *et seq.*, are those which are provided with some specialized apparatus for the utilization of animal matters.

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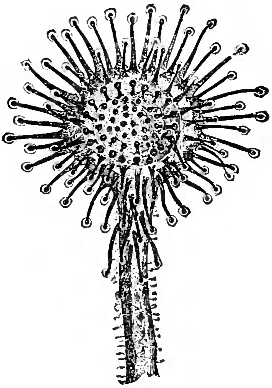
[1] For an interesting account of the more striking effects produced upon the host-plant, the reader should consult Frank: Die Pflanzenkrankheiten, 1879.

The relations which exist between the ash-constituents of the parasite and its host have been examined by Reinsch.

FIG. 152. Cuscuta, a parasite. The coiled embryo and seedling are shown in the right-hand sketches; in the other sketch, the adult plant, with its flower-clusters, attached to the living stem of another plant.

The structure and office of the prehensile and digestive apparatus are now to be illustrated by the following examples: —

889. **Drosera rotundifolia,** or round-leaved sundew, grows abundantly in northern peat-bogs and in sand mixed with vegetable mould, both in the Old World and the New. The plant has a few (4 to 12) leaves, arranged in a flat tuft at the base of the flower-stalk, and narrowed at their bases into hairy petioles. The most striking character of the leaves is the thick clothing of peculiar hairs, otherwise known as *tentacles* or *glands*, from the tip of each of which exudes a drop of a clear viscid liquid. These hairs are complicated in structure. They contain all the histological elements proper to the leaf itself; for this reason it has been thought by some that they should be regarded as processes from the leaf rather than as hairs. The marginal tentacles are long, have purple stalks, and are terminated by elongated purple glands; those towards the middle of the leaf are shorter, have greenish stalks and ovoid glands. Each gland consists of a double layer of polygonal cells which surround a central body composed of elongated cells and a few tracheïds. The protoplasmic lining of all the cells is transparent and thin, and the cavity is filled with an homogeneous purple fluid. The tracheïds pass by insensible gradations into minute spiral ducts.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890. The mode of action in Drosera is as follows: When a small object is placed on the middle glands, a sluggish movement is soon detected in the marginal tentacles. If the object is a fragment of animal matter, the motor impulse is communicated rapidly, and the marginal tentacles curve sharply over upon the fragment, bringing the glands in contact with it. The blade of the leaf also sometimes becomes curved, forming a shallow cup. Inorganic and such organic matters as are not acted on by the secretion from the glands act more slowly in causing movement of the tentacles than do soluble organic substances, and no movement follows unless the object rests upon the glands themselves, not merely on the secretion which covers

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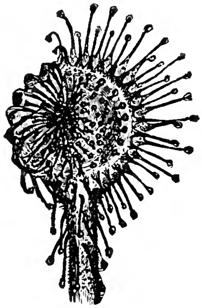
FIG. 153. Drosera rotundifolia. View of leaf from above. (Darwin.)

them. Darwin found that movement was caused by the contact of a particle weighing only .0008 milligram ($\frac{1}{78740}$ of a grain).



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When a tentacle has been excited by contact with a solid particle, there is seen, after some hours, a remarkable change in its cells near the gland. "Instead of being filled with homogeneous purple fluid, they now contain variously shaped masses of purple matter suspended in a colorless or almost colorless fluid."[1] Tentacles which have been thus acted on by contact of particles have a mottled appearance, and can be picked out with ease from all the others. The change of contents is termed by Darwin *aggregation*. "The little masses of aggregated matter are of the most diversified shapes, often spherical or oval, sometimes much elongated, or quite irregular with thread or necklace-like or club-formed projections. They consist of thick, apparently viscid matter, which in the exterior tentacles is of a purplish, and in the short discal tentacles of a greenish, color. These little masses incessantly change their forms and positions, being never at rest. . . .

"Shortly after the purple fluid within the cells has become aggregated, the little masses float about in a colorless or almost colorless fluid; and the layer of white granular protoplasm which flows along the walls can now be seen much more distinctly. The stream flows at an irregular rate, up one wall and down the opposite one, generally at a slower rate across the narrow ends of the elongated cells, and so round and round. But the current sometimes ceases. The movement is often in waves, and their crests sometimes stretch almost across the whole width of the cell and then sink down again. Small spheres of protoplasm, apparently quite free, are often driven by the current round the cells; and filaments attached to the central masses are swayed to and fro, as if struggling to escape. Altogether, one of these cells, with the ever-changing central masses and with the layer of protoplasm flowing round the walls, presents a wonderful scene of vital activity."[2]

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[1] Darwin: Insectivorous Plants, 1875, p. 39.

[2] Darwin: Insectivorous Plants, pp. 40, 42.

FIG. 154. Drosera rotundifolia. Leaf with the tentacles on one side inflected over a bit of meat placed on the disc. (Darwin.)

The aggregation is caused by various nitrogenous organic fluids and salts of ammonia; the most efficient agent for its production being ammonic carbonate, .000482 milligram ($\frac{1}{134400}$ of a grain) being enough to cause aggregation in all the cells of a tentacle. These figures show the extreme sensitiveness of the tentacles and glands to slight external impressions.

891. "If the glands are excited either by the absorption of nitrogenous matter or by mechanical irritation, their secretion increases in quantity and becomes acid." That it contains an unorganized ferment admits of no question. The secretion after excitation possesses the power of dissolving the albuminoids substantially as the gastric juice of animals does. When an insect alights upon the leaf of Drosera, its violent struggles to escape only wind more closely about it the threads of viscid matter from the glands. Soon the tentacles close around it, and the increased secretion of the digestive fluid brings about a true digestion of the nitrogenous matter.

892. That the digested matters can be absorbed, appears from numerous experiments. In these, after the disappearance of albuminous matters impregnated with a salt of lithium, it was possible with the spectroscope to detect the salt in the plant. Parts of the leaves remote from the seat of digestion, being dried, calcined, moistened with hydrochloric acid, and placed in the colorless flame of a Bunsen burner, gave the characteristic lithium line.

893. *Does the plant gain any advantage by this absorption of organic matter?* Francis Darwin's[1] experiments upon this subject may be briefly stated as follows: —

Two sets of thrifty plants of Drosera were cultivated under the same conditions, with the single exception of a provision of animal food to the leaves of one set. At the conclusion of an experiment extending through three months, the ratios between the unfed and the fed plants were as follows: —

	Unfed.		Fed.
Weight of plants, exclusive of flower-stems	100	:	121.5
Number of flower-stems	100	:	164.9
Total weight of flower-stems	100	:	231.9
Total number of capsules	100	:	194.4
Average weight per seed	100	:	157.3
Total calculated number of seeds produced	100	:	241.5
Total calculated weight of seeds	100	:	379.7

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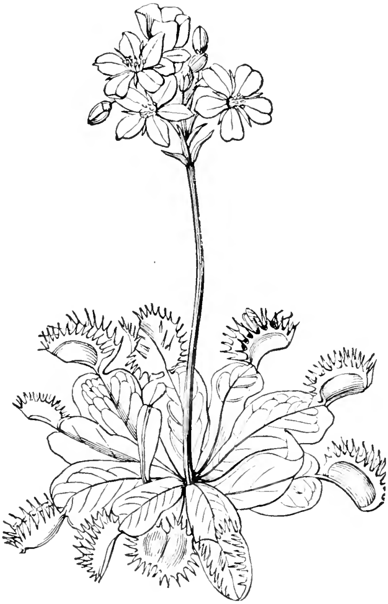
[1] Journal of the Linnæan Society, xvii., 1880, p. 17.

"Two hundred plants of Drosera rotundifolia were transplanted in June and cultivated in soup-plates filled with moss during the rest of the summer. Each

894. **Dionæa muscipula,** or Venus's fly-trap, grows sparingly in sandy soil near Wilmington, North Carolina, and in one or two other localities along the Carolina coast. Its leaf consists of two rather distinct parts, — the two-valved trap at the extremity, and a petiole-like support. It is probable that the support is not a true petiole, but a leaf-blade, while the trap is a special appendage developed upon the tip of the leaf-blade.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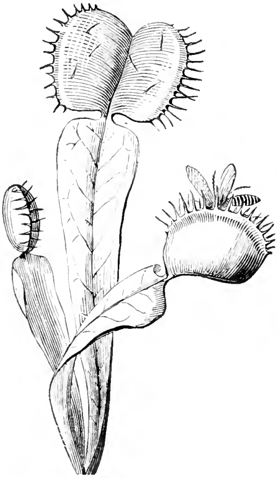
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895. The spring-trap is made up of two symmetrical halves meeting at a median hinge. The outer border of each half is

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plate was divided into halves by a low wooden partition, one side being destined to be fed with meat, while the plants in the opposite half were to be starved. The plates were placed altogether under a gauze case, so that the 'starved' plants might be prevented from obtaining food by the capture of insects. The method of feeding consisted in supplying each leaf (on the fed sides of the six plates) with one or two small bits of roast meat, each weighing about one-fiftieth of a grain. This operation was repeated every few days from the beginning of July to the first days of September, when the final comparison of the two sets of plants was made" (Nature, xvii., 1878, p. 223).

FIG. 155. A plant of Dionæa muscipula, reduced in size.

FIG. 156. Three of the leaves of almost the natural size; one of them open, the others closed. Probably a fly is never caught by the teeth as here represented.

fringed with stiff bristles so placed as to interlock when the trap is shut. The upper face of each half is somewhat convex when the trap is open, and upon it there are three delicate hairs which are exceedingly sensitive. Supposing the plant to be in health and under favorable conditions, the lightest touch upon one of the hairs upon the face of the trap will cause the valves to close instantly, bringing their edges in apposition. A light touch in the median line, that is, at the hinge, will produce the same effect. The sensitive hairs each consist of several rows of elongated cells so arranged as to form a conical filament resting on a constricted base and attached by an articulation to a rounded group of cells. This structure enables the hairs to bend when the trap is shut.

896. The digestive apparatus consists of minute reddish short-stalked glands made up of a few polyhedral cells. These do not secrete any fluid unless excited by the presence of food-materials, when they secrete copiously a colorless, glairy, acid liquid, containing an unorganized ferment similar to that produced by the stomach of animals, if not identical with it. Scattered among the secretory glands are numerous compound hairs formed of eight divergent cells, which are generally orange or brown in color.

897. From experiments by Darwin and others it is clear that dry albuminous solids do not excite the action of the glands, but if moistened very slightly, they call the glands into activity. Moreover, if the bit of meat or other albuminous matter be placed on the valves in such a way as not to spring the trap, the valves will soon slowly close without further touch. Aggregation takes place in the cells of the glands in much the same way as in Drosera.

898. When a small insect is caught by the springing of the trap, it can escape after a time through the spaces left between the bristles at the border; but if the insect is of moderate size, its escape is impossible: the valves shut down more and more tightly upon it, and digestion soon begins.

899. The opening of the valves after digestion takes place in different times according to the vigor of the plant and nature of the prey. After a mere touch by which the trap is sprung without anything in it, the valves will again open of themselves in a day or even less. When the trap is closed by a bit of meat, the valves open in from three or four days to rather more than a week; when it closes over a large insect, they remain shut for a much longer time, even for a month.

900. Canby[1] states that he has known "vigorous leaves to devour their prey several times; but ordinarily twice, or quite often once, was enough to render them unserviceable." Mrs. Treat[1] observes that "several leaves caught successively three insects each, but most of them were not able to digest the third fly, but died in the attempt. Five leaves, however, digested each three flies and closed over the fourth, but died soon after the fourth capture. Many leaves did not digest even one large insect."

901. The following experiments by Darwin illustrate the flow of the secretion: "A bit of albumin $\frac{1}{10}$ of an inch square but only $\frac{1}{20}$ in thickness, and a piece of gelatin $\frac{1}{5}$ inch long and $\frac{1}{10}$ broad, were placed on a leaf which eight days afterwards was cut open. The surface was bathed with slightly adhesive acid secretion, and the glands were all in an aggregated condition. Not a vestige of the albumin or gelatin was left. Similarly sized pieces were placed, at the same time, on wet moss in the same pot, so as to be subjected to nearly similar conditions; after eight days these were brown, decayed, and matted with fibres of mould, but had not disappeared."[2]

902. That the digested matters are absorbed by the leaf has been shown by the spectroscope, as in the case of Drosera; but no experiments are yet on record as to the effect of this nutritive matter on the plant.

The character of the movement by which the trap is sprung is spoken of in the chapter on "Movements."[3]

903. **Other insect-catching Droseraceæ.** Drosera and Dionæa are members of the order Droseraceæ. Its four remaining genera have also the power of capturing insects.

Aldrovanda has been well called a miniature Dionæa. Its bilobed leaves float in water (the plant being destitute of roots). Each leaf is two-valved, something after the fashion of Dionæa, but each valve is made up of two parts. One, near the hinge in the median line, is provided with colorless glands; the other, a sort of thin film outside, has no true glands. On the inner part there are some extremely delicate hairs which

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[1] Cited by Darwin: Insectivorous Plants, 1875, p. 311.

[2] Insectivorous Plants, p. 302.

[3] Burdon Sanderson has investigated the electrical disturbance which takes place when the trap of Dionæa is sprung. For details and conclusions see the following papers: Proceedings of the Royal Society, vol. xxi. p. 495, and Nature, x., 1874, pp. 105, 127. But similar electrical disturbances are exhibited when any fresh vegetable structure is sharply bent.

have been shown to be sensitive, and on touching them the valves close. By this plant minute water-insects and crustaceans are captured (see Fig. 190).

Drosophyllum, a rare plant found in Portugal, catches insects by a viscid secretion from minute mushroom-shaped glands. The tentacles do not have the power of movement possessed by those of Drosera. That its glands can secrete a digestive fluid appears from Mr. Darwin's experiments.

Roridula, found at the Cape of Good Hope, and *Byblis*, of western Australia, closely resemble the viscid-haired Droseraceæ, which have been examined in a fresh state, and they have been added to the list of the insect-catching plants of the order.

904. **Pinguicula** is so called from the greasy appearance presented by the upper surface of its leaf, due to the existence of great numbers of disc-like glandular hairs with short stalks. The glandular character of the hairs is shown by the secretion which exudes from them even when they are not irritated.

905. The secretion which flows when the leaves of Pinguicula are not excited by the presence of albuminous matter is neutral; but upon excitation of the leaf it becomes acid, far more copious in amount, and has the power of digesting nitrogenous organic substances. At that time the clear contents of the cells of the glands also become aggregated, much as in the case of the cells in Drosera; and this fact is adduced by Darwin as proof that the digested matters are absorbed.

906. In about three hours after an insect alights upon a leaf of Pinguicula the margin begins to roll over it and envelop it, in the manner shown by the accompanying figure. The following experiment by Darwin shows what takes place in this incurving: "A young and almost upright leaf was selected with its two lateral edges equally and very slightly incurved. A row of small flies was placed along one margin. When looked at next day, after fifteen hours, this margin but not the other was found folded inwards, like the helix of the human ear, to the breadth of one tenth of an inch, so as to lie partly over the row of flies. The glands on which the flies rested, as well as those on the over-

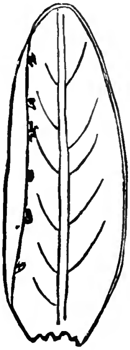
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FIG. 157. Pinguicula vulgaris. Outline of leaf with its left margin inflected over a row of small flies. (Darwin.)

lapping margin which had been brought into contact with the flies, were all secreting copiously."[1]

The incurvation lasts for only a day or two, after which the leaf assumes its former position: fragments of glass keep the margins incurved for a shorter time than do nitrogenous bodies.[2]

907. Darwin suggests the two following advantages which the plant can derive from even this transient inrolling: (1) the captured food and the secretion are protected from rain, and (2) the food is brought into contact with a larger number of glands than if the leaf remained flat.

908. It appears probable that the leaves of Pinguicula derive some nourishment from the seeds, etc., which may fall upon them. "We may therefore conclude that Pinguicula vulgaris, with its small roots, is not only supported to a large extent by the extraordinary number of insects which it habitually captures, but likewise draws some nourishment from the pollen, leaves, and seeds of other plants which often adhere to its leaves. It is therefore partly a vegetable as well as an animal feeder."[3]

909. **Utricularia,** a genus named from the utriculi or little bladders found on the dissected leaves of some of its species, belongs to the same natural order as Pinguicula. Its members capture minute aquatic animals by means of peculiar traps. Each bladder has at its mouth a few diverging hairs, while just within the orifice there is a sort of trap-door, which can be lifted by a slight touch and then falls by its own weight, covering the mouth and preventing egress. If a small aquatic animal passes through the entrance and pushes by the funnel-shaped trap-door, it is securely imprisoned. The interior of the bladders is lined more or less thickly with peculiar glandular hairs not very unlike those intermingled with the glands of Drosera, and found also on the valves of Dionæa. These are either bifid or quadrifid.

910. According to Darwin these hairs have the power of absorbing dissolved matters in a state of decay, but there is in them no true digestive capacity. If the plants can utilize animal matter at all, it is only after it has become dissolved during the process of decay.

911. **Genlisea.** The plants belonging to the genus **Genlisea** — a genus allied to Utricularia — have two kinds of leaves, ordinary and bladder-bearing, and the bladders have something of the same arrangement at the orifice as has already been alluded to under Utricularia.

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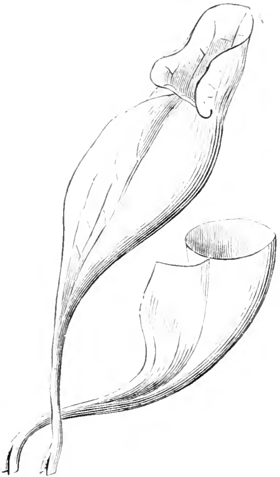
[1] Insectivorous Plants, p. 371.

[2] Insectivorous Plants, p. 377.

[3] Insectivorous Plants, p. 390.

912. **Sarracenia.** All of the eight species of this genus have hollowed phyllodia, which form slender pitchers or urns. In the best-known species, S. purpurea,[1] the urn is generally so held that rain can fall directly into it; in fact, the upright foliar expansion would seem to insure that none be lost. In S. flava, Drummondii, and rubra, the pitchers are more nearly vertical, and the lid at the mouth of the tube so disposed when the leaf is young as to shed for the most part rain that falls thereon; but in the older leaves the lid becomes somewhat erect. Even in the latter position a portion of the rain that falls upon the leaves is carried off. In the remaining species, S. variolaris and psittacina, the lid is a roof which keeps the rain from entering the tube. In all the cases there is usually considerable water in the pitchers; in the last two species it probably all comes from within as a secretion.



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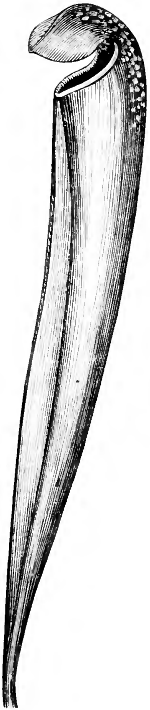

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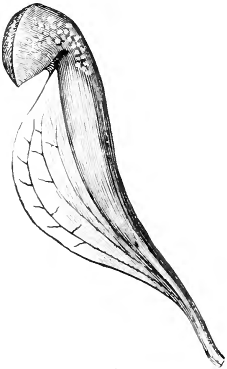

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913. Sarracenia variolaris has been long known to attract insects to the leaves. Passing over the earlier notices referred to in the Bibliography, page 351, the following quotation from MacBride,[2] written in 1815, will indicate sufficiently the character of the attraction: —

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[1] Schimper: Botanische Zeitung, 1882, p. 225.

[2] Transactions of the Linnæan Society, xii., 1818, p. 48.

FIG. 158. Pitcher-leaves of Sarracenia purpurea; one has the upper part cut away.
FIG. 159. Pitcher of Sarracenia variolaris.
FIG. 160. Pitcher of Sarracenia psittacina.

"The cause which attracts flies is evidently a viscid substance, resembling honey, secreted by or exuding from the internal surface of the tube. From the margin where it commences, it does not extend lower than one fourth of an inch. The falling of the insect as soon as it enters the tube is wholly attributable to the downward or inverted position of the hairs of the internal surface of the leaf. At the bottom of the tube, split open, the hairs are plainly discernible, pointing downwards; as the eye ranges upward they gradually become shorter and attenuated, till at or just below the surface covered with the bait, they are no longer perceptible to the naked eye nor to the most delicate touch. It is here that the fly cannot take a hold sufficiently strong to support itself, but falls."

914. The tissues of the internal surfaces of the pitchers have been classified by Hooker in the following manner: —

"(1) *An attractive surface*, occupying the inner surface of the lid, which possesses stomata, and (in common with the mouth of the pitcher) minute honey-secreting glands; it is, further, often more highly colored than any other part of the pitcher, in order to attract insects to the honey.

"(2) *A conducting surface*, which is opaque, formed of glassy cells, which are produced into deflexed, short, conical processes. These processes, overlapping like the tiles of a house, form a surface down which an insect slips, and affords no foothold to one attempting to crawl up again.

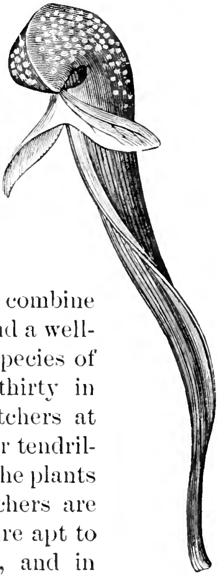
"(3) *A glandular surface* (seen in S. purpurea), which occupies a considerable portion of the cavity of the pitcher below the conducting surface. It is formed of a layer of epidermis with sinuous cells, and is studded with glands. Being smooth and polished, this, too, affords no foothold for escaping insects.

"(4) *A detentive surface*, which occupies the lower part of the pitcher, in some cases for nearly its whole length. It possesses no cuticle, and is studded with deflexed, rigid, glass-like, needle-formed hairs, which further converge towards the axis of the diminishing cavity; so that an insect, if once amongst them, is effectually detained, and its struggles have no other result than to wedge it lower and more firmly in the pitcher."

915. Mellichamp describes a line of saccharine liquid which leads up from the base of the leaf to its brim. This secretion comes from glands at the mouth of the pitcher; but it is found only at certain periods. Led by this lure, insects are drawn towards the brim of the pitcher, and sooner or later they are caught in considerable numbers in the pitchers themselves.

916. The exact nature of the liquid in the pitchers is not fully understood. Mellichamp's observations seem to indicate that it has the power of accelerating the decomposition of animal matter. Nothing is yet known positively as to the manner in which the products of decomposition are utilized by the plant, if, indeed, they are at all serviceable to it.[1]

917. **Darlingtonia** has been examined by Canby, who finds strong indications that it allures insects much as the Sarracenias do.



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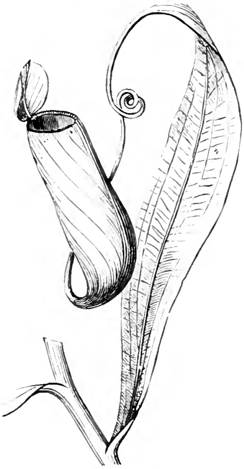

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918. **Nepenthes.** This striking plant has long been a favorite in the greenhouse on account of its peculiar leaves, which often combine a blade, a tendril, and a well-formed urn. The species of Nepenthes (about thirty in number) produce pitchers at the extremity of their tendril-like leaves. When the plants are young these pitchers are less elongated and are apt to rest on the ground, and in such plants their whole interior is clothed with secreting glands. When the plant is older, the pitchers become more distinctly tubular, and do not possess such conspicuous wings as those found in the form just mentioned. All of them have lids; in one case the lid is

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[1] It is interesting to observe some of the early conjectures as to the probable use of these pitchers. "Morrison speaks of the lid, which in all the species is tolerably rigidly fixed, as being furnished by Providence with a hinge. This idea was adopted by Linnæus, and somewhat amplified by succeeding writers, who declared that in dry weather the lid closed over the mouth and checked the loss of water by evaporation. Catesby, in his fine work on the 'Natural History of Carolina,' supposed that these water-receptacles might 'serve as an asylum or secure retreat for numerous insects, from frogs and other animals which feed on them;' and others followed Linnæus in regarding the pitchers as reservoirs for birds and other animals, more especially in times of drought" (Hooker's Address before British Association, 1874). But Burnett regarded the tubes as closely analogous to the stomachs of animals.

Fig. 161. Pitcher of Darlingtonia Californica.
Fig. 162. Leaf of Nepenthes; leaf, tendril, and pitcher combined.

thrown back, but in the others its overarching is a conspicuous feature. The mouth of the pitcher is strengthened by a thick rim, near which are very numerous glands secreting a sweet liquid. In the interior of the pitcher there is a conductive surface, somewhat like that seen in Sarracenia. This extends for some distance down from the mouth, and is frequently crowned by a sort of funnel-like appendage of the rim. Below the conductive surface there is a secreting surface dotted with innumerable glands. According to Hooker, from whose notice many of the facts here given are taken, there are three thousand of these glands in a square inch.

The fluid which collects in the pitchers has been shown by Gorup-Besanez and Will to be neutral, or only very slightly acid in reaction, unless animal matter has been introduced. If, however, any animal matter has been placed in the pitchers, the glands give forth an acid secretion, which contains an active ferment that resembles pepsin and has the power of digesting albuminous substances. It is an interesting fact that the neutral secretion, although it has not the power of digesting albuminous matters, becomes efficient at once upon the addition of a small amount of acid (formic). During digestion the glands exhibit the same phenomena of aggregation as observed in Drosera.

The absorption of animal matter by Nepenthes has been proved by the Lithium method.

919. By the viscid or glandular hairs of a large number of plants insects are sometimes caught, but to what extent these hairs serve in digestion and absorption is not yet clear. From experiments by Darwin, it appears that in some cases at least they may aid the plant in absorbing ammonia compounds found in rain and in the atmosphere, and that the glands may also "obtain animal matter from the insects which are occasionally entangled by the viscid secretion."[1] One case merits particular attention; namely, that of

920. **Dipsacus, or Teasel.** Francis Darwin has called attention to the extraordinary character of some of the hairs of this plant. The following abstract gives only the briefest outline of his interesting paper.

The glandular hairs are multicellular and pear-shaped, being supported by the small end on a cylindrical stalk, which rests on an epidermal cell. At the summit of the gland where several of

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[1] Darwin: Insectivorous Plants, p. 355. The catchfly (Silene) should be examined with reference to this point.

the radiating cells meet, threads of gelatinous matter can be seen to protrude under certain circumstances. No apertures, however, can be seen through which the filaments come, therefore it is thought that they extend directly through the cell-walls. They have been shown to consist of protoplasmic matter with which a certain amount of resinous substance is combined, and at times they contract violently, become thicker, and at last form a small ball on the summit of the gland. The contraction can be produced by many chemical and physical agents, *e. g.*, ammonic carbonate. If a filament under the microscope is treated with a drop of a 2 per cent solution of the carbonate, the following changes occur: The filament contracts, but almost instantly recovers itself, and is once more protruded; it does not, however, regain its original form or appearance; instead of consisting of thin elongated ropes of a highly refracting substance, it is converted into necklace-like masses which strongly resemble the aggregations found in the true insectivorous plants.

Beal has described somewhat similar hairs on some thistles.

It is not the province of this volume to discuss the singular relationships which are presented by these groups of insectivorous plants. Attention must be directed, however, to the fact that Dionæa and Drosera, with their widely different mechanisms for the capture of insects, belong to the same natural family; and that Pinguicula and Utricularia, with methods equally diverse, are very nearly allied plants. Such facts can be explained in part by the theory presented in Volume I. page 328, — the "Theory of Descent."[1]

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[1] The following list will introduce the student to some of the principal works upon insectivorous plants. As the list is chronologically arranged, it may serve as a brief history of the subject.

1768. John Ellis: "De Dionæa muscipula." A letter to Sir Charles Linnæus descriptive of the method by which this fly-trap captures insects.

1782. Roth: "Von der Reizbarkeit des sogenannten Sonnenthaues, Drosera rotundifolia und longifolia" (Beiträge zur Botanik, Bremen, Th. 1, no. iv, pp. 60–76). An account of observations begun in 1779 on the irritability of the glands of sun-dew leaves, showing that they respond to contact with insects, but not to a pin or bit of straw. Roth suggests that the plant may possibly receive some nourishment from the insects. (In Darwin's Botanic Garden, 1780, p. 24, it is stated that Whately had made in England observations similar to those of Roth.)

1791. Bartram: "Travels through North and South Carolina, etc." This book contains a short sketch of the capture of insects by Sarracenia.

1815. Macbride: "On the power of Sarracenia adunca to entrap insects" (Transactions of the Linnæan Society, xii., 1818, 48–52).

1829. Burnett, in the Quarterly Journal of Science, Literature, and Arts,

921. **Epiphytes, or air-plants,** obtain their food-materials wholly without contact with the soil. It is supposed that the ash materials

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ii. 290, also gives an account of Sarracenia, together with a description of its digestive powers, and compares its hollow leaf to an animal stomach.

1834. Curtis, in the Journal of the Boston Society of Natural History, i., pp. 123–125, gives a description of the irritability of Dionæa, and of its mode of action.

1848. Benjamin: "Ueber den Bau und die Physiologie der Utricularien" (Botanische Zeitung, vi., pp. 1, 17, *et seq.*).

1850. Cohn: "Ueber Aldrovanda vesiculosa" (Flora, p. 673).

1855. Grœnland: "Note sur les organes glanduleux des Drosera" (Ann. des Sc. nat. bot., sér. 4, tome iii. p. 297).

1855. Trécul: "Organization des glandes pédicellées de la feuille du Drosera rotundifolia" (Ann. des. Sc. nat. bot., sér. 4, tome iii. p. 303).

1859. Caspary: "Aldrovanda vesiculosa" (Botanische Zeitung, xvii. p. 125).

1860. Nitschke in Botanische Zeitung, xviii. p. 57, and xix., 1861, p. 145, gives an excellent description of Drosera, and an account of simple but telling experiments upon the sensitiveness of the leaves.

1860. Darwin began his experiments upon Drosera, not published until much later.

1862. Botanische Zeitung of this year (p. 185) contains a second article on the subject of Aldrovanda by Caspary.

1863. Scott: "On the Propagation and Irritability of Drosera" (Gardeners' Chronicle, p. 30).

1868. Canby published an account of experiments on feeding Dionæa, in the Gardener's Monthly, p. 229.

1872. Ziegler: "Sur un fait physiologique observé sur des feuilles de Drosera" (Comptes Rendus, lxxiv. p. 1227).

1873. Treat: "Observations on the Sun-dew" (American Naturalist, vii. p. 705). In this paper Mrs. Treat describes experiments relative to feeding Drosera carried on in 1871.

1873. A. W. Bennett: "On the movements of the glands of Drosera" (British Association Reports, xliii. p. 123).

1873. Stein: "Ueber die Reizbarkeit der Blätter von Aldrovanda" (Verhandlungen des bot. Vereins für die Prov. Brandenburg).

1874. Burdon Sanderson: "Venus's Fly-Trap" (Nature, x. p. 105).

1874. Asa Gray: "Insectivorous Plants" (Nation, xviii. pp. 216, 232). An account of the observations communicated by Darwin, and a short résumé of the subject up to that date.

1874. Mellichamp: "Researches on the pitchers of Sarracenia variolaris, and the way in which insects are caught in them" (Nature, x. p. 253).

1874. Hooker: Address before the British Association for the Advancement of Science, published in full in the Report for 1874. This address gives an excellent account of the digestive powers of various carnivorous plants, especially Nepenthes.

1875. J. W. Clark: "On the absorption of nutrient material by the leaves of some insectivorous plants." This article gives the results of experiments on the absorptive capacity of Drosera and Pinguicula, conducted with the aid of the spectroscope.

which they incorporate come to them in the form of dust, which subsequently dissolves and is absorbed. The sources of their carbon and nitrogen have already been sufficiently explained.

1875. Darwin: "Insectivorous Plants." A work of 462 pages, more than half of which is devoted to Drosera. At the close of his exhaustive discussion of his experiments upon this plant, Mr. Darwin says: "I have now given a brief recapitulation of the chief points observed by me with respect to the structure, movements, constitution, and habits of Drosera rotundifolia; and we see how little has been made out in comparison with what remains unexplained and unknown."

1875. Reess and Will: "Einige Bemerkungen über fleischessende Pflanzen" (Botanische Zeitung, p. 713).

1875. Canby: "Darlingtonia Californica" (Proceedings American Association, p. 64).

1875. Cohn: "Ueber die Function der Blasen von Aldrovanda und Utricularia" (Beiträge zur Biologie der Pflanzen).

1875–6. Morren published in the Bulletin of the Royal Academy of Belgium the results of experiments which may be interpreted as showing that the plants derive no benefit from their insects.

1875–6. Gorup-Besanez and Will published some observations regarding a pepton-forming ferment in plants, in Sitzungsberichte der physikalisch-medicinisches Societät zu Erlangen.

1876. Francis Darwin: "The process of aggregation in the tentacles of Drosera rotundifolia" (Quarterly Journal of Microscopical Science, xvi. p. 309).

1876. Sydney H. Vines: "On the digestive ferment of Nepenthes" (Journal of Anatomy and Physiology, xi. p. 124).

1876. Faivre: "Recherches sur la structure, le mode de formation, et quelques points relatifs aux fonctions des urnes chez le Nepenthes" (Comptes Rendus, lxxxiii. p. 1155).

1876. Munk: "Die elektrischen und Bewegungserscheinungen am Blatter der Dionæa muscipula."

1877. Cramer: "Ueber die insectenfressenden Pflanzen."

1877. Aschman: "Les plantes insectivores," Luxemburg.

1877. Pfeffer: "Ueber fleischfressende Pflanzen und über die Ernährung durch Aufnahme organischer Stoffe überhaupt" (Landwirthsch. Jahrb. v. Nathusius, p. 969). An excellent account of the mechanism and absorptive properties of carnivorous plants.

1879. Drude: "Die insektenfressenden Pflanzen." A full and interesting examination of the subject in Schenk's Handbuch der Botanik.

1882. Schimper: "Notizen über insectenfressenden Pflanzen" (Botanische Zeitung, xl. p. 225).

Several *jeux d'esprit* have been published, in which the remarkable properties of a few humble plants have been exaggerated into accounts of man-catching and man-eating trees of large size.

CHAPTER XI.

CHANGES OF ORGANIC MATTER IN THE PLANT.

922. It has now been shown that under the influence of sunlight green plants produce organic matter out of inorganic materials. This organic matter is conveyed to points where it is to be used, or to temporary reservoirs where it is stored for future use. It undergoes manifold changes in the plant, until in the ordinary course of nature it is resolved at last into the very materials from which it originally came; namely, carbonic acid and water.

923. But as the organic matter of the plant represents in its construction a definite amount of energy of motion derived from solar radiance transformed into the energy of position, in its apparent destruction is involved the reconversion of this energy of position into energy of motion. Between the first and last terms of these constructive and destructive processes very different periods of time may elapse in different cases, according to the changes which the organic matter undergoes.

924. That portion of the organic matter which is built into the fabric of the plant in the form of cellulose more or less modified is not often broken down into its original components while the organism is living; but, by decay and by combustion, even this relatively permanent substance is decomposed, and its elements are finally given back to the air and soil. A certain portion of the organic matter, however, undergoes speedy and striking changes, and all of these are now to be examined from another point of view.

TRANSMUTATION, OR METASTASIS.

925. The physiological expression for the substance formed by chlorophyll in the sunlight is **food.** This substance is utilized by the organism in many ways; but of these only the following need now be noticed: (1) for the supply of energy for movements and other work; (2) for the repair of waste; (3) for

the construction of new parts. The changes by which these processes are performed take place in the protoplasm which receives and in some way disposes of the newly formed food.

926. **Supply of energy for work.** This is furnished by the process of oxidation. It will be remembered that the inorganic materials concerned in the production of the food of the plant, namely, carbonic acid and water, are highly oxidized compounds. By assimilation a part of the oxygen is liberated, and the organic matter formed is some carbohydrate capable of oxidation. The reception of oxygen, the oxidation of the oxidizable matter, and the release of the products of oxidation by the plant are collectively termed *respiration*.

927. **Repair of waste.** The living matter of plants, like the living matter of animals, being the seat of all the activities manifested by the organism, is constantly undergoing waste and demanding repair. The repair of waste is proper *nutrition*.

928. **The construction of new parts.** It has been shown (Chapter X.) that by the appropriation of nitrogen by the plant proteids are formed, and these are in great part utilized in the production of new protoplasmic matter. So far as the latter is an actual increase in substance, and not a mere repair of waste, it represents true *growth*. The growth of any root, stem, or leaf consists in the formation of new cells and the increase of these in size. In this process the production of new cell-wall is of course the most conspicuous phenomenon. The permanent increase in size of the cell-walls of a plant disposes of a large part of the organic matter which is prepared by assimilation, and this phase of growth is apt to divert attention from that which really underlies it; namely, growth of the protoplasm itself.

929. For convenience, the various chemical changes which go on within the plant may be divided into two groups; namely, **transmutation** and **complete oxidation.** In the former, the organic matter changes its properties in some way, either by the addition of new materials or by the reconstruction of its existing molecules, but, notwithstanding the change, still remains organic matter; while in the latter it is resolved into its original inorganic components. The change of one kind of food into another, the transformation of starch into cellulose, and the formation of proteids, are good examples of transmutation: the consumption of food for the release of energy, an example of complete oxidation. The first of these groups of changes cor-

responds nearly to what has been called *metastasis*,[1] the second to *respiration*. But it must be remembered that the distinction between the two groups is not absolute.

930. **The contrast between assimilation and respiration** is very marked: one is substantially the opposite of the other. The following tabular view displays the essential differences between them.

Assimilation proper	Respiration
Takes place only in cells containing chlorophyll.	Takes place in all active cells.
Requires light.	Can proceed in darkness.
Carbonic acid absorbed, oxygen set free.	Oxygen absorbed, carbonic acid set free.
Carbohydrates formed.	Carbohydrates consumed.
Energy of motion becomes energy of position.	Energy of position becomes energy of motion.
The plant gains in dry-weight.	The plant loses dry-weight.

Some of the changes which are grouped under transmutation, or metastasis, present almost as great a contrast to assimilation proper as that shown in the above table.

931. **Course of transfer of assimilated matters.** In the present state of knowledge it is impossible to trace all the chemical changes which assimilated matters undergo in the plant, or even the course which such matters take; only a few of the more obvious modifications have been investigated. Before proceeding to describe the important forms of organic substance in the plant, the following general considerations should be presented.

The carbohydrates are believed to be transferred from one part to another, in the higher plants, through the thin-walled parenchyma. The reaction of these cells is almost uniformly acid. The transfer takes place only when the carbohydrates are in solution.

The albuminoids are probably carried chiefly by means of the soft bast of the fibro-vascular bundles; the cells of this bast have a slightly alkaline reaction.

But that these are not the only paths of transfer, appears from the frequent occurrence of minute starch-grains in the sieve-cells, and, on the other hand, of dissolved albuminoids in parenchyma cells.

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[1] The German word Stoffwechsel is usually translated *metastasis*, — a word long known in medicine with a totally different signification from that above. Schwann's term, *metabolism*, much used in human physiology, expresses its idea better, but for some reasons the term *transmutation* appears preferable.

The direction of transfer of the above compounds is towards the point of use, or of storing; there is never any approach to a true circulation throughout the plant, corresponding, as was formerly taught, to the circulation in animals.

932. **Classification of the principal organic products.** For the present purpose these may be conveniently grouped into (1) those which are free from nitrogen, and (2) those which contain nitrogen. Some have been already treated of in earlier pages of this volume; of the rest, little more than a mere enumeration can here be given.

933. **Products free from nitrogen. I. Carbohydrates.** In general these are solid bodies many of which are soluble in water. They are conveniently divided into the cellulose group, having the empirical formula, $C_6H_{10}O_5$, and the sugars, — grape-sugar, fruit-sugar, and cane-sugar.

THE CELLULOSE GROUP comprises the following isomeric bodies: —

934. *Cellulose.* This substance (see page 31) is regarded as a product of the direct transformation of starch or its equivalent. When once separated from the protoplasm as cell-wall, cellulose is not again dissolved save in the exceptional cases of germination where it serves as a food. Sachs has shown that in the germination of the date, the pitted thickening masses of the cell-walls of the endosperm are dissolved and utilized by the embryo.

935. *Starch* (see pages 47–50). The occurrence of this substance in the chlorophyll granules under certain conditions has already been described. Its occurrence in reservoirs of food, and the relation of this to the starch-generators, have been discussed in 174.

The following table gives some idea of the amount of starch found in the ordinary commercial sources: —

Source.	Amount of starch present.
Grains of wheat	64 per cent.
Grains of corn	65 " "
Grains of rice	76 " "
Potato tubers	15–29 " "

When starch is to be transferred from the places where it is held in reserve to the points where it is to be consumed, it is converted into a form of sugar by some one or more of the unorganized ferments occurring in plants. Although the sugar thus formed passes at once into solution, it is a curious fact that at certain points during its course this solution may transiently exhibit more or less fine-grained starch. The tendency of starch to form in this way is very remarkable in the process of germination.

936. *Inulin.* This substance is dissolved in cell-sap (see 183), but is easily separated from it upon immersion of the plant sections in alcohol. It replaces starch in the roots and root-like stems of many perennials belonging to the following orders, — Liguliforæ (Compositæ), Campanulaceæ, and Lobeliaceæ.

937. *Lichenin* is abundant in certain lichens, amounting in Cetraria Islandica to more than 40 per cent.

938. *Dextrin.* Under this name are comprised at least two substances[1] which are produced during the transformation of starch into sugar. Dextrin occurs in the young sprouts of potato, in most bulbs as they are starting, and in the spring sap of many trees.

939. *The Gums.* These are amorphous substances which either dissolve in water or merely swell in it to form soft masses or thick viscous liquids. An example is

Arabin ($2C_6H_{10}O_5+H_2O$), the chief constituent of Gum Arabic, obtained from a species of Acacia. It is found associated with arabic acid, which is supposed to be combined with calcium. It occurs in cherry-tree gum, and to a slight amount in the gum of many other plants.

Of those gums which do not truly dissolve, must be mentioned Cerasin, abounding in cherry-tree gum; Bassorin, or the essential constituent of gum-tragacanth; and Vegetable Mucus, which occurs in the seed-coats of flax, the pseudo-bulbs of many orchids, and the leaves of some mallows.

940. *The Pectin Bodies.* According to Fremy these are derivatives from pectose, a neutral insoluble substance found in unripe fruits and in some fleshy roots. Pectose undergoes various changes not yet understood. Vegetable jelly, obtained by boiling subacid fruits, is a familiar example of one of the products of such changes.

941. THE SUGAR GROUP. The more common members of this group are grape-sugar, fruit-sugar, and cane-sugar. The empirical formulas of these substances have simple relations, exhibited in the following table, in which they are compared with that of starch: —

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[1] For an account of the allied substances, amylodextrin and achroodextrin, see W. Nägeli, Beiträge zur näheren Kenntniss der Stärkegruppe, 1874.

Starch,	$C_6H_{10}O_5$
Cane-sugar,	$C_{12}H_{22}O_{11}$
Grape-sugar and fruit-sugar,	$C_6H_{12}O_6$

Thus,

$$\underset{\text{Starch.}}{2C_6H_{10}O_5} + \underset{\text{Water.}}{H_2O} = \underset{\text{Cane-sugar.}}{C_{12}H_{22}O_{11}}$$

$$\underset{\text{Cane-sugar.}}{C_{12}H_{22}O_{11}} + \underset{\text{Water.}}{H_2O} = \underset{\text{Grape-sugar.}}{C_6H_{12}O_6} + \underset{\text{Fruit-sugar.}}{C_6H_{12}O_6}$$

The three following classes of sugars, based upon their relations to fermentation, have been made: (1) directly fermentable, (2) indirectly fermentable, (3) non-fermentable sugars. To the third class belong Arabinose, Sorbit, etc., which need no further notice here.

The directly fermentable sugars are grape-sugar, fruit-sugar, and inverted sugar.

942. *Grape-sugar*, otherwise termed glucose (or, on account of its turning the plane of polarization to the right, dextrose), is, as its name indicates, abundant in the grape, where it may form from 10 to 30 per cent of the juice. Figs contain, on an average, 12 per cent; sweet cherries, 9 to 10 per cent; apples and pears, 7 to 10 per cent; plums, 2 to 5 per cent; and peaches less than 2 per cent of this sugar.

943. *Fruit-sugar*, sometimes known as lævulose, is uncrystallizable. It is associated in most ripe fruits with dextrose.

944. *Inverted sugar* occurs in some ripe fruits, where, as Buignet has shown, it is formed from cane-sugar by the action of a ferment and not of a fruit-acid. It is also found in the so-called honey-dew of the leaves of the Linden.[1]

945. The indirectly fermentable sugars, of which common cane-sugar may be taken as the best example, ferment under the influence of yeast only when they have first undergone a change by which they are converted into other sugars.

946. *Cane-sugar* occurs in the cell-sap of many plants, often in large amount. The following percentages are regarded as average ones: —

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[1] According to Boussingault, 120 square metres of linden leaves yield in a single warm July day between two and three kilograms of honey-dew. As to whether this substance is a product of an insect, or an exudation from leaves under peculiar conditions, is not yet settled (Ebermayer: Chemie der Pflanzen, 1882, p. 255).

Sugar-cane stem	16–18 per cent.
Sugar-beet	10–14 "
Sorghum	10–11 "
Indian corn	5–7 "
Sugar maple	8 "

947. **Products free from nitrogen. II. Vegetable acids.** Of these the most widely distributed are oxalic, tartaric, citric, and malic acids.

948. *Oxalic acid* ($C_2H_2O_4$) occurs in almost every plant, the amount in some reaching as high as 4 per cent. Most of it is combined with calcium or with potassium, a part remaining uncombined. According to Müller,[1] the fresh leaves of sugar-beet contain 4 per cent of this acid, of which one third is in solution.

949. *Tartaric acid* ($C_4H_6O_6$) occurs free, and also combined with potassium in the juice of the grape and many other fruits.

950. *Citric acid* ($C_6H_8O_7$) occurs in the amount of 6 to 9 per cent in the juice of lemons and allied fruits, and is associated with other acids in most of our subacid fruits, such as currants, cherries, etc.

951. *Malic acid* ($C_4H_6O_5$) occurs free, or combined with calcium, in the juices of many fruits and in the sap of many plants. It imparts the sour taste to our most common fruits.

952. **Products free from nitrogen. III. Fats, or Glycerides.** According to Ebermayer most of the fats which occur in plants are mixtures (not compounds) of the following three kinds of fats in different proportions: Tristearin or stearin, tripalmatin or palmatin, triolein or olein. The oils in most seeds, however, are free, fatty acids; namely, stearic, palmitic, and oleic.

The fats are regarded as compound ethers formed from the triatomic alcohol glycerin, whence they have been sometimes termed Glycerin ethers. The following formulas exhibit one view as to their constitution: —

Tristearin	$\left.\begin{matrix}(C_{18}H_{35}O)_3\\C_3H_5\end{matrix}\right\}O_3$
Tripalmatin	$\left.\begin{matrix}(C_{16}H_{31}O)_3\\C_3H_5\end{matrix}\right\}O_3$
Triolein	$\left.\begin{matrix}(C_{18}H_{33}O)_3\\C_3H_5\end{matrix}\right\}O_3$
Stearic acid	$C_{18}H_{36}O_2$
Palmitic acid	$C_{16}H_{32}O_2$
Oleic acid	$C_{18}H_{34}O_2$
(Glycerin	$C_3H_5(OH)_3$)

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[1] Quoted by Ebermayer, Chemie der Pflanzen, p. 320.

The oils form very intimate mixtures with the albuminoids in many cases, especially in seeds of such plants as Ricinus, etc. According to Sachs, "in the germination of all oily seeds, sugar and starch are produced in the parenchyma of every growing part, disappearing from them only when the growth of the masses of tissue concerned has been completed. Since, in the case of Ricinus, the endosperm grows also independently, starch and sugar are, in accordance with the general rule, temporarily produced in it. The cotyledons apparently absorb the oil as such out of the endosperm, whence it is distributed into the parenchyma of the hypocotyledonary stem and of the root, serving in the growing tissues as material for the formation of starch and sugar, which on their part are only precursors in the production of cellulose. In these processes tannin is also formed, which is of no further use, but remains in isolated cells, where it collects apparently unchanged until germination is completed. It can scarcely be doubted that the material for the formation of this tannin is also derived from the endosperm, although perhaps only after a series of metamorphoses. The absorption of oxygen, which is an essential accompaniment of every process of growth and especially of germination, has in this case, as in that of all oily seeds, an additional significance, inasmuch as the formation of carbohydrates at the expense of the oil involves the appropriation of oxygen."[1]

Vegetable wax is closely allied to the fats.

953. **Products free from nitrogen. IV. Certain astringents.** This indefinite group comprises various matters differing slightly from one another in some particulars, but agreeing in possessing a faint acid character, in changing color with salts of iron, and in combining with certain protein matters. Tannin is sometimes placed in the next category, namely, among the glucosides; but according to Schiff it is digallic acid. The most important members of this group are *Tannin* (the so-called tannic acid), *Gallic acid*, and the astringent principle in Cinchona, Catechu, and Kino. According to Nägeli, these matters are to be found in buds, in unripe fruits, and in those petals which become red or blue, dissolved in the cell-sap and diffusing through cell-walls. Tannin sometimes exists in little globules of solution, enveloped by a delicate film of albuminous matter; for example, in the cells of the pulvinus of Mimosa and in the bark of many ligneous plants (Birch, Poplar, etc.). The following views are held as to

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[1] Text-book, 2d English ed., p. 716.

the formation of this substance: Many authors regard it as a product of the retrograde metamorphosis of certain carbohydrates; Sachsse thinks that it always attends the formation of cellulose from starch, and that there is a slight evolution of carbonic acid; Wiesner regards it as intermediate in the series which begins with the carbohydrates and ends with the resins. This last view is also held by Hlasiwetz, who has obtained the same products from tannin as from the resins, when each was fused with potassic hydrate.

It is a significant fact that all the barks which are rich in tannin are also rich in starch.

Nothing is positively known as to the function of tannin and its associated bodies in the plant. By Hartig they have been looked upon as reserve materials; but Schroeder was not able to verify Hartig's observations. By most observers these substances are regarded as waste products, having no further nutritive function, but possibly playing some part in the formation of colors. The following table[1] shows their amount in some of the barks and other parts used in tanning: —

Galls	30–77	per cent.
Catechu	40–50	"
Divi-Divi	30–40	"
Sumach	12–18	"
Oak bark	7–20	"
Willow bark	8–12	"
Hemlock bark	13–16	"

954. **Products free from nitrogen. V. Most Glucosides.** These are substances which under certain conditions, especially by the action of unorganized ferments, are broken up into glucose or some allied sugar, and at the same time some other body capable of further decomposition. Most of them are soluble in water. The following are among some of the best known: salicin, coniferin, æsculin. quercitrin. Tannin is often placed among the Glucosides.

955. **Products free from nitrogen. VI. Ethereal oils.** These are volatile liquids generally approaching Terpene ($C_{10}H_{16}$) in chemical composition. Nothing is certainly known as to their formation in the plant. They are not again taken up as plastic matter, but simply serve some function, often that of attraction

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[1] For other determinations see Ebermayer's Chemie der Pflanzen, p. 452, from which most of the above are taken; also see the excellent table in the Tenth Census, vol. ix., p. 265.

or of protection. To their presence is due the fragrance of many fruits and flowers, notably those of orange, bergamot, and the mints. Associated with the ethereal oils, the camphors occupy a prominent place. They are generally regarded as the products of the slight oxidation of some ethereal oils. The following is the best known, $C_{10}H_{16}O$ (Laurel-camphor).

956. **Products free from nitrogen. VII. Resins and Balsams.** These substances, which differ much in consistence, color, and other physical properties, contain comparatively little oxygen, are mostly amorphous, insoluble in water, and sometimes possess a slight acid reaction.

Balsams are defined as "mixtures of resins with volatile oils, the resins being produced from the oils by oxidation, so that a balsam may be regarded as an intermediate product between a volatile oil and a perfect resin." [1]

The Balsams are generally divided into two groups: (1) those containing much cinnamic acid, as Balsam of Tolu, Peru, etc.; and (2) those which are purely oleo-resinous, as Balsam Copaiba, Fir, etc.[2]

Certain resins and caoutchouc-like matters are found in large amount in the latex.

957. **Products containing nitrogen. I. The albumin-like matters.** Ritthausen classifies these substances into (1) Albumin of plants; (2) Casein of plants; (3) Gelatin of plants.

Albumin of plants is the term applied to the protein matters which readily coagulate from their aqueous solutions upon the action of heat or acids. The coagula dissolve more or less readily in potassic hydrate, exhibiting considerable differences in respect to solubility. They contain from 2.6 to 4.6 per cent of ash, and have the following elementary composition: —

Carbon	52.31–54.33	per cent.
Hydrogen	7.13– 7.73	"
Nitrogen	15.49–17.60	"
Sulphur	.76– 1.55	"
Oxygen	20.55–22.98	"

Casein of plants comprises the following substances: legumin, gluten-casein, conglutin. Solutions of these are precipitated by dilute acids and by rennet. The precipitates are readily

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[1] Watts: Dictionary of Chemistry, i., 1863, p. 491.

[2] A solution of the coloring-matter of alkanet root in dilute alcohol applied to a thin section of a plant containing resins colors the resins red after a few minutes, but does not serve to distinguish one from another.

soluble in a solution of basic potassic phosphate. Their ultimate composition is nearly the same as that of the group just mentioned.

Gelatin of plants. The associated matters are (1) Gliadin, (2) Mucedin, (3) Gluten-fibrin. These bodies are soluble in alcohol, and in water containing a small amount of acid or alkali. In their fresh state they are tough, viscid masses, only slightly soluble in water.[1]

958. Weyl does not accept Ritthausen's classification, but holds that legumin is a mixture of vegetable vitellin and casein; and further, that there is no true casein in seeds, — the substance called by this name being a product of secondary changes in the laboratory.

959. **Products containing nitrogen. II. Asparagin** ($C_4H_8N_2O_3$). This substance occurs in the shoots of Asparagus officinalis and many other plants, from which it can be obtained in the form of transparent crystals of the orthorhombic system. It is merely necessary to evaporate the juice of the plants to the consistence of a thin syrup, and after allowing it to stand for a time the crystals will separate, and may be purified by recrystallization. Pfeffer describes the following useful method of preparing them upon the slide of the microscope: A moderately thick section of the tissue suspected of containing asparagin is placed on a slide, covered with a bit of glass, and treated with absolute alcohol, when the crystals will be thrown down in the cells, or will form in the alcohol outside of the specimen. The character of the crystals can be known certainly by their insolubility in a concentrated aqueous solution of the same substance (see 46).

The amount of asparagin in certain plants has been given as follows: —

Name of Plant.	Per cent of Asparagin.	Observer.
Roots of Althæa	2. . . .	Plisson and Henry.
Vetch germs	1.5 . . .	Piria.
Radicles of a germinating plant dried at 100 C. . .	10.5 . . .	Beyer.

960. Asparagin possesses its chief interest from the part which it probably plays in the transfer of nitrogenous matters through the plant. According to Pfeffer, although it cannot be detected with certainty in the seeds of the vetch and pea, it appears in the young parts, especially in the lines of transfer (for

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[1] Hunt has called attention to a curious relation between the composition of animal gelatin and that of starch to which ammonia is added.

example, the petioles of the cotyledons). That the source of the asparagin must be the reserve albuminous matters in the seed, appears from the following consideration : "The absolute amount of nitrogen remains the same during germination, and the nitrogen of seeds is all or nearly all contained in their albuminous ingredients."[1] Asparagin and the chief proteid of the seeds in leguminous plants have been thus compared : —

	Asparagin.	Legumin.	Difference.
Carbon	36.4	64.9	+28.5
Hydrogen	6.1	8.8	+2.7
Nitrogen	21.2	21.2	0.0
Oxygen	36.4	30.6	—5.8

"Asparagin contains less carbon and hydrogen but more oxygen than legumin and other proteids. Consequently if the whole of the nitrogen of legumin is used in the formation of asparagin, a considerable quantity of carbon and hydrogen must be given off and a certain amount of oxygen absorbed. Exactly the opposite will take place upon the conversion of asparagin into proteid."[1]

961. **Products containing nitrogen. III. The alkaloids.** These substances all possess the power of uniting with acids to form salts, and they are often described as basic alkaloids. Among the most important are *Morphia*, *Quinia*, and *Strychnia.*

The number of alkaloids now known is very great, and the modes in which they are found combined in the plant are very diverse. They are more abundant in those plants which are grown under conditions of considerable warmth, and are much more abundant in some parts of the plant than in others, as is shown by the case of morphia. Nothing is positively known as to their origin or proper function in the organism. It should be mentioned, however, that many of them when applied to the very plants from which they were prepared prove to be poisonous ; thus, morphia poisons the poppy.

962. **Products containing nitrogen. IV. Unorganized ferments.** It has long been known that there must exist in certain parts of

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[1] Pfeffer, in Sachs's Text-Book, 1882, p. 719. For a full account by Pfeffer, see Pringsheim's Jahrbücher, viii., 1872, p. 429 ; and Monatsbericht der Berlin Akademie, 1873, p. 780. See also Husemann and Hilger : Die Pflanzenstoffe, i., 1882, p. 264.

plants, notably in seeds, compounds which possess the power of effecting changes in the character of starch, etc.; but it was not until 1873 that a method was given which enables us to isolate these compounds in a state of comparative purity. This method is based upon their solubility in glycerin, and their ready precipitation from glycerin solutions by means of common alcohol.[1]

By the use of this method Gorup-Besanez has been able to obtain from the seeds of vetch, flax, etc., a ferment which is soluble in water and glycerin. The substance contains 7.76 per cent of ash constituents and 4.5 per cent of nitrogen. Its solutions convert starch into sugar very rapidly at the temperature of 20°–30° C.; and in the presence of a dilute acid, for instance hydrochloric, it has the power of peptonizing proteids. In solution, it loses its activity at 80° C.; but if carefully dried, it can stand a temperature of 120° C. Up to the present time no ferment capable of effecting changes in the fats of plants has been isolated.[2]

963. Baranetzky has shown that in the conversion of starch into sugar there are two phases: (1) the formation of dextrin, and (2), at a somewhat higher temperature, the formation of sugar. He observed an acid reaction in the ferment.

964. In the sap of Carica papaya, Wurtz and Bouchut[3] have isolated a peptonizing ferment which acts promptly upon albuminoids. The juices of several tropical fruits are said to have the property of softening meats, and this action is regarded as dependent upon some unorganized ferment.

965. Besides the products already enumerated, there are some bitter and extractive matters and some coloring substances which do not naturally fall into any of the groups described.

966. From the facts which have now been presented, it is clear that the composition of the sap which escapes from a plant when it is wounded must be very complex. The juices of a plant contain all its dissolved mineral matters, gases in solution, and numerous members of both of the nitrogenous and non-nitrogenous groups already mentioned.

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[1] Hüfner. Journal für praktische Chemie, v., 1872, p. 372, and xi., 1875, p. 43.

[2] For a short account of the work of Kosmann (Journal de Pharmacie et de Chimie, sér. 4, tome xxii. p. 335) and that of Krauch (Versuchs-Stationen, xxiii. p. 77), see Husemann and Hilger: Die Pflanzenstoffe, i., 1882, p. 238.

[3] Comptes Rendus, lxxxix., 1879, p. 425; xci., 1880, p. 787. See also the following: Duclaux: Comptes Rendus, xci. p. 731, and Hansen: Sitz. der physikmedicin. Societät zu Erlangen, 1880.

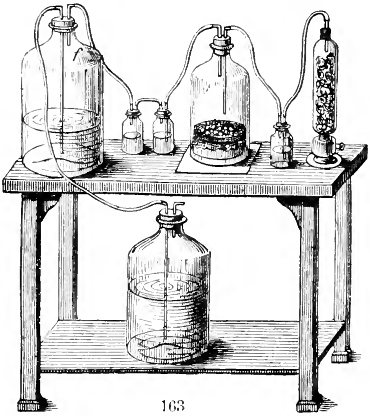
RESPIRATION.

967. It has been long known that air is necessary for the germination of seeds.[1] In 1777 Scheele[2] pointed out that in this process, as in the breathing of animals, oxygen (called by him fire air) is consumed and carbonic acid (called by him air-acid) is given off. Two years later, Ingenhousz[3] showed that all plants at night give off fixed air (carbonic acid), and in 1804 Saussure proved that all plants require oxygen for their growth. In 1838 Meyen[4] clearly defined the scope of respiration in plants, since which time it has been carefully examined in most of its relations.

968. The relations of gases to plants, so far as their absorption and elimination are concerned, have been sufficiently discussed in Chapter X. It is merely necessary to state at present that oxygen is readily absorbed by all parts of plants, and that the intercellular passages (519) form a means by which it can traverse the whole plant very rapidly.

969. In its simplest phases respiration consists in the absorption of oxygen, the oxidation of oxidizable organic matters, and the evolution of the products of oxidation; namely, carbonic acid and water. Some other products are often formed in minute amount, but these may be here disregarded.

970. **Measurement of Respiration.** Respiration can be measured very nearly by the amount of oxygen which disappears or by the amount of carbonic acid which is given off. The ordinary apparatus for examining respiration is based upon the measurement of the latter, and consists essentially of some application of potash-bulbs, or wash-bottles (see Fig. 163), for the interception of all evolved carbonic acid. The



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[1] See Malpighi: Opera omnia, 1686.

[2] Chemische Abhandlung von der Luft, 1777.

[3] Experiments upon Vegetables, 1779, p. xxxvi.

[4] Pflanzenphysiologie, ii., 1838, p. 162.

air supplied to the seeds in the bell-jar, of course first carefully freed from every trace of carbonic acid, is drawn through by means of an aspirator, and in the bulbs all the carbonic acid derived from the germinating seeds is retained.

971. **Plants in dwelling-houses.** To what extent can house-plants injure the air of rooms at night? The carbonic acid which is given off by plants comes from the breaking up of assimilated matters in the various activities of the organism, such as growth, movements, etc. But the total amount of work done by any plant under the conditions to which ordinary house-plants are subjected is represented by the oxidation of a very small amount of food. From the most trustworthy data it is safe to say that in the case of one hundred average house-plants the whole amount of carbonic acid resulting from such oxidation during work would not vitiate the atmosphere of a moderate-sized room to any appreciable extent; in fact, would be exceeded by the amount evolved from a common candle burning for the same length of time.

972. **Relation of the carbonic acid given off to the oxygen absorbed.** Owing to the fact that part of the carbonic acid produced during respiration is retained within the plant, and that water is formed as a product of respiration, it is difficult to determine the exact relations of volume of the absorbed oxygen and the evolved carbonic acid. It is known, however, that in certain cases the amount of carbonic acid evolved is less than would be expected from the amount of oxygen absorbed. This is well shown when the germination of oily seeds is compared with that of seeds containing chiefly starch. When oily seeds germinate, the amount of carbonic acid is appreciably less than that given off by starchy seeds. Hellriegel has shown that in one instance the fixation of oxygen amounted to an increase in weight of 1.15 per cent.

973. **The free oxygen of the atmosphere is ample for the respiratory process.** Saussure[1] has shown that the amount in the atmosphere can even be reduced one half without materially interfering with the functions of the plant.

Most observers have found that in pure oxygen there is an increase in the activity of the respiratory function.

Bert[2] has conducted interesting experiments upon the effect

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[1] Quoted by Pfeffer, Pflanzenphysiologie, i. p. 373.

[2] For a discussion of this question, particularly with reference to the lower organisms, consult Bert: La pression barométrique, 1878.

of pressure on the various functions, by which it appears that in ordinary air, under a pressure of six atmospheres, Mimosa perished quickly. In an atmosphere under high compression seeds germinated, if at all, very slowly.

974. **Influence of temperature upon respiration.** Respiration can go on at low temperatures, even near the freezing-point of water. The rate of respiration increases with rise of temperature, as will be seen from the following figures for germinating beans: —[1]

Temperature.	Amount of carbonic acid given off each hour.
2° C	10.56 mgr.
6°	21.22 "
18°	32.34 "
20°	39.60 "
30°	47.52 "

975. **Influence of light upon respiration.** It is not yet known positively whether light has any effect upon respiration. In some experiments there has been a slight increase,[2] in others a diminution,[3] in the rate, with increased illumination; but it is not certain whether all other factors were excluded.

If the produced carbonic acid does not escape readily from the tissues, respiration goes on more slowly.[4]

976. **Periods of rest.** Although all plants require oxygen for the performance of their normal functions, it by no means follows that when a plant is supplied with oxygen the normal activities will be necessarily exhibited. In the case of certain bulbs, seeds, etc., even with the most favorable surroundings, there may be no signs of respiratory or other activity until after the lapse of

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[1] Rischawi: Versuchs-Stationen, xix., 1876, p. 338.

[2] Wolkoff and Mayer: Landwirthschaftliche Jahrbücher, 1874, Heft iv.; Cahours: Comptes Rendus, lviii., 1864, p. 1206.

[3] Dumas: Annales de Chimie et de Physique, sér. 5, tome iii., 1874, p. 105; Borodin: Just's Botan. Jahresbericht, iv., 1878, p. 920.

[4] For the bearings of this upon alcoholic fermentation, which, according to Melsens, is not arrested until a pressure of 25 atmospheres of carbonic acid is reached, see Pasteur: Annales de Chimie et de Physique, sér 3, tome lii., 1858, p. 415; and Nägeli: Die niederen Pilze, 1877, p. 31.

Alcoholic Fermentation. This process is so intimately connected with that of respiration that it requires a brief description at this point. Reduced to its simplest terms, it consists of the changes which are produced in a solution of sugar by the growth of a microscopic organism. This is some one of the Saccharomycetes (a group of low fungi which are propagated by a process of budding). By the growth of this fungus the solution of sugar is broken up into various products, the most noteworthy being alcohol and carbonic acid.

a given period of time. There is little doubt that this refusal of the resting part to start is an inherited trait connected in some way with the protection of the plant against untoward influences.

977. Respiration is accompanied by an **evolution of heat.** The flowers of the melon and tuberose were examined by Saussure, who found that in the opening of the former there was an elevation of 4 to 5 C.°, in that of the latter, .3°. Caspary detected a noticeable rise of temperature in the opening flowers of Victoria regia, and the same has been observed in flowers of species of Cactus.

978. In those cases where it is possible to examine an organ in which the process of respiration is rapid, as in a compact cluster of flowers of Araceæ, the difference between the temperature of the air outside and that inside the spathe is very marked.

979. The following results by Senebier, obtained by two methods of experimenting, are very instructive, showing the remarkable and rapid changes of temperature in such cases. The plant in this instance was Arum maculatum.

Time.		Temperature of air. C.°	Temperature of spathe. C.°
3	P. M.	15.6	16.1
5	"	14.7	17.9
5¾	"	15.	19.8
6¼	"	15.	21.
6¾	"	14.9	21.8
7	"	14.3	21.2
9¼	"	15.	18.5
10½	"	14.	15.7
5	A. M.	14.1	14.1

Even higher differences have been observed.

980. Light is produced during the growth of certain of the lower fungi under certain conditions. The phenomenon called phosphorescence is not known in any of the higher plants.[1] According to Fabre, it is associated with the absorption and consumption of oxygen, and the evolution of carbonic acid.

981. **Intramolecular respiration.** Under certain circumstances plants can continue to give off carbonic acid when no free oxygen is supplied, and when they are kept in an atmosphere

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[1] For an account of supposed cases of luminous flowers see Balfour's Class Book of Botany, 1854, p. 676.

of some other gas.[1] The following experiment will illustrate this: —

If a mass of active seedlings be placed in a current of some neutral gas, for instance nitrogen, the seedlings will continue to evolve carbonic acid. Since the amount of carbonic acid given off is greater than can be derived from the oxygen which might be fairly assumed to have been retained in the plants at the beginning of the experiment, the conclusion has been drawn that the production of this gas is at the expense of substances within the tissues containing combined oxygen. In other words, this process, which is like respiration in some particulars, differs from it in this respect: in ordinary respiration free oxygen enters into the plant and there oxidizes certain matters; while in this case the molecules of certain compounds break up, and the released oxygen at once forms, with carbon, carbonic acid, which is evolved. This process is known as intramolecular respiration.

982. Wortmann[2] has proved that when seedlings of Vicia Faba are placed for short periods in an atmosphere free from oxygen, they give off the same amount of carbonic acid as they do when oxygen is furnished. Hence he was naturally led to believe that all the carbonic acid produced by plants has its origin in intramolecular respiration, and that the free oxygen of the air takes no direct part in the formation of the carbonic acid evolved.

983. But, on the other hand, Wilson[3] has shown that most plants evolve much larger quantities of carbonic acid when free oxygen is provided, and that Vicia Faba forms a remarkable exception to this rule. His experiments were made upon seedlings, buds, leaves, flowers, fruits, and cryptogamous plants, and with uniform results. He cites Pfeffer as saying: "If an equal amount of carbonic acid were formed in both intramolecular and normal respiration, this would only prove that the same

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[1] The same phenomenon has been observed in the case of some of the lower animals: Pflüger (Archives fur Physiologie, x., 1875, p. 251) has shown that when these animals are kept in an atmosphere of nitrogen, they evolve during the first few hours nearly the same amount of carbonic acid as if they had been placed in common air. The chemical processes which cause the production and evolution of carbonic acid in the absence of free oxygen are grouped by Pflüger under the term *intramolecular respiration.*

[2] Arbeiten des botanischen Instituts, Würzburg, 1880, p. 500.

[3] Flora, 1882, and American Journal, xxiii., 1882, p. 423. For an interesting account of the literature of intramolecular respiration see Pflüger's paper, mentioned above. Observations upon the subject were made even during the last century and early in the present century. For Broughton's and Pfeffer's work see Botanische Zeitung, 1870, and Pflanzenphysiologie.

number of carbon affinities for oxygen had been satisfied in each case, and would in no way indicate from whence the supply of oxygen came. And in case free oxygen was active in normal respiration, in intramolecular respiration, when free oxygen was absent, its full supply might still be obtained through constant powerful attractive forces which could take oxygen from other combinations and thus give rise to secondary changes."

984. Eriksson[1] has shown that a slight elevation of temperature occurs during intramolecular respiration, amounting in the case of a mass of seedlings, flowers, or fruits, 125 cc. in bulk, to .1°–.3° C. In the experiments which he made with yeast, he obtained a much larger increase of temperature. Thus, when he employed 500 cc. of a fluid containing five parts by weight of water and one part by weight of yeast, together with 10 per cent of sugar, he obtained an increase of 3°.9 C. He found, further, that in intramolecular respiration, both in the case of germination and in that of yeast, the elevation of temperature can be noticed for one week. After this time, with diminution of the respiration, the temperature becomes the same as the surrounding air; but even then life is not extinct.

985. The curious experiment of introducing the smallest possible amount of organized ferment into a liquid from which all air has been expelled, but which is otherwise fitted to undergo fermentation or putrefaction, has resulted in setting up one or the other of these processes, and causing the liberation of considerable quantities of carbonic acid. It is believed that in this case likewise the needed oxygen is supplied by that in the molecules of oxygen-compounds, which are easily broken down.

986. While the non-nitrogenous compounds are those which play the most important part in furnishing material for oxidation and the release of energy, the nitrogenous matters share in this activity. Some physiologists[2] look upon the latter as the chief matters concerned in the process of respiration, and would regard the non-nitrogenous compounds as merely supplying waste. According to this view, asparagin is a waste product somewhat analogous to urea in animal economy.

987. From what has been said, it is plain that respiration does not consist merely in the direct absorption of oxygen and the immediate oxidation of compounds within the organism, but that it is a complicated process of which the absorption of oxygen and the evolution of carbonic acid are the extreme terms.

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[1] Untersuchungen aus dem bot. Inst. zu Tübingen, 1881, p. 105.

[2] Borodin: Botanische Zeitung, 1878.

CHAPTER XII.

VEGETABLE GROWTH.

988. As already shown, vegetable growth consists (1) in the formation of new cells, (2) in the increase in size of previously existing ones, or, (3) as is commonly the case, in both of these processes taking place simultaneously. In the production of new cells and in the augmentation of cells in size there are certain chemical and physical phenomena which always accompany the morphological changes.

989. The chemical changes are essentially those which have been described under Transmutation and Respiration; available matters change their character in order to be utilized in the formation and increase in size of cells. The physical phenomena are chiefly those which accompany oxidation; namely, the evolution of heat and the production of electrical disturbances.

990. The materials used by the plant for the formation of new structures are produced by assimilation; and in annuals a large part of the assimilated matter is consumed in growth as soon as it is made. But, in perennials, especially in those which belong to climates where vegetation has periods of rest, a portion of the assimilated matter is stored up for future use. The rapidity of the growth from buds in the spring is due to the abundant supply of assimilated matters prepared during the preceding summer.

991. Hence growth is not necessarily associated with increase in weight. In fact, in the growth of new parts from a bulb or tuber, although there is a marked increase of volume, there is, at first, an actual loss of dry substance through oxidation. Moreover, one part may grow at the expense of another; and we may have under certain conditions the anomaly of an increase in volume of new organs, with simultaneous but larger decrease in size of older parts, so that the result, as regards the whole, is diminution of weight.

992. **Morphological changes in the cells.** The two processes involved in ordinary growth, namely, increase of cells in number and in size, may go on together. But growing cells belong to

one of two classes: either they are capable of producing other cells, or, incapable of this, they develop into cells for some special office. To the former class belong all merismatic tissues; (see 201) from the latter all the permanent tissues are derived. Since growing cells have such different destinies, we must examine them in their earliest stage to find what they have in common.

993. The simplicity of structure in many of the lower plants is so great that a living cell can be kept under observation throughout its various stages, and through its transparent wall all the changes which go on within it can be noted. But the points of growth in most plants, especially those of the higher grade, are hidden by more superficial cells; and upon removal of these protecting parts, pathological changes are brought about at once, from exposure and mechanical injury, and healthy growth is arrested. In a few instances only, such as plant-hairs and other epidermal structures, is it possible to observe directly the progress of cell-division. Growth in deeper parts must be examined by an indirect method; that is, like parts must be compared at different stages of development, care being taken to select those which have been kept under nearly the same external conditions. By judicious selection of material for the examination of growth, specimens can be found which exhibit in a single section several different phases of cell-division.

994. When fresh material is employed, the sections are so much distorted that it is difficult to secure satisfactory results; in fact, the discordant views relative to the formation of cells are largely attributable to this source of error. If, however, the tissue to be examined is placed for a while in absolute alcohol, either with or without a little chromic acid, the cell-wall is rendered so much harder that the sections are not seriously distorted, and the contents of the cells are more clearly seen. When the treatment is supplemented by the use of staining agents adapted to special cases, the course of development ot new cells can be followed out with comparative certainty.

995. In the protoplasm of nearly all vegetable cells there is a spheroidal or lenticular body apparently denser than the protoplasm itself. It retains the name *nucleus*, given to it by Robert Brown, who first called attention to its importance. Under ordinary circumstances it can readily be detected in all active cells of the higher plants.

When living, it resists, like the protoplasm in which it is embedded, the entrance of all coloring agents; but when dead it is at once tinged by them. Upon the application of iodine it becomes deeper brown-yellow than protoplasm, and this led Hofmeister to the belief that it is richer in albuminoidal matters.[1] Its behavior with digestive fluid and other reagents indicates that, like the nucleus in the animal kingdom,[2] it contains a substance rich in phosphorus.[3]

996. The surface of the nucleus generally appears to be firmer and more highly refringent than the interior mass, and in these respects is like the superficial layer of protoplasm. Even with low powers of the microscope and without reagents the inner mass of the nucleus is often seen to be far from homogeneous, generally containing granules, which are sometimes irregular, sometimes regular in form. When a single large granule is present, it is known as the nucleolus; when two or more, the nucleoli. These vary widely in number, size, and shape. Besides such granules, vacuoles are frequently present. Upon the application of suitable staining agents, and by the use of high powers, the nucleus, formerly thought to be nearly homogeneous, is shown to be a basic substance possessing a finely reticulated structure. At times the nucleus appears to be simply dotted throughout with fine points.

997. When the bodies which are associated with its basic substance are granular, they are distinct from each other; but when in the shape of rods, fibres, or delicate threads, they are usually conjoined to form a sort of network, or so connected together as to make a long thread which is tangled in a complicated manner. The basic substance of the nucleus, less highly colored by staining agents than the rest, has been called Achromatin; while the portions which take color readily are termed Chromatin by Flemming, nuclein[4] by Strasburger.

During cell-division these portions of the nucleus undergo remarkable changes of shape and position, which, with the changes observable in the nucleus as a whole, can be illustrated by a few special cases taken from Strasburger's treatise, and given in nearly his words.

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[1] Hofmeister: Die Lehre von der Pflanzenzelle, 1867, pp. 78, 79.

[2] Hoppe-Seyler: Physiologische Chemie, i. p. 84, which contains a good account of the literature of the subject.

[3] Zacharias: Botanische Zeitung, 1881, p. 169.

[4] The only objection to the term *nuclein* is its previous application to the proximate chemical substance rich in phosphorus which, although a part of the nucleus, is not proved to be identical with the part which receives colors most deeply.

998. **Development of stomata.** Each of the mother-cells from which the guardian-cells of stomata are formed contains at first a large nucleus with one large nucleolus or several small nucleoli (Fig. 164, No. 1). The nucleus grows in size and becomes granular, but does not lose its identity in the protoplasmic mass (Fig. 164, Nos. 2, 3). At this period faint stripes appear which converge towards the poles of the spheroidal nucleus, while there is developed midway, at what has been well called the equator, a row of granules lying in one plane and forming a sort of disc or plate (Fig. 164, No. 4). The granules next pass for the most part in the meridian lines towards the poles, and there accumulate to constitute new nuclei (Fig. 164, No. 5). The polar masses are connected by faint stripes, and from this stage (Fig. 164, No. 6) go rapidly to their fuller development. In them rods appear which, though somewhat curved, generally lie in the direction of the axis of the spindle, and the contour of the two masses becomes clearly defined (Fig. 164, No. 7). Next, the faint stripes thicken somewhat, while at the equator there is developed a plane of minute granules (Fig. 164, No. 8), which become confluent and form a coherent film. This soon splits into halves between which cellulose is secreted. At first the secretion takes place in spots, but it soon becomes uniform. The splitting of the film for the formation of the cellulose is similar to that of the nuclear disc, except that in the former the

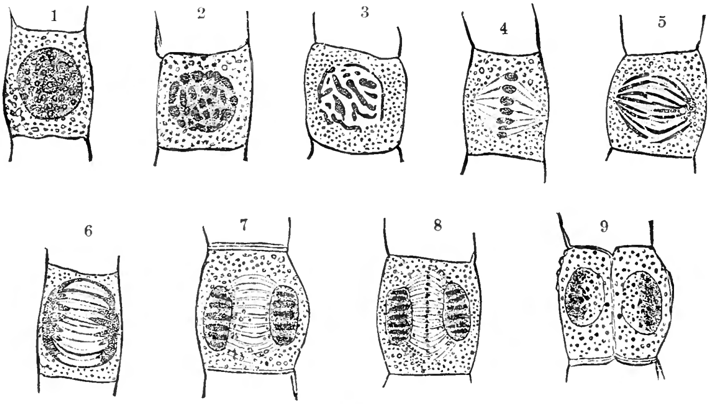

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Fig. 164. Changes in the nucleus during cell-division in the mother-cell of a stoma of Iris pumila. The dark parts in all the figures represent the *nuclein*. In No. 9 the cell-division is complete. (Strasburger.)

separation is very slight. At the time of the formation of the cellulose film certain nuclear threads may stretch as far as the wall of the mother-cell; but often they do not extend to it, and in this case the gap is filled out by a corresponding plate from the protoplasm. The cellulose film is produced almost simultaneously throughout the whole extent of the mother-cell, which is cut into two guardian-cells, forming a stoma (Fig. 164, No. 9).[1] Although the process goes on without interruption, it may be divided into three phases; namely, (1) the arranging of the nucleolar bodies to form a disc in the middle plane of the nucleus; (2) the splitting of the nuclear disc into two parts which pass over towards the poles, there becoming new nuclei, leaving faint meridional lines connecting them; (3) the thickening of these lines, and the appearance of granules at the equator, so as to form a plate which divides into halves. The cellulose film secreted between these halves sooner or later goes across the cell cavity, making a partition-wall between two new cells.

The mother-cell from which guardian-cells are developed in the manner just described is itself produced in nearly the same manner from an epidermal cell. The latter contains a spherical nucleus having a diameter about two thirds that of the cell. It is not wholly filled with protoplasm, as is usually the case with cells capable of division, but has a very thick lining of protoplasm along the wall, and in this the nucleus is embedded. The nucleus extends completely across the cell-cavity, while above it and below it is cell-sap. If, now, the epidermal cell is to give rise to a new one, the nucleus passes over to one end of it and there divides into two parts, essentially as before described, except that the halves remain close together. Between these new nuclei the cell disc or plate, and the cellulose plate, are successively produced, cutting the old cell into unequal parts.

999. **The division of cells in cambium** was examined by Strasburger[2] in young shoots of Pinus sylvestris, which had completed their growth in length and had begun to thicken. These were selected on account of their rapid development. The cambium cells of this pine have a lining of protoplasm, together with a nucleus which occupies the middle of the cell and completely fills the smaller diameter. The nucleus is nearly spherical, or

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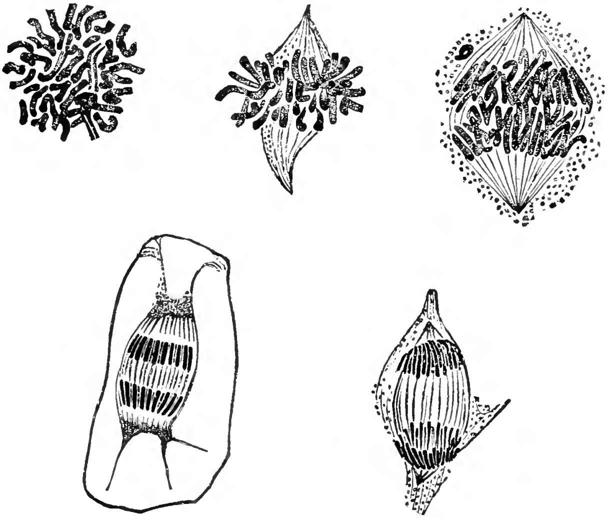
[1] Strasburger: Ueber Zellbildung und Zelltheilung, 1876, p. 110. This account is somewhat but not essentially different in the edition of 1880.

[2] Ueber Zellbildung und Zelltheilung, 1876, p. 116.

somewhat lengthened in the direction of the long axis of the cell, and contains several nucleoli. When it begins to grow, these nucleoli disappear, and the characteristic striation previously described appears transverse to the direction of future division and of the nuclear disc. The latter is not clearly defined, and its halves do not recede from one another very far, since, in fact, there is not space for much expansion in any event. The partition wall at first is confined to the space between the halves, and these are found in close contact with it, but later it extends completely across. The remarkable thickness of the radial walls of the cambium is explained by Sanio as due to the non-absorption of a part of the mother-cell; but Strasburger ascribes it to the uninterrupted nutrition of the radial wall from the contents of the cell itself. The newly formed partition-wall is thin, and cannot be shown by reagents to be double.[1]



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[1] The student should consult Strasburger's work: Ueber den Theilungsvorgang der Zellkerne, 1882; also Das botanische Practicum, chap. xxxiv.

FIG. 165. Behavior of nucleus during cell-division in the endosperm of Allium to illustrate the extraordinary complexity of the stained bodies. The dark lines represent the chromatin. (Flemming.)

1000. **Development of pollen-grains.** This affords some of the most instructive examples of cell-division, and owing to the facility with which material can be procured and studied, has received much attention.

(1) *Superficial phenomena.* These, which can be easily traced without the employment of staining agents, are in brief as follows: At the period when the loculi of the anthers begin as minute elevations at the end of the stamen, the external layer of cells, which is to serve as epidermis, is underlaid by a group of small cells which give rise to the mother-cells of the pollen and to the lining of the anther itself. This group is termed the archesporium; by division of its inner layer, large mother-cells are produced which divide to form the pollen-grains. The division of a mother-cell may give rise to two, three, or four pollen-grains, and in some cases more, according to the

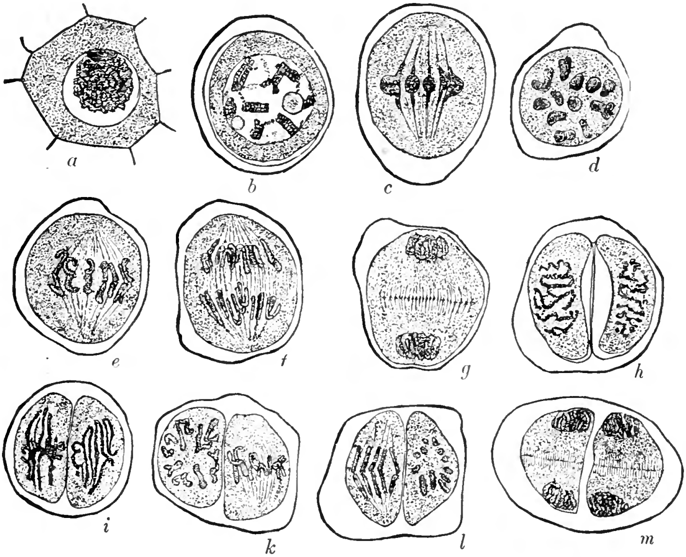

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FIG. 166. Fritillaria Persica. Division of the mother-cells of pollen. *a*, early stage, in which the threads are confused; *b*, the segments in course of longitudinal division; *c*, the nuclear spindle in profile; *d*, the same seen from its extremity or pole; *e*, division of the nuclear plate; *f*, separation of the derivative or daughter-segments; *g*, formation of the derivative tangles and the cell plate; *h*, the course of the nuclear threads in the derivative nuclei; *i*, longitudinal extension; *k*, nuclear spindle, on the right, in profile, on the left, from its extremity; *l*, separation of the segments, on the left seen in profile, on the right from the extremity; *m*, formation of the cell-plates. (Strasburger.)

direction of the lines of fission. It is possible to distinguish differences in the mode of division which are fairly characteristic of Angiosperms and Gymnosperms, of Monocotyledons and Dicotyledons. Although the morphology of the tissues involved and the course of development are not yet completely understood, it may be said that the formation of pollen-grains suggests throughout the mode in which the male elements are produced in the higher cryptogams.

(2) *Changes in the Nucleus.* The following suggestions by Strasburger for demonstrating the nuclear changes in pollen-grains can be applied with few modifications to all cases of cell-division: Place the young part, in this case a very young anther, in a solution of methyl-green in acetic acid, and subject it to slight pressure by which the contents of the anther-cells will be discharged. Those parts susceptible of staining will take the color readily and the different stages can be followed out substantially as shown in the figures. For the staining-agent above mentioned the following may be substituted, — gentian-violet in acetic acid, or nigrosin with picric acid. Preparations made with the latter can be preserved in glycerin without losing color.

Another and better method is to place sections of the tissue which has been kept for a few days in absolute alcohol, in an alcoholic solution of safranin, and after twelve hours wash with absolute alcohol; then transfer them to oil of origanum and thence to a thick solution of Damar in turpentine, for mounting.

By the safranin the delicate threads of the spindle are not much colored; they take, however, a good color with hæmatoxylin. Other combinations of coloring agents give good results.[1]

1001. **Cell-division in plant-hairs.** The stamen-hairs of Tradescantia Virginica afford excellent material for this examination. The last or upper three cells while still young are capable of division. If the very young hairs are transferred carefully to a slide on which is a three per cent solution of cane-sugar, they will continue the process of cell-division as shown in Fig. 167. If the specimen is a good one, and has not been much injured during its removal, it will remain active for several hours.

All the examinations of cell-division require the use of high powers of the microscope, none being better for the purpose than the so-called homogeneous immersion lenses.

1002. **The direction in which the new cell-wall is laid down** at the point of growth has been exhaustively examined by Sachs.

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[1] Das botanische Practicum, 1884, p. 598.

According to him, the planes of the walls at a point of growth may be thus classified :[1] —

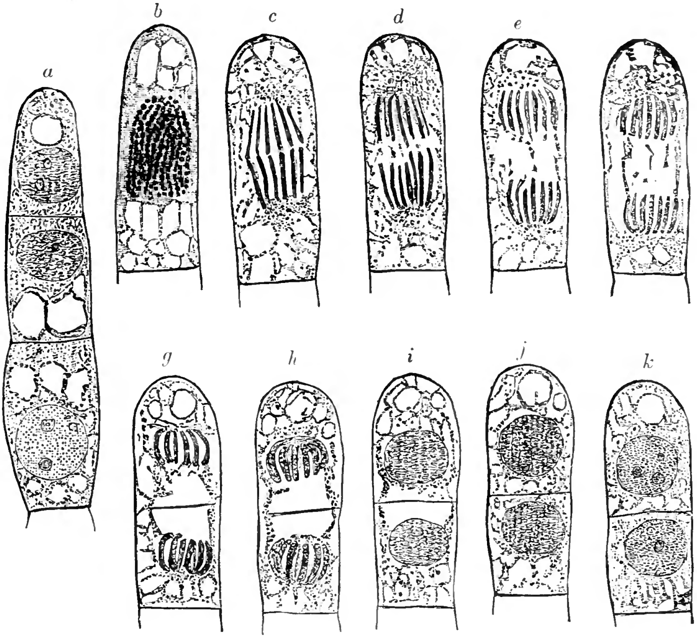

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Fig. 167. Tradescantia Virginica. Process of cell-division in the stamen-hairs. *a*, with a quiescent nucleus in the lower cell, and in the upper, one which has just finished its division; *b*, nucleus showing a coarse granular structure with a tendency to linear arrangement of the particles. The drawings from *c* to *k* inclusive exhibit the different stages of cell-division at the following points of time: *c*, at 10 o'clock and 10 minutes; *d*, 10.20; *e*, 10.25; *f*, 10.30; *g*, 10.35; *h*, 10.40; *i*, 10.50; *j*, 11.10; *k*, 11.30. (Strasburger.)

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[1] "The relations of the periclinal and anticlinal planes are illustrated by the following cases : —

(*a*) If the outline (in longitudinal section) of the growing point is a parabola, the periclinals will constitute a system of confocal parabolas of different parameter, the focus of the system being at the point of intersection of two lines, of which one is the direction of the axis and the other of the parameter. In this case the anticlinals, being the orthogonal trajectories of the periclinals, constitute a system of confocal parabolas, the axis and focus of which coincide with those of the periclinals.

(*b*) If the outline of the growing point is a hyperbola, the periclinals will be confocal hyperbolas, with the same axis but different parameter ; the anticlinals will be confocal ellipses, with the same focus and axis as the periclinals.

(*c*) If the outline of the growing point is an ellipse, the periclinals will be confocal ellipses ; the anticlinals will be confocal hyperbolas" (Abstract from

1. *Periclinal*, those which exhibit in longitudinal section curves in the same direction as the surface.

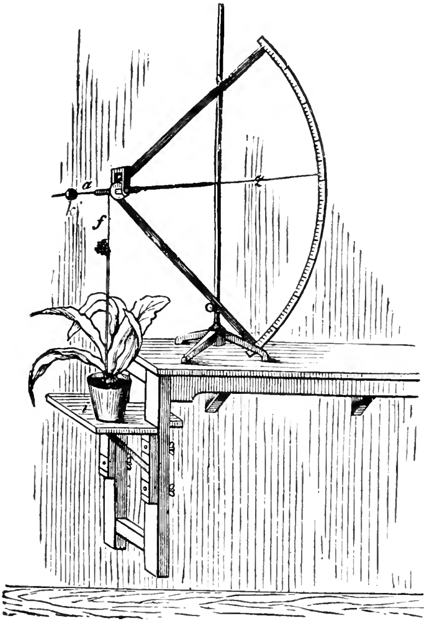
2. *Anticlinal*, those which cut the surface and the periclinal walls at right angles (forming a system of orthogonal trajectories for the periclinal walls).

3. *Radial*, those which pass through the axis of growth and cut the surface at right angles.

4. *Transverse*, those which cut both the axis of growth and the surface at right angles.

1003. **Growth of the cell-wall.** When the new cell is formed it undergoes changes in size, and often in shape and thickness. If it increases in size regularly at all points of the surface, it preserves, of course, its original shape; but if its growth is irregular at different points, great modifications of form result. Pollen-grains afford instances of the former method of growth, while the latter is seen in the multicellular organs, for example stems and leaves. At the growing points of the stem and leaf the cells when first formed are nearly alike in appearance; but wide differences are soon presented.

The growth of a cell in size may be terminal, when it gives rise to elongated forms; or localized at a point, line, or zone, when projections and swellings of various kinds are produced.[1]



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Arbeiten des botan. Inst. in Würzburg, 1878, in appendix to Text-book, 2d Eng. ed., p. 951).

The student should also read Sachs's Vorlesungen, 1882, pp. 523–557.

[1] These have already been sufficiently considered in the histological part of this volume, and it is not necessary to again call attention to the adaptations of the resultant structures to their respective kinds of work in the organism.

FIG. 168. Arc-auxanometer *f*, thread connecting plant with short arm of lever *a z*. The weight of long arm balanced by movable weight at *k*. (Pfeffer.)

1004. **Measurement of growth.** In some cases it is very easy to make direct measurements of the amount of increase in volume; but in general it is necessary to employ some form of apparatus by which the amount can be more or less exaggerated by a multiplier.

Several forms of growth-measurers, or auxanometers, have been devised for attaining this end. The simplest consists of a fixed arc of large radius (see Fig. 168), on which a delicate arm moves up or down according to the direction in which a small wheel at the centre, to which the arm is attached, is moved by the action of a thread fastened to the plant. Care must be taken to balance the arm as perfectly as possible, in order to prevent any strain on the plant by the weight of the index.

This form of apparatus is well adapted to demonstration before a class; and if a rapidly growing seedling or strong scape is chosen for experiment, the movement of the arm through the arc in an hour will be sufficient to be clearly seen at a considerable distance. A modification of the apparatus by Professor Bessey reduces its cost to a mere trifle. Both the arc and its supporting radii are made of strong manila paper; the wheel is a common spool, and the arm may be a slender straight straw.

1005. **Recording Auxanometers.** For the purpose of registering growth, several applications of the chronograph have been made. One of the most satisfactory of these consists of a slowly revolving cylinder covered with smoked paper, upon which a needle, attached to the end of a balanced thread passing over a

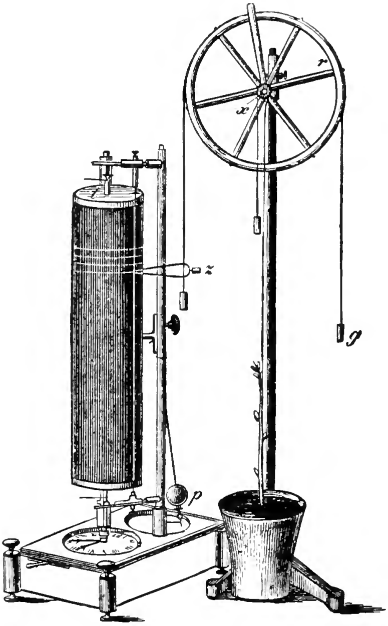

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Fig. 169. Registering auxanometer. The thread attached to the plant passes over the small wheel at x, and is balanced by a weight. The index z is balanced by the weight g; the thread between them goes over the wheel r. The cylinder is carried round by the clock-work, which is regulated by the pendulum weight at p. (Pfeffer.)

wheel, leaves its trace as it ascends or descends. The wheel is caused to move by means of a second balanced thread which passes over its axis, and which is fastened at one end to the growing part of the plant.

1006. Pfeffer's modification of this apparatus provides that the cylinder shall turn a short distance at regular intervals of time, so that the line made by the needle becomes interrupted and thus exhibits the appearance of steps; in which the height of the step represents the total ascent or descent of the needle during a given time, while the other line of the step merely marks the distance through which the cylinder moves at the close of one of its intervals.

1007. Examples of very rapid growth are afforded by many fungi; for instance the common puff-ball, which increases enormously in size during a single night.

Shoots of bamboo have been observed at Kew to grow at the rate of two to three inches in the twenty-four hours; and in its native habitat, Bambusa gigantea has been known to grow more than ten inches a day.

The expansion of the leaves of Victoria regia is extremely rapid, under favorable conditions reaching a foot in the twenty-four hours. The scapes of many plants develop at a rapid rate, and afford excellent material for practice with the auxanometer.

1008. **Conditions of growth.** Vegetable growth does not take place unless there is an available supply of assimilated matter, access of free oxygen, and a sufficiently high temperature. The assimilated matter may be furnished to the growing parts directly from green tissues, or from reservoirs where it has been stored up. In either case it must come in a state of solution to the growing cells, and hence a certain amount of water is required for the transfer. That the amount of water demanded is not necessarily large, is shown by the starting of shoots from bulbs, tubers, etc., in the spring, even when no water has been furnished from outside.

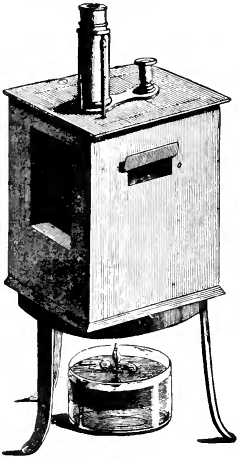
1009. Although the process of respiration in green plants may go on for a time without free oxygen, as has been shown by the experiments described on page 371, there is no proof that growth occurs under such circumstances. In an atmosphere of hydrogen, nitrogen, carbonic acid, or nitrous oxide, — gases which are not in themselves harmful to plants, — growth does not take place, as has been proved by experiments upon seeds and seedlings. Detmer has shown that growth is immediately checked when the plant is deprived of free oxygen, but death does not ensue until after a considerable time. During the period of inactivity the plant is ready to respond at once to the influence of oxygen, growth being then immediately resumed.

1010. If assimilated matters and free oxygen, both essential to growth, are abundantly supplied to a plant which is kept at too low a temperature, growth does not occur. The minimum limit for growth is different for different plants, and is not the same for all organs.

Again, it must be noted that there is a maximum limit of temperature above which growth does not take place, and this limit is also different for different plants. Between the lower and upper limits there is, for the plants which have been thus far studied with respect to the effect of heat on growth, an optimum of temperature at which growth is most rapid.

1011. **Relations of growth to temperature.** *The minimum temperature* required for growth is generally much higher for plants of warm regions than for plants of cold climates, and there are wide differences even among plants belonging to the same climate. A few of the earliest spring plants begin their growth at or very near the freezing-point of water: it is thought by some observers that growth may, in a few cases, take place even below this point. Kjellmann states that the marine algæ at Spitzbergen continue to develop their thallus during the polar night of three months, and that most of them during this time produce their spores, the temperature of the sea-water being on the average one degree below zero, Centigrade.[1]

But, on the other hand, many of the tropical plants[2] cultivated in hot-houses cease growing when the temperature falls below 10° or 15° C.



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1012. *The maximum temperature* for growth is as wide in its range for different plants as the minimum. Aside from the

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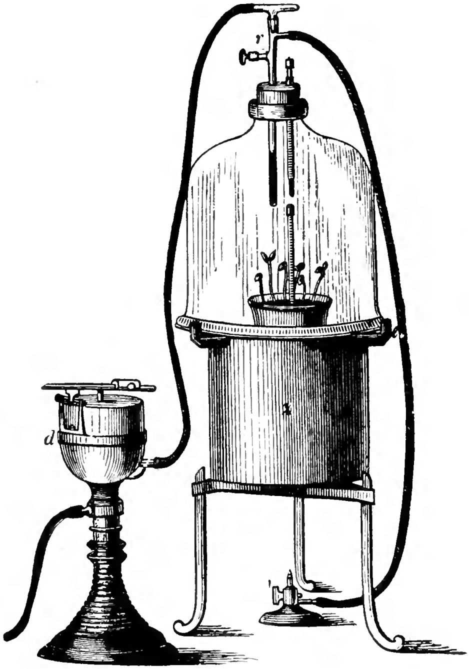
[1] Comptes Rendus, lxxx., 1875, p. 474. See also Falkenberg: Die Algen im weitesten Sinne, in Schenk's Botanik, 1882.

[2] See De Candolle: Physiologie végétale, 1832.

FIG. 170. Double-walled metallic box for keeping microscopic objects at a given temperature while under observation. (Sachs.)

instances of plants growing in hot springs, it may be said to lie at or very near 50° C. The figures obtained by Sachs for the common plants he experimented upon are in general between 36° and 46° C. It is a curious fact that some tropical plants are not capable of bearing a higher temperature than a few plants of cold countries.[1]



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1013. *The optimum temperature for growth* lies in most cases between 20° and 36° C.

1014. The following table, compiled by Pfeffer, exhibits at a glance the cardinal points of temperature as they have been determined by four observers: —

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[1] Pfeffer: Pflanzenphysiologie, ii., 1881, p. 123.

Fig. 171. Apparatus for keeping seedlings in a constant temperature. The drum at *d* is an ordinary thermo-regulator by which the flow of illuminating gas can be controlled within narrow limits To insure still greater control, the more sensitive regulator, *r*, is also employed. The cylindrical vessel, *z*, has double walls, the space between them being filled with water. Under this vessel a very small burner is sufficient even for optimum temperature. (Pfeffer.)

Name of Plant.	Temperature for Growth.			Observer.
	Minimum. ° C.	Optimum. ° C.	Maximum. ° C.	
Triticum vulgare	5.0	28.7	42.5	Sachs.[1]
	7.5	29.7		Köppen.[2]
Hordeum vulgare	5.	28.7	37.7	Sachs.
Sinapis alba	0.	21.	28.0	De Candolle.[3]
		27.4	over 37.2	De Vries.[4]
Lepidium sativum	1.8	21.	28.	De Candolle.
		27.4	below 37.2	De Vries.
Linum usitatissimum	1.8	21.	28.	De Candolle.
		27.4	over 37.2	De Vries.
Trifolium repens	5.7	21–25.	below 28.	De Candolle.
Phaseolus multiflorus	9.5	33.7	46.2	Sachs.
Pisum sativum	6.7	26.6		Köppen.
Lupinus albus	7.5	28.		Köppen.
Zea Mais	9.5	33.7	46.2	Sachs.
	9.6	32.4		Köppen.
	9.	21–28.	35.	De Candolle.
Cucurbita Pepo	13.7	33.7	46.2	Sachs.
Sesamum orientale	13.	25–28.	below 45.	De Candolle.

Köppen has given an instructive table which exhibits the relations of growth to temperature in a few common plants. The figures denote the growth in forty-eight hours of the whole descending axis of each plantlet.

Temperature. ° C.	Lupinus albus.	Pisum sativum.	Vicia Faba.	Zea Mais.	Triticum vulgare.
10.4		5.5			4.6
14.4	9.1	5.0			4.5
17.	11.0	5.3			6.9
21.4	25.0	25.5	9.3	3.0	41.8
24.5	31.0	30.0	10.1	10.8	59.1
25.1	40.0	27.8	11.2	18.5	59.2
26.6	*54.1*	*53.9*	*21.5*	29.6	86.0
28.5	50.1	40.4	15.3	26.5	73.4
30.2	43.8	38.5	5.6	*64.6*	*104.9*
31.1	43.3	38.9	8.0	49.4	91.4
33.6	12.9	8.0		50.2	40.3
36.5	12.6	8.7		20.7	5.4
39.6	6.1			11.2	

1015. **Relations of growth to light.** It is only under the influence of light that the plant can prepare from inorganic matter

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[1] Text-book, 2d Eng. ed., p. 830.

[2] Wärme und Pflanzensachsthum, 1870, p. 43.

[3] Bibliothèque universelle d. Genève, Archives des Sciences physiques, xxiv., 1865, p. 243.

[4] Matériaux pour la connaissance de l'influence de la température sur les plantes, Archives Néerlandaises, v., 1870, p. 385.

materials for its growth; but if an adequate amount of assimilated substance has been stored up, growth can go on in the dark until this store is exhausted. It is, in fact, in the dark that nearly all vegetable growth takes place. It is well known that all the points of growth in the ordinary higher plants are more or less protected from the action of light. Thus, the growing tissues of buds are concealed beneath external structures; so also is the cambium by which dicotyledons increase in thickness.

1016. When, however, a shoot develops in darkness it is apt to become much more attenuated than when it develops in light; its leaves are etiolated, and of abnormal shape and diminished size. Such shoots are said to be "drawn."

1017. There is considerable difference in the degree to which different parts of plants are affected by the withdrawal of light, and there are also differences in this respect between different species. The effect of darkness upon shoots is well shown by the simple experiment of conducting a branch of some strong plant like Tropæolum or a gourd into a dark box, all its other leaves being kept in the light. The effects are more striking when the shoot is a flowering one; the internodes will become much drawn, the leaves will be small and blanched, the calyx will be pale, but the rest of the flower will be hardly affected either in shape or size. It sometimes happens, however, that the flowers will be abnormal.

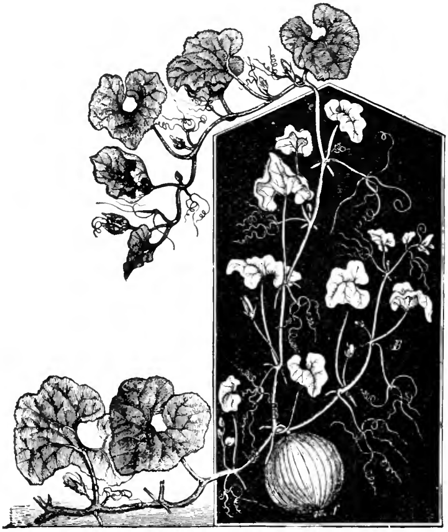

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FIG. 172. Growth of gourd in light and darkness. (Sachs.)

1018. **The relations of growth to oxygen.** All growth is accompanied by the oxidation of assimilated substance, or food. Can growth be stimulated by furnishing to the plant a larger amount of oxygen than it would obtain under natural conditions? This question is not yet positively answered by any experiments. It has been shown that some plants grow, for a time at least, more rapidly when they are subjected to a slight increase of pressure of the atmosphere by which they are surrounded; but there are also a few cases which indicate that some other plants may grow more rapidly under a diminished pressure.

The "resting" state of some plants cannot be shortened by any increase in the amount of oxygen furnished; it is only after the normal time of rest has ended that any growth begins. When periods of rest cannot be disturbed by any ordinary change in the surroundings, they may be held to be conservative, since they are generally correlated with the climatic conditions of peril from cold or from dryness, under which these plants naturally live.[1]

1019. **Periodical changes in the rate of growth.** Even under external conditions which are as nearly constant as possible growth is not quite uniform in its rate. Thus, an extending internode grows in length at first slowly, then with gradually accelerating rapidity until a maximum of growth is reached, from which point the rate declines until with maturity of the part growth ceases. The line of growth, when given graphically, is a curve known as the great curve of growth; and the period of rise and decline is the grand period, to distinguish this from the minor periods of accelerated growth, which appear on the curve as small fluctuations.

1020. **Properties of new cells and tissues.** Newly formed cells are generally characterized by the possession of a certain amount of turgidity; the young cell-wall exerting more or less resistance to the expansive contents within. The contents are therefore compressed to some degree by the confining wall; the action and reaction varying, of course, with changes in the surroundings. If a part of its water be withdrawn from the cell, the compression is materially lessened; while, on the other hand, an increase in the amount of water must augment it.

1021. These features have been recently re-examined by De Vries, who has suggested a quantitative method for determining the amount of turgidity at any given time. The method, when reduced to its simplest terms, consists in the use of solutions of

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[1] For a very curious account of experiments upon the influence of electricity upon growth, the student should see Grandeau: De l'influence de l'électricité atmosphérique sur la nutrition des végétaux, Annales de Chimie et de Physique, sér. 5, tome xvi., 1879, p. 145.

salts of known strength in which the tissues are placed, and which are then allowed to act upon the contents of the cells. When the solutions are more dense than the fluids in the cavity of the cell, an exosmotic action withdraws a certain amount of the water from the cell, causing thereby a shrinking of its contents which can be easily observed under the microscope, or noted by curvature of the whole section. The method permits the experimenter to ascertain within narrow limits the density of the contents of a given cell, and to determine the relative degree of turgidity in different cases. When a cell undergoes no change of form upon being placed in a solution of a given strength, that solution is taken as a measure of the density of its contents.[1]

1022. **Tensions in cell-wall.** There may frequently be observed a tension of different layers of the cell-wall. This can be easily demonstrated by making thin sections of any succulent tissues from which cells can be readily detached; a curvature will be detected at the moment of cutting.

1023. Young cell-walls are elastic to a certain extent; but their limit of elasticity is easily exceeded, and then they remain in the stretched condition. When an internode is strongly stretched in the direction of its length, it undergoes permanent elongation. This elongation may amount in some cases to three or even five per cent; whereas the temporary extension in the same instances may range from seven to seventeen per cent. The extensibility diminishes, while the elasticity increases, with the age of the internode.

1024. From his experiments Sachs draws the following conclusions regarding growing internodes: (1) After flexion they do not completely recover their straightness; (2) one vigorous bending, and to a still greater extent repeated ones in opposite directions, leave the internode flaccid, or deprive it of its rigidity; (3) when growing internodes are sharply struck, there is a sudden curvature, the concavity of which lies towards the direction of the blow.[2]

1025. **Tension of tissues.** Under the ordinary circumstances of growth walls of young cells continue to be somewhat elastic

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[1] *Plasmolysis.* For a full account of the quantitative action of numerous plasmolytic agents the student should consult De Vries's paper in Pringsheim's Jahrbücher for 1884, where the effect of potassic nitrate and other substances upon the protoplasmic film is detailed at length. In the Laboratory at Cambridge, Mr. Puffer has confirmed most of De Vries's observations.

[2] Sachs: Text-book, 2d Eng. ed., 1882, pp. 784–788.

and hence exhibit distinct tensions. If there is a marked difference in the rate of growth between the internal and the external cells in any organ, as is the case in most young stems, the more superficial tissues are stretched to some extent by the internal ones; hence arise tensions of tissues, the organ in this state being in a balanced condition, in which the equilibrium can be disturbed by slight external or internal causes. The following experiment exhibits the phenomenon of tension very strikingly: From a long and thrifty young internode of grapevine cut a piece which shall measure exactly one hundred units, for instance, millimeters. From this section, which measures exactly one hundred millimeters, carefully separate the epidermal structures in strips, and place the strips at once under an inverted glass to prevent drying; next, separate the pith in a single unbroken piece wholly freed from the ligneous tissue. Finally, remeasure the isolated portions, and compare with the original measure of the internode. There will be found an appreciable shortening of the epidermal tissues and a marked increase in length of the pith.[1] The young ligneous tissue is generally shortened by its release, but this result is by no means constant. The most astonishing feature is the great difference which exists between the length of the external tissues and that of the internal tissues which up to the period of isolation they had compressed. The external parts had been plainly stretched to a certain extent, while the internal had been as obviously confined by them. The tensions are not only in the direction of the length, but are also transverse. Similar tensions are to be found also in foliar organs. But there are

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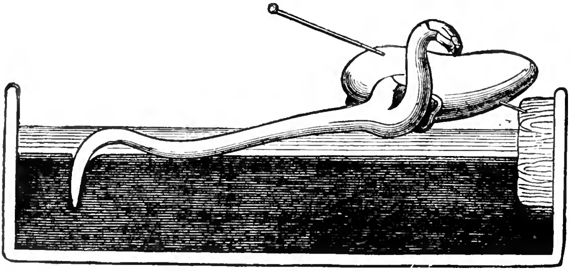
[1] The following table exhibits the remarkable differences in tension between the outer and the inner parts of young shoots of Nicotiana Tabacum. Each internode is first cut squarely off at both ends, and then carefully sliced lengthwise so as to separate the bark, wood, and pith from each other. Supposing the length of the whole internode to be one hundred units, the length of the cortex will fall short of this, while that of the pith will considerably exceed it.

Number of the Internode, counting from the youngest.	Length of the Isolated Tissue.		
	Cortex.	Woody part.	Pith.
I.-IV.	94.1	98.5	102.9
V.-VII.	96.9	98.9	103.5
VIII.-IX.	96.5	98.5	100.9
X.-XI..	99.5	99.5	102.4

some parts, as for example most roots near their extremity, which do not exhibit this phenomenon.

1026. **Geotropism.** Suppose a young shoot to possess the tension already described; let this be placed, while growing, in an horizontal position. In consequence of its position the nutrient fluids will, from the force of gravitation, have a tendency to collect in greater amount in the cells upon its under side. Their presence on that side will not only cause an increase of turgescence there, but will offer to the growing cells a larger amount of available material for immediate use in growth, especially for laying down the cell-wall. From one or from both of these causes there will therefore be an appreciable elongation of the tissues on the under side, and hence a curving upwards will occur, which finally results in the assumption of the erect position by the organ in question.



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1027. If, on the other hand, the organ possesses little or no tension, it is conceivable that the growth would result in a curvature of the extremity towards the ground; this is seen in the case of roots. The same factors produce an upward curvature where there is marked tension of tissues, and permit a downward curvature where there is little or no tension. It is a significant fact that in the case of certain branches from roots the direction of growth is oblique.

1028. Organs which turn towards the earth are termed *geotropic;* those which turn upwards are *apogeotropic;* those which pursue in their growth oblique directions have been termed *diageotropic.*

1029. **Heliotropism.** It can be shown by exact measurement that in many cases light, especially the more refrangible part of

FIG. 173. Vicia Faba. Descent of root into mercury. (Sachs.)

the spectrum, has a retarding effect upon the growth of certain parts, — for instance, upon that of shoots, — exhibiting itself in the curvature of the part towards the side of greatest illumination. Such curvatures are said to be *heliotropic.* It is, however, well known that the shoots and some other parts of a few plants turn away from the light; such are termed *apheliotropic.*[1]

1030. Little is known positively as to the nature of the influence which light exerts upon growth. The studies of Vines have shown that the influence is largely due to the modification of the turgescence of growing cells. "The conditions of growing and of contractile cells are in some respects the same. Turgidity is essential to the proper fulfilment of the functions of both, and it has been shown that light has the power of inhibiting, more or less completely, the activity of both. The most general case of the action of light upon growing cells has been shown to be a diminution in the rapidity of their growth. The cell with diminished or arrested growth may be fairly compared with one of the cells of a rigid motile organ. In both, the micellæ of the protoplasm are in a state of stable equilibrium so that they do not yield, in the former case to the force which tends to separate them, namely, the pressure of the cell contents, and in the latter to the force which tends to bring them nearer together. The theory that the action of light upon growing cells and upon those of motile organs is due to such a modification of the relations existing between the micellæ of the protoplasm that the mobility of the micellæ is diminished, thus gives a satisfactory explanation of many phenomena which at first sight seem not to have much in common."[2]

1031. **Hydrotropism.** It has been shown by several experimenters that rootlets when developing in moist air deviate towards a moist surface. This phenomenon, which has been examined in detail by Sachs, is termed *Hydrotropism.* The

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[1] In order to examine the effects of the different parts of the spectrum upon the growth and movements of plants, the student should cultivate in cases of glass of different colors two or three seedlings, as many bulbous plants, and some well-rooted cuttings of hardy house-plants, for instance Pelargonium. Observe whether the growth is more or less rapid under blue glass, and note whether all the seedlings circumnutate in the same manner in the different cases. It should be borne in mind that the bulbous plant as it starts has a generous supply of available food, whereas the seedling has a more scanty store, and the cutting very little.

[2] Arbeiten des bot. Inst. in Würzburg, 1878, p. 147.

accompanying figure shows an easy method of demonstrating this mode of governing the direction of growing roots.

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1032. **Thermotropism.** As might be expected from what has been said regarding the tensions of tissues and the facility with which their balance is disturbed, the effect of warmth in governing the direction of a growing organ must be considerable. Curvatures dependent upon temperature are called *thermotropic.*

1033. **Assumption of definite form** during growth depends, of course, chiefly upon inherited tendencies; but there have been experiments which show that to a slight extent it may be possible by external influences to induce special shapes of growing structures. Among the most interesting of these are the experiments by Pfeffer[1] upon the growth of bilateral organs in some of the lower plants, especially Marchantia; by De Vries[2] upon

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[1] Arbeiten des bot. Inst. in Würzburg, 1871, p. 77.

[2] Arbeiten des bot. Inst. in Würzburg, 1872, p. 223.

FIG. 174. Roots of seedlings affected by moisture during their descent. The apparatus consists of a network frame filled with moist sawdust in which the seedlings germinate. (Sachs.)

bilateral symmetry; by Vöchting[1] upon the modification of foliar and axial organs.

1034. **The amount of force** which is exerted by certain organs during their growth has been accurately measured for only a few cases. Thus Darwin[2] found that the transverse growth of the radicle of a germinating bean was able to displace a weight of 1,500 grams, or 3 lbs. 4 oz., and in another instance, 8 lbs. 8 oz. "With these facts before us, there seems little difficulty in understanding how a radicle penetrates the ground. The apex is pointed, and is protected by the root-cap; the terminal growing point is rigid, and increases in length with a force equal, as far as our observations can be trusted, to the pressure of at least a quarter of a pound, probably with a much greater force when prevented from bending to any side by the surrounding earth. Whilst thus increasing in length it increases in thickness, pushing away the damp earth on all sides, with a force of above eight pounds in one case, of three pounds in another case. . . . The growing part does not therefore act like a nail when hammered into a board, but more like a wedge of wood, which, whilst slowly driven into a crevice, continually expands at the same time by the absorption of water; and a wedge thus acting will split even a mass of rock."

By means of a framework placed around the fruit of a vigorous squash kept under conditions most favorable to its rapid development, Clark[3] estimated the force exerted by growth to be about 5,000 pounds.

1035. That external pressure can retard growth is well shown by the experiments of De Vries[4] upon the formation of autumn wood (see page 138). By increasing the external pressure exerted by the bark he was able to diminish the calibre of the wood-cells and ducts; whereas, by diminishing the pressure (by making longitudinal incisions into the bark) he was able to

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[1] Botanische Zeitung, 1880, p. 593.

[2] The Power of Movement in Plants, 1881, p. 76.

[3] For a full account of this experiment, see Report of the Secretary of the Massachusetts Board of Agriculture for 1874.

The great force exerted by the increase in size of the stems and roots of woody plants is sometimes demonstrated in an extraordinary manner by the development of seedlings in crevices. Thus, at the Marien Cemetery in Hanover, Germany, the base of a tree has dislodged the heavy stones of a strongly built tomb. One of the stones, which measures 23 × 28 × 56 inches, has been lifted upon one side to the height of five inches. The tree measures just above its base from ten to fourteen inches in diameter.

[4] Flora, 1872, p. 241.

cause a considerable enlargement of the similar elements. Further observations led him to the conclusion that the striking differences between spring and autumn wood, upon which the annual rings depend, are due to the greater pressure which is exerted by the bark in the latter part of the summer.

CHAPTER XIII.

MOVEMENTS.

1036. Most of the movements exhibited by plants are associated with growth. In the preceding chapter attention has been called to some of these movements, especially those which are characterized by a change in the direction of growing parts (see Geotropism, Heliotropism, etc.). In the present chapter it is proposed to examine continuous and recurrent movements, and indicate to what extent these are likewise the accompaniment of growth.

In the existing state of knowledge no satisfactory classification of the movements of plants can be made. The provisional one now to be followed is adopted only for convenience.

1037. **Locomotion,** or movement of the whole organism from place to place, can be observed in some of the lower plants. One of the most interesting examples is furnished by Æthalium septicum, which at certain stages of its existence consists of approximately pure protoplasm in a naked state. Under favorable conditions this naked mass (the plasmodium), which frequently attains considerable size, passes in a creeping manner over a moist surface, thrusting out processes in an apparently irregular manner, sometimes retracting them, but more often bringing up to the advanced part the rest of the uneven mass.

The sensitiveness of this mass to the action of external influences renders it a suitable object for the examination of the essential properties of protoplasm, and many of the more important facts relative to its movement have therefore already been given (see 550). It is important to notice particularly that there is a rhythmical pulsation of the sap-cavities or vacuoles in the plasmodium, dependent, it is supposed, upon the irregular absorption of water with a varying imbibition power. This spontaneous pulsation is somewhat affected by external conditions; for instance, it is increased in rate by heat and diminished by cold.

1038. Portions of protoplasmic matter concerned in the reproduction of many of the lower plants, especially those which live wholly in the water, as the algæ, have the power of independent locomotion. This is exhibited strikingly in the motile spores, which are provided with cilia, and can thereby propel themselves from place to place with considerable rapidity. Similar independent motion is shown also by the antherozoids of many of the lower and even some of the higher cryptogams.

The protoplasmic movement by which such locomotion is secured is essentially identical with certain ciliary movements observed in the animal kingdom.

1039. It is a familiar fact that some minute algæ, furnished either with walls of cellulose (Desmids) or cellulose impregnated with silicic acid (Diatoms), possess the power of motion, but the cause is not well understood. In the case of the skiff-shaped diatom the motion is somewhat spasmodic, and the course of the organism through the water is not in a straight line, but it is nevertheless enabled to traverse a considerable distance in a short time. Owing to the absence of any distinct cilia, it is difficult to conceive the mechanism of propulsion. According to Max Schultze there is a minute slit on the under side of the motile diatoms, and through this slit a delicate film of protoplasmic matter projects. By contact of this motile film with surrounding objects, the diatom, as it is supported in the water, is transported from place to place.

These three cases of locomotion, namely, of (1) naked protoplasm, (2) of ciliated structures, (3) of apparently closed cells, do not exhaust the list of instances of motion of vegetable organisms from place to place; other cases are referred to the succeeding volume upon the lower plants.

1040. **The movement of protoplasm within cell-walls** has already been sufficiently examined (see 546); but attention should now be called to the fact that chlorophyll granules (which are always embedded in the protoplasmic mass) frequently assume at night, or when a portion of the leaf is darkened, positions different from those which they have during strong exposure to light. This change

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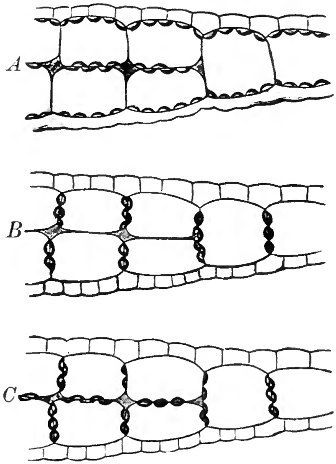
FIG. 175. Circulation of protoplasm in hair of Gourd. (Sachs.)

of position is well observed in the thin leaves of some mosses, the grains generally (1) gathering on the side walls under bright light, but (2) occupying the upper and lower faces of the cells when the intensity of the light is much diminished. The first mode of arrangement is termed *apostrophe*, the second *epistrophe*.[1]

1041. **Hygroscopic movements** are dependent upon the property possessed by dry vegetable tissues of swelling more or less under the influence of moisture. They are most strikingly exhibited in the case of simple parts, like the filamentous appendages of the spores of Equisetum and the teeth of the peristome of certain mosses, notably that of Funaria hygrometrica. They are also seen in the long appendages of many fruits; for example, in the awns of some grasses, in some Geraniaceæ, etc., where they serve the useful purpose of fastening the fruit with its enclosed seed in favorable soil. When the fruit falls upon moist soil, it at first lies flat; later, the extremity of the appendage and the tip of the fruit form fixed points in the ground; and then, as moisture is absorbed by the dry tissue, a spiral curvature throughout the whole takes place. This continues to twist the tip of the fruit down into the soil, much after the fashion of a corkscrew. This kind of movement is most surprisingly shown in some of the grasses of South America, and in our native Stipa.



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In not a few instances the whole plant becomes relatively dry, rolling up into a roundish mass which becomes expanded again upon access of water. Good examples of such action are afforded

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[1] In some cases the aggregation of the chlorophyll granules differs somewhat from that described in the text. For a discussion of this subject, consult Frank (Botanische Zeitung, 1871, and Pringsheim's Jahrbücher, viii., 1872), also Stahl (Botanische Zeitung, 1880). Sachs, Prillieux, and Famintzin have contributed much to the discussion.

FIG. 176. Cross-section through the leaf of Lemna triscula, showing the position of the chlorophyll granules: *A*, during the day; *B*, during exposure to strong light; *C*, during the night. (Stahl.)

by the so-called Resurrection plant of California (Selaginella lepidophylla), and by the Oriental plant known as the Rose of Jericho. The latter plant, when dry and shrunken into small compass, takes the shape of an irregular ball, becomes detached from the ground where it has grown, and may be blown about over great distances; if it has ripe seeds, these are scattered during transit.

1042. **Movements due to changes in structure during ripening of fruits.** The fruit of the common Impatiens, or Touch-me-not, affords a familiar instance of the movements of this class. As it approaches maturity, the valves of the capsule become tense, each one, so to speak, holding the others in place; and when they are disturbed by even a slight touch they separate violently, and by their spring throw the seeds to considerable distances. In some cases the mechanism is more elaborate, notably in the cucumber-like fruit of Momordica Elaterium. In this the separation of the fruit-stalk permits a sudden shrinking of the whole pericarp and a violent escape of the seeds with a viscid liquid through the opening made by the separation. The seeds are projected considerable distances from the fruit.

Hildebrand[1] distinguishes between (1) *dry* explosive fruits (such as Violet, Witch-Hazel, and Lupinus luteus), and (2) *fleshy* explosive fruits (such as Impatiens, Momordica, and Cardamine hirsuta).

1043. **Revolving movements, or Circumnutation.** The tips of all young growing parts of the higher plants, as well as the tips of many of the lower, revolve through some orbit, either a circle or some form of the ellipse, the latter sometimes being so narrow that it becomes practically a straight line. During its revolution a tip bows or nods successively to all points of the compass; whence the name nutation, or, as termed by Sachs, revolving nutation. Darwin, who re-examined the whole subject, has suggested a more general term, namely, *circumnutation.*

"Circumnutation depends on one side of an organ growing quickest (probably preceded by increased turgescence), and then another side, generally almost the opposite one, growing quickest."[2]

1044. Owing to the fact that there are numerous instances in which the revolving movements are variously modified, that is, "a movement already in progress is temporarily increased in

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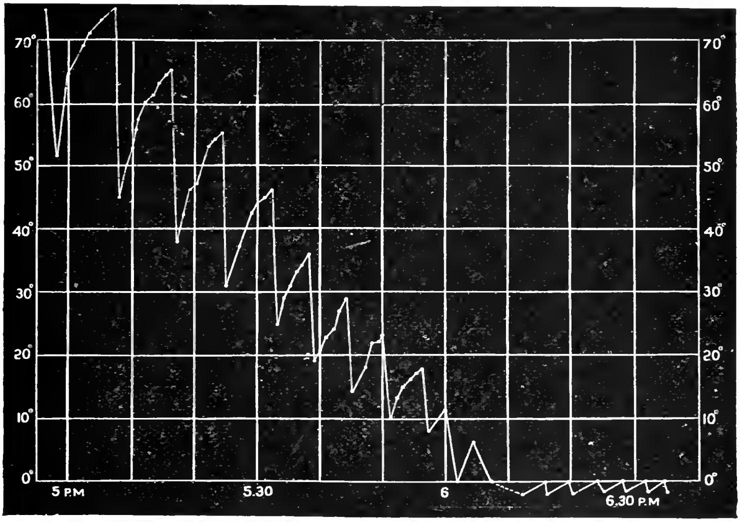
[1] Pringsheim's Jahrbücher, ix., 1873, p. 235, where the whole subject is discussed in an interesting manner.

[2] Darwin: Power of Movement in Plants, 1880, p. 99.

some one direction and temporarily diminished or arrested in other directions," it has been found convenient to discriminate between circumnutation and modified circumnutation. Darwin divides the latter into two classes of movements: (1) those dependent on innate or constitutional causes, and independent of external conditions, except that the proper ones for growth must be present; (2) those in which the modification depends to a large extent on external agencies, such as the daily alternations of light and darkness, light alone, temperature, or the action of gravity. It is plain that such a division cannot be absolute; in fact, numerous intermediate cases are known to exist.



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1045. **Methods of observation of circumnutation.** For measuring the rate and determining the exact direction of the movements of circumnutating parts when the parts are small and the movements slight, the following methods described by Darwin[1] can be employed in nearly all cases where it is necessary to magnify the amount of displacement.

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[1] Power of Movement in Plants, 1880, p. 6.

FIG. 177. Angular movements of a leaflet of Averrhoa bilimbi during its evening descent, when going to sleep. Temp. 78-81° F. The ordinates represent the angles which the leaflet made with the vertical at successive instants. A fall in the curve represents an actual dropping of the leaf, and the zero line represents a vertically dependent position. Each oscillation consists of a gradual rise followed by a sudden fall. (Darwin.)

A very slender filament of glass, made by drawing out a thin glass tube until it is no larger than a hair, is to be affixed to the tip of the root, stem, or leaf under observation; this is easily done by means of a quickly drying varnish, for instance shellac dissolved in alcohol. In order to mark the path made by the filament it is best to cement to the tip of the slender hair of glass a very minute bead of black sealing-wax, "behind which a bit of card with a black dot is fixed to a stick driven into the ground. The bead and the dot on the card are viewed through the horizontal or vertical glass plate (according to the position of the object), and when one exactly covers the other, a dot is made on the glass plate with a sharply pointed stick dipped in thick India ink. Other dots are made at short intervals of time, and these afterwards joined by straight lines. The figures thus traced are angular; but if the dots are made every one or two minutes the lines are more curvilinear, as occurs when radicles are allowed to trace their own course on smoked glass plates."

"Whenever a great increase of the movement is not required, another and in some respects a better method of observation is followed. This consists in fixing two minute triangles of thin paper, about one twentieth of an inch in height, to the two ends of the attached glass filament; and when their tips are brought into a line so that they cover one another, dots are made as before on the glass plate."[1]

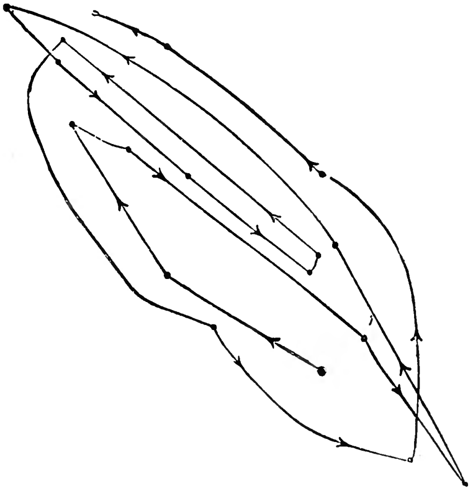

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FIG. 178. Tracing, showing the conjoint circumnutation of the hypocotyl and cotyledons of Brassica oleracea during 10 hours and 45 minutes. Figure reduced to one half original scale. (Darwin.)

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[1] It is very convenient to employ large bell-jars, or hemispherical glasses, as glass screens upon which to record the dots indicating the position of the tip at any given moment. It must be remembered that in all these cases there

1046. **Circumnutation in seedlings.** That part of the axis which is below the cotyledons is made up of a rudimentary stem known as the *caulicle* or *hypocotyl*, and a rudimentary root or *radicle* proper. The part of the young stemlet above the cotyledons is termed the *epicotyl.* In the cotyledons of the plantlet, when freed from the seed-coats, and in all parts of the young axis, slight movements can be observed. In all observations it is necessary to remove the plantlet as far as possible from disturbing conditions; thus, all light must be excluded until the moment of making the observation, when only a faint light should be employed.

1047. Two facts are easily apparent with regard to the revolving *radicle:* (1) its extreme sensitiveness to contact; (2) its tendency to yield to geotropism (see 1026).

1048. The *caulicle*, upon emerging from the seed-coats, is often more or less arched; but it may become straight after a short time, when it can be seen to pass through an elliptical orbit by which the plane of the cotyledons is somewhat inclined successively to all points of the compass. Darwin has shown that even before the liberation of the caulicle from the seed-coats, when both columns of the arch are held in the soil, the top of the arch moves with considerable regularity. It is difficult to understand how the summit of the arch formed by the curved caulicle can revolve when both of its supporting columns are fixed in the soil. Darwin has accepted an explanation suggested by Wiesner, which is briefly as follows: In a given internode (it must be remembered that the caulicle represents the first internode of the seedling, as shown in Volume I. page 9) there may be a zone in which the growth is equal on all sides, and which may be termed the zone of indifferent growth, while on each side of this there may be two others in which there is unequal growth at intervals of time. Then by the faster growth on one side of the arch the summit would be thrown to one side, and this process

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is more or less distortion produced by the best methods of projection, and in all accurate observations this must be taken into account.

When seedlings are inverted so that the glass filament is held upwards, it must be noted that the influence of gravitation must come in as a modifying element. To mark the amount of influence exerted by gravitation, it is well to vary the length and weight of the filament employed. But it must be observed that the weight of the organ itself is the most important element in the problem. Moreover, it has been observed that all young growing parts, especially the extremity of the radicle, are more or less sensitive; and hence the course of the filament may be somewhat modified by even slight contact.

would sooner or later be succeeded by its reversal; and thus the summit would be made to circumnutate.

1049. Darwin's[1] illustration of the movements of the parts of seedlings gives a clear idea of their sequence. "A man thrown down on his hands and knees and at the same time to one side by a load of hay falling on him, would first endeavor to get his arched back upright, wriggling at the same time in all directions to free himself a little from the surrounding pressure; and this may represent the combined effects of apogeotropism and circumnutation when a seed is so buried that the arched hypocotyl or epicotyl protrudes at first in a horizontal or inclined plane. The man, still wriggling, would then raise his arched back as high as he could; and this may represent the growth and continued circumnutation of an arched hypocotyl or epicotyl before it has reached the surface of the ground. As soon as the man felt himself at all free, he would raise the upper part of his body, whilst still on his knees and still wriggling; and this may represent the bowing backwards of the basal leg of the arch, which in most cases aids in the withdrawal of the cotyledons from the buried and ruptured seed-coats, and the subsequent straightening of the whole hypocotyl or epicotyl, circumnutation still continuing."

1050. The *cotyledons* not only share the movement of the caulicle, but they have also an independent movement which is greatly modified by slight changes in the surroundings. Freed from their seed-coats, they move upwards and downwards in very narrow ellipses, and at different rates in different plants. Generally their movement takes place only once in the course of the twenty-four hours: in Cassia tora, on an average, once in about two hours; in Oxalis rosea, once in about three hours; while in Ipomœa cœrulea Darwin observed the change of position to occur almost hourly. It is noticeable that the cotyledons may change the direction of their movement slightly at different times of the day, and may thus have a zigzag course during a part of the day and a nearly regular orbit during the rest.

1051. In some of the seedlings which have been examined with especial reference to their movements there is a joint or swelling to be detected at the base of the petiole. This is the equivalent of the pulvinus commonly found in Sensitive plants; changes in the position of cotyledons provided with such joints depend, as in the case of sensitive leaves, upon variations in the turgescence

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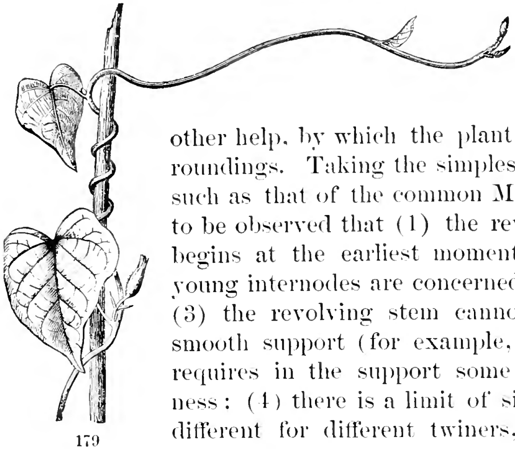
[1] Power of Movement in Plants, 1880, p. 106.

of the cells composing it, while changes in the position of cotyledons devoid of them are due to unequal growth.

1052. **Circumnutation of the young parts of mature plants.** By methods similar to those described in 1045, it can be shown that the growing extremities of stems, branches, leaves, and their numerous modifications possess the power of movement; in some instances exhibiting essentially the same phenomena as those presented by the parts of the seedling, while in other cases they show differences at an early stage. The most striking of these differences is that observed in twining stems. In this case there is a greatly increased amplitude of the orbit through which the tip of the stem passes. Although only a special case under a general class, twining stems may well receive a somewhat detailed description.

1053. **Twiners** are distinguished from proper climbers by the absence of any special organs, other than the stem itself, for grasping supports; climbers being provided with some sort of tendrils, or other help, by which the plant is held to its surroundings. Taking the simplest cases of twiners, such as that of the common Morning Glory, it is to be observed that (1) the revolving movement begins at the earliest moment; (2) only a few young internodes are concerned in the revolving; (3) the revolving stem cannot twine around a smooth support (for example, a glass rod), but requires in the support some degree of roughness: (4) there is a limit of size to the support, different for different twiners, beyond which it cannot be grasped by the revolving stem; (5) the direction of the revolution is not the same for all twiners; (6) the rate differs with the plant and with the surroundings.



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1054. In the early state of a twining plant the movements are in narrow ellipses; but with even a slight increase in size of the seedling, the transverse axis of the ellipse becomes greater, and soon the orbit is practically a circle.

1055. The number of internodes concerned in the twining movement is usually not more than three or four, and sometimes

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FIG. 179. Revolving shoot of Morning Glory.

only two are involved. The internodes below the seat of movement are rigid. The revolving is associated with growth, but the growth alone is probably not the sole cause of the movement.

1056. It is only the young internodes which are capable of spontaneous movement; but growth itself, unassociated with changes in the turgescence of the tissues upon the different sides, would not be sufficient to account for the movement. It must be remembered that the young stem possesses remarkable tensions, which are easily disturbed by slight internal as well as external causes. The increased turgescence of its cells upon one side, or their diminished turgescence on the other, or the action of both conjointly, followed as this is by an increased growth of the turgescent part, would produce sufficient change in the curvature of the stem to bring about the twining movement.

1057. When a twining stem comes in contact with a smooth support, it generally slides up the support, but fails to grasp it. The check which is given by a smooth support sometimes brings about a change of position in the revolving stem, which is thus described by Darwin: "When a tall stick was so placed as to arrest the lower and rigid internodes of Ceropegia, at the distance at first of fifteen and then of twenty-one inches from the centre of revolution, the straight shoot slowly and gradually slid up the stick, so as to become more and more highly inclined, but did not pass over the summit. Then after an interval sufficient to have allowed of a semi-revolution, the shoot suddenly bounded from the stick, and fell over to the opposite side or point of the compass, and reassumed its previous slight inclination. It now recommenced revolving in its usual course, so that after a semi-revolution it again came in contact with the stick, again slid up it, and again bounded from it and fell over to the opposite side. This movement of the shoot had a very odd appearance, as if it were disgusted with its failure, but was resolved to try again."[1]

1058. Many of the common twiners of temperate climates are able to twine round very slender supports, for instance a small cord, but are unable to twine round a post or trunk of a tree. This does not, however, appear to be wholly dependent upon the amplitude of the revolution. In tropical regions some of the twiners ascend trunks of immense size, but they are generally assisted by adventitious roots, etc.

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[1] Climbing Plants, 1875, p. 21.

1059. Any given twiner generally twines in one direction only; for instance, the hop moves in the direction of the hands of a watch, or to use another expression, follows the sun; the Morning Glory moves in an opposite direction. But there are some cases in which the direction of twining is reversed even during a comparatively short distance. In the tropics this reversal is said to be common.[1]

1060. The time required for the revolution of a twiner varies in different plants, and is by no means constant for the same plant at different stages of its development. In the case of the Morning Glory, the average time required for the revolution of a thrifty shoot under favorable conditions is about three hours.

1061. Twiners are affected somewhat by the amount of light received, but the revolving goes on uninterruptedly night and day. The increase of rate when a revolving shoot is approaching a window may be equal to a tenth, or somewhat more, of the whole period of the revolution. Such acceleration is very different for different plants.

1062. **Modified circumnutation.** The effect of the influence of light in increasing the rate of movement in a twiner is a good example of a large class of modified movements. These movements have already been considered in the chapter on "Growth," under the terms Heliotropism, Geotropism, etc., but must be again referred to in connection with the universal movement, circumnutation. When it is desirable to free any circumnutating part from the influence of a disturbing factor, for instance light, great care must be taken to avoid subjecting it to abnormal conditions such as result when a seedling is kept in the dark in order to free it from the influence of light on its movements. When so kept it undergoes changes of form with its blanching, and therefore little security is felt that all its behavior is normal. In the instance of green plants which demand light for their healthy activity the removal of disturbing factors is a task of considerable difficulty.

A part of the difficulty is removed by the use of some instrument by which the plants can be made to revolve slowly in a given plane, thus exposing the different sides successively to the action of the force. A simple form of this appliance is

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[1] Fritz Müller is quoted by Darwin as saying, that the stem of Davilla twines indifferently from left to right or from right to left; and that he once saw a shoot which had ascended a tree about five inches in diameter reverse its course.

known as the *clinostat*. It consists of a clock-work which carries a disc on which can be placed growing plants: by the revolution of this horizontal disc all parts are in turn given the same amount of illumination. If the clock-work is so arranged as to rotate a horizontal shaft to which a growing plant can be affixed, any one part of the plant will be exposed to the influence of gravitation in precisely the same manner and to the same extent as all other parts.

When circumnutation is plainly modified by unequal growth. striking disturbances are produced which have received much investigation. Among these cases are the changes of position which many peduncles undergo during the development of flowers and fruits. Although the extremity of the flower-stalk passes through its definite orbit, it is in some instances so affected by the greater growth of the upper side as to curve downwards, while a similar excessive growth on the under side will produce an upward curvature. De Vries, who has given much attention to these phenomena, has coined the adjectives *epinastic*, denoting curvature from growth on the upper side, and *hyponastic*, that from growth on the under side of an extending organ.

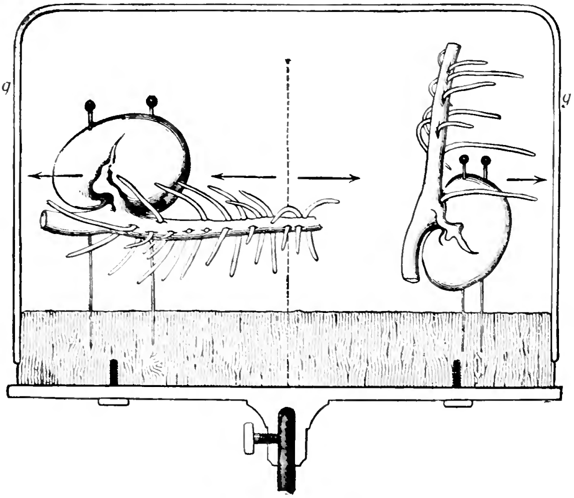

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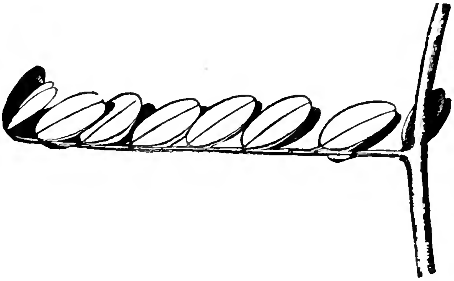
FIG. 180. Disc of a clinostat covered by a glass case *g*, and bearing two Windsor beans with primary and secondary roots.

1063. The ample revolving movement is not confined to stems, but is observed in some modified branches and leaves, for example in certain tendrils, etc. A single instance will serve to show the remarkable nature of the movement in the case of the tendrils of Echinocystis lobata, as described by Darwin:[1] "These are usually inclined at about 45° above the horizon, but they stiffen and straighten themselves so as to stand upright in a part of their circular course; namely, when they approach and have to pass over the summit of the shoot from which they arise. If they had not possessed and exercised this curious power, they would infallibly have struck against the summit of the shoot and been arrested in their course. As soon as one of these tendrils with its three branches begins to stiffen itself and rise up vertically, the revolving motion becomes more rapid; and as soon as it has passed over the point of difficulty, its motion coinciding with that from its own weight causes it to fall into its previously inclined position so quickly that the apex can be seen travelling like the hand of a gigantic clock."



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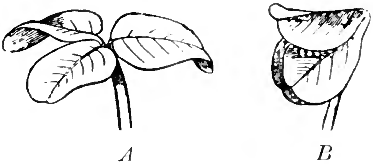

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1064. **Nyctitropic, or sleep, movements.** The foliar organs of many plants assume at nightfall, or just before, positions unlike those which they have maintained during the day. In many cases the drooping of the leaves at night is suggestive of rest, and the name given by Linnæus to this group of phenomena, namely, "the sleep of plants," seems appropriate. But in numerous cases the nocturnal position is one of obvious constraint, and considerable force has to be expended in lifting the leaf to

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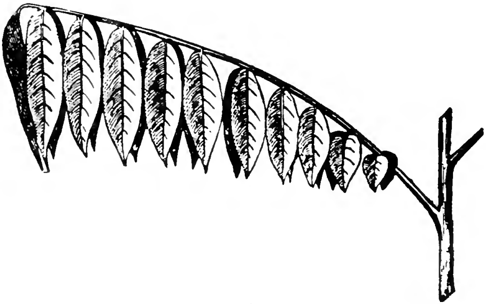
[1] Power of Movement in Plants, 1880, p. 266.

Fig. 181. Leaf of Coronilla rosea at night. (Darwin.)
Fig. 182. Leaf of White Clover. *A*, day position; *B*, night position. (Darwin.)

the new position. The diversity of positions can be only imperfectly indicated by the accompanying illustrations.

According to Pfeffer, the sleep-movements of leaves and of cotyledons depend upon increased growth on one side of the median line of the petiole and midrib, followed after a certain interval of time by a corresponding growth on the opposite side. Thus in ordinary leaves which droop at night the depression is produced by a slightly increased growth on the upper side, and the rise in the morning by a similar growth on the under side. But in the most striking cases there is a distinct apparatus at the base of the leaf-stalk, which accomplishes the same movement by simple turgescence of the opposite sides.



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The apparatus consists of an enlargement formed of cellular tissue in which there is often an appreciable difference between the character of the cell-walls on the upper and under side of the swelling. This swelling, known as the pulvinus, permits the movement to be

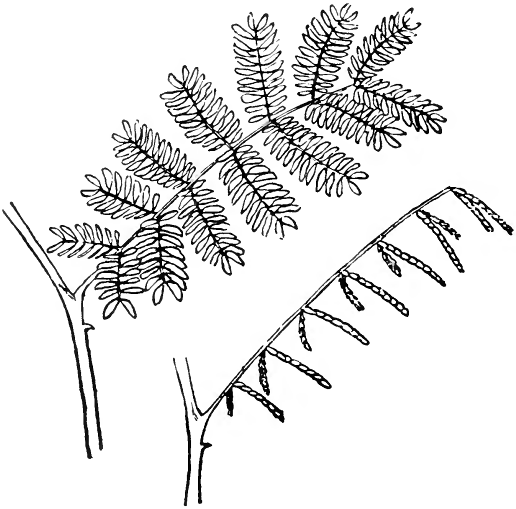

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FIG. 183 Leaflets of Averrhoa bilimbi at night. (Darwin.)

FIG. 184. Leaf of Acacia Farnesiana during the day and at night. (Darwin.)

continued long after the movements in young leaves destitute of such an apparatus have ceased.

1065. **The sleep-movements of cotyledons** are extremely diverse, but in general consist in an elevation of the tips, bringing the upper faces into proximity, and sometimes into contact. It may happen also that one or more of the early leaves developed from the plumule approaches the elevated cotyledons. Darwin has noted that in some cases the cotyledons of plants, with ordinary leaves which exhibit sleep-movements, may not change their position at night, except as they do in simple circumnutation.

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1066. **The utility of the sleep-movements** of leaves and cotyledons is believed to consist in protection from too great radiation during the night. Darwin has shown by simple and conclusive experiments that in the case of some plants this change of the position of leaves at the approach of a chilly night is a matter of life and death.

When leaves which naturally assume nyctitropic positions are pinned or otherwise kept from changing their position, and the plant is exposed to a temperature a little below freezing, under a clear sky, into which the radiation of heat must go on rapidly from the upper surface of the leaves, serious injuries result, the leaves becoming browned and even killed; whereas, leaves on

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FIG. 185. Desmodium gyrans. *A*, position during the day; *B*, position at night.

the same plant which are allowed to take the protective position, escape.

1067. **Sleep-movements of floral organs.** These are, in general, dependent, as Pfeffer has clearly shown, upon the alternate growth of the opposed surfaces. For instance in a crocus, the greater growth of the inner surface of the parts of the perianth will bring about an opening of the flower, whereas the greater growth of the outer surface will effect a closing.

Pfeffer's method of investigation is capable of application, provided one has a microscope which admits of being held with its tube horizontal. A perianth leaf is carefully detached without too much violence from the flower, and immediately placed in a small tube containing water, so that the expanded part may be brought within the field of the microscope. If fine lines are measured off upon its inner and outer surfaces in India ink, their gradually increasing distance from each other can be watched to good advantage. It can then be clearly seen that when the part curves outward it is owing to an increased growth upon the inner surface, and *vice versa*. That there is an antecedent turgescence is very likely, as has been repeatedly pointed out by De Vries and others. It is probable also that in a few cases the opening and closing are due to a temporary turgescence unaccompanied by much growth.

Changes in illumination and in temperature are sufficient to effect the alternations of growth and of turgescence in delicately constituted parts, where there is a balanced tension existing between the outer and inner tissues.

1068. **Times of opening and closing in the open air.** Under the ordinary conditions of an equable climate the times of opening and closing of the flowers of a given plant do not vary widely. Hence it is possible to construct a floral clock which shall mark the hours with tolerable regularity. The dial at Upsala, Sweden, suggested by Linnæus, and that designed for Paris by De Candolle,[1] are approximately correct; but in a climate having the sharp and sudden differences of heat and of moisture which characterize eastern North America such floral clocks are not successful.

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[1] The following list from De Candolle's Physiologie gives the hours of the opening of certain flowers in Paris: —

Ipomœa purpurea	2	A. M.
Calystegia sepium	3–4	"
Matricaria suaveolens	4–5	"

1069. **The Telegraph plant.** The most surprising instance of rapid spontaneous movement is that which is exhibited by the lateral leaflets of Desmodium gyrans. Each complete leaf of Desmodium consists of a large terminal leaflet and two little lateral leaflets. At nightfall the terminal leaflets sink vertically, and the petioles are somewhat raised, so that the terminal leaflets are much crowded together upon the stem (see Fig. 185.) The cotyledons do not have this nyctitropic movement, but the first true leaf sleeps just as do the older ones.

The lateral leaflets do not fall at night, but at the temperature of 36 to 38° C., or even somewhat higher, keep up, night and day, an irregular jerking movement, which has been compared to the ticking of the second-hand of a watch (or, formerly, to the movements of the arms of a Semaphore Telegraph). The tip of the moving leaflet passes


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FIG. 186. Desmodium gyrans.

Papaver nudicaule and most Cichoriaceæ	5	A. M.
Convolvulus tricolor	5–6	"
Convolvulus siculus	6	"
Species of Sonchus and Hieracium	6–7	"
Species of Lactuca	7	"
Anagallis arvensis	8	"
Calendula arvensis	9	"
Arenaria rubra	9–10	"
Mesembryanthemum nodiflorum	10–11	"
Ornithogalum umbellatum	11	"
Passiflora cœrulea	12	M.
Pyrethrum corymbosum	2	P. M.
Silene noctiflora	5–6	"
Œnothera biennis	6	"
Mirabilis Jalapa	6–7	"
Lychnis vespertina	7	"
Cereus grandiflorus	7–8	"

through its elliptical orbit in a period of from half a minute to a minute or more, the time varying greatly according to the external conditions, but being nearly uniform under uniform high temperature. The lateral leaflets move independently of one another, one sometimes passing downwards while the other is ascending, but there is no distinct relation between them.

At the base of the terminal leaflet, the base of the lateral leaflets, and the base of the main petiole, are pulvini, to changes in which the several movements are due.

1070. **The cause of autonomic movements not fully known.** As to the cause of the periodic changes in turgescence and associated growth which give rise to "spontaneous" movements, little is at present known. The fact that in the naked protoplasm of the plasmodium of the Myxomycetes the sap cavities exhibit a rhythmical pulsation which is thought to be dependent upon variations in the imbibition power of the protoplasm for water, throws little light upon the ultimate cause which underlies variable turgescence in one case and variable pulsation in the other. Although variations in turgescence and associated growth are everywhere observable in young and still parts of plants, in some instances similar phenomena can be observed, as we have just seen, in specialized organs which are no longer capable of growth.

1071. DeVries[1] calls attention to the fact that organic acids or their salts, as they are formed in tissues, have a marked effect upon the turgescence of the cells composing the tissue. If these compounds were produced first in the cells on one side of a shoot or other motile organ, and then in the cells next to these, and so on, the phenomena of circumnutation would be exhibited. Its cause will probably be found in chemical processes which cause the osmotic power of the cell-contents to vary.[2]

1072. **Sensitiveness.** By this is meant the capacity to react against an irritation; thus, the root is said to be sensitive to moisture, some leaves to light, etc. But it is usual to employ the term in a more restricted signification; following Darwin's cautious definition, "a part or organ may be called sensitive, when its irritation excites movement in an adjoining part."[3] The irritant may be shock, prolonged contact, a light touch, or a chemical agent.

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[1] Botanische Zeitung, 1879, pp. 830, 847, and in an independent communication.

[2] Pfeffer: Periodischen Bewegungen (1875).

[3] Power of Movement in Plants, 1880, p. 191.

1073. It has been shown (1024) that young shoots react, although somewhat sluggishly, against mechanical shock, their change of form or direction depending on the character or direction of the blows received. In certain delicate tissues, especially those which possess much simplicity of structure, change of form and of direction may be produced in response to comparatively slight mechanical or chemical irritation. It is to these that the term *sensitive tissues* is properly applied.

1074. **Sensitiveness of roots.** The tip of the caulicle is generally sensitive to contact and to caustics. There are, however, great differences in the degree of sensitiveness; in some cases slight contact being sufficient to cause reaction, while in others the contact must be prolonged and accompanied by direct pressure. If the caulicle with its unformed root is placed under conditions where growth can take place with great rapidity, the sensitiveness is much impaired and sometimes is wholly lost; it is partially lost also when the caulicle grows slowly, or is forced to grow out of season. Under natural conditions and at a normal rate of growth the tip is sensitive for about one twentieth of an inch. If a piece of caustic is applied to the tip (not more than 1.5 mm. from the very end), the caulicle will curve away from the irritated side. The reaction is as plainly seen in those cases where the caulicle does not elongate, but where the root itself descends.

1075. The length of the portion of these organs which *reacts* is about ten millimetres. The time of reaction varies for different plants, being sometimes in five hours, and, according to Darwin, almost always within twenty-four hours.

1076. "The curvature often amounts to a rectangle; that is, the terminal part bends upwards until the tip, which is but little curved, projects almost horizontally. Occasionally the tip, from the continued irritation of the attached object, continues to bend up until it forms a hook with the point directed towards the zenith, or a loop, or even a spire. After a time the radicle apparently becomes accustomed to the irritation, as occurs in the case of tendrils; for it again grows downwards, although the bit of card or other object may remain attached to the tip."[1]

1077. The tip of the radicle has been shown (1046) to be constantly circumnutating. By this movement the sensitive tip is brought into contact with different sides of minute crevices in

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[1] Power of Movement in Plants, 1880, p. 193.

the soil,[1] and "as it is always endeavoring to bend to all sides, it will press on all sides, and will thus be able to discriminate between the harder and softer adjoining surfaces . . . consequently it will tend to bend from the harder soil, and will thus follow the lines of least resistance."[2]

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[1] Darwin: Power of Movement in Plants, p. 197.

[2] The two following passages should be carefully studied by the student, since they embody in a few words Darwin's summary of most of the results of his experiments upon radicles. Both passages are from the "Power of Movement in Plants," 1880: —

"We see that the course followed by a root through the soil is governed by extraordinarily complex and diversified agencies, — by geotropism acting in a different manner on the primary, secondary, and tertiary radicles, — by sensitiveness to contact, different in kind in the apex and in the part immediately above the apex, and apparently by sensitiveness to the varying dampness of different parts of the soil. These several stimuli to movement are all more powerful than geotropism, when this acts obliquely on a radicle which has been deflected from its perpendicular downward course. The roots, moreover, of most plants are excited by light to bend either to or from it; but as roots are not naturally exposed to the light, it is doubtful whether this sensitiveness, which is perhaps only the indirect result of the radicles being highly sensitive to other stimuli, is of any service to the plant. The direction which the apex takes at each successive period of the growth of a root ultimately determines its whole course; it is therefore highly important that the apex should pursue from the first the most advantageous direction; and we can thus understand why sensitiveness to geotropism, to contact, and to moisture, all reside in the tip, and why the tip determines the upper growing part to bend either from or to the exciting cause. A radicle may be compared with a burrowing animal such as a mole, which wishes to penetrate perpendicularly down into the ground. By continually moving his head from side to side, or circumnutating, he will feel any stone or other obstacle, as well as any difference in the hardness of the soil, and he will turn from that side; if the earth is damper on one than on the other side, he will turn thitherward as a better hunting-ground. Nevertheless, after each interruption, guided by the sense of gravity, he will be able to recover his downward course and to burrow to a greater depth" (p. 199).

"We believe that there is no structure in plants more wonderful, as far as its functions are concerned, than the tip of the radicle. If the tip be lightly pressed or burnt or cut, it transmits an influence to the upper adjoining part, causing it to bend away from the affected side; and, what is more surprising, the tip can distinguish between a slightly harder and softer object, by which it is simultaneously pressed on opposite sides.

"If, however, the radicle is pressed by a similar object a little above the tip, the pressed part does not transmit any influence to the more distant parts, but bends abruptly towards the object. If the tip perceives the air to be moister on one side than on the other, it likewise transmits an influence to the upper adjoining part, which bends towards the source of moisture. When the tip is excited by light (though in the case of radicles this was ascertained in only a single instance) the adjoining part bends from the light; but when

1078. **Sensitiveness of stems and branches.** Under ordinary conditions even twining stems are not sensitive to slight mechanical irritation. The reactions to moisture, light, gravitation, etc., have been already noticed, and it is now intended to call attention to the extraordinary sensitiveness of certain tendrils, some of which are modified branches, while others are modified leaves or parts of leaves.

1079. **Tendrils** circumnutate, and by their revolving movement reach out for a proper support. Moreover, they are produced on the young and circumnutating extremities of shoots, so that two modes of revolution are frequently to be observed simultaneously. But in this revolving movement the tendrils are prevented from becoming entangled with the rest of the shoot. The manner in which this is done is thus described: "When a tendril, sweeping horizontally, comes round so that its base nears the parent stem rising above it, it stops short, rises stiffly upright, moves on in this position until it passes by the stem, then rapidly comes down again to the horizontal position, and moves on so until it again approaches and again avoids the impending obstacle."[1]

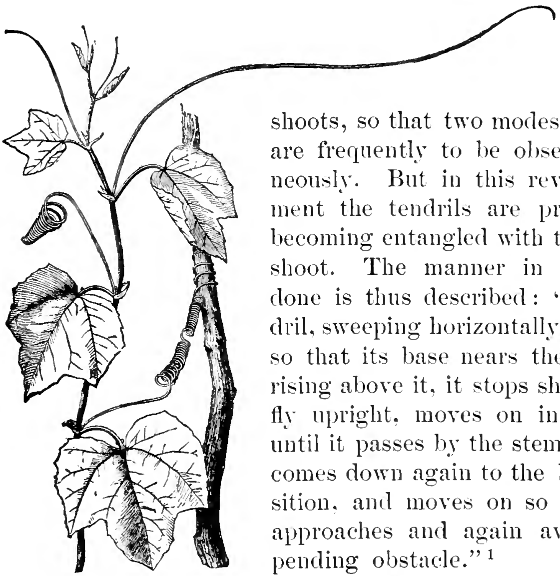

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Fig. 187. Shoot of Passiflora, showing tendrils.

1080. When a light thread is placed upon a long revolving tendril of Passiflora, Echinocystis, or

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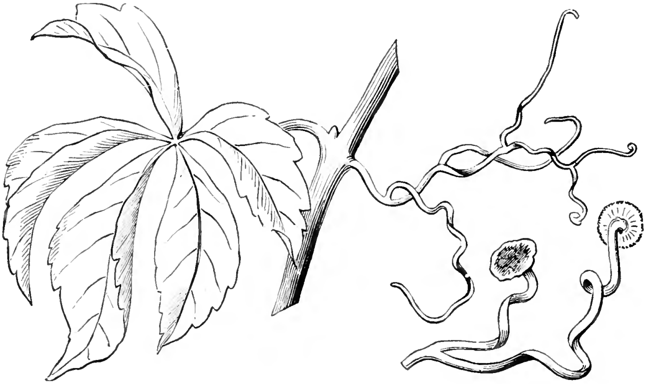
excited by gravitation the same part bends towards the centre of gravity. In almost every case we can clearly perceive the final purpose or advantage of the several movements. Two, or perhaps more, of the exciting causes often act simultaneously on the tip, and one conquers the other, no doubt in accordance with its importance for the life of the plant. The course pursued by the radicle in penetrating the ground must be determined by the tip; hence it has acquired such diverse kinds of sensitiveness. It is hardly an exaggeration to say that the tip of the radicle thus endowed, and having the power of directing the movements of the adjoining parts, acts like the brain of one of the lower animals; the brain being seated within the anterior end of the body, receiving impressions from the sense organs, and directing the several movements" (p. 572).

[1] Gray: How Plants Behave, 1872, p. 18.

Sicyos, a curvature soon takes place in the direction of the contact. If the plant is in a vigorous condition and the tendril is young, a slight touch is generally sufficient to cause immediate flexion. If a solid object, for instance a staff, is placed in contact with such a tendril, the bending and coiling takes place at once, and thus the organ is brought into close apposition with the support.

1081. As soon as the tendril has coiled around its support, a striking phenomenon is observed in the portion between the shoot and the support: it begins to twist, throwing the whole thread into a double coil, a part of which winds one way and the rest another. There can be no doubt that this comes from the action of the same force which causes the revolution in the tendril before it becomes attached to the support, and the further exercise of this force must necessarily produce two coils running in opposite directions. After the tendril has made fast to its support, its structure begins to change in a remarkable manner, becoming much firmer and more elastic than before, — a provision adapting it admirably to resist sudden strains upon the main shoot from gusts of wind.



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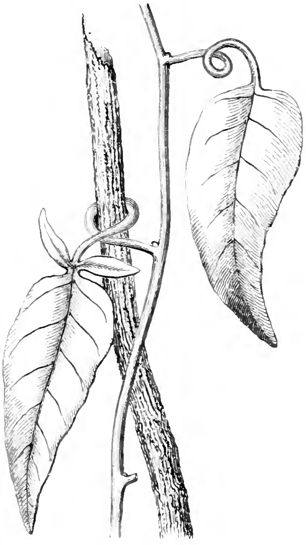
1082. But if the tendril in its revolution has failed to come in contact with any proper support, it is thrown into a single coil, which runs from the extremity of the tendril, and extends for a short distance, perhaps half the whole length of the organ. Sometimes, however, it simply becomes flaccid.

FIG. 188. Ampelopsis quinquefolia, or Virginia creeper.

1083. In some cases tendrils are not sensitive to contact, but are distinctly apheliotropic, turning away from the light, and in this way securing for the plant an adequate mechanical support upon some wall or the like. Grape-vines and Virginia creeper furnish good examples of such tendrils. The branches of the tendrils of the grape-vine sometimes clasp around a slender support, somewhat in the same way as an object would be grasped by a thumb and finger.

The much-branched tendrils of species of Ampelopsis are also apheliotropic; but when the tips of the branches of the tendrils come in contact with a wall, they become expanded into flat discs which cling to the surface.

1084. **Sensitiveness of petioles.** This can be easily examined in the common climbing species of Clematis, in Solanum jasminoides, etc. The leaves circumnutate and, in the case of compound leaves, the separate leaflets also. When young the sides of the petioles are sensitive to touch, bending towards where the pressure or compact is. Shortly after clasping the support by means of this bending the petioles increase in thickness, become stronger and tougher than before, and sometimes take on a structure suggestive of a rigid branch. In Gloriosa the sensitiveness is very marked in the leaf-tips, but only on the under surface of the prolonged thread-like extremity.



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1085. **Sensitiveness of leaf-blades.** The fly-trap of Dionæa (considered by some an appendage to the proper leaf-blade) is exquisitely sensitive to any touch upon the hairs which grow on the faces of the trap. As soon as these are touched the trap instantly closes, and the same effect follows a slight touch on the median line. A cross-section through the leaf shows that the parenchyma is thin-walled. The leaf of the small water-plant Aldrovanda has likewise been shown to be sensitive.

FIG. 189. Solanum jasminoides.

1086. The leaflets of numerous plants exhibit a peculiar degree of sensitiveness even to a slight touch. Among these are several species of Mimosa and Oxalis. The plant which has received the fullest investigation is the easily cultivated

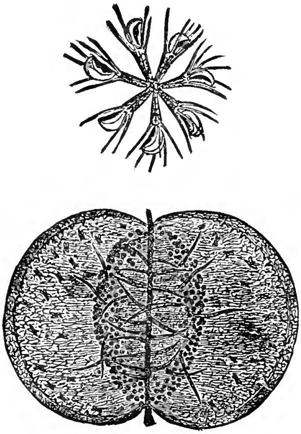
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Fig. 190. Aldrovanda vesiculosa; the lower illustration shows the expanded leaf much enlarged.

1087. *Mimosa pudica* (the Sensitive plant). This has compound leaves consisting of four long leaflets, each of which is divided into numerous minor leaflets arranged in pairs. At the base of each leaflet, and also at the base of the petiole, there is a pulvinus, composed of peculiar cells. On the upper half of the pulvinus these are thicker-walled than on the lower; most of them contain roundish globules made up of a strong solution of tannin in water, surrounded by a film of some albuminoid matter. These globules are not, however, of any significance as concerns the motility, since they are found in the parenchyma of the bark of some ligneous plants (see 953).

1088. When a fully spread leaf is touched at its extremity the many leaflets successively close in pairs, the upper surfaces approaching and the tips falling somewhat forward; the four branches of the leaf then draw near each other, and the main petiole inclines downwards and finally droops passively at the joint. The recovery from this position of collapse takes place in a few minutes, generally in about a quarter of an hour.

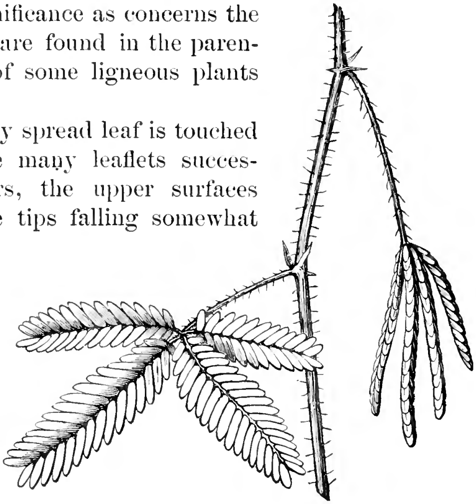
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Fig. 191. Mimosa pudica.

1089. If an irritant is applied to a single leaflet, the opposite one may be the only other affected; or, if the effect is more pronounced, all the leaflets on a single division of the leaf may be closed without affecting any on the other branches. But if a still sharper impulse is given, not only will all the leaflets on a single leaf close, but other leaves on the plant may be affected. Thus it is possible by applying a hot needle to a single leaflet to affect all those on a small plant. A drop of strong sulphuric acid acts in the same way.[1]

When a leaf of Mimosa is separated from its plant by a sharp cut through its pulvinus, and is at once placed in a saturated atmosphere, it soon recovers its normal expanded condition; if now it is touched the leaflets will collapse as usual, and at the moment of closing a drop of water can be seen exuding from the cut surface. According to Pfeffer it is possible to observe that the water comes from the parenchyma of the lower half of the pulvinus.[2]

1090. According to Bert,[3] who made use of a thermo-electric apparatus, the pulvinus of a leaf of Mimosa in its normal condi-

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[1] For a study of the transmission of the shock, see Pfeffer, Pringsheim's Jahrbücher, ix., 1873, p. 308.

Some of the effects produced by irritants upon the hairs of certain insectivorous plants have been already described. The phenomena of *aggregation* then alluded to must be now treated more in detail. It is described by Pfeffer in the following words: "Suddenly the contents of the cell acted on become clouded by a separation of minute particles which aggregate to form masses. These masses consist essentially of albuminous matters, which, from their collecting the coloring substance in the cell-sap, become tinged. The whole process of aggregation takes place in the cell-sap."

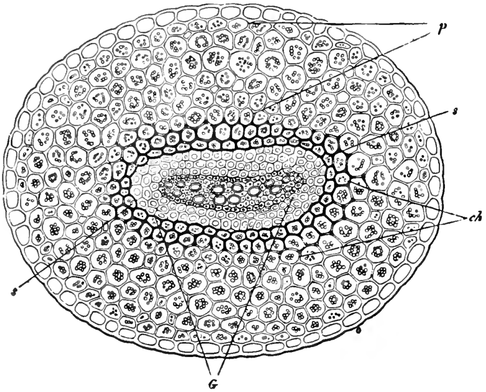
Pfeffer points out the curious fact that while ammonic carbonate, without any other irritant, will cause this aggregation, acetic acid will make it disappear.

Such changes as aggregation and variations in turgescence are connected in some way, not yet understood, with the imbibition power of protoplasm for watery fluids. The mechanical or chemical irritants which temporarily diminish the capacity of protoplasm for retaining within the cell the maximum quantity of water will produce a distinct effect upon the tension of the cell-wall, and result in a change of its size or form, or both. The irritation thus caused can be transmitted to a distant part. The intimate relations which exist between the young cell-wall and the protoplasmic lining must not be overlooked in any consideration of the subject of sensitiveness in plants. Lastly, the continuity of protoplasm in many mobile and sensitive organs must be borne in mind in the consideration of this subject.

[2] Pflanzenphysiologie, ii., 1881, p. 237. See also Pfeffer's Physiologische Untersuchungen, 1873, p. 32.

[3] Comptes Rendus, lxix., 1869, p. 895.

tion is always slightly cooler than the rest of the petiole, but upon the movement from irritation it rises in temperature; not enough, however, to account for the raising of so considerable a weight as that of the leaf.



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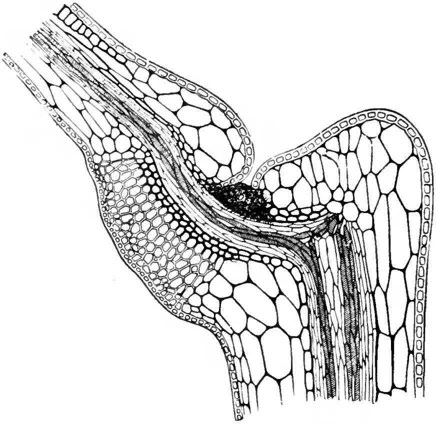
1091. Some physiologists have regarded the sensitiveness of the pulvinus of the Sensitive plant and of other motile parts as residing chiefly if not wholly in the cell-wall, while others have thought that it resided in the contractile protoplasm. It is now generally held to be due to some sudden variation in the osmotic power of the protoplasm, particularly in its peripheral portion in contact with the cell-wall, by which the turgescence of the cell is suddenly changed.[1]



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1092. If a plant with motile leaves is kept in darkness for a day or so, even if the temperature is favorable to motion, its power of movement is either greatly impaired or for a time wholly lost. A diminished amount of light is sufficient to produce the same effect in the case of the Sensitive plant.

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[1] Compare Hofmeister: Die Lehre von der Pflanzenzelle, 1867, p. 300; Brücke: Archiv für Anatomie, Physiologie, und wiss. Medicin, 1848, p. 434; Unger: Botanische Zeitung, 1862, p. 113; 1863, p. 349.

FIG. 192 Transverse section of the motile organ of a leaflet of Oxalis carnea. (Sachs.)

FIG. 193. Vertical section through the motile organ of a leaflet of Oxalis carnea. (Sachs.)

Sachs has given the name Phototonus to the normal motile condition resulting from alternation of day and night. "A plant in this condition, if placed in the dark, will remain for some time (hours or even days) in a state of phototonus, which then disappears gradually; the plant is therefore under normal conditions in a state of phototonus even during the night. In the same manner a plant which has become rigid in continued darkness retains its rigidity for some time (hours or even days) after being exposed to light. The two conditions therefore pass over into one another only slowly."

1093. Temporary rigidity is produced in the case of the Sensitive plant by an exposure to a temperature of 15° C. The same effect is produced by a temperature above 50° C., according to Bert's observations at about 60° C. It is stated by him that the sensitiveness of Mimosa is destroyed by exposure to a green light, while plants placed under bell-jars of the following colors remained healthy: white, red, yellow, blue, and violet.[1]

1094. **Sensitiveness of stamens.** No better illustration of this is afforded than that given by stamens of the common Barberry. The six stamens lie curved under the arching petals, but if a filament is lightly touched it is jerked suddenly forward, bringing the anther into apposition with the pistil.

1095. The filaments of certain Compositæ are sensitive. The case of the common Chicory has been thus described: The anthers are conjoined to form a tube supported upon five disconnected filaments which are at first more or less curved outwards. If the filaments in this condition are lightly touched they instantly straighten, carrying the anther-tube up a little higher, and thus bringing the pollen all along the style which is enclosed. After a short time they resume their former curved condition, retracting the anther-tube to the place which it occupied before. It is to be observed that the irritation of a single filament excites only that one, and thus the tube of anthers may be pushed over to one side for a few minutes, again recovering itself after a little while.

1096. Sparmannia Africana has a cluster of beaded filaments surrounding the pistil and variously intermingled with the stamens. When these are touched lightly they open out from the centre with considerable rapidity, and remain thus expanded for a certain period, after which they revert to the closed position. Somewhat the same phenomenon is to be observed in

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[1] Comptes Rendus, lxx., 1870, p. 339.

species of Portulaca, where the stamens, upon contact, move outwards.

1097. The gynandrous style of Stylidium is curved downwards; when it is lightly touched it suddenly flies to the other side of the flower, although sometimes it merely straightens itself.

Sensitive lobes of the style or stigma are possessed by Mimulus and some other Scrophulariaceæ,[1] by Martynia, and some allied plants.

1098. In all the foregoing cases the sensitiveness is greatest when the plants, or their sensitive parts, are kept at a tolerably high temperature. Sachs has shown that the most favorable temperature for Mimosa movements is about 36° or 37° C.

1099. **Effects of anæsthetics upon sensitiveness in plants.** When a young plant of Mimosa is placed under a bell-jar in which a sponge wet with chloroform or an equivalent anæsthetic has filled the confined atmosphere with its vapor, some of the leaflets droop and remain so, while others retain their normal position. But after a while the leaflets will be found to have lost all power of reacting to a touch; in short, they have become insensitive. The same effect is observed in the case of Barberry stamens. Its explanation is looked for in the changed relation of the sensitive cells to water when they are subjected to the influence of an anæsthetic.

1100. **Plants possess no nervous system.** That sensitive plants must have nerves, or their equivalent, for the recognition of impressions and the transmission of their influence to a somewhat distant point was formerly held by many writers, but this opinion is not now entertained by any physiologist.[2]

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[1] See Heckel's Memoir, Comptes Rendus, lxxix., 1874, p. 702.

[2] "Finally, it is impossible not to be struck with the resemblance between the foregoing movements of plants and many of the actions performed unconsciously by the lower animals. With plants an astonishingly small stimulus suffices; and even with allied plants one may be highly sensitive to the slightest continued pressure, and another highly sensitive to a slight momentary touch. The habit of moving at certain periods is inherited both by plants and animals; and several other points of similitude have been specified. But the most striking resemblance is the localization of their sensitiveness, and the transmission of an influence from the excited part to another, which consequently moves. Yet plants do not of course possess nerves or a central nervous system; and we may infer that with animals such structures serve only for the more perfect transmission of impressions, and for the more complete intercommunication of the several parts" (Darwin: Power of Movement in Plants, 1880, p. 571).

CHAPTER XIV.

REPRODUCTION.

1101. In scientific as well as popular language the term *individual* is commonly applied to each and every plant; but if by individual is meant an organism incapable of subdivision without loss of its identity, the term as applied thus to the higher plants is obviously a misnomer. It has been shown both in Volume I. of this series,[1] and in Part I. of the present volume,[2] that under certain circumstances any of the higher plants may be separated into parts, each of which may afterwards lead an independent existence. Thus buds may be severed from the parent plant and soon establish themselves as independent organisms, capable of increase in size, and becoming sooner or later distinguishable in no wise from the stock from which they came. But there are serious difficulties in the way of regarding these separable buds as true individuals:[3] each bud is the promise of a branch, and consists of parts which, under certain conditions, may be separated from each other. In fact, the vegetable individual is not reached in such mechanical subdivision until we come to the cells of which all the parts are composed. Nor do these satisfy completely the definition of an individual, since in exceptional cases the cell itself may spontaneously divide into viable parts.[4]

1102. **In plants, individuality is more or less completely merged in community.** Under normal conditions the separable parts, while still attached to their common stock, co-operate for the common good. If separated under favorable conditions they in their turn become stocks in which are combined congeries of similar separable parts, or, in other words, become individual plants, in the ordinary acceptation of the term. For instance, the tuber of the potato, which is the thickened extremity of an underground branch, possesses a certain number of buds, each

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[1] Page 316. [2] Pages 152, 162. [3] Volume i. p. 316.

[4] Such a phenomenon is seen in the formation of swarm-spores (or zoögonidia) from a terminal cell of Achlya.

of which may, in suitable soil, give rise to a thrifty plant: the new plants will in their turn produce new tubers likewise with buds, and these again new plants, and so on in unlimited succession. Nevertheless, the divisible organisms are for our present purpose conveniently termed vegetable individuals.[1]

1103. Plants of the higher grade (Phaenogamous plants) are propagated either by buds or by seeds. In the former case, a portion of the axis with incipient leaves is separated from the parent; in the latter case, a new structure (the embryo), capable of independent existence, is formed by means of a special apparatus, — the flower. In the flower, two sets of sexual organs, the stamens, constituting the andrœcium, and the pistils, constituting the gynœcium, produce by their conjoint action an embryo, or undeveloped plant, within the seed.

Reproduction by buds is non-sexual or asexual; that by the formation of an embryo is sexual.

1104. Non-sexual reproduction (Agamogenesis) can be traced through all classes of plants, — from the higher, where it takes place through proper buds, down to the very lowest, where it takes place by a single cell dividing spontaneously to form two or more separated individuals.

1105. Sexual reproduction (Gamogenesis) likewise can be traced through all classes of plants except the very lowest, where it has not as yet been demonstrated to exist. As the series is followed from above downwards, the flower gives place to other structures, and the seed is replaced by simpler bodies, known as spores.

FERTILIZATION IN ANGIOSPERMS.

1106. Flowering plants are naturally divided into Angiosperms and Gymnosperms: the former are distinguished by the possession of a closed ovary in which the ovules are contained. The latter have no closed ovary, and hence the ovules are naked. A part of the reproductive apparatus is simpler in Gymnosperms than in Angiosperms; but owing to certain practical difficulties in the treatment of microscopic material, the demonstration of the reproductive process is less easy in the former than in the latter. It is proposed, therefore, to begin with an examination of the reproductive process, or fertilization, of Angiosperms.

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[1] The view has been held by some that all the derivatives from one seed, whether united or separated, constitute collectively a single individual.

1107. Three subjects must be briefly reviewed before entering upon the study of the process itself; namely, the *pistil*, the *ovule*, and the *pollen-grain*. For all details regarding particulars of form and special morphological relations, pages 249–285 of Volume I., and Chapter IV. of the present volume may be consulted.

1108. **The angiospermous pistil** (see Fig. 196) consists of a closed *ovary* containing the ovules, which is generally prolonged into a slender organ known as the *style*. Either some portion of the style, or, when this is wanting, some portion of the ovary, is furnished with a peculiar secreting surface known as the *stigma*. The manifold shapes of ovary, style, and stigma have been sufficiently described in Volume I., and the microscopic structure of each has been examined in a general way in Part I. of the present volume. From what was there said, it will be remembered that the form and structure of pistil and stamens have intimate relations to the transfer of pollen and its reception by the stigma.

1109. **The stigmatic secretion.** The surface from which this exudes may exist as an expanse of considerable extent, or it may have the form of single or double lines, or be reduced even to a mere point. The extent of the stigmatic surface bears a fixed relation to the number of ovules in the ovary.

At a certain period in the development of the flower, the stigma, which up to that time may have been apparently free from moisture, becomes covered with a glutinous secretion of a saccharine nature. At this period, known as that of maturity, the stigma is from its stickiness likely to catch and retain upon its surface any pollen which may fall thereon. The secretion is generally slightly acid[1] in reaction, and is as variable in the amount of sugar which it contains as ordinary nectar.

1110. The pollen-grains of angiosperms when set free from the cells in which they are produced may become completely isolated (simple grains), or they may remain firmly coherent in clusters of four (Typha, Rhododendron, etc.), eight, sixteen, thirty-two, or even, as in some species of Acacia, sixty-four ("compound grains"). In many Orchidaceæ the grains are more or less compactly fastened together into masses by a glutinous matter forming pollinia, and much the same grouping into masses occurs in Asclepiadaceæ.

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[1] Van Tieghem: Traité de Botanique, 1884, p. 850.

1111. **Structure of pollen-grains.**[1] The grains consist of single cells having a firm membrane and heterogeneous contents. The membrane is rarely single (as in Zostera), being generally composed of two coats, — an outer, the *extine* (called *exine* by Schacht), and an inner, the *intine*. The extine may be smooth, but it is frequently beset with protuberances of some kind, points, prickles, or other sculpturings, which may be characteristic of genera or even larger groups. It is also provided generally with one or more partial or complete perforations, which are of course fully closed by the intine which is pressed up against them. The number of these perforations is constant in certain groups of plants: for instance, one in most monocotyledonous plants; two in Ficus, Justicia, Beloperone; three in Onagraceæ, Geraniaceæ, Compositæ; four to six in Impatiens, Ulmus, and Alnus; many in Nyctaginaceæ, Convolvulaceæ, Malvaceæ, and some Caryophyllaceæ. Under the action of concentrated sulphuric acid the intine is destroyed, while the extine generally remains unchanged except in color.[2]

When the pollen of Thunbergia is acted on by strong sulphuric acid, the destruction of the intine permits the extine to uncoil as a band. In no case did Schacht detect any perforation of the intine.

1112. **The contents of a pollen-grain** are (1) protoplasmic matter; (2) granular food materials, such as starch, oil, and, according to Schacht, inulin; (3) dissolved food matters, sugar and dextrin. These heterogeneous contents form what was formerly called the fovilla.

In the granular protoplasmic matter of pollen-grains it is possible to demonstrate the existence of a nucleus, and in some cases two nuclei can be made out distinctly. It is considered well established[3] that the single nucleus which exists in the simple grain at the period of its separation from the mother-cell divides in most cases into two nuclei of unequal size. The larger of the two fragmental nuclei remains with no change; while the smaller may become partitioned off from the rest of the cell either by a true cell-wall or by a peripheral film of protoplasm, and may later divide and form a group of two or four minute cells.

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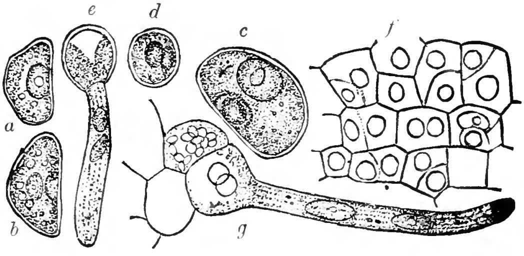
[1] These details are summarized chiefly from Schacht's exhaustive treatise on the subject in Pringsheim's Jahrbücher, ii., 1860, p. 109.

[2] In some cases a double membrane can be shown in the extine, for instance Œnothera, where the extine separates into a true extine and an *intextine*.

[3] Strasburger: Ueber Befruchtung und Zelltheilung, 1878. See also Quarterly Journal of Microscopical Science, 1880, p. 19.

1113. The pollen-grains of many plants burst when placed in water, and the fovilla escapes as a slightly coherent mass which soon becomes more diffused and allows the finer granules to pass into the water, where they immediately exhibit the Brownian movement, common to all minute particles suspended in a liquid.[1]

1114. If pollen-grains are placed in a solution of sugar instead of in pure water, they will increase somewhat in size; and in a few hours, if the specimen is kept at the right temperature, there will appear at some point of the surface of each grain a minute tube, which by great care can be cultivated in a proper medium until it attains a length of several millimeters.[2]



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1115. The pollen-grains of Tulipa Gesneriana emit their tubes in a 1 to 3 per cent solution of cane-sugar; the following require a somewhat stronger syrup: Leucojum æstivum and Narcissus poeticus, 3 to 5 per cent; most orchids, 5 to 10 per cent; Convallaria majalis, 5 to 20 per cent; Iris sibirica, 30 to 40 per cent.[3]

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[1] For an extended account of the speculations once based upon the occurrence in water of motion of the particles of the fovilla, the reader should consult Meyen: Pflanzenphysiologie, iii., 1839, pp. 192 *et seq.*; and also the remarkable treatise by Robert Brown.

[2] Schleiden states that pollen-grains which come accidentally in contact with nectar readily send out tubes; and that we often find at the base of the flower a whole mass of confervoid web, which consists of entangled pollen-tubes emitted in this manner (Principles of Scientific Botany, 1849, p. 408).

[3] Strasburger: Das botanische Practicum, 1884, p. 511.

FIG. 194. *a*, young pollen-grain of Allium fistulosum, before its division; *b*, after the division of the nucleus; *c*, after the division of the protoplasm; *d*, young pollen-grain of Monotropa Hypopitys divided; *e*, same emitting its tube, into which the two nuclei pass; *f*, coalescent grains of the pollen of Platanthera bifolia during their division; *g*, formation of the pollen-tube of Orchis mascula, into which the two nuclei pass. (Strasburger.)

1116. When a pollen-grain is deposited upon a fitting stigma,[1] at the period when the stigmatic secretion is sufficiently abundant, it increases somewhat in size, and soon[2] a tube,[3] sometimes more than one, is thrust forth and passes immediately into the loose tissue of the stigmatic surface. The tube consists of a protrusion of the intine, and its place of emerging is at some one of the perforations of the extine. In some instances the wall separating the larger and the smaller fragments of the original nucleus of the pollen-grain becomes absorbed, and then the two nuclei make their way into the tube as it is prolonged. During its descent the pollen-tube is slender, of about the same calibre throughout, and has extremely thin walls. It extends through the conducting tissue of the style, being nourished by the nutrient matter secreted from the cells of that tissue, until it at last reaches the cavity of the ovary.

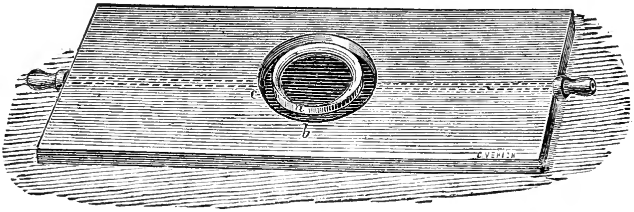

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FIG. 195. Apparatus for cultivating pollen-grains, etc. The object is placed on the under side of a glass cover over the circle at *a*. If necessary, air can be drawn through the tube. A simpler contrivance may be made from a piece of moist pasteboard.

1117. According to Capus,[4] the extent of the stigmatic surface bears a definite relation to that of the conductive tissue of the style, one surface being in fact a mere expansion of the other; and the volume of the conductive tissue of the style is governed by the number of ovules which are to be fertilized. Thus, in a

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[1] An interesting account of the artificial fertilization of certain plants of the Poppy family after removal of the stigmas is given by Hooker in "The Gardeners' Chronicle," 1847. It is not known that the experiments have yet been repeated.

[2] According to Gärtner, the emission of the pollen-tube begins in some cases in half a minute after the pollen has been applied to the stigma ; but in some others, as in Mirabilis Jalapa and in the Malvaceæ, it takes from 24 to 36 hours.

[3] Amici, in 1822, appears to have been the first to detect the pollen-tube. His earliest observations were made upon Portulaca oleracea.

[4] Annales des Sc. nat., sér. 6, tome vii. p. 204.

pistil with a large number of ovules the stigmatic surface is large, as is also the amount of conductive tissue of the style through which the pollen-tubes are to descend.

1118. **The conductive tissue** through which the pollen-tube descends, and by which it is nourished, is formed at the stigma by a modification of epidermal cells, and below this arises from modifications in the parenchyma; in the style it may constitute a solid mass of delicate cells, sometimes with walls which have undergone the mucilaginous modification, or it may simply line the hollow tube which is frequently found, as in the pistil of the violet.

1119. **The time required for the descent of the pollen-tube** depends upon the length and character of the path the tube is to traverse, and is very different in different cases. Hofmeister states that in Crocus vernus, with a style which is from one to two inches in length or sometimes more, the tube reaches the ovary in from one to three days. Schleiden[1] gives the following times required for descent of the tube: Cereus grandiflorus, having a style nine inches long, a few hours; Colchicum autumnale, with a style thirteen inches long, twelve hours. In some other cases (certain orchids) it is weeks before the end of the tube has descended for even a very short distance.

1120. A single pollen-grain of some flowers can emit more than one pollen-tube: thus Amici has seen twenty to thirty tubes proceed from one grain. Pollen-tubes sometimes branch in their course downward.

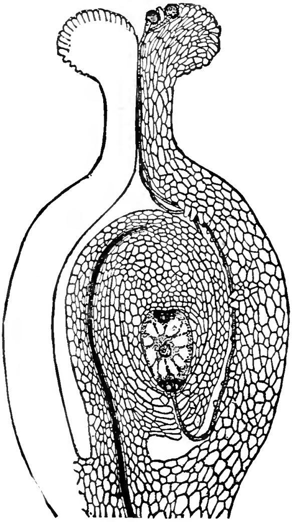

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FIG 196. Diagram of a longitudinal section of an ovary having only one ovule with basal placentation, designed to exhibit the course of the pollen-tube from the stigma to the summit of the embryonal sac above the oösphere. The ovule is anatropous, and is inserted, as is usually the case in Compositæ. (Luerssen.)

1121. The length of time during which pollen-grains can preserve their vitality has been determined for a few cases:[2]

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[1] Schleiden: Principles of Scientific Botany, 1849, p. 407.

[2] Gärtner, quoted by Mohl: Vegetable Cell, p. 134.

Those of Hibiscus Trionum at least three days after removal from the anther; those of Cheiranthus Cheiri, fourteen days; those of Camellia, Cannabis, Zea, and Phœnix dactylifera (Date), one year.

1122. Although each ovule requires for its impregnation only one pollen-tube, the number of pollen-grains in flowers which open at maturity is far in excess of the number of ovules. The ratio has been ascertained in a few cases, among which are the following: Cereus grandiflorus,[1] 250,000 grains of pollen to 30,000 ovules; Wistaria sinensis,[2] about 7,000 grains of pollen to each ovule; Hibiscus Trionum,[3] 4,863 grains of pollen to about 30 ovules. In some other cases, for instance Geum urbanum,[4] the excess of pollen over ovules is about 10 : 1.

1123. The localization of the conductive tissue in the ovary itself is sometimes very marked; thus in ovaries with parietal placentation, the ovarian walls in the immediate vicinity of the ovules are seen to be distinctly conductive, while in those with axile placentation, the modified tissue is found in the axis. Capus distinguishes the following varieties of conductive placentæ: (1) with a smooth surface, the micropyle being close to the placenta, *e. g.*, Solanum; (2) papillar, the papillæ either simple or compound, sometimes serving to guide the pollen-tube to the micropyle, *e. g.*, some Cucurbitaceæ; (3) hairy, the hairs sometimes secreting a mucus or even breaking down into a gelatinous mass through which the pollen-tube may penetrate with facility, *e. g.*, some Aroids. Special names were formerly given to peculiar forms of the conductive tissue, but the terms now possess no utility. For special examples of the forms, the reader must consult the practical exercises at the end of this volume.

1124. **Structure of the ovule.** As shown on page 175, the ovules arise as minute protuberances at some part of the ovarian wall or upon the axis of the ovary. In orchids the protuberance consists of only a single row of cells; but in most

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[1] Morren.

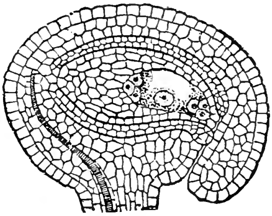
[2] Gardeners' Chronicle, 1846, p. 771.

[3] Kölreuter: Vorläufige Nachricht (quoted by Balfour: Class Book of Botany, p. 564).

[4] Gärtner: Beiträge zur Kenntniss, p. 346 (quoted by Darwin in "Effects of Cross and Self Fertilization in the Vegetable Kingdom," p. 377).

The following are some of Hassall's determinations of the number of pollen-grains (Annals of Nat. Hist. viii., 1842, p. 108): Dandelion, 243,600 grains; a flower of Peony, with 174 stamens each containing 21,000 pollen-grains, 3,654,000; while in a plant of Rhododendron the number of grains was estimated to be 72,620,000.

other cases several rows of cells are superposed, forming the body known in morphology as the nucleus of the ovule. This, to avoid the possibility of even slight confusion, will be now spoken of as the *nucellus.*



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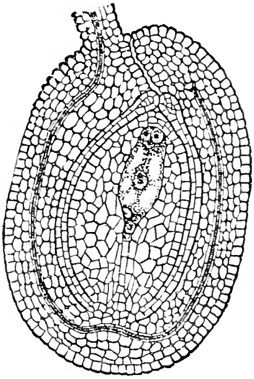
That this distinction is necessary, will appear from the fact that in one of the large cells of this body there is a true cell-nucleus which undergoes remarkable changes, all of which must be described. It should therefore be remembered that in the following discussion the term *nucellus* means exactly that which in Volume I. page 277 is called *nucleus of the ovule.*



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1125. Around the nucellus there is developed in most instances a double ring, which soon nearly invests it, forming an inner and an outer coat. Attention has been called in Volume I. to the fact that the integuments of the ovule do not completely invest the nucellus, but that there is at its true apex an orifice known as the foramen or micropyle. It has also been shown that by a peculiar distortion during its development the ovule may be so bent round upon its support, the funiculus, as to have the micropyle present itself towards the placental attachment. Hence, when the apex of the ovule is spoken of, the micropylar extremity is meant.

1126. At the micropylar extremity of the forming ovule, a single cell, beneath the surface (except in orchids and some saprophytes), elongates in the direction of the length of the ovule, and by one or sometimes many transverse and vertical partitions becomes divided into segments of unequal size. The lowest segment continues the elongation and the enlargement of the structure thus formed within the ovule, known as the embryo

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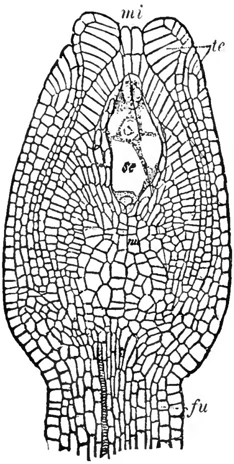
FIG. 197. Longitudinal section of the amphitropous ovule of Baptisia australis. (Van Tieghem.)

FIG. 198. Longitudinal section of the anatropous ovule of Mimosa pudica. (Van Tieghem).

sac. During the subsequent development of the ovule the embryonal sac continues to increase in size, often irregularly, and displaces or obliterates by absorption many of the cells around it.



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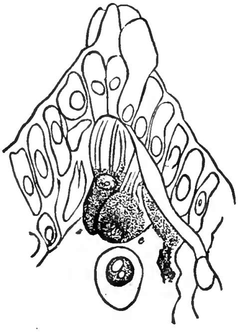
1127. At an early period in the development of the embryonal sac it is completely filled with protoplasm containing a cell-nucleus. This nucleus divides, and the two new nuclei are soon found at opposite ends of the sac, where each divides into four nuclei. Between the two groups of four nuclei there may be a vacuole of considerable size.

The next stage is marked by the passage of a nucleus from each extremity of the embryonal sac towards its centre, where they become united to form a secondary nucleus.

1128. The nuclei at the lower end of the sac become surrounded with other protoplasmic matter, and later by cell-walls; they then constitute what have been termed the *antipodal cells.* At the upper end of the sac, also, the three nuclei become surrounded by



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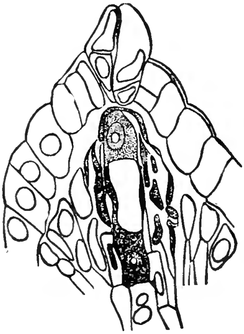

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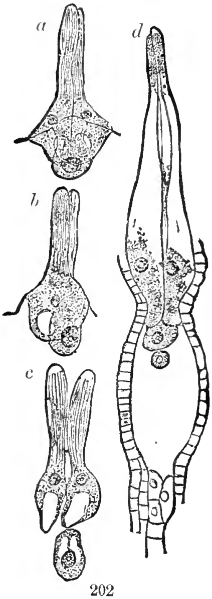
FIG. 199. Longitudinal section of the orthotropous ovule of Polygonum divaricatum. *fu*, funiculus; *te*, the two integuments; *nu*, the nucellus, whose summit is prolonged towards the micropyle, *mi*; *se*, the embryonal sac. (Strasburger.)

FIG. 200. Polygonum divaricatum. Summit of the ovule with the apex of the embryo sac, and the complete embryonal apparatus. *e*, the oöspore; *s*, one of the synergidae, the other being hidden from view. (Strasburger.)

FIG. 201. Polygonum divaricatum. Summit of the ovule, showing the encroachment of the embryo sac upon the adjoining cells. (Strasburger.)

more or less protoplasmic matter, but are not invested by a true cell-wall; these have been termed the egg-apparatus. Two of these naked nucleated bodies are somewhat attenuated at their upper part and rounded below; the slender portion contains the nucleus, the rounded a vacuole. The bodies are termed the *synergidæ.* The remaining cell is near the lower extremity of the two just described, and is known as the *oösphere.* All of these parts are shown in the figures.



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Such, then, is the structure of the embryonal sac and of the egg-apparatus, when the extremity of the pollen-tube emerges into the cavity of the ovary and comes in contact with the micropyle, or foramen. It has been shown by Strasburger, that when contact takes place between the pollen-tube and the summit of the embryonal sac, one of the synergidæ changes its character; its rather clear protoplasm becomes turbid, its vacuole and nucleus vanish, and with a slight contraction the mass becomes finely granular, after which it may wholly disappear. At this time the oösphere also undergoes the following changes: it clothes itself with a thin film of cellulose, and in its protoplasmic mass a well-marked nucleus, probably derived as such from the pollen-tube, appears by the side of the nucleus of the oösphere, sometimes of the same size, sometimes smaller. The two nuclei blend, forming a single ovoid body, with distinct or with confluent nucleoli. Even if at first distinct the nucleoli may become confluent at a later period. The

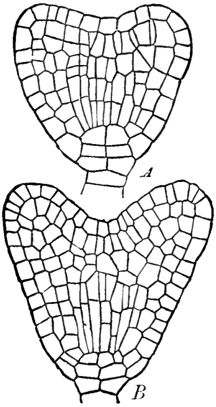

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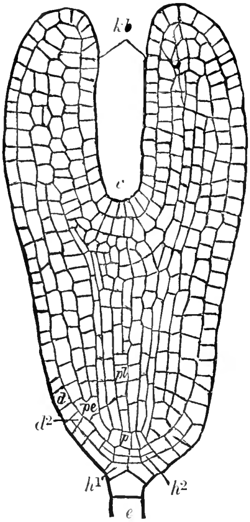
FIG. 202. Synergidæ prolonged across the membrane of the embryonal sac. *a*, *b*, *c*, from Gladiolus communis; *d*, from Bartonia aurea. *a*, plane perpendicular to the plane of the symmetry of the ovule; *b*, in the plane of symmetry; *c*, after separation of the three parts; *d*. (Strasburger.)

FIG. 203. Capsella Bursa-pastoris. Two embryos with cotyledons distinctly developed. *B* more advanced than *A*. (Luerssen.)



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other synergide remains unchanged, or passes through nearly the same changes as those described. It should be said that in some instances the pollen-tube passes down without apparently affecting the synergidæ to any very marked extent, but producing its influence directly upon the oösphere.

1129. These changes now described in the oösphere are known collectively as those of fertilization or impregnation; the fertilized or impregnated oösphere is termed an oöspore. It passes through a series of changes by which a second cell is formed, then others in a linear series, or in a more complex chain, termed the proembryo or suspensor. In some cases, however, no suspensor at all is produced.

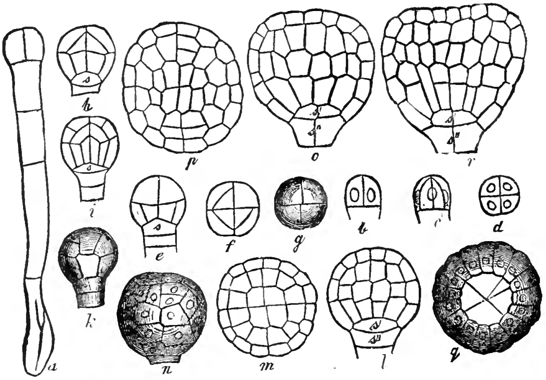

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FIG. 204. Capsella Bursa-pastoris. Embryo developed more than in Fig. 203. A longitudinal section showing cotyledons, *kb*: *c*, point of growth; *e*, suspensor; *pl*, plerom; *p* and *pe*, periblem; *d*, and d^2, dermatogen; h^1, and h^2. root-cap. (Hanstein.)

FIG. 205. Camelina sativa. *a*, two-celled embryo, much exceeded in size by the long suspensor. Capsella Bursa-pastoris, the figures *b*, *r*, showing different stages in the development of the embryo; *b*, *c*, *d*, aspects of the embryo divided into quadrants; *e*, *f*, *g*, different views of the embryo at the formation of the dermatogen; *i*, longitudinal section showing further divisions and the formation of the periblem and plerom; *k*, same as *i*, but given in perspective; *l*, longitudinal, *m*, transverse, section of the same embryo at a later stage; *n*, perspective view of embryo at a little earlier stage than *l* and *m*; *o*, *p*, *r*, later stages; *q*, same embryo seen from below, exhibiting the first divisions near the suspensor; *s*, *s′*, *s″*, cells nearest the suspensor. (Luerssen, after Prazmowski.)

1130. The terminal cell of the suspensor is followed by the initial cell or cells of the embryo proper; the different stages of the development of the embryo can be traced in the ovule of one of our most common weeds, Capsella (compare Figs. 203–205).

The case above described is a simple one, but may serve as a type of all normal cases of fertilization in angiosperms, the innumerable deviations from which cannot be further alluded to here.[1]

1131. With the changes in the embryo sac there are concomitant changes in the whole nucellus and its integuments. A certain amount of food of some kind (see 509) is stored either in the sac or in the developing tissues around it, constituting the so-called albumen of the seed. The food within the developing embryo sac is termed endosperm; if around it, perisperm. But the changes do not stop with the ovule as it ripens into a seed: they go on also in the surrounding parts. In fact, as soon as fertilization has begun, the flower wilts, and in most cases the external organs fall. The ovary, sometimes with associated parts such as the calyx, the receptacle, etc., passes through changes by which it becomes the fruit.

FERTILIZATION IN GYMNOSPERMS.

1132. The chief differences between the reproduction in these plants and that in those just described are in the preliminary development of the pollen and the ovule.

1133. *Pollen of gymnosperms.* The grain is distinctly divided by a curved partition into two portions, and one of these portions is frequently divided in much the same way into two parts. Comparison of this pollen with that of

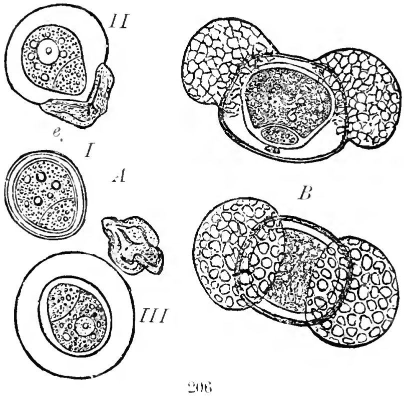

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Fig. 206. *A*, pollen-grains of Biota before their escape from the pollen-sac. *I*, fresh, *II* and *III* swollen by water; the extine *e* having split off, the protoplasmic contents are seen. *B*, pollen-grains of Pinus pinaster before their escape from the pollen-sac; a side and a dorsal view. (Sachs.)

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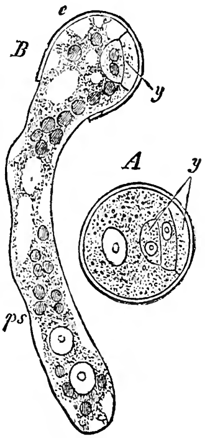
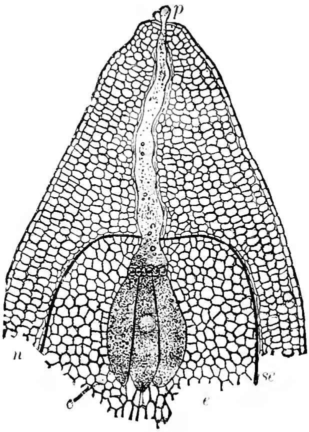
[1] The student is urged to study with great care the masterly treatise by Strasburger, Ueber Befruchtung und Zelltheilung, 1878, and the more succinct account in his Practicum, 1884.

angiosperms shows that in the latter the nucleus divides, but that the division stops here, no true dividing-wall being formed.



1134. *Ovule of gymnosperms.* The ovule is always orthotropous. It has an integument which is sometimes prolonged so as to form a fleshy tube communicating with the nucellus.

The nucellus, like that of angiosperms, contains an embryonal sac; at an early stage this is filled with endosperm, which it will be remembered is not developed in angiosperms until after fertilization. Some of the upper cells of the endosperm are rather larger than the others, elongated in the direction of the axis of the ovule, and each surmounted by a "rosette" of minute cells which comes between the group and the summit of the embryo sac. These large cells, with their rosettes, are termed *corpuscules.* These corpuscules are considered oöspheres. Around them in the embryo sac there appears to be nothing corresponding strictly to the synergidæ, the antipodal cells, etc., observed in the angiosperms, although some homologies have been pointed out.



In some cases, like that figured, there is a sort of depression at the summit of the endosperm, which has been called the pollinic chamber.

1135. *Contact of pollen with the ovule.* As the name indicates, the gymnosperms are naked seeded; no stigma or style intervenes between the pollen and the ovule. When the divided pollen of the gymnosperm falls upon the micropyle of the ovule, it

Fig. 207. Pollen-grain of Ceratozamia longifolia. *A*, grain with partial partitions; *B*, the same emitting its tube, *ps*, which has ruptured the outer coat; *y*, minute inactive cells. (Juranyi.)

Fig. 208. Longitudinal section of the nucellus of the naked ovule of Juniperus Virginiana. *n*, nucellus; *se*, membrane of the embryonal sac; *e*, endosperm; *c*, corpuscles; *p*, a pollen-grain which has protruded its large tube as far as the corpuscles. (Strasburger.)

finds there a certain amount of moisture by means of which a tube is formed from one of the large cells. This extends directly into the tissue of the nucellus, coming sooner or later into contact with the summit of the embryonal sac, and then affecting the corpuscules below. From the fertilized corpuscule the embryo is developed.[1]

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[1] For the purpose of affording some means of comparison of the methods of reproduction in flowering plants and in those of a lower grade, the following brief notes concerning the reproduction in several of the groups of Cryptogams have been inserted: —

(1) No sexual reproduction has yet been demonstrated in the very lowest forms of vegetation. Such plants are termed Protophytes. The fungi which are associated with fermentation and putrefaction, and certain of the simplest algæ, are examples of the group.

In the study of the Protophytes the beginner can examine with profit the cells of *common yeast*. Care should be taken to distinguish between the cells of the plant and the grains of starch with which compressed yeast is generally associated.

The simple one-celled plants with chlorophyll which belong to this group can be found in almost any stagnant water. They are spherical, and are frequently grouped in twos or fours.

(2) The sexual process in Zygophytes is characterized by the confluence of the protoplasmic masses of two very similar cells by which a new mass is formed as the starting-point of the new individual. In most of these zygophytes there is no plain distinction of sex. Some of the lower moulds and many of the filamentous algæ are examples of the group.

Excellent specimens for study may be found in stagnant or slow-running water in spring and through the summer. By careful search it is possible to detect cases in which the process of conjugation has advanced somewhat: such specimens can be kept under observation by having the slide sufficiently warm and constantly supplied with fresh water, when the different stages of conjugation and of cell-division may be examined.

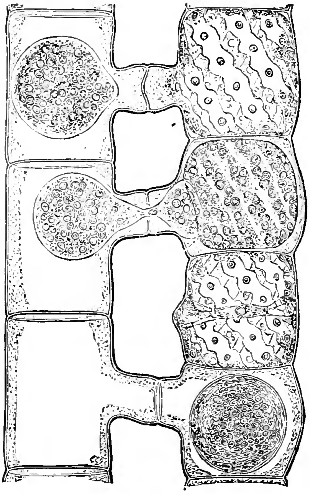

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Fig. 209. Spirogyra, illustrating the mode of fertilization in the Zygophytes. Approximating cells of two filaments produce extensions which become conjoined; the protoplasmic masses in these cells become confluent, forming a single mass which after escaping becomes clothed with a cell-wall and develops into a filamentous chain of cells. In this case there is no appreciable distinction of sex.

1136. It was formerly thought that no clear gradations could be detected between the flowering plants and the higher groups

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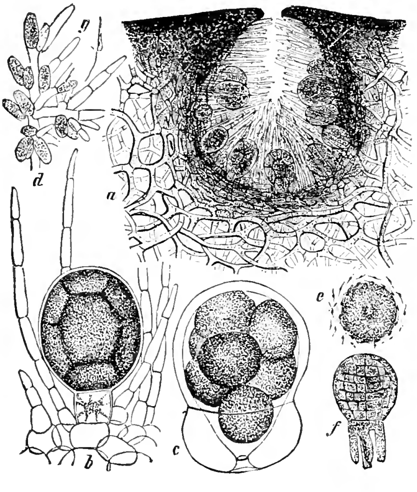
(3) Oöphytes. In this group a mass of protoplasm, known as an oösphere, is fertilized by specialized threads or slender masses of protoplasmic matter termed antherozoids, coming from another part of the same or of another plant. By contact with these antherozoids the oösphere becomes an oöspore, the starting-point of a new individual. In this group, of which Fucus or rock-weed may be taken as an example, the fertilization is direct.

In the examination of this group the student may employ the common rock-weed which carpets the boulders along the coast. Sections should be made in the uneven pustulated part of the frond, and in a vertical direction. Good preparations can be obtained from material which has been dried or from that which has been kept in alcohol, and winter specimens will be found especially good.



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Some of the species are diœcious, having the male elements in the conceptacles on one plant and the female elements in those upon another.

(4) Carpophytes. The simplest plants of this heterogeneous group are illustrated by Fig. 211. The oösphere is contained in a specialized organ (the carpogonium), which is frequently prolonged to form a style-like process (the trichogyne). The antherozoids are carried by water to this process, and fertilization results; the product of

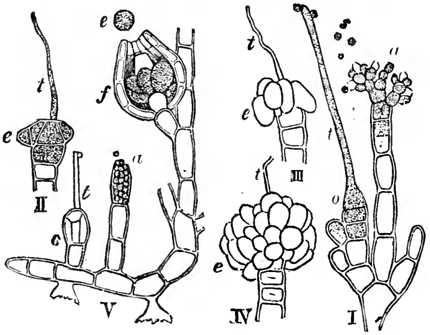

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FIG. 210. Fucus, illustrating the fertilization of an oöphyte. *a*, section through a conceptacle exhibiting the reproductive organs; *b* and *c*, the oöspheres in different stages of development; *d*, antheridia with a single antherozoid (*g*); *e*, an oösphere surrounded by antherozoids; *f*, an oösphere germinating. (Thuret.)

FIG. 211. Nemalion. I.-IV., a carpophyte. I., a branch showing antheridia, *a*, and a carpogonium, *o*, with the trichogyne, *t* (*e*, spermatium). V., Lejolisia exhibiting *a*, antheridium, *c*, carpogonium, and *f*, ripe fruit; *e*, an escaping spore. (Thuret and Bornet.)

of flowerless plants. Comparative investigations have, however, shown that such gradations do exist, and that the chain of exist-

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fertilization is shown in the figure. Of the more complicated cases this is not the place to speak; their treatment, as well as that of all the simpler forms, may be looked for in Volume III.

Specimens for this demonstration of the different stages of reproduction are to be procured at different seasons. As will be seen from the figure, most of the features are so nearly superficial as to need no particular sections for their exhibition.

(5) True mosses and their allies are characterized by the possession of an archegonium or flask-shaped body containing a central cell in which is the oösphere. The oösphere is fertilized by immediate contact with antherozoids which are formed in antheridia; as a result of the fertilization, there is produced a spore-case filled with spores.

In the examination of the fructification of a moss, the plant must be taken at an early stage, and search must be made for the sexual organs by removal of the flower-like cluster of leaves at the summit of the minute stalk. If the removal is successfully performed, and the plant is in the right condition, a group of threads like those shown in the figure will be plainly seen. Among these are to be found some flask-like bodies, the archegonia, and either on the same receptacle or on another plant of the same species the male organs, one of which, greatly magnified, is shown in Fig. 212. Under a very high power the escaping antherozoids can be seen. When fertilization has taken place, the archegonium goes on in its development, becoming, after many intermediate steps, the capsule or "fruit" of the moss, covered by a sort of hood or cap, and tightly closed at its mouth by a lid. Removal of the lid discloses the teeth of the mouth (peristome) and the spores within. Upon germination, a spore gives rise to slender filaments among which is produced the minute moss-plant with the sexual organs figured in the sketch.

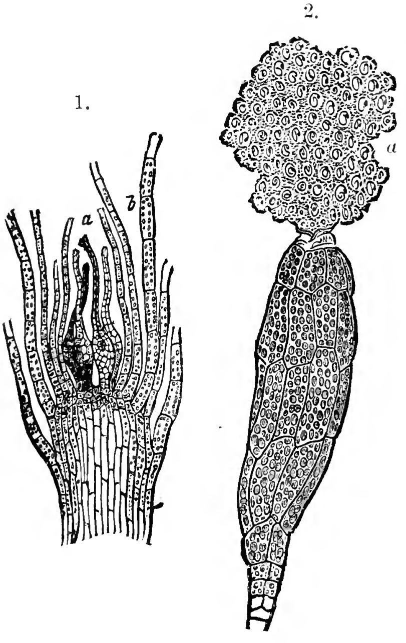

FIG. 212. Funaria hygrometrica, a moss. 1. Longitudinal section through the upper part of the plant with archegonia, *a*, and leaves, *b*. 2. Antheridium bursting and allowing escape of the antherozoids, *a*. (Thomé.)

ences is practically unbroken, reaching from the lowest to the highest forms. The character of this evidence will appear in the succeeding volume of this series.

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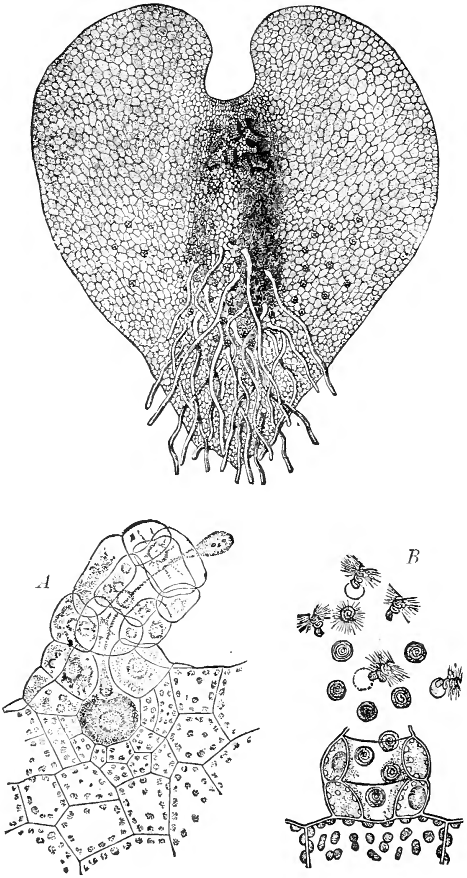
(6) True ferns exhibit the following phenomena of fertilization. On the back of the frond there are formed spores in spore-cases, which are variously grouped and protected. The spores on reaching a fit surface soon give rise to thin films (prothalli), on the under side of which are produced the sexual organs, all of which are shown in the figures. As a result of the process of fertilization there is produced a fern-plant, which at its adult age bears the spores above spoken of.

In any greenhouse where ferns are kept it is easy to procure, by careful search on the soil of the flower-pots, abundance of the prothalli in different stages. The most minute of these exhibit the sexual organs just forming, while those which are more advanced give all the features shown in the figures. The student must observe that on the surface of the soil in the flower-pots many other growths are to be found, and care must be taken not to confound other flat films (belonging, for instance, to Hepaticæ) with the prothalli of the ferns.



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Sections through the prothallus will exhibit the sexual organs in different stages of development. The best material is procured by the cultivation of

FIG. 213. Prothallus of a fern, exhibiting the reproductive organs. At the sinus of the heart-shaped film are to be seen the archegonia, one of which, more highly magnified, is displayed in section in *A*. *B*, an enlarged antheridium with escaping antherozoids. (Luerssen.)

1137. **Contrast between non-sexual and sexual reproduction as regards results.** In non-sexual reproduction a certain portion of living matter is separated from the rest of the living matter of the plant, and, coming under favorable conditions, pursues an independent existence; in sexual reproduction, two portions of living matter, from different parts of the organism or from different organisms, unite to constitute a new individual.

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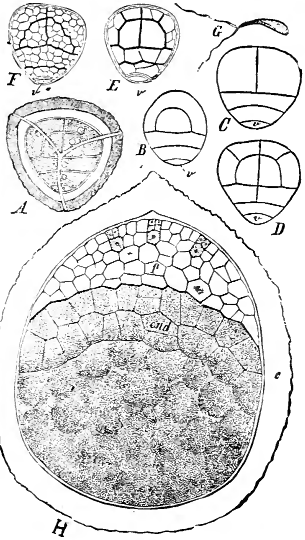
fern-spores. On a piece of unglazed earthenware, for instance a broken flower-pot, which has been first boiled for a time in water to destroy any injurious moulds, a few spores are to be lightly dusted. If the whole is covered by a bell-jar and kept dark and warm, after a certain time the delicate films will be detected and can then be traced through their development.

(7) Some of the allies of the ferns produce spores of more than one sort, differing in size and subsequent development. The larger spores, known as macrospores, give rise to an included prothallus which subsequently becomes exposed at one portion, where there is developed an archegonium (or sometimes more than one). Previous to or coincident with this development there is formed within the spore-walls a peculiar tissue which has been termed the endosperm, and which is regarded as the homologue of the endosperm in gymnospermous seeds. The smaller spores are denominated microspores, and pursue a peculiar course of development. One of the cells (seldom more than one) remains essentially unchanged, while the others give rise to the mother-cells of the antherozoids. It is therefore thought proper to consider the sterile cell as the homologue of a rudimentary male prothallus, and the others of rudimentary antheridia. From the mother-cells are produced, sooner or later, the antherozoids by which the archegonium is fertilized.



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If these allies of the ferns are compared with the angiosperms, wide differences are found to exist which can be bridged over, in part at least, by the gymnosperms. Hence, in some systems of classification the gymnosperms are placed between the angiosperms and cryptogams instead of between the monocotyledons and dicotyledons.

Fig. 214. Selaginella. *A*, *F*, microspores in different stages of formation of the antheridia. *G*, antherozoid; *H*, axile longitudinal section of a macrospore six weeks after fertilization, but before germination; *v*, rudimentary prothallus of the microspore; *p*, prothallus of the macrospore with three archegonia; *end*, endosperm; *e*, exosporium. (Pfeffer.)

1138. The new individual, for instance a bud, arising from non-sexual reproduction, generally repeats in itself all the peculiarities of the organism from which it took its origin; the new individual, the seed or spore, arising from sexual reproduction, usually differs in some particulars from the organism or organisms by which it was produced.

1139. Hence, in the higher plants individual peculiarities are perpetuable by bud-reproduction, whereas the seed gives rise to variations. If the horticulturist wishes to keep the descendants of a given stock true to all the characters which give them value, he relies upon some method of multiplying the plant by buds; if, on the contrary, he desires to induce or increase some variation from the stock, he makes use of seeds.

1140. The ordinary horticultural operations by which buds are severed from the parent stock and suitably placed for further advantageous development are: (1) layering, — the fastening a branch in earth, so that while yet connected with its main stem it may form new roots and afterwards live independently of the stem; (2) the forcing of cuttings or slips, which in congenial soil will produce a supply of roots; (3) grafting, or the transfer of a shoot (a scion) from the parent plant to some other plant by which it can be nourished; (4) budding, the transfer of a single bud to another plant (see 426).

1141. While in most cases buds produce shoots or plants very closely resembling the parent, it sometimes happens that remarkable variations arise. These are known as *bud-variations*, and are commonly called *sports*. In general, when once originated they are perpetuable by any of the processes of bud-propagation just described, but are not likely to be reproduced by seed. From the long list of them given by Darwin only a few familiar cases are here mentioned: (1) the moss-rose, from the Provence rose (Rosa centifolia); (2) Pelargonium, giving rise to numerous varieties; (3) Dianthus, Sweet William, Carnations, and Pinks, which vary very widely in cuttings from a single plant.

1142. Many of the cases of sports, especially those which have descended from hybrids, are attributable to reversion to an ancestral form; a few seem to be dependent on changes in the surroundings; while others have been attributed to the influence exerted by a graft.

1143. Ordinarily the scion produces no marked effect upon the stock, and, conversely, the stock exerts no effect upon the shoot growing from the scion. But when, for instance, some of the variegated forms of Abutilon have been grafted on green-leaved stocks, they have been known to affect many of the subsequent shoots. Such cases are known as *graft-hybrids*. The most remarkable example is that of Cytisus Adami, a form midway between Cytisus laburnum and purpureus. Of this plant Darwin says: "Throughout Europe, in different soils and under different climates, branches on this tree have repeatedly and suddenly reverted to both parent species in their flowers and leaves. To behold mingled on the same tree tufts of dingy red, bright yellow, and purple flowers, borne on branches having widely different leaves and manner of growth, is a surprising sight. The same raceme sometimes bears two kinds of flowers, and I have seen a single flower exactly divided in halves, one side being bright yellow and the other purple; so that one half of the standard-petal was yellow and of larger size, and the other half purple and smaller. In another flower the whole corolla was bright yellow, but exactly half the calyx was purple. In another, one of the dingy-red wing-petals had a bright yellow narrow stripe on it; and lastly, in another flower one of the stamens, which had become slightly foliaceous, was half yellow and half purple; so that the tendency to segregation of character or reversion affects even single parts and organs. The most remarkable fact about this tree is that in its intermediate state, even when growing near both its parent species, it is quite sterile; but when the flowers become pure yellow or pure purple they yield seed." Passing over the views expressed by many that Cytisus Adami is a hybrid produced by seed, the account of its origin, quoted by Darwin, is here given. M. Adam inserted a shield of Cytisus laburnum in the stem of C. purpureus; the bud lay dormant a year and then produced a shoot which was rather more vigorous than those of C. purpureus; this shoot was propagated and the plants therefrom were sold as a variety of Cytisus purpureus, before they had come into flower.[1]

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[1] The account of the budding was published after they had flowered, but before this extraordinary tendency to reversion had been manifested. Upon a review of the testimony Darwin was inclined to accept the foregoing account of the origin of Cytisus Adami as a graft-hybrid as true. Other cases are to be placed in the same category.

For a full statement of bud-variations and graft-hybrids the student should read: Darwin, Variation in Animals and Plants under Domestication, 1868, vol. 1, chap. xi.; also Focke, Die Pflanzen-mischlinge, 1881, p. 519. In the latter is an interesting account of the mixed oranges (Bizarria). Consult also Braun, On the Phenomenon of Rejuvenescence in Nature (Ray Society, 1853); and numerous papers by Caspary.

1144. **Apogamy.** The prothallus which develops from a fern-spore bears upon its under side the sexual organs; from their interaction a bud is produced which grows into the fern-plant. Farlow[1] has shown that in some cases the prothallus can give rise to a bud without sexual intervention. De Bary[2] has traced out the connection between this mode of budding and that which is found in certain other plants. To the abnormal budding of the prothallus and homologous structures he has given the name *apogamy*.

1145. **Parthenogenesis**[3] is the production of an embryo without the intervention of pollen (or the equivalent of pollen in the lower plants). Cœlebogyne ilicifolia, a species belonging to the order Euphorbiaceæ, has been known to produce seeds with more than one embryo, and without access of pollen. It has been held by some that the embryos in this case are formed from oöspheres which had not been fertilized, but investigations by Strasburger indicate that they are adventitious outgrowths from the cellular tissue of the nucellus, and are outside of, not in, the embryo-sac.

In some other cases examined, Strasburger regards the formation of embryos outside the embryo-sac as dependent upon the fertilization of the oösphere, but in only one case of this kind did he observe any embryo form also from the fertilized oöspore.

1146. **Polyembryony**, the production of two or more viable embryos in a seed after the manner just described, is of frequent occurrence in oranges, onions, and Funkia (Day Lily).

1147. **Fertilization in different degrees of consanguinity.** It has been shown in Volume I. that "no two individuals are exactly alike; and offspring of the same stock may differ (or in their progeny may come to differ) strikingly in some particulars. So two or more forms which would have been regarded as wholly distinct are sometimes proved to be of one species by evidence of their common origin, or more commonly are inferred

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[1] Quart. Journ. Mic. Science, xiv., 1874, p. 266; Proceedings Am. Acad., ix. p. 68.

[2] Botanische Zeitung, 1878, p. 449 *et seq.*

[3] Braun: Ueber Parthenogenesis bei Pflanzen, 1857; Hanstein: Die Parthenogenesis der Cœlebogyne ilicifolia, 1877; Hanstein: Botanische Abhandlungen, 1877; Strasburger: Befruchtung und Zelltheilung, 1878.

Cases of parthenogenesis occur in the lower plants, where they have been followed out in cultures continued for a considerable time. Their consideration belongs to the next volume of this series.

For an account of parthenogenesis in animals, see Balfour: Treatise on Comparative Embryology, 1880; also Brooks on Heredity, 1883, p. 55.

to be so from the observation of a series of intermediate forms which bridge over the differences. Only observation can inform us how much difference is compatible with a common origin. The general result of observation is that plants and animals breed true from generation to generation within certain somewhat indeterminate limits of variation; that those individuals which resemble each other within such limits interbreed freely, while those with wider differences do not. Hence, on the one hand, the naturalist recognizes *Varieties* or differences within the species, and on the other, *Genera* and other superior associations indicative of remoter relationship of the species themselves."

"Most varieties originate in the seed, and therefore the foundation for them, whatever it may be, is laid in sexual reproduction. . . . Upon the general principle that progeny inherits or tends to inherit the whole character of the parent, all varieties must have a tendency to be reproduced by seed. But the inheritance of the new features of the immediate parent will commonly be overborne by atavism; that is, the tendency to inherit from grandparents, great-grandparents, etc. Atavism, acting through a long line of ancestry, is generally more powerful than the heredity of a single generation. But when the offspring does inherit the peculiarities of the immediate parent, or a part of them, its offspring has a redoubled tendency to do the same, and the next generation still more; for the tendencies to be like parent, grandparent, and great-grandparent now all conspire to this result and overpower the influence of a remoter ancestry."[1]

1148. The reproductive elements in a complete flower may combine to produce an embryo. In this case the pollen and ovule have originated upon a single shoot, within very narrow limits of difference as regards the time, place, and conditions of their development, and the result of their union is what might be expected, — a close copy of the parent plant. The fecundation of a flower by its own pollen is termed *close-fertilization*, or self-fertilization.

1149. In *cross-fertilization* the pollen fertilizing the ovule of a flower comes from another flower of the same species, and here the reproductive elements have been developed under dissimilar conditions.

1150. In *hybridization* the pollen comes from a flower of a different species; and in this case the conditions, external and

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[1] Volume I. pp. 318, 319. The student is urged to review carefully the following sections also in that volume: 619 to 640, and 657 to 662 inclusive.

internal, under which the reproductive elements have been produced are widely dissimilar.

The mechanism by which close-fertilization is secured in some instances and absolutely prevented in others has been fully explained in Volume I. The account of the mechanism is now to be supplemented by a statement of the results of reproduction in the different degrees of relationship.

1151. **The results of close-fertilization contrasted with those of cross-fertilization.** It has long been known to cultivators of plants, that in order to keep the desirable varieties which are under cultivation "true to seed" they must be close bred; that is, all pollen from other varieties of the same species must be excluded. The whole subject is best illustrated by reference to the numerous experiments by Darwin; the exhaustive nature of which is indicated by an account of a single series given nearly in his own words.

1152. The plants experimented upon in all cases were raised from carefully ripened seed, and, when ready to flower, were placed under nets with meshes of one tenth of an inch in diameter, in order that all pollen-carrying insects might be excluded.

A plant of Ipomœa purpurea (Morning Glory), growing in the greenhouse, was protected in the manner just described, after ten of its flowers had been fertilized by pollen from their own stamens, and ten others by pollen from a distinct plant of the same species. The seeds from the first ten flowers may be termed *self-fertilized*, those from the other ten, *crossed*. The two kinds of seeds were placed on damp sand on opposite sides of a glass tumbler covered by a glass plate, with a partition between the seeds, and the glass was put in a warm place. As often as a pair of seeds germinated they were put on opposite sides of a pot, with a superficial partition between them, and the same procedure was followed until five or more seedlings of exactly the same age were planted on the opposite sides of several pots. The soil in the pots in which the plants grew was well mixed, and the plants on the two sides were always watered at the same time; thus the seedlings were subjected to practically the same conditions from a very early stage.

In the same manner self-fertilized and crossed seeds were secured during ten generations. The results, so far as these can be shown by measurement of the plants, are exhibited in the following table:[1] —

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[1] Darwin: Effects of Cross and Self Fertilization, 1876, p. 52.

IPOMŒA PURPUREA.

Number of the Generation.	Number of crossed Plants.	Average height of crossed Plants in inches.	Number of self-fertilized Plants.	Average height of self-fertilized Plants in inches.	Ratio between average heights of crossed and self-fertilized Plants.
First	6	86.	6	65.66	100 : 76
Second . . .	6	84.16	6	66.33	100 : 79
Third	6	77.41	6	52.83	100 : 68
Fourth . . .	7	69.78	7	60.14	100 : 86
Fifth	6	82.54	6	62.33	100 : 75
Sixth	6	87.50	6	63.16	100 : 72
Seventh . . .	9	83.94	9	68.25	100 : 81
Eighth . . .	8	113.25	8	96.65	100 : 85
Ninth . . .	14	81.39	14	64.07	100 : 79
Tenth . . .	5	93.70	5	50.40	100 : 54
All ten generations taken together.	73	85.84	73	66.02	100 : 77

1153. The results of close and cross fertilization, as shown by the weight of the seed-capsules, are given by Darwin thus: "The offspring of intercrossed plants of the ninth generation, crossed by a fresh stock, compared with plants of the same stock intercrossed during ten generations, both sets of plants left uncovered and naturally fertilized, produced capsules by weight as 100 to 51."[1]

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[1] The following summary (Darwin: Effects of Cross and Self Fertilization, p. 56) shows more of the results: —

First generation of crossed and self-fertilized plants growing in competition with one another. Sixty-five capsules produced from flowers on five crossed plants fertilized by pollen from a distinct plant, and fifty-five capsules produced from flowers on five self-fertilized plants, fertilized by their own pollen, contained seeds in the proportion of . . . . 100 to 93.

Fifty-six spontaneously self-fertilized capsules on the above five crossed plants, and twenty-five spontaneously self-fertilized capsules on the above five self-fertilized plants, yielded seeds in the proportion of . . . 100 to 99.

Combining the total number of capsules produced by these plants and the average number of seeds in each, the above crossed and self-fertilized plants yielded seeds in the proportion of . . . . 100 to 64.

Other plants of this generation grown under unfavorable conditions and spontaneously self-fertilized yielded seeds in the proportion of . 100 to 45.

1154. "All the self-fertilized plants of the seventh generation, and I believe of one or two previous generations, produced flowers of exactly the same tint; namely, of a rich dark purple. So did all the plants, without any exception, in the three succeeding generations of self-fertilized plants; and very many were raised on account of other experiments in progress not here recorded. . . . The flowers were as uniform in tint as those of a wild species growing in a state of nature. . . . The crossed plants continued to the tenth generation to vary in the same manner as before, but to a much less degree, owing probably to their having become more or less closely inter-related."[1]

1155. In the sixth self-fertilized generation there appeared a plant which was larger than its crossed competitor, and its powers of growth and fertility were transmitted to its descendants. Thus it appears that even with the exclusion of foreign pollen new characters can assert themselves.

1156. It was not found in these experiments that simply crossing a flower from another flower on the same plant was productive of any advantage; on the contrary, there are some cases which show that it may result in an actual disadvantage. "The benefits which so generally follow from a cross between two

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Third generation of crossed and self-fertilized plants. Crossed capsules compared with self-fertilized capsules yielded seeds in the ratio of . 100 to 94.

An equal number of crossed and self-fertilized plants, both spontaneously self-fertilized, produced capsules in the ratio of 100 to 38. And these capsules contained seeds in the ratio of 100 to 94. Combining these data, the productiveness of the crossed to the self-fertilized plants, both spontaneously self-fertilized, was as . . . . 100 to 35.

Fourth generation of crossed and self-fertilized plants. Capsules from flowers on the crossed plants fertilized by pollen from another plant, and capsules from flowers on the self-fertilized plants fertilized with their own pollen, contained seeds in the proportion of . . . . 100 to 94.

Fifth generation of crossed and self-fertilized plants. The crossed plants produced spontaneously a vast number more pods (not actually counted) than the self-fertilized, and these contained seeds in the proportion of 100 to 89.

Ninth generation of crossed and self-fertilized plants. Fourteen crossed plants spontaneously self-fertilized, and fourteen self-fertilized plants spontaneously self-fertilized, yielded capsules (the average number of seeds per capsule not having been ascertained) in the proportion of . . . . . 100 to 26.

Plants derived from a cross with a fresh stock compared with intercrossed plants. The offspring of intercrossed plants of the ninth generation, crossed by a fresh stock, compared with plants of the same stock intercrossed during ten generations, both sets of plants left uncovered and naturally fertilized, produced capsules by weight as . . . . 100 to 51.

[1] Darwin: Effects of Cross and Self Fertilization, p. 59.

plants apparently depend on the two differing somewhat in constitution or character. . . . The mere act of crossing two distinct plants which are in some degree inter-related and which have been subjected to nearly the same conditions does little good as compared with that from a cross between plants belonging to different stocks or families and which have been subjected to somewhat different conditions." [1]

1157. In Volume I. the different methods by which cross-fertilization is effected were sufficiently described, but certain special questions were then purposely left unanswered; namely, those in regard to the anatomical and chemical nature and the distribution of the attractions by which insects are allured to flowers to insure cross-pollination.

1158. **The nectar** which certain flowers offer to insects is made known by color or odor, or both. It is the sweetish liquid commonly called the "honey" of the flower, secreted by certain specialized organs known as nectar-glands. Mention has already been made (453) of the occurrence of these glands on leaves. In the flower they consist usually of specialized parenchyma not unlike the secreting surface of the stigma (see 1109). They are sometimes raised by a stalk, or *adenophore*, more or less above the surface of the floral organ on which they are developed, but often not elevated at all.

1159. Nectar-glands may occur upon any part of the flower, upon its bracts, or even upon some part of the flower-stalk near it. The "Cow-pea" of the Southern States affords a good example of nectar-glands on the flower-stalk. Many species of Euphorbia have them on bracts; the common Passion-flower and the cotton plant of the South also have them on the same organs. The most remarkable case of arrangement of the glands is found in a tropical plant, Marcgravia nepenthoides; this has been thus described: "The flowers are disposed in a circle, hanging downwards like an inverted candelabrum. From the centre of the circle of flowers is suspended a number of pitcher-like vessels, which, when the flowers expand in February and March, are filled with a sweetish liquid. This liquid attracts insects, and the insects numerous insectivorous birds. The flowers are so disposed, with the stamens hanging downwards, that the birds to get at the pitchers must brush against them, and thus convey the pollen from one plant to another." [2]

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[1] Darwin: Effects of Cross and Self Fertilization, p. 61.

[2] Belt: Naturalist in Nicaragua, 1874, p. 128.

1160. From the nectar-glands of proper floral organs the secretion of nectar is generally copious and is prone to collect in minute cavities such as shallow pits, or in conspicuous special receptacles, the so-called *nectaries.* The morphology of these organs has been sufficiently described in Volume I., Chapter VI.

1161. **The specific gravity of nectar** is very variable. The following figures are from Unger's[1] determinations: —

Agave Americana	1.05
" geminiflora	1.09
" lurida	1.20

If it is assumed that the solid matter in nectar is wholly sugar, these figures would correspond respectively to the following amounts of cane-sugar; namely, 10, 18, and 41.66 per cent.[2]

1162. **The period of most copious secretion of the nectar** usually coincides with the maturity of the anthers or of the stigma, but in some cases the nectar is prepared in considerable quantity before the flower opens.[3]

1163. The secretion of nectar can be arrested, as Wilson has shown, by carefully washing the secreting surface with a jet of water and then drying it with filter-paper. Nectaries which have been thus made inactive through removal of the nectar can be again brought into activity by adding to the surface a little strong syrup.

1164. The secretion from nectar-glands is not dependent upon the pressure exerted by contiguous cells. When the flow of the nectar from a nectar-secreting surface has been arrested in the manner described above, a pressure of even 40 centimetres of mercury upon the stem is insufficient to produce any effect; but the activity of the surface is at once resumed when a little syrup is placed upon it.

The secretion of nectar can proceed even when the tissues are not turgescent.[4]

1165. The colors of flowers depend, as indicated in 477, upon the existence in the cells of minute granules or of colored sap. The shades may be modified to some extent by accidents

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[1] Sitzungsberichte, Berlin Akademie, xxv., 1857, p. 446.

[2] Wilson: in Untersuchungen aus dem bot. Inst., Tübingen, 1881, p. 7.

[3] Bonnier: Les nectaires, Ann. des Sc. nat., sér. 6, tome viii., 1879, p. 5.

[4] For details see an important memoir by Wilson in Untersuchungen aus dem bot. Inst., Tübingen, 1881, i. p. 1; also an excellent paper by Trelease, "Nectar and its Uses" (in Report on Cotton Insects, U. S. Dept. of Agriculture, 1879), which contains a comprehensive bibliography.

of surface: *e. g.*, in the case of velvety petals the color is often softened, sometimes to a remarkable extent.

1166. Contrasted colors are often seen in a single flower. In general these are so disposed in spots or lines as to suggest that they bear a direct relation to the point where the nectar is secreted; hence such color-marks were called by Sprengel *nectar-spots* or *nectar-guides*. But in some cases flowers have conspicuous spots without being nectariferous; *e. g.* certain poppies.

1167. Darwin cites the following case as showing that nectar-marks have been developed in connection with the nectaries: "The two upper petals of the common Pelargonium are thus marked near their bases, and I have repeatedly observed that when the flowers vary so as to become peloric, or regular, they lose their nectaries and at the same time the dark marks. When the nectary is only partially aborted, only one of the upper petals loses its mark. Therefore the nectary and these marks stand in some sort of close relation to one another, and the simplest view is that they were developed together for a special purpose; the only conceivable one being that the marks serve as a guide to the nectary."[1]

1168. The colors of the flowers in certain species change more or less after opening; thus many Borraginaceæ turn from red to blue even during a short space of time. One of the most interesting cases of this change of color is presented by Arnebia. When the flower opens each lobe of the yellow corolla is conspicuously marked by a deep purple spot; after a few hours this begins to fade, and by the next day entirely vanishes.

1169. Of all colors of flowers white, pale yellow, and yellow[2] are the most common.

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[1] Effects of Cross and Self Fertilization, 1876, p. 373.

[2] The following table by Kohler and Schübeler (cited by Balfour) exhibits the relative frequency of certain colors in the plants of twenty-seven different families of plants: —

Color of flower.	In 4200 species.	Mean of 1000.
White	1193	284
Yellow	951	226
Red	923	220
Blue	594	141
Violet	307	73
Green	153	36
Orange	50	12
Brown	18	4
Black	8	2

1170. The colors of flowers have been variously classified; thus De Candolle divides them into a xanthic (yellow) and a cyanic (blue) series, both of which can pass into red and white. With few exceptions, these two series are not represented in the same blossom.

1171. The odors of flowers depend in some cases (*e. g.* orange-blossoms) upon the presence of a volatile oil which can be extracted by distillation; but in many other instances the odoriferous principle cannot be separated by chemical or other means.

1172. White flowers are more generally fragrant than those of any other color. "The fact of a larger proportion of white flowers smelling sweetly may depend in part on those which are fertilized by moths, requiring the double aid of conspicuousness in the dusk and of odor. So great is the economy of nature that most flowers which are fertilized by crepuscular or nocturnal insects emit their odor chiefly or exclusively in the evening."[1]

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[1] Darwin: The Effects of Cross and Self Fertilization in the Vegetable Kingdom, 1876, p. 374.

According to Kohler and Schübeler (cited by Balfour), the distribution of odor with regard to color is as follows:—

Color.	Species.	Odoriferous.	Odors agreeable.	Odors disagreeable.
White	1193	187	175	12
Yellow	951	75	61	14
Red	923	85	76	9
Blue	594	31	23	7
Violet	307	23	17	6
Green	153	12	10	2
Orange	50	3	1	2
Brown	18	1	0	1

The following classification, taken partly from Trinchinetti, as cited by Balfour, indicates the diversity which exists in regard to the periods and permanence of odors of flowers.

(1) Flowers which are odoriferous at the time of opening and which remain so throughout; *e. g.* most Roses.

(2) Flowers in which the intermission of odor is connected with their opening and closing; and in this class there are two subdivisions:—

(*a*) Those which are closed and scentless during the day, and are open and odoriferous at night; *e. g.* Mirabilis Jalapa, Cereus grandiflorus, etc.

(*b*) Those which are closed and scentless at night, and are open and odoriferous during the day; *e. g.* Convolvulus arvensis, Cucurbita Pepo, some species of Nymphæa.

1173. Nectar is protected in various ways from unwelcome insects; that is, from those which cannot aid cross-fertilization. The chief of these is by the structure of the flower itself or the parts below. Characteristic odors and certain colors may contribute to this protection. Thus, as Müller has pointed out, dull yellow flowers are entirely, or almost entirely, avoided by beetles, while they are visited by Diptera and Hymenoptera (flies and bees).

1174. **Hybrids** are the offspring of crossed species. But, as shown in Volume I. page 320, the limits which separate varieties from species are sometimes not sharply defined; hence it happens that the term *hybrid* has been also applied to crosses between strongly marked varieties of the same species. Such offspring should, however, be termed either variety-hybrids or cross-breeds, and the word hybrid kept to its proper signification.

1175. Wide differences exist in the degrees of capacity for producing hybrids. Thus certain closely allied species cannot be made to cross, while others much more remote in apparent relationship are crossed without difficulty.

1176. In general the limits of capacity for hybridizing do not extend beyond the genus; a few cases, however, are known in which species usually assigned to different genera have been successfully crossed.[1] Hence it cannot be known beforehand whether the attempt to cross two species will be successful.

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(3) Flowers which are always open, but which are odoriferous at one time and scentless at another. Under this class there are also two subdivisions:

(*a*) Those always open, and only odoriferous during the day; *e. g.* Cestrum diurnum, Coronilla glauca, etc.

(*b*) Those always open, and only odoriferous at night; *e. g.* Cestrum nocturnum, Hesperis tristis, etc.

In certain cases odors are given out by flowers in an intermittent manner. This is strikingly shown in some of the larger night-flowering species of Cactaceæ.

Delpino has given (Ulteriori Osservazioni sulla Dicogamia nel Regno Vegetale, 1868–1874) an elaborate classification of odors as they exist in flowers. He makes forty-five kinds which are readily distinguishable as peculiar, while between these kinds there are of course innumerable gradations.

[1] Focke notes that hybrids between species belonging to different genera are comparatively common in the following families: Caryophyllaceæ, Melastomaceæ, Passifloraceæ, Cactaceæ, Gesneriaceæ, Orchidaceæ, Amaryllidaceæ, and Gramineæ; and he cites also the following instances outside of these families: Brassica × Raphanus, Galium × Asperula, Centropogon × Siphocampylus, Campanula × Phyteuma, Verbascum × Celsia, Philesia × Lapageria. (Pflanzen-mischlinge, 1881, p. 456).

1177. In reciprocal hybridization the pollen of *A* is effective when applied to the stigma of *B*; and, conversely, the pollen of *B* is potent when applied to the stigma of *A*. But it sometimes happens that the rule will not work both ways. Thus the pollen of Mirabilis longiflora was found by Kölreuter to produce hybrids when applied to the stigma of Mirabilis Jalapa; but the pollen of the latter was without effect upon the stigma of the former. Other cases are known, but the cause of this extraordinary preference is not understood.

1178. Hybrids are produced artificially by the transfer of pollen from one species to the stigma of another species, care being taken to exclude all pollen of the second species from its own stigma. The pollen is best transferred by means of a sable or camel's hair pencil.[1] Exclusion of the pollen of the flower to be fertilized must be secured by removal of the anthers before the flower opens. This is easily effected by the use of delicate forceps, an incision being carefully made in the side of the corolla. After the application of the pollen to the stigma, the plant or blossom must be covered by some close netting.

1179. Following the application of the pollen, changes take place in the fertilized flower. But, as Nägeli has pointed out, these changes in many cases fall far short of yielding satisfactory results to the experimenter. Nägeli describes several grades of partial fertilization: (1) that in which the ovary, and perhaps the persistent calyx, grows somewhat without appreciably affecting the ovules; (2) that marked by greater growth of the ovary, and by slight enlargement of the ovules, which afterwards shrivel up; (3) that with small imperfect fruits with empty seeds; (4) that having good fruits with empty seeds; (5) that with normal fruits with apparently perfect seeds which have no germs; (6) that producing good fruits with seeds which have only minute germs incapable of further development.

In successful fertilization there are produced good fruits holding sound seeds.

Some of the cases in which hybrids have been produced between the species of different genera are given by Nägeli (Sitz. d. k. Akad. d. Wiss. z. München, 1865 and 1866), as follows: Rhododendron and Azalea, Rhododendron and Rhodora, Rhodora and Azalea, Rhododendron and Kalmia. Of those above mentioned, Rhododendron, Rhodora, and Azalea are now placed by Bentham and Hooker in a single genus, — Rhododendron.

[1] It is of great importance that the pollen should be applied at exactly the proper period for impregnation. This is usually indicated by the moisture of the stigmatic surface.

1180. If to a stigma pollen from two species is applied simultaneously, only that will be potent which has the greatest sexual affinity, and no apparent effect will be produced by the other.

1181. With some remarkable exceptions, hybrids share the general characters of their parents, and are intermediate between them. It sometimes happens that part of the offspring of a single union will have certain characters, while the rest,[1] raised from the same seed-pod, will possess others.

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[1] This and certain other points referred to in the text are well illustrated by the case of Parkman's Lily, which is here described nearly in full: —

"My first attempt was to combine the two superb Japanese lilies, L. speciosum (lancifolium) and L. auratum. The former was used as the female parent. Four or five varieties of it, varying from pure white to deep red, were brought forward in pots under glass. This was necessary, because L. speciosum does not ripen its seed in the open air in the climate of New England. When the flowers were on the point of opening, the anthers were carefully removed from the expanding buds by means of forceps. As the pollen was entirely unripe, and as pains were taken to leave not a single anther in any of the flowers, self-impregnation was impossible. The pollen of L. auratum was then applied to the pistils as soon as they were in condition to receive it. Impregnation took place in most cases. The seed-pods swelled, and promised an ample crop of seed; but the experiment was spoiled by the bad management of the man in charge of the greenhouse, in consequence of which the pods were attacked by mildew.

"In the next year I repeated the attempt, with the same precautions. This time the seed was successfully ripened. Being sown immediately, a portion of it germinated in the following spring, and the rest a year later. In regard to this seed, two points were noticeable: first, it was scanty, the pods (though looking well) being in great part filled with abortive seed, or mere chaff; and, next, such good seed as there was differed in appearance from the seed of the same lily fertilized by the pollen of its own species. The latter is smooth, whereas the hybrid seed was rough and wrinkled. About fifty young seedlings resulted from it; and their appearance was very encouraging, because the stems of nearly all were mottled in a manner characteristic of L. auratum, but not of L. speciosum. Here, then, was a plain indication of the influence of the male parent. The infant bulbs were pricked out into a cold-frame, and left there three or four years, when, having reached the size of a pigeon's egg, they were planted in a bed for blooming. This was in 1869. Towards midsummer, one of the young hybrids showed a large flower-bud much like that of its male parent, L. auratum. The rest, about fifty in all, showed no buds until some time after; and when the buds at length appeared, they were precisely like those of the female parent, L. speciosum. The first bud opened on the 7th of August, and proved a magnificent flower, nine and a half inches in diameter, resembling L. auratum in fragrance and form, and the most brilliant varieties of L. speciosum in color. In the following year it measured nearly twelve inches from tip to tip of the extended petals; and in England it has since reached fourteen inches. . . . In this one instance the experiment had been a great success; but of the remaining fifty hybrids, not one produced a flower in the least distinguishable from that of the pure L. speciosum. The

1182. Focke has shown that hybrids between remotely related species are generally delicate and difficult of cultivation, but that those which result from nearly related species are remarkable for the vigor of their vegetative organs. Nägeli has also pointed out that the latter have a somewhat longer lease of life than the parents; thus annuals can become biennials or even perennials.

1183. Hybrids between closely related species usually have larger or more showy flowers than either of the parents, but their reproductive organs are much weaker. This diminution of fertility may be complete, but it is usually only partial. The pollen-grains are generally fewer and often less developed, the ovules are less likely to afford sound germs. As a rule, the stamens are more affected than the pistils.

1184. Derivative hybrids are the offspring resulting from a union of a hybrid with one of the parent forms, or with another hybrid from a different source. In the former case there is frequently observed a marked tendency towards reversion, which may be heightened by repeated experiments in the same direction, until at last it is complete.[1]

1185. Hybrids and their offspring exhibit a marked tendency to vary. This fact is utilized by horticulturists in the production of new varieties. Varieties thus produced must, however, be perpetuated by other means than by seed.[2]

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influence of the alien pollen was shown, as before noticed, in the markings of the stem, and also in a diminished power of seed-bearing; but this was all.

"In the next year, wishing to see if the male parent would not make his influence appear more distinctly in the second generation, I fertilized several of these fifty hybrids with the pollen of L. auratum, precisely as their female parent had been fertilized. The crop of seed was extremely scanty; but there was enough to produce eight or ten young bulbs. Of these, when they bloomed, one bore a flower combining the features of both parents; but, though large, it was far inferior to L. Parkmanni in form and color. The remaining flowers were not distinguishable from those of the pure L. speciosum" (Bulletin of the Bussey Institution, ii., 1878, p. 161).

[1] For a full treatment of this subject, the student should examine Nägeli's treatise in Sitzungsberichte der Königl.-bayer.-Akad. der Wissenschaften zu München, 1865, ii.; and that by Focke, Pflanzen-mischlinge, 1881.

[2] For a full account of the variation of hybrids, the student should see Naudin, Ann. des Sc. nat., sér. 4, 1863, tome xix.

For a study of the influence of foreign pollen on the form of the fruit, see a paper by Maximowicz: St. Pétersb. Acad. Sci. Bull. xvii., 1872, col. 275.

CHAPTER XV.

THE SEED AND ITS GERMINATION.

1186. Thus far this treatise has dealt chiefly with the phenomena presented by the organs of adult plants, especially while these are in a healthy state. It is necessary to consider in conclusion a special case; namely, that of the seed, and the earliest phases of its independent existence.

1187. When a fertilized ovule approaches maturity, its activities become notably lessened in degree until, with perfect ripeness of the seed, the embryo manifests no indication of life. In a few cases the seed is so precocious that it will germinate even before it is detached from the parent plant; but there is usually a period of suspended activity.

1188. Two views are held as to the nature of the life of the embryo during this period of arrested activity: (1) that it is simply potential, and may be roughly compared to the fire in a match, ready to manifest itself under favorable conditions; (2) that it is a sluggish, dormant state, which differs from active life only in degree.

1189. From the first point of view it is easy to regard the seed as representing a certain amount of potential energy indirectly derived from solar radiance, and held for a time in a condition from which it may be released in many ways: thus, it may be liberated by rapid combustion, as when corn is burned for fuel; by slow oxidation, as when seeds decay; or by the act of germination.

1190. The second view takes into account, although it does not explain, the slight changes which take place in certain seeds and some other parts, especially buds, during what has been called the resting state.

1191. It has been stated (976) that many seeds cannot be made to start into active growth, even under the most favorable external conditions, until after the lapse of a definite period. Nothing is yet known as to the exact structural and other changes which go on by virtue of this peculiarity.

1192. **Ripening of fruits and seeds.** The structural changes attending this process, taken together, result in adaptations for providing the embryo with an ample supply of food, for giving it adequate protection during its resting state, and for securing its dissemination.

1193. The chemical changes comprise chiefly the storing up of a sufficiency of food of a proper character to support the embryo for a time. In pulpy fruits they are mostly associated with the consumption of a certain amount of oxygen and the liberation of more or less carbonic acid. Many of the chemical changes can go on after the separation of the fruit or seed from the parent plant.

In the ripening of pulpy fruits the important changes in texture are attended by the formation of sugars, acids, etc., and by modifications in the character of the walls of cells.

1194. **Dissemination** is most frequently secured by (1) some mechanism for transport by air, water, fleece, or plumage; (2) the construction of some expulsive apparatus; (3) the existence of certain attractions of taste, color, and odor, by which the seeds are made the food of birds. In the last case the germ itself, protected against the action of digestive juices, is often carried to great distances from the parent plant.

1195. **Ripeness of seeds.** The embryo is sometimes viable, or capable of independent life, at a very early stage. Immature seeds are of course deficient in their supply of proper food for the embryo, which is only imperfectly developed, and their integuments are not yet adapted to protect the germ adequately. But in certain instances such seeds may germinate, giving rise to strong and healthy plants. Cohn[1] has shown that seeds which are not perfectly ripe germinate somewhat sooner than those which are more mature; this means that the store of food is in a condition which admits of immediate use. He has further pointed out that seeds separated from the plant, but still enclosed in the pericarp, ripen; and he believes that those seeds which have reached a medium stage of ripeness germinate most readily. "Viability does not coincide with ripeness; it precedes it."[2]

1196. Shortly before the period of ripening, the part which

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[1] Flora, 1849, p. 481.

[2] There is some reason to believe that in the case of certain cultivated vegetables unripe seeds may give rise to earlier varieties than come from ripe seeds. For numerous citations from the extensive literature of the subject see a paper by the author in the Report of the Secretary of the Massachusetts Board of Agriculture for 1878.

connects the fruit or seed with the parent plant undergoes marked changes, which ultimately effect or permit complete separation of the seed from the plant without any injury. The process of separation has been compared to that by which the leaf is detached from the branch in the autumn.

1197. **How long can a seed retain its vitality?** Some seeds perish shortly after separation from the parent unless they are at once planted, while others preserve their vitality for long periods. In experiments by De Candolle seeds of three hundred and sixty-eight species of plants were kept in the same place and under the same conditions for fifteen years. The following results are recorded: —

Of	1 Balsaminaceæ	1	came up,	or 100 per cent.
"	10 Malvaceæ	5	" "	" 50 " "
"	45 Leguminosæ	9	" "	" 20 " "
"	30 Labiatæ	1	" "	" 3⅓ " "
"	10 Scrophulariaceæ	0	" "	
"	10 Umbelliferæ	0	" "	
"	16 Caryophyllaceæ	0	" "	
"	32 Gramineæ	0	" "	
"	34 Cruciferæ	0	" "	
"	45 Compositæ	0	" "	

1198. Daubeny, Henslow, and Lindley found that the seeds of a species of Colutea germinated when forty-three years old, and those of a Coronilla when forty-two years old. They ascertained that the seeds of plants belonging to twenty genera experimented on, germinated after from twenty to twenty-nine years' separation from the parent plant.[1]

There is no unquestioned evidence that wheat-grains from the wrappings of mummies have been made to germinate.[2]

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[1] Report of the British Association for the Advancement of Science, 1850, p. 165.

[2] The following notes of cases of prolonged vitality may be of interest: —

M. R. Brown m'a dit avoir fait germer des graines de Nelumbium speciosum extraites par lui de l'herbier de Sloane, c'est-à-dire ayant au moins 150 ans (De Candolle: Géographie Botanique raisonnée, 1855, p. 542).

Seeds of Nelumbium (*jaune*) have sprouted after they had been in the ground for a century (Lyell's Second Visit to the United States, ii., 1849, p. 328).

The grains of wheat found in mummy-wrappings are uniformly blackened as if by slow charring (*eremacausis*), and there is no evidence of a trustworthy character that such seeds have ever been made to germinate. The account by Count von Sternberg of the germination of wheat supposed to have been procured at the unrolling of a mummy will be found in Isis, 1836, col. 715–717.

GERMINATION.

1199. Germination,[1] the process by which an embryo unfolds its parts, is complete when the plantlet can lead an independent existence.

1200. **The conditions necessary for germination** are (1) moisture, (2) free oxygen, (3) warmth.

1201. *The amount of water required* to initiate the process of germination is, in general, that which will completely saturate and soften the seed. Germination does, however, begin in certain cases even when only the radicle and the albumen directly around it have become soaked.

The amount of water requisite for the saturation of a seed has been determined for a large number of plants, and will be seen by a comparison of the results to vary within wide limits, depending on the percentage of water already present and the character of the albumen. It is plain that in very exact determinations account must be taken of the possibility of a loss by the seed of a portion of its contents while in water; in three days this amounts in the common bean to a little over two per cent. The cereals require a comparatively small amount of water for saturation, while leguminous seeds absorb a much larger quantity.[2]

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[1] It is well to distinguish between two stages in the process of germination, (1) that marked by the protrusion of the first rootlet, (2) the subsequent development of the embryo into an independent plant. The reason for making this distinction is, that most of the experiments upon the relations of temperature, etc., to germination have usually terminated at the first stage; whereas the vigor of the plantlet as seen at a later stage is an important factor in deducing results to guide practice in sowing seeds.

[2] The table below, by Hoffmann (Versuchs-Stationen, vii., 1865, p. 52), has a parallel column of results obtained at Tharandt (Nobbe: Samenkunde, p. 119):

Species.	Percentage of liquid water absorbed.	
	Observations by Hoffmann.	Observations at Tharandt.
Indian corn	44.	39.8
Wheat	45.5	60.
Buckwheat	46.9	
Rye	57.7	
Oats	59.8	
White beans	92.1	
Windsor bean	104.	157.
Peas	106.8	*a.* 96. *b.* 71.
Red clover	117.5	105.3
Sugar beet	120.5	
White clover	126.7	89.

1202. The increase of seeds in size accompanying the absorption of water is ascertained by placing them from time to time in a narrow graduated cylinder, pouring over enough water to completely cover them, and noting the height at which the water stands; then pouring it into another graduated glass and accurately measuring it. The difference in amount of water in each case indicates the volume of the seeds. The work must be done expeditiously in order to avoid the error arising from absorption during the period of measuring; but this error in any case is slight.

1203. The following results may be of interest and serve as a guide to the student.[1]

65.418 grams of air-dried peas, having a volume of 43 cubic centimetres, were soaked in water at a temperature of 19°–21° C. The soaked seeds were at each measurement carefully dried by blotting-paper: —

Time.	1. In absolute figures.		2. In percentages.	
	Weight.	Volume.	Weight.	Volume.
14 hours . . .	46.41 gr.	46 cc.	70.9	107
41 " . . .	8.02 "	19 "	12.3	44.1
70 " . . .	8.52 "	7 "	13	16.3
70 hours . . .	62.95 gr.	72 cc.	96.2	167.4

The gain in weight in 70 hours was therefore 96 per cent, and in volume 167 per cent.

In another experiment the changes were as follows: Phaseolus vulgaris gained in weight, in 48 hours, 100.7 per cent, and in volume, 134.14 per cent. In still another experiment, with the same species, the gain in weight in 72 hours was 114.5 per cent (or, taking into account some loss by extraction, 117.5 per cent), and in volume, 140.9 per cent. The gain in volume is considerably greater than the gain in weight.[2]

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[1] Nobbe: Handbuch der Samenkunde, 1876, p. 122.

[2] It must be noted that in many dry seeds, for instance between the cotyledons of some peas and beans, there are cavities which must be filled before there can be any marked increase of volume (Nobbe: Handbuch der Samenkunde, 1876, p. 125).

1204. The greater part of the increase in weight and volume from the absorption of water by dry seeds takes place in a short time; for example: —

Phaseolus vulgaris.	Increase in weight.	Increase in volume.
In 6 hours	13.99 per cent.	28.28 per cent.
“ 9 “	18.63 “ “	13.10 “ “
“ 23 “	49.42 “ “	62.07 “ “
“ 28 “	3.35 “ “	3.45 “ “

After this there was very little gain either in weight or volume.

1205. *Access of free oxygen* must be provided to secure germination. Even if all other conditions are favorable, germination does not take place in pure water devoid of any free oxygen, or in an atmosphere of nitrogen.

1206. The oxygen accessible to the seed must be diluted to about the degree found in common atmospheric air, although it is not necessary that the dilution should be made with nitrogen, as is the case with air. Boehm[1] has shown that a mixture of proper proportions of hydrogen and oxygen answers about as well as a mixture of nitrogen and oxygen for germination of seeds, provided it is furnished to them under ordinary atmospheric pressure. That the degree of pressure is an important factor, is proved by Bert's[2] experiments. Barley gave the following results: —

	Percentage germinated.
In ordinary air (76 cm. pressure)	84
In air 50 “ “	40
“ “ 25 “ “	28
“ “ 6 “ “	10

The proportion of oxygen to nitrogen in atmospheric air is approximately 1 : 5 (oxygen, 21, nitrogen, 79 parts).

1207. *The temperature requisite for germination* to begin differs considerably in different species. The lowest temperature recorded is the following, noted by Uloth:[3] In a perfectly dark ice-cellar seeds of Acer platanoides sprouted on ice, the rootlets penetrating to a depth of 5 to 7.5 cm. into the dense

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[1] Sitzber.: Wien Akad., lxviii., 1873, p. 132.

[2] Comptes Rendus, lxxvi., 1875, p. 1493.

[3] Flora, 1871, p. 185.

clear ice; the seeds themselves being in hollows on its surface. The temperature must of course be given as 0° C. Uloth found also that wheat-grains germinated in the same cellar upon pieces of ice. Kerner[1] placed seeds with some earth in glass tubes and exposed them to the cold springs on the edge of snow-fields in Alpine regions. He found that the seeds of most Alpine plants could germinate at 2° C., and that some might even at 0°. It was shown that at all growing points there is some heat evolved. In Uloth's observations, above noted, attention is called to the fact that the rootlets descended into solid ice in a number of cylindrical cavities which they melted out for themselves.

1208. The *minimum* temperature for germination of the seeds of many plants in common cultivation is given by Haberlandt[2] as 4°.75 C. (although some can start even below this). Between 4°.75 and 10°.5 we have the minimum temperature for Indian corn, timothy grass, sunflower; between 10°.5 and 15°.6, that for tobacco and squash; between 15°.6 and 18°.5, that for cucumber and melon.

1209. The *maximum* temperature, or that beyond which germination cannot begin, differs greatly in different species. Haberlandt has shown that degree of ripeness, freshness, the "race," and several other influences considerably modify the result. The maximum temperature for a few of the more common plants is here noted: —

	C°.
Wheat, rye, barley, oats, peas, timothy grass, cabbage, poppy, flax, and tobacco	31–37
Red clover, lucerne, buckwheat, and sunflower	37.5–44
Indian corn, millet, squash, cucumber, and sugar melon	44–50

In no case was germination observed above 50° C.

1210. Between the minimum temperature below which and the maximum temperature above which germination of a certain kind of plant does not ordinarily take place there lies an *optimum* temperature; that is, the degree at which germination begins most speedily.[3] The short table on the following page is by Sachs: —

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[1] Berichte der naturw-med. Vereines in Innsbruck, 1873, and Botanische Zeitung, 1873, p. 437.

[2] Versuchs-Stationen, xvii. p. 104.

[3] The difference in regard to the degree of warmth demanded by seeds of the same species raised in different climates has been examined by Schübeler (Die Culturpflanzen Norwegens, 1862, p. 27).

	Minimum.	Maximum.	Optimum.
Barley	5°	38°	29°
Wheat	5°	42°	29°
Scarlet runner	9.°5	46°	33°
Indian corn	9.°5	46°	33°
Squash	11°	46°	33°

1211. The time required after planting for germination to begin, a point indicated by the protrusion of the radicle, has been determined[1] for a large number of plants. A few examples are here mentioned: —

	Indian corn.	Red clover.	Birch.
At 16° C.	144 hours.	32 hours.	120 hours.
" 25° C.	56 "	24 "	24 "
" 31° C.	48 "	24 "	24 "
" 37°.5 C.	48 "	24 "	24 "
" 44° C.	80 "		72 "

1212. The influence of light upon the earliest stages of germination has been shown by careful investigations to be inappreciable so far as most plants are concerned.[2]

The unqualified statement found in some works,[3] that light is in general prejudicial to germination, is not borne out by facts.

1213. **The phenomena of germination** are: (1) forcible absorption of water, (2) absorption of oxygen, (3) solution of nutrient matters, (4) their transfer to points of consumption, (5) their employment in building up new parts. After the initial step these processes may go on simultaneously.

1214. The enormous imbibition power of dry seeds can be demonstrated by confining sound seeds in a strong receptacle to which water can obtain access. If a closed manometer is attached, the pressure they exert can be measured. Boehm[4]

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[1] Versuchs-Stationen, xvii., 1874, p. 104; and Storer: Bulletin Bussey Inst., 1884.

[2] Hoffmann: Jahresber., über Agricultur-Chem., 1864, p. 110.

[3] Ingenhousz; Senebier, Physiologie végétale, iii. 1800, p. 396; Johnston's Lectures on Agricultural Chemistry, 1842, p. 194.

[4] Müller: Botan. Unters. ii., 1872, p. 29, quoted by Nobbe (Handbuch der Samenkunde, p. 118). Similar experiments at Wellesley College gave results somewhat lower than this.

found that peas in swelling could overcome a pressure of 18 atmospheres, corresponding to a height of the mercurial column of 13.5 metres.

1215. The influence of oxygen upon the absorption of water by the seed is not marked, as will be seen by the following experiment:[1] —

200 fresh seeds of red clover were placed in pure water for 20 hours; 200 more were placed in water into which oxygen gas was conducted; 200 more in water through which carbonic acid gas was conducted for a while and then the water covered with a layer of oil to exclude the air. The results, so far as swelling is concerned, were as follows: —

Seeds in water	83 per cent swollen.
" " with oxygen	86 " "
" " " carbonic acid . .	71 " "

1216. The oxygen absorbed by seeds in germination was thought by Schönbein to undergo the active or ozone modification. By his experiments the seeds of two plants, Cynara Scolymus and Scorzonera Hispanica, were shown to possess to a considerable degree the power of converting atmospheric oxygen into ozone.

1217. Oily seeds absorb a large amount of oxygen. Siewert has pointed out the fact that the neutral oil of the rape-seed very soon after access of oxygen and water to it possesses an acid reaction. Oleic acid can absorb at ordinary temperatures about twenty times its volume of oxygen.

1218. Nutrient matters must become liquid before they can be utilized by the embryo. Some of these in the form in which they are stored up in seeds are soluble in water; such are the sugars, dextrin, and a part of the albumin. The other nutrient matters, such as starch, the oils, and most nitrogenous substances, must undergo changes before they can enter into solution. Some of these changes have already been alluded to in Chapter XI., and are here presented in brief review.

1219. The conversion of starch into soluble matters is effected in the seed by means of one or more "ferments." In the process of malting,[2] which consists essentially in forcing germination up to the point of protrusion of the radicle and then checking it, the starch appears to undergo little change. But if the ground malted grains are kept in water of a temperature of 68° C. for

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[1] Nobbe: Handbuch der Samenkunde, 1876, pp. 102, 103.

[2] See Watts's Dictionary of Chemistry, under "Beer."

two hours, all the starch will be found to have been converted into and dissolved as soluble carbohydrates, sugar, and dextrin. The change in this case is attributed to the ferment, *diastase*, one part of which, it is claimed, can convert two thousand parts of starch into sugar. It will be noted that in the process above described the temperature (68° C.) is much higher than that at which ordinary germination proceeds.

Dubrunfaut[1] has given the name *maltin* to a ferment far more active than diastase, found in all germinating cereals. This is able to convert into a soluble state from one hundred thousand to two hundred thousand times its weight of starch. It forms with tannic acid an insoluble compound which retains its power for a long time. In good barley meal there is one per cent of maltin.

1220. The oil in oily seeds is in germination carried through a long series of changes. It is first transformed into starch, and then follows the same course as starch, already described.[2]

1221. Van Tieghem has shown that oleaginous albumen, rich in aleuron, has an activity of its own which enables it to digest itself, so to speak, and thus become at once fit for the embryo to use; on the other hand starchy albumen and cellulosic albumen must be first acted on by the embryo, and thus become dissolved and ready for use.[3]

1222. The changes which take place in a germinating seed are accompanied by direct or indirect oxidation of a portion of the nutrient matters, a release of energy, and an evolution of carbonic acid.[4] The amount of CO_2 given off by germinating seeds and the rise of temperature serve as measures of the process of oxidation.

1223. It is not proved that germination can be hastened by chemical means. Experiments with dilute chlorine water seem to show that the time can be somewhat lessened, but the results are discordant.[5]

1224. It has been asserted recently that the presence of microbes, the minute organisms to which putrefaction is due, is

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[1] Comptes Rendus, lxvi., p. 274.

[2] Peters, Versuchs-Stationen, iii., 1861, p. 1; Müntz, Ann. de Chimie et de Physique, sér. 4, tome xxii. p. 472.

[3] Ann. des Sc. nat., sér. 6, tome iv., 1877, p. 189.

[4] For the changes in the horny endosperm of the date palm see Sachs, Botanische Zeitung, 1862, p. 241.

[5] See M. Carey Lea, American Journal of Science, xxvii., 1864, p. 373, and xliii., 1867, p. 197.

essential to the beginning of the process of germination. It is said that in soil which has been completely sterilized, that is, freed from microbes or their germs, seeds provided with all other requisites for germination will fail to sprout. These experiments by Duclaux[1] have not been repeated by other observers.

1225. The appearance of abundant crops of certain plants upon ground recently cleared by fire is one of the most noteworthy phenomena in connection with germination. At the North, two plants have obtained, *par excellence*, the name of "fire-weeds;" namely, Erechtites hieracifolia, and the more common willow-herb, or Epilobium angustifolium. They are later replaced by shrubs, and later still by soft-wooded trees, which are characteristic of burnt districts. The following suggestions have been made in regard to their appearance: (1) that the seeds have been long buried in the soil, under conditions which have preserved their vitality, but which did not permit them to germinate; (2) that the seeds find their way to the ground of a clearing which affords, in the ash released from wood by burning, a soil most fit for germination. But no exact observations have yet been made upon the subject.

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[1] Comptes Rendus, c., 1885, p. 67.

CHAPTER XVI.

RESISTANCE OF PLANTS TO UNTOWARD INFLUENCES.

1226. Claude Bernard has shown that life presents itself under three forms: (1) latent, dormant, or inactive, illustrated by the seed; (2) variable, or oscillating, exemplified by the plant during periods of apparent rest, when its activities are nearly suspended, but when, in fact, some chemical changes are going on, though very slight in degree; (3) active, or free, exhibited by a plant in full vigor.

It has been repeatedly pointed out in previous chapters that during their resting periods seeds and other parts can be subjected to the action of influences which would destroy the life of plants in full activity.[1]

1227. Inquiry as to the kind and amount of injury caused to active plants by hurtful agents must deal with the influence of extremes of temperature, too intense light, improper food, poisons, and mechanical agents. Many of these injurious influences and their effects upon special parts of the plant have already been alluded to in previous chapters; but it is proper to consider them now with regard to the whole organism.

1228. **Effects of too high temperature upon the plant.** Here, as in most other cases, there is wide diversity among plants, depending upon their constitutional peculiarities; thus, plants of the tropics not only demand higher temperatures than those of

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[1] For some account of various recent views in regard to the nature of life, the student is referred to the following works: Herbert Spencer, Principles of Biology, 1870; Claude Bernard, Leçons sur les Phénomènes de la Vie communs aux Animaux et aux Végétaux, 1879; and Nägeli's recent treatises.

For an interesting account of the reactions of living matter to very dilute solutions of certain substances which are poisonous when used in greater strength, see Loew and Bokorny. These investigators use a dilute alkaline solution of argentic nitrate in the discrimination between living and dead protoplasm; upon application of the reagent the former turns black, the latter remains uncolored. The solution is made by mixing 1 cc. of a one per cent solution of the nitrate in distilled water with an equal amount of a solution containing 13 parts of potassic hydrate solution, 10 parts of ammonia, and 77 parts of distilled water (Pflüger's Archiv. xxv., 1881, p. 150).

colder climates for the exercise of their normal functions, but they will also generally sustain much higher degrees of heat without injury. The differences of temperature in favor of tropical plants are not, however, always very marked.

The following table[1] indicates sufficiently the highest temperatures which a few common plants can bear. The line at the top shows what were the immediate surroundings of the plants experimented upon; the columns marked A show the highest temperatures short of proving fatal; those marked B, the lowest fatal temperatures. The plants were exposed to the high temperatures from fifteen to thirty minutes.

Name of Plant.	Roots in water, stems in air.		Roots in soil, stems in air.		Plant in water.	
	A.	B.	A.	B.	A.	B.
	° C.	°	°	°	°	°
Zea Mais	45.5	47.	50.1	52.2	46.	46.8
Tropæolum majus	45.5	47.	50.5	52.	44.1	45.8
Citrus Aurantium	47.8	50.5			50.3	52.5
Phaseolus vulgaris	45.5	47.	50.	51.5		

1229. After a plant has been subjected to too high a temperature, its foliage wilts and soon becomes dry; and its leaves, having once taken on a scorched appearance, are unable to recover their turgescence. It may happen, however, that the injury does not proceed so far as to affect the latent or even the partially developed buds; if this is the case, partial recovery takes place through their unfolding. The curious fact[2] that many algæ can resist very high temperatures has been already adverted to (see 566).

1230. **Effects of cold upon the plant.** Certain plants are seriously injured by low temperatures which are considerably above the freezing-point of water, but these are exceptional cases. Most northern plants can readily endure cold, provided their tissues are not frozen.

Frost produces very different effects upon different plants. In some of our familiar spring plants the leaves may be frozen and thawed without apparent mischief, but in general the thawing must take place slowly; if it proceeds rapidly, the plant may be

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[1] De Vries: Archives Néerlandaises, v., 1870.

[2] Consult also American Journal of Science and Arts, xliv., 1867, p. 152.

irreparably injured. There are well-known cases in which plants may be thawed quickly without serious injury.[1]

1231. Göppert[2] and others have shown that the flowers of certain orchids, turned blue by the formation of indigo in their cells when they are slightly frozen and suddenly thawed, will preserve their usual colors unchanged if made to thaw very slowly.[3]

1232. As to the length of time during which the vitality of a frozen plant persists, we have no exact observations; but it is stated that after the recession of a glacier in Chamouni several plants which had been covered by ice for at least four years resumed their growth.[4]

1233. It is still an open question whether much of the injury to certain plants by freezing is not strictly mechanical, resulting from the expansion during the formation of ice in the cells.[5]

1234. **"Winterkilling."** The destruction of many plants by exposure to the influences of a variable winter is sometimes attributed to the injurious effects of drying winds rather than to cold alone. It has been shown (748) that the amount of water absorbed by roots is governed largely by the temperature of the soil. Although the exhalation of moisture from the leaves of evergreens in winter is not large, it is, however, sufficient to create a certain demand upon the soil for a supply. This demand, slight as it is, is of course greater during very dry weather; and it is from this that the injuries may be supposed largely to result.

1235. The behavior of certain plants during exposure to low temperatures affords some of the best illustrations of the adaptation of vegetation to its surroundings; and the question as to increasing the tolerance of a given species or variety to the

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[1] Sachs has shown that the leaves of cabbage, turnip, and certain beans frozen at a temperature of from —5° C. to —7° C., and placed in water at 0° C., are immediately covered with a crust of ice, upon the slow disappearance of which they resume their former turgescence (Versuchs-Stationen, ii. 1860, p. 167). If such frozen leaves are placed in water of 7.5° C. they become flaccid immediately.

[2] Botanische Zeitung, 1871, p. 399.

[3] According to Kunisch (quoted by Pfeffer: Pflanzenphysiologie, ii., p. 436), this blue discoloration is observed when the flowers, placed in an atmosphere of carbonic acid, are subjected to a freezing temperature: in this case, of course, the indigo is produced from chromogen without free oxygen.

[4] Botanische Zeitung, 1843, p. 13.

[5] Hoffmann (Grundzüge der Pflanzenklimatologie, 1875, p. 325) attributes a part of the mechanical injury from freezing to the separation from the cell-sap of the air previously contained therein.

untoward influence of cold, by careful selection of seed for a series of years, has been successfully answered by cultivators in some northern countries of Europe.[1]

1236. Among the protective adaptations of seedlings to cold is that described by De Vries,[2] who has noted that in certain instances there is a marked retraction of the caulicle into the ground upon the approach of a lower temperature. The withdrawal is due to the contraction of the cellular tissue composing the root.

1237. **Effects of too intense light upon the plant.** All other conditions being natural, living plants containing chlorophyll can perform their functions normally when placed in the brightest sunlight.[3] Even when the rays of light are moderately concentrated upon the foliage by a large convex lens there is no serious disturbance of function. But when, as in Pringsheim's experiments (see 824), the sunlight is rendered very intense, assimilation is arrested and destruction of the protoplasm soon ensues.

1238. **Effects of improper food upon the plant.** It has been shown (Chapters VIII. and X.) that certain substances are indispensable to the healthful growth of plants; and it has further been pointed out that most of these substances may be offered to the plant in excess with no marked results. It should now be noted that a few of these substances, notably nitrogen compounds, applied in excess may induce a more luxuriant growth than is desirable to the cultivator. Penhallow[4] and others have pointed out that certain maladies of plants are largely dependent upon malnutrition. In such maladies fungi are frequent concomitants, in many cases invading plants already enfeebled by improper or insufficient food; in others, obviously causing by their presence and activity the diseased conditions.

1239. **Effects of poisons upon the plant.** *Noxious Gases.* The most hurtful of these, considered from a practical point of view, come as products of the combustion of inferior sorts of coal,

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[1] Schübeler (see note on page 465).

For an account of the formation of ice in plants, and the different degrees of temperature at which it takes place, consult Müller: Landwirthschaftl. Jahrbücher, ix., 1880.

[2] Botanische Zeitung, 1879, p. 649. Haberlandt has also examined the same mechanism to some extent.

[3] It is a familiar fact that many plants thrive best in deeply shaded glens. Success in the cultivation of such plants is attained only by regarding their natural condition.

[4] Houghton Farm Experiment Department, series 3, no. iii.

especially those which contain sulphur compounds as impurities.[1] Formerly, in the vicinity of large chemical factories, the escaping gases were productive of wide-spread injury to vegetation; but improved methods of manufacture have diminished this evil to a considerable extent.

1240. Sulphurous acid, formed by combustion of sulphur in the open air, produces, even when existing in the air in the proportion of only one part in 9,000, the following effects upon leaves: their blades shrivel from the tips, become grayish yellow, and soon dry so that they fall off at a slight touch. The phenomena observed are somewhat like those occurring at the time of the fall of the leaf in autumn. Yet in the experiments by Turner and Christison mentioned in the note,[2] the amount of sulphurous gas present in the air was so small as to escape detection by smell.

Hydrochloric acid gas, nitric acid in vapor, and chlorine are also very destructive to plants, even when in such minute amounts as to be unnoticed on account of their odor.

Injurious effects are often produced upon shade trees by the leakage of illuminating gas from street mains.

1241. *Wardian Cases.* In 1829 Ward accidentally discovered that plants could thrive in tightly closed cases, in which there could not be any interchange of the air with the outside atmosphere.[3] This discovery led him to institute experiments rela-

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[1] R. Angus Smith: Air and Rain, 1872, pp. 465, 553.

[2] For accounts of experiments in this interesting field, the student may consult the following works: Turner and Christison, Edinburgh Medical and Surgical Journal, xxviii. p. 356; and Gladstone in Report of British Association for Advancement of Science, 1850.

[3] N. B. Ward: On the Growth of Plants in Closely Glazed Cases, 1852.

The table on the following page, based on researches by T. W. Harris, shows the agents, the effects of which were tried upon chlorophyll, and the results in each case as to the extrusion of chlorophyll pigment (see 772). The figures in the third column indicate results as follows: —

1. Chlorophyll grains large and well defined. Sponge-like structure evident. One or two globules of large size on almost every grain; sometimes almost as large as the grain itself, which is colorless or nearly so.

2. Globules still plentiful but smaller; frequently several on each grain. Structure of the grains evident. The protoplasm in this and the two following grades (3 and 4) is often contracted by the chemicals used, rendering the result more or less obscure.

3. Globules small, and fewer than in 2. Grains still retain some coloring-matter in their substance, and are not so well defined either in form or structure.

4. Globules few; only seen on a few grains. Structure of the grain not defined, but under a high power it frequently has a granular and sometimes a

tive to the systematic cultivation of plants in such cases in the impure air of manufacturing towns. In the glass cases, now

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stellate appearance. In the latter case each grain is generally surrounded by an irregular mass of colored protoplasm, these masses being often connected together by threads. This stellate structure is also often brought out after dissolving out all the coloring-matter by prolonged treatment with benzoic acid.

5. No result.

Agent.	Time of Action.	Result.
Alcohol (95 %)	1 day.	Grains bleached, but form remains.
Steam	1 hour.	2
Boiled in H_2O	7 min.	2
" " then cold in HCl	2 days.	3 } Chlorophyll stellate.
" " " " HNO_3	2 "	3
" " " " Benzoic Acid	2 "	3
H_2SO_4 conc.	1 "	Specimen destroyed.
H_2SO_4 dilute	1 "	3
HNO_3 conc.	1 "	Protoplasm contracted.
HNO_3 dilute	1 "	1
HCl	1 "	2
$HCl + HNO_3$ (3 parts HCl, 1 part HNO_3)	1 "	Protoplasm much contracted.
$H_2SO_4 + HCl$ (equal parts)	2 "	3
$H_2SO_4 + HNO_3$ "	2 "	3
$H_2SO_4 + HCl + HNO_3$ (equal parts)	2 "	3
$HC_2H_3O_2$	7 "	3
$H_2C_2O_4$	7 "	3
H_3PO_4	7 "	2
$H_2C_4H_4O_6$ (Tartaric acid) { Slight result after 3 days. }	7 "	2
H_2CrO_4	7 "	4
Picric Acid	7 "	4
Citric Acid	7 "	3
Boracic Acid	7 "	3
Benzoic Acid { sat. sol. in a sol. of 1½ parts Na_2HPO_4 to 100 H_2O }	1 "	1
Benzoic Acid	2 "	Grains bleached.
Salicylic Acid	3 "	3
Na_2HPO_4	6 "	5
$Na(NH_4)HPO_4$	6 "	5
$NaHSO_4$	6 "	5
NaOH	2 "	Grains destroyed and pigment diffused through the protoplasm.
NH_4OH	2 "	5
K_2CO_3	2 "	5
Ether	1 "	Grains swell and become homogeneous, but no extrusion or escape of the pigment.

everywhere known as Wardian cases, the plants are supplied with sufficient water, and the atmosphere is practically saturated with moisture. When exposed to sunlight, the plants in the cases can carry on all the operations of assimilation, growth, and respiration.

Comparing the conditions which surround the plants in a Wardian case with those which prevail in a furnace-heated house, it is plain that the plants in the case are placed in what is essentially a humid tropical climate, while those in the house are exposed to excessive dryness, and to an atmosphere which may contain minute traces of the poisonous gases arising from combustion.

1242. *Liquids and Solids.* Comparatively few substances except those possessing strong acid or alkaline properties are injurious to a plant. As indicated in 685, preparations of arsenic which are extensively employed for the destruction of insects upon crops in cultivated fields are not absorbed by plants to an appreciable extent. This is further illustrated by the impunity with which various other insecticides can be applied to greenhouse plants.

1243. Numerous experiments, more curious than profitable, have been made to test the effect of poisonous alkaloids upon vegetation. Many observers have proved that some plants yielding poisonous alkaloids may be poisoned by applications to their roots of solutions of the very alkaloids which they have themselves produced; thus morphia may poison the poppy (see 961). Strasburger[1] says that morphia speedily kills motile spores.

Kühne[2] has noted that the protoplasmic movement in the stamen-hairs of Tradescantia is not wholly arrested, even after many hours, by a solution of veratrin; and Pfeffer[3] has observed that the cells in sections of certain fleshy roots are not killed even when immersed for several days in a saturated solution of morphia acetate.

As Frank[4] suggests, these discrepancies in effects depend on the differences in the power possessed by the various parts in the absorption of such matters.

1244. **Effects of mechanical injuries upon the plant.** The most important of these are caused by destructive fungi. The destruc-

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[1] Wirkung des Lichtes und der Wärme auf Schwärmsporen, 1878, p. 66.

[2] Untersuchungen über das Protoplasma, 1864, p. 100.

[3] Pflanzenphysiologie, ii., 1881, p. 454.

[4] Pflanzenkrankheiten, 1879.

tion primarily affects the cell-contents, and later the cell-wall. It is very highly probable that in certain cases various products of decomposition arising from the progress of the fungi may themselves prove poisonous to contiguous parts of the plant.

One of the most important problems of practical horticulture and agriculture is the search for efficient means by which invading fungi may be destroyed without at the same time injuring the host-plant to which they have attached themselves.[1]

1245. The presence of certain fungi in plants sometimes gives rise to abnormal growths and to various distortions. When once their disturbing influence is felt, the subsequent growth may be affected for a long time, and the malformations become of an extraordinary character.

1246. Considerable distortions are often produced by bites or other injuries by insects.[2] Galls — for instance those of the oak and willow — are among the most noteworthy instances of this kind.

1247. The effects of lightning upon trees have been examined by many observers. Cohn[3] and Colladon[4] have pointed out some of the characteristic injuries sustained by species of poplar, elm, and oak, stating that the stroke does not usually affect the summit of the first two, but that oaks are frequently struck at their uppermost branches. The course of the injury is often spiral, winding around the trunk in stripes which involve part of the sap-wood and bark.

It is not now believed that any species of trees are exempt from injury from lightning, although the ash was formerly thought to possess a remarkable degree of immunity.

1248. **Partial or complete blanching** of otherwise healthy leaves exposed to light has been regarded by some observers as an indication of a diseased condition. In some cases the blanching is dependent upon a lack of iron in the soil (see 791), but in others it appears to be strictly hereditary, being propagable both by bud and by seed. Nothing is known, however, as to its causes in these cases, and they are generally referred to the unsatisfactory category of sports.

It is worthy of notice that a considerable proportion of the so-called variegated plants, especially of those which have only

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[1] For an account of some experiments in this field, see Frank : Pflanzenkrankheiten, 1879 ; and Nobbe : Handbuch der Samenkunde.

[2] For a bibliography of this subject, see Frank's Pflanzenkrankheiten.

[3] Denkschrift. d. Schles. Ges. f. vaterl. Kult. Breslau, 1853, p. 267.

[4] Mém. de la Soc. de Phys. et d' Hist. Nat. de Genève, 1872, p. 501.

white spots intermingled with the green of the leaf, come from eastern Asia, notably from Japan.[1]

1249. The lease of life of any given plant is fixed primarily by the inherited character:[2] hence we have annuals, biennials, and perennials; but these differences are not in all cases absolute, in some they are even ill-defined. The lease of life is modified secondarily by external influences, which have been sufficiently discussed in the present volume. In conclusion, attention should be called again to the fact (see Chapter V.) that in many instances the duration of the life of the plant is determined largely by mechanical factors, especially the strength of materials.

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[1] Morren: Hérédité de la Panachure, 1865, p. 7; Frank: Pflanzenkrankheiten, p. 465.

[2] The student should examine Minot on "Life and Growth."

GLOSSARIAL INDEX.

GLOSSARIAL INDEX.

The numbers following the titles refer to pages. An italicized page-number indicates that the term which it follows is defined on the page to which it refers.

PRACTICAL EXERCISES.

SUGGESTIONS FOR STUDIES IN HISTOLOGY AND PHYSIOLOGY OF PHÆNOGAMS.

THE following hints are designed chiefly to aid students who have at their command the simpler appliances described in the foregoing pages. In addition to the simpler exercises there are also suggested a few which are quite within the power of students having access to a small chemical laboratory and a small cabinet of physical apparatus. The chemical and physical outfits now found in many of our high schools will prove ample for the successful prosecution of these experiments.

HISTOLOGICAL PRACTICE.

Material for study. The supply of material for histology should be abundant and of the best quality, all inferior or imperfect specimens being carefully excluded. It (except that distinctly referred to as *fresh*) should be collected at proper seasons and preserved at once in strong alcohol, great care being exercised to have every specimen accurately labelled; name, locality, time of gathering, etc., being noted. When alcoholic material is required for immediate use in the preparation of sections, it can be softened, if necessary, by soaking in pure water, as directed in 37.

Delineation. When a satisfactory section or preparation has been secured, the student should make an accurate drawing of its essential features. The employment of a camera lucida (12) insures correct proportions in all parts of the sketch, and is always to be recommended. Drawings made by its aid are conveniently designated by the following abbreviated term, *ad nat. del.* It may seem scarcely necessary to caution students against obscuring any part of their histological sketches by meaningless shading; a few clean and clear outlines suffice to express the character of the preparation better than any attempt to give the effects of light and shade. There are some exceptions to this broad statement; for instance, preparations of nascent flowers are shown equally well by shaded figures, and the same is true of many pollen-grains, etc. The use of slips of drawing-paper of uniform size and the arrangement of these under appropriate heads will render the keeping of a systematic record of work much easier.

Permanent preparations. In most cases the sections or other preparations should be permanently mounted in some suitable preservative medium, and properly labelled with the name of the plant and of the special part exhibited, date of preparation, medium in which it is mounted, etc. The drawings should be numbered or labelled to correspond with the permanent preparations.

Histological elements, their modifications and combinations. In the following enumeration of the more important elements the sequence is (1) form, (2) contents, (3) distribution, (4) development.

FORMS OF THE STRUCTURAL ELEMENTS AND SIMPLE TISSUES.

I. Parenchyma Proper and its Chief Modifications.

(*a*) Soak a few peas or beans in water until they become soft enough to be cut without difficulty, remove the seed-coats, and make with a wet razor (see 8) three very thin sections through the cotyledons. These sections for comparison should be at right angles to one another, in order to exhibit the length, breadth, and thickness of the cells. On removing them from the knife or razor (by means of a camel's-hair brush), float them in water and move them gently about, in order to detach the cell-contents which have partly escaped from the cut cells. When the sections appear clear, transfer them to the middle of a glass slide, add a little pure water and cover with thin glass, being very careful to exclude all air-bubbles. If the sections are thin and wholly free from bubbles of air, compare the outlines of the cells with one another, making drawings of the specimens.

(*b*) Make similar sections (1) through the pulp of any unripe fruit — apple, pear, snow-berry, etc.; (2) through the pith of Elder, Lilac, or any soft shoots; (3) through the pulp of any succulent leaves, for instance those of Sedum, Purslane, or Begonia.

(*c*) Make a transverse and a vertical section through the petiole of any water-lily, or through the soft interior of any rush (Juncus).

(*d*) When, after considerable practice, the student succeeds in making *very* thin sections of the foregoing plants, let the reagents for the demonstration of cellulose be applied to them, as directed in 143.

It is not superfluous to state (1) that success in the application of these and most of the other reagents employed under the microscope is generally preceded by many failures, and (2) that carelessness in the use of some of the reagents may irreparably ruin the microscope lenses.

Sclerotic Parenchyma. Excellent material can be obtained from the flesh of pears and quinces (see 211 and Fig. 40).

From the tough shells of many sorts of nuts and seeds (see Fig. 41) good preparations can be made by the method described in 495. For the Canada balsam there recommended good shellac can be advantageously substituted.

Collenchyma cells are well exhibited by cross-sections of the stem of any common Labiate, for instance Spearmint, or of the stem of almost any of the Umbelliferæ (see 216). Apply dilute hydrochloric acid to the sections.

Wood parenchyma cells are easily obtained by careful maceration (70). Dilute solutions of Schulze's liquid are preferable to strong, although much slower in action. Excellent material is afforded by most of the oaks and other hard woods (see 254, 255). Nearly all possible intermediate forms can be found by careful search. Apply the tests for "lignin" (154). Use also upon different specimens red and blue coal-tar colors.

II. Epidermal Cells.

(*a*) Examine a film removed from the upper surface of some fleshy leaf; for instance, Sedum, the cultivated Cotyledon or Eccheveria, Purslane, or Begonia, etc.

(*b*) Compare the cells of this film with those found on the upper surface of a shining petal; *e. g.*, that of Buttercup or Poppy.

(*c*) Remove a moderately thin film from the young stem or branch of some Cactus, and examine the exposed surface of the epidermal cells for cutinization (156 and 224). Apply any of the coal-tar colors to similar fragments, and note differences of tint.

(*d*) Examine the "bloom" (226) on the following: (1) stem of Indian corn, (2) stem of castor-oil plant, (3) leaf of cabbage, (4) fruit of plum, juniper, or Myrica cerifera (Bayberry).

(*e*) Make a thin vertical section through the leaf of Ficus elastica (India-rubber plant), noting the epidermis and cystoliths (see 164 and Fig. 6).

(*f*) Examine the examples of multiple epidermis afforded by many of the cultivated species of Begonia.

Trichomes. (*a*) Examine the velvety petals of any flower, and compare their very short trichomes, or hairs, with those on downy, rough, and bristly stems and leaves.

(*b*) Examine also a vertical section of a young rose-prickle.

The variety of glandular trichomes at hand in any locality is so great that no special directions need be given for their selection.

(*c*) Root-hairs are easily obtained by allowing the seeds of flax, or the grains of corn, wheat, etc., to germinate on wet filtering-paper, or even on moist glass.

Stomata (pp. 70–73). For the proper study of these a micrometer eye-piece (11) is very necessary. By its employment the dimensions of individual stomata and the number of stomata on a given space can be easily determined.

Sections of stomata are made best by aid of the processes of imbedding (8). Examination of the table by Weiss (page 71) will afford hints as to the selection of large stomata for examination in section.

Water-pores and rifts (242). (*a*) Water-pores are furnished by the tips of the teeth of the leaves from some species of Fuchsia. Sections showing their constituent cells are best made vertically and lengthwise through the leaf. Tropæolum, or the so-called Garden Nasturtium, also gives good examples.

(*b*) Compare with these water-pores the irregular rifts in the leaves of some grasses; for instance, Indian corn.

III. Cork-Cells.

For the examination of these cells, the student should begin with the soft and close-textured "velvet" cork procurable at any apothecary shop. Let the sections be made in at least two directions at right angles to each other, and if possible let them pass through one of the lines of demarcation of the cork: note any differences of shape and size presented by the cells at that place.

The young stems of any of our common currants give in cross-section excellent illustrations of cork-cells (see pages 74–76) and of their development. Test these and similar specimens of cork-cells for the presence of cutin or suberin (see 26, 54, 161).

IV. Prosenchymatic Wood-Elements.

These elements (see pages 78–87) can be studied to best advantage after very careful maceration, as directed in 70. Long wood-cells, woody fibres, and tracheæ (or ducts), are easily separable from each other by such chemical means, and are generally identified with facility. Abundant material for the demonstration of tracheæ is afforded by the fibro-vascular bundles (198) of herbs and by the ligneous parts of our common trees *other than the Coniferæ.* There appears to be no special need of specifying the ligneous plants which can be most successfully employed for demonstrations of the woody elements. Magnolias, Tulip-tree, woody Leguminosæ and Rosaceæ, Urticaceæ, and Cupuliferæ are all satisfactory as sources of material.

Good examples of tracheïds are procurable from species of Coniferæ, such as Pines, Firs, Spruces, etc. These should be examined in all stages of development and from all points of view, particular attention being directed to the marked difference between the radial and tangential aspects of the cells.

Cells which have been separated from each other mechanically and have not been previously acted on by chemicals should be studied with reference to their behavior under the action of iodine and other reagents, it being possible to demonstrate the existence of thin layers or "plates" which compose the wall. Iodine colors the fresh cells yellow; investigation shows, however, that the inner wall or plate of the cell is not much, if at all, colored by the reagent, the color being confined to an outer and a middle wall or plate. When the cells thus treated with iodine are touched with concentrated sulphuric acid, the outer and middle plates remain yellow, while the inner plate turns blue. Soon the inner and middle plates dissolve, the outer not being attacked until somewhat later. If Schulze's macerating solution (full strength) is employed, the outer plate dissolves quickly, but the others are not much affected for some time. Careful management of these powerful solvents is demanded to insure even a moderate degree of success in this demonstration.

V. Bast-Fibres.

Isolation of these cells is easily effected by teasing with needles under the dissecting microscope. The use of macerating solutions for this purpose is also admissible, but the results are not quite so satisfactory as with the wood-elements. Examination of the table on page 90 shows the wide difference which exists between the dimensions of the raw fibres and their structural elements, into which they can be separated mechanically.

Most bast-fibres take the coal-tar colors very well, and it would be best for the student (without giving too much time to it) to note the different effects which are produced on various fibres by the colors described on page 19. The changes produced in the dimensions of the fibres by dilute acids should also be observed. After this preliminary practice the reactions given on page 90 should be carefully repeated with such material as is at hand. Full directions for the preparation and use of the prescribed reagents will be found in the introductory chapter. Lastly, determinations of the average dimensions of the commercial fibres, flax, hemp, jute, etc., should be carefully made.

VI. Cribrose-Cells or Sieve-Cells.

These can be very easily demonstrated in thin vertical sections of the stems of any large Cucurbitaceous plants; for instance, squashes, melons, etc. If the student fails to detect in fresh material forms similar to those shown in Fig. 73, a little tincture of iodine should be added to the specimen, in order to contract the lining and other contents of the cells. By this reagent the contents become more or less distinctly colored, and the discrimination between the cells and the surrounding tissues is generally very plain. In other common plants, grape-vines, etc., the detection of cribrose-cells is not always easy, but a diligent search will bring out these characteristic constituents of soft bast.

The study of the structure of the sieve-plates requires the use of much higher powers of the microscope than most beginners are likely to possess. Much can, however, be done in the examination of the *callus* by the employment of the reagents mentioned in 282 and 283. The student should not fail to submit a thin section showing the larger cribrose-cells to the action of concentrated sulphuric acid, and remove in this way the whole of the cell-wall, leaving (if the manipulation has been careful) the contents slightly connected together and showing the intercommunication between the cells.

VII. LATEX-CELLS.

Latex-cells are abundant for demonstration in many wild and cultivated plants; but few afford material better adapted to the use of beginners than the greenhouse plant, Euphorbia splendens. Other cultivated species of the same genus are about as good. With the younger and softer stems of this plant one has merely to secure thin sections through their outer or cortical portion, when, in a good section, the latex-tubes can be found ramifying irregularly. The peculiar dumb-bell shaped grains in the tubes form a characteristic feature.

When a thin section of any tissue containing latex-tubes is gently heated in a dilute solution of potassic hydrate, or for a shorter time in a stronger solution, the parts become so much softened that the tubes can be easily separated from the surrounding tissue, after which they can be floated on to a fresh slide and examined by themselves.

Abundant material for the study of latex-cells is furnished by plants of the following groups: Lobeliaceæ, Campanulaceæ, Liguliforæ, and many Papaveraceæ.

VIII. SPECIAL RECEPTACLES FOR SECRETIONS.

These are constantly met with in sections of many stems, leaves, and fruits. A few examples for study are here given.

(*a*) *Crystal-cells.* Look for these in the leaves of the Araceæ, Onagraceæ, and Chenopodiaceæ, and in the bark of almost any of the ligneous Rosaceæ (Pomeæ), where they are especially associated with the bast-fibres.

(*b*) *Resin-cells and resin-reservoirs* are found in the bark of many Coniferæ and Umbelliferæ, etc., in the leaves of Rutaceæ, Hypericaceæ, and Myrtaceæ.

(*c*) *Tannin receptacles* are found in very many kinds of bark. For the detection of tannin, solutions of potassic chromate or ammonic chromate may be employed, a brown color being promptly produced. This test is preferable in some respects to the solutions of iron alluded to in 59.

Intercellular spaces of various shapes and sizes containing air, or air and water, are met with in many of the plants already enumerated. The most interesting are found in monocotyledonous plants, notably Araceæ and Juncaceæ.

CELL-CONTENTS.

I. Protoplasm.

No better material for the demonstration of the physical and chemical properties of protoplasm in its active state can be employed by a beginner than the *young* stamen-hairs of Spiderwort. Several garden species of Spiderwort are available for this purpose, especially Tradescantia Virginica and pilosa. The greenhouse species can also be employed. If none of these are at hand. any young large plant-hairs with thin transparent walls will answer for the demonstration. If the hairs are sufficiently young. the protoplasm appears as a nearly transparent mass filling the cell-cavity; but even when they are only slightly advanced in development the mass becomes honey-combed by sap-cavities or vacuoles. With further development these become confluent, and traversed here and there by slender threads; the wall of the cell, however, as long as it is alive, being lined by a delicate film of protoplasm.

When the protoplasm exists in a cell only in the latter condition, it is well to place the cell in a solution of sugar (a five per cent one will answer) or in dilute glycerin. By this means the protoplasmic lining is contracted somewhat by the withdrawal of water from its cavity, and in shrinking from the wall its shrivelled contour can be easily distinguished.

It is best for a beginner to use in his early demonstrations very young plant-hairs in which the vacuoles do not occupy much space within the cell. The cells composing the growing points of most roots, stems, and leaves are too small for satisfactory study at the very outset; it is well to defer the examination of the protoplasm in these until its reactions have been clearly demonstrated in young plant-hairs.

Directions for the demonstration of active protoplasm can be found in section 124. The tests there given should be repeated by the student four or five times with different kinds of cells, after which the effect upon fresh material of potassic hydrate, both the concentrated and the dilute solutions, should be carefully watched. In these examinations it will be well to practise with the reagents without lifting the cover-glass (see 17 and 20).

II. Chloroplastids.

Examine the *chlorophyll granules* (see page 41) in the following material: —

(*a*) The parenchyma cells of any thick leaves, for instance those of Purslane, Begonia, etc., noting in the drawing the relative size and abundance of the granules in different cells.

(*b*) The epidermis of the same leaves, noting in what cells, if any, the granules are found.

Examine also the green bodies in the leaves of any true moss, and in any filamentous alga, *e. g.*, Spirogyra, and the cotyledons of the following seeds for any green granules: sunflower, maple, and pine.

Raise three seedlings of flax and pine. Let one of the seedlings of each be kept in darkness, to the second seedling of each give only a very little light, to the third give as much light as possible; and when the plumules have begun to develop, examine the cotyledons and young stems for any color-granules.

Do well-blanched celery petioles contain chlorophyll? To answer this, examine the base, middle, and summit of the leaf-stalk.

The next three studies can be advantageously deferred until after that of starch.

III. Leucoplastids.

These bodies (see 174) require for their detection very careful manipulation, but by following the directions given on page 44 they can usually be made out without much difficulty. For the pseudo-bulb of Phajus, which is there recommended, the same organ in almost any of the cultivated exotic orchids may be substituted.

IV. Chromoplastids.

These can be examined in any of the colored fruits; for instance, in winter, the berries of Solanum Pseudocapsicum (Jerusalem Cherry) may be used (as directed in 498). The granules there found should be compared with colored granules in the petals of almost any flower. For examination of the color-granules in flowers, common pansies answer very well (see 477.)

V. Protein Granules (pages 44–47 and 182).

Examine thin sections of the endosperm of the seed of Ricinus after the specimen has been treated as directed in 176, and also of the seed of Bertholletia (Brazil-nut). Permanent preparations from the latter should be made as directed on page 47.

Search also for cubical crystalloids in the cells just under the skin of a potato-tuber.

VI. Starch.

In the examination of starch (pages 47 and 181) make thin sections of (*a*) a potato-tuber, (*b*) the cereal grains figured in the pages cited, (*c*) seeds of the pea and bean.

Detach some medium-sized starch-granules and measure them with the micrometer; after this apply a solution of iodine, employing the most dilute one which will impart a decided color to the granules. Is the color given by iodine permanent? Does exposure of the colored specimen to light make any difference in permanence of color?

In all cases note very carefully any appearance of stratification which the different granules present, and determine the distinctive characters by which each of the common commercial starches can be recognized, such as rice-starch (toilet-powder), laundry starch (either wheat or potato), etc. After sufficient familiarity has been acquired by an examination of all the kinds of starch figured in Part I., try to identify under the microscope specimens of laundry starch and of various kinds of flour.

Can starch be detected in the following: —

Seeds of flax and mustard?

Roots of beets and turnips?

Pulp of the ripe and the unripe apple?

Bark of willow and maple?

Young shoots of pine?

For the detection of starch in minute amount in chlorophyll granules the directions given on page 42 must be carefully followed.

From this time on, the character of the granules seen in any specimen should be determined by iodine and the result noted in the drawing.

VII. CRYSTALS.

In many of the sections already spoken of, for instance those of Begonia, single crystals and clusters of crystals have attracted attention. For a brief study of different forms of crystals (see pages 52–55) the following are very serviceable: petioles of Begonia, scales of onion, leaves of Tradescantia, Fuchsia, and the common "Calla" (Richardia), bark of many woody plants.

If a thin section of the leaf of almost any Araceous plant, for instance "Calla," is placed in a little water under the microscope, it frequently happens that the discharge of acicular crystals (raphides), described on page 52, can be seen without difficulty.

Apply to the specimens containing crystals the two reagents spoken of in the table on page 54, and carefully note results.

Repeat Vesque's experiment (188).

VIII. CARBOHYDRATES DISSOLVED IN THE CELL-SAP.

(*a*) *Inulin* (183) is deposited from its solution in cell-sap whenever the cells are placed for a time in alcohol or even in glycerin. Its characteristic forms are not likely to be mistaken for anything else met with in the tissues. Excellent material is afforded not only by the common Dahlia, but by Cichory and Dandelion (see Fig. 35).

(*b*) *The sugars.* Examine a thin section of beet-root by the method described in 184. Compare with it a thin section of any ripe fruit.

IX. OTHER CELL-CONTENTS.

Oil Globules, sometimes of large size, but generally minute, are to be looked for in those seeds which do not contain starch (compare 511). Examine in these the effect of ether on the particles of oil, and also make sections through the leaves of St. John's-wort, Rue, and Dictamnus, and through the rind of an orange or lemon to determine the shape of the receptacles containing oily matters.

Resins, etc. For a study of these, proceed as directed in 56, employing young shoots of Pine.

Tannin, etc. For the detection of tannin, solutions of iron (see 59) may be used; but the results are generally more satisfactory when a solution of potassic or ammonic dichromate is employed. The color imparted to the cells containing much tannin is brownish or even almost black. The student should examine the very peculiar globules of tannin-solution found in the sensitive pulvinus, or cushion, at the base of the petiole of Mimosa (Sensitive plant). Similar globules have been detected in different barks.

DISTRIBUTION OF THE HISTOLOGICAL ELEMENTS.

The various histological elements after being examined as directed in Chapter II. should be investigated with regard to their mutual relations. It is advisable to begin with the skeleton or framework of the plant, afterwards taking up the latex-cells, etc.

As shown in Chapter III., the framework of the higher plants, which we are now to consider, consists of fibro-vascular bundles variously arranged and conjoined. The bundles, which in some cases may run for some distance as isolated threads, and in others exist as compact masses, are surrounded with larger or smaller amounts of cellular tissue, the exterior portions of which are specially adapted to come into contact with the surroundings of the plant.

I. Structure of Fibro-vascular Bundles.

For the demonstration of the structure of fibro-vascular bundles, seedlings of the following plants will afford good material: Bean, Indian corn, Castor-oil plant, and Squash. The roots of these plants give examples of *radial* bundles (313), in which the strands of liber and of wood are in different radii, while from their stems (including the hypocotyledonary stem of the bean, castor-oil, and squash) may be obtained excellent illustrations of *collateral* bundles.

The sections for displaying the structure of the bundles are best made in the three directions, transverse, vertical-tangential, and vertical-radial. In a few cases sections made obliquely to the axis of the organ are instructive; but unless great care is exercised in observing all their relations, they may be rather misleading.

In all cases examine fully the character of the bundle-sheath (see 212). The student should not be satisfied with anything less than a clear interpretation of all the structural elements which he meets in a given bundle. If the structure of a bundle is not revealed by the sections already prepared, fresh ones should be made and carefully compared with the others, and with the figures in Part I. In order to identify some of the structural elements composing a bundle, it is sometimes advisable to resort to cautious maceration (see 70), so that the parts may be isolated. It has been found advantageous, in a few instances, to very securely fasten the section under examination to thin rubber membrane by means of the best "rubber" cement or marine glue, and then subject the membrane and section together to the action of the macerating liquid, great care being exercised to have the process gradual. After the maceration is complete, the membrane is removed from the liquid, washed, and then slowly stretched until the adherent wood-elements are somewhat torn apart. It will be observed that by this method their former relations need not be greatly disturbed.

After examining the fibro-vascular bundles in the seedlings above named, proceed to the study of the bundles in the roots, stems, and leaves of two adult herbaceous plants, for instance Indian corn and Bean, in order to ascertain what differences, if any, exist in the composition of the bundles in a given organ at different periods of growth.

It was stated in 309 that the simplest form of a fibro-vascular bundle consists of merely a few tracheal cells (or sometimes tracheæ) together with some cribrose or sieve cells. The student should search for tracheïds, which may occur disconnected from any bundle; as for example in the stems of species of Salicornia (a seaside plant of succulent texture), and in the petiole and pitchers of Nepenthes. Tracheïds occur also, often in a continuous layer, as a sheath of the aerial roots of orchids. Sieve-tubes may be looked for at a little distance from the bundles in the stems of potato and tobacco, where they occur in the periphery of the pith.

Two supplementary studies are strongly advised: (1) of the bundles in ferns, (2) of those in aquatic phænogams. In the former, "concentric" bundles are met with; in the latter, rudimentary bundles.

II. COURSE OF THE BUNDLES.

The course of the fibro-vascular bundles can be traced in some cases, especially in young and rather juicy stems, like those of Impatiens, with little or no difficulty; but it is generally necessary to treat somewhat thick sections of the stem under examination by a macerating liquid, for instance potassic hydrate, after which the course can be made out. In most cases the course of the bundles can also be made out by series of sections made at different points in the organ, care being taken to arrange the sections in their proper sequence.

The following material will be useful for practice in the determination of the course of the bundles: young shoots of Clematis, Vitis, and Phaseolus (all dicotyledons); and, after these, shoots of Spiderwort, the rootstock of Convallaria (Lily of the Valley), or of Smilacina, and if possible the bud of a young palm.

The course of the bundles in leaves and dry fruits can be easily demonstrated by "skeletonizing" them. This is effected by keeping the leaves for a long time in a dilute solution of calcic hypochlorite (see 50).

DEVELOPMENT OF THE ELEMENTS.

This must be examined in the youngest seedlings of the plants now spoken of. The sections must be through the growing points, and should be well cleared by one of the processes described in 16 or 24. For the development of special structural elements, for example latex-cells, see Part I.

HISTOLOGY OF THE VARIOUS ORGANS.

I. The Root.

The student may use, for demonstration of the histology of the root-tip, any seedlings which have been grown either in water or on a clean support, and are therefore free from grains of earth. Root-hairs are best examined on seedlings sprouted upon moist sponge or bibulous paper.

II. The Stem.

It is advised that the student now prepare, in addition to the sections of stems previously examined, sections through two and three year old shoots of any common dicotyledon, and note all differences which exist between the different woody elements forming the rings, and all changes in the bast. The growth of cambium should be carefully examined in the young shoots of Pine and of Oak.

For the study of the secondary changes in the bark, the twigs of black currant or of white birch afford good material, the successive changes being easily followed.

The occurrence of true cork in out-of-the-way places is illustrated by Catalpa, Professor Barnes reporting that it sometimes occurs between the annual layers in the stem of Catalpa speciosa. Other cases should be looked for.

III. The Leaf.

The leaf presents few difficulties in histological manipulation. For all necessary details consult pp. 155–164. The following plants afford excellent material for study: —

Of the centric arrangement of parenchyma in the blade, Triticum vulgare, Acorus, and many of the Cactaceæ.

Of the bifacial arrangement of parenchyma, many plants with flat horizontal leaves.

IV. The Flower.

It is assumed that the student has thoroughly familiarized himself with the morphology of the simpler flowers as explained in Volume I., and has acquired some facility in examining, as there directed, those of more complicated structure.

The study of the microscopic anatomy of all the floral organs in their adult state should precede any attempt to examine their development. Since the flower should be examined in *all* stages of its development, it is well to select for study only those flowers which can be readily obtained in large numbers, and furthermore, by preference, those which are not thickly covered with hairs. The common weeds Lepidium Virginicum and Capsella Bursa-pastoris afford excellent material for the study of the flower and its development, and have the signal advantage of being much alike in the most essential respects, yet possessing minor differences which are not likely to be overlooked.

An exhaustive examination of the histology of the organs of the flower should begin with the study of the sepals, the other organs being taken up in their turn, and the following points receiving special attention: (1) the possible occurrence of stomata upon all the parts of the blossom; (2) the peculiarities in the proper epidermal cells of the petals; (3) the character of the parenchyma in all parts of the flower, and all differences in the nature of the cell contents, notably the plastids; (4) the character and the distribution of the fibro-vascular bundles in their course from the pedicel to their ultimate attenuated ramifications in the several organs.

Stamens. The character of the pollen demands special attention, and its examination should be followed by a comparison between as many kinds as possible taken from various flowers. The character of the integuments and the contents of the grains should also be demonstrated.

The *pistil* requires little special study, except in regard to its development. It will be well to examine the conductive tissue of the style and trace it down to the ovarian walls. (Other minute matters connected with the stamens and pistils are considered under "Fertilization.")

V. Development of the Flower.

From the youngest flower-cluster of any plant having indeterminate inflorescence, for instance that of Lepidium or Capsella, cut squarely off a short piece of the tip, place it on a glass slide in a little alcohol, in order to remove the air, and cover with thin glass. (If the student has an air-pump, the specimen can be placed at once in water on the slide, and then subjected to the action of a partial vacuum, which will of course free the whole preparation from any air-bubbles.) After the air has been removed, add water, and if the specimen requires clearing, as is usually the case, some potassa. On gently warming the slide the specimen will grow somewhat darker, but after a time will be made tolerably clear. If not, proceed as directed in 25. The specimen, if a good one and well prepared, ought to show all the relations of the several flowers of the cluster to each other. Prepare a second specimen by removing the flowers in succession under the dissecting lens, beginning with the larger, and placing them in a row which will comprise all the stages of development. With the material thus obtained, which it is well to keep moist with glycerin, the examination of all the different parts can be successfully carried out. The study will be far more instructive if the student makes a parallel series with an allied species. Comparison of the two species above mentioned shows exactly when and where some of the parts are arrested in development.

VI. Development of the Pollen.

The examination of the anther for this study should begin at a very early stage in the growth of the flower, and particular attention should be given to the cells which line the pollen cavities. Great advantage is gained from the skilful employment of staining agents, by which the parts are brought out more clearly (see 77 *et seq.*). All changes in the character of the nucleus of the grains during their differentiation demand for their identification the use of staining agents without the previous application of potassa.

VII. Development of Ovules.

In this examination the wall of the ovary must be removed, and the minute eminences which are to become the ovules observed in their earliest stage. The successive external productions which are to become the integuments of the ovule should be traced with great care. It is also well to examine minutely the changes in form of the embryonal sac in the nucleus (or nucellus) of the ovule. These will be further adverted to under "Fertilization."

VIII. Minute Structure of the Seed.

Since in the previous exercises some parts of the seed have been already examined, it is necessary here merely to call attention to the desirability of studying the character of the integuments in at least two common and a few exceptional cases. For the former, no seeds are better than those of the common Bean, Pea, or Lupine. After a clear idea has been obtained of the nature of the cells which compose the greater part of the two integuments, the student should make careful sections through the hilum in order to display the peculiar sac-like body there seen. For the exceptional types of integuments, examine the seeds of Flax (showing the gelatinous modification, etc.), or better, if they can be procured, the seeds of Collomia and Cotton. It will be well also to examine the closely united ovarian and ovular coats in the common grains, like Wheat or Indian corn.

The student should examine as many seeds as possible, including those containing much, little, and no starch, and observe also whether or not there is any difference between ripe and unripe seeds in the amount of starch which they contain. He should examine the contents of the cells nearest the integuments in any of the seeds above mentioned, and ascertain the relative amount of albuminoid matters present compared with those in the cells in the interior of the seed.

Further microscopic examination of the seed is to be taken up when germination is studied.

PRACTICAL EXERCISES IN VEGETABLE PHYSIOLOGY.

This course of experiments in Vegetable Physiology is divided into two parts: the first series comprises a few exercises which can be undertaken by any one having only the simplest appliances; the second requires more complicated apparatus. The first series, if faithfully and intelligently followed, should place the student in possession of the leading facts regarding the principal activities of the plant; while the second series should acquaint him with the chief methods employed for the investigation of the special offices of the organs of the plant, and fix the principal results in his mind. It should, however, be frankly stated that for the proper and satisfactory performance of the experiments detailed in this second or special series the student should first become familiar with the ordinary methods of chemical and physical manipulation, and have at command the fundamental principles of chemistry and of physics.

FIRST SERIES.

In this series are discussed experimentally the following cardinal topics: (1) The behavior of protoplasm in a living cell; (2) The gain in substance by assimilation and the loss of substance by growth; (3) The chief conditions under which plants assimilate; (4) The dependence of the principal activities of the plant upon certain external conditions.

The experiments can be conducted with the following appliances: —

1. A small balance with weights ranging from twenty grams to one centigram. If a balance is not procurable, ordinary hand-scales with horn or brass pans will answer very well.
2. A water-bath, or in place of it a small porcelain-lined kettle of one or two pints capacity, fitting into a larger iron kettle. Water placed in the larger kettle prevents the inner one from being heated above the boiling-point of water.
3. Half a dozen test-tubes.
4. Three or four pieces of glass tubing, six inches long.
5. A small camel's-hair pencil, and India ink.
6. Pieces of colored glass or colored gelatin (red, yellow, green, blue, violet), six inches square or larger.

For the first study, the examination of protoplasm, a microscope magnifying from two hundred to six hundred diameters will be required, together with a small outfit of slides and covers; and for the examination of growth a zinc box constructed as directed in "The Dependence of Growth upon Heat."

I. The Behavior of Protoplasm in a Living Vegetable Cell.

For all necessary details as to the chemical reactions of protoplasm, see 124 and the exercise on page 8 of this "Praxis." At present it is proposed to call attention to the various

Movements of Protoplasm.

(*a*) *Material.* The delicate hairs from the young leaves of almost any pubescent plant will serve for the demonstration of these movements, but the following are recommended on account of their abundance and excellence: stamen-hairs of Spiderwort (Tradescantia), hairs from the young leaves of squash and nettle, and from the velvety leaves of many cultivated exotics.

(*b*) *Preparation of specimens.* Remove by needles, forceps, or scalpel a very little of the epidermis with its attached hairs, and place it at once in a little water on a glass slide. In placing the thin glass cover on the specimen be careful to exclude all air-bubbles and not to crush the cells. If necessary, put a fragment of glass under one edge of the cover, to lighten the pressure on the object. If the hairs are suitable for the examination, the delicate threads of protoplasm ought to be distinctly seen through the cell-walls, and, after a little time, a movement of translucent granules should be seen in them. If, after a few moments, no movement can be detected, warm the slide a little with the hand and again observe. If no movement should now be seen, add to the water on the slide a little dilute glycerin; this causes slight contraction of the protoplasmic lining of the cell, and probably the movement can then be observed in the threads. If not, do not waste time over the specimen, but try a fresh one. A power of 200 diameters will answer for this work, but one of 500 is better.

(*c*) *Questions to be answered by the specimen.* If the student has secured a good preparation, in which the movement of granules in the threads can be seen distinctly, he can easily answer the following queries: What is the rate of motion of the granules at the temperature of the room? Do the threads remain unchanged in shape? Do any granules pass from one cell to the next one? Where is the motion fastest?

While the observations are in progress, be careful not to allow the preparation to become dry: add a little water occasionally, and note whether the rate of motion is increased or diminished for the next minute or so.

(*d*) *Questions to be answered by experiment.* (1) What effect upon the rate of protoplasmic movement does increase of temperature produce?

In order to keep the slide with the specimen, prepared as above, from touching the metallic stage of the microscope, place under each end of it a piece of thick pasteboard, and then clamp it down firmly by means of the stage-clips, so that it cannot be easily displaced. After the slide has been in position for a few minutes, note the rate of movement of the granules at the ordinary temperature of the room. When this has been accurately determined, place near the specimen, on the slide, a coin or other small piece of metal which has been heated to 40° C., and note the change of rate. Afterwards apply more and more heat by a second and a third application of the coin, heated each time higher by immersion in hot water, and note the result. Of course this very simple method of experiment does not allow one to determine the exact temperature to which the specimen is heated, but its temperature is only a little lower than that of the coin.

For exact experiments employ the apparatus described in 557 or 558.

(2) What effect upon the rate of movement does a decrease of temperature cause?

Prepare a fresh specimen as directed under (*b*), lower the temperature of the slide by the application of a coin which has been immersed in ice-water, and note all changes in the rate of movement. Still lower temperatures are easily secured by placing in a small copper cup on the slide (an ordinary copper cartridge-shell answers very well) a mixture of ice and salt.

If in either of the preceding experiments the motion of the granules has been arrested, endeavor, by reversing the application, to re-establish movement: thus, if the movement was arrested at the higher temperature, apply cold; if it was arrested by cold, apply heat.

II. The Gain in Substance by Assimilation, and the Loss of Substance during Growth.

Select a number of beans (Windsor, Horticultural, Lima, or white), of nearly the same size, weigh ten of them, and dry them carefully in a water-bath to ascertain the amount of water which they contain. Take two other lots of ten each, weigh them carefully, plant them on moist blotting-paper or wet sponge, and keep them in a warm place until they have sprouted. When the beans have fairly started, suspend them over the surface of water, with their roots in it, as directed in 669. From this time on, keep one set of the seedlings in the light and the other set in the dark, being careful in each case that the water is supplied in sufficient quantity to make up for all loss by evaporation, and that it is changed every third day. Let all the conditions under which the two sets are cultivated be as nearly alike as possible, with the single exception that light is present in one case and completely absent in the other. In a couple of weeks the two sets of seedlings will have become large enough for further study: the set grown in the light will be green and thrifty, the others may be as large, but they will have a yellow, unhealthy appearance. Remove the two sets from the water and carefully dry them separately over the water-bath as directed in the case of the seeds. When they do not further lose weight, weigh carefully. Compare the weight of the dried seedlings with the weight of the dried seeds.

III. The Chief Conditions of Assimilation.

In the examination of these, repeat with great care the experiments detailed on page 305.

IV. The Dependence of Growth upon Heat.

This may be shown in the following manner: Take a sheet of tin or zinc about 6 to 8 inches in width and 24 inches in length. Turn up its ends at right angles 6 inches. Turn them once more at right angles, rather less than half an inch at the top and two and a half inches at the bottom. This last turn will hold a sheet of glass which will form the fourth side of a box, narrower by two inches at the bottom than at the top; that is, the glass side will not be vertical, but inclined. Cut out a piece of wire-gauze of the right size for the bottom, and either solder or rivet it in place. Fill this box with well-moistened sawdust. Plant a row of six or eight large Windsor beans in regular order in the sawdust, near the glass side, so that the tip of each radicle will start down about one fourth of an inch from it. If the glass is properly inclined, the radicle will quickly press itself against it and thus be the more readily seen and studied in its subsequent growth. When the radicles are about two inches in length, withdraw them, and by the aid of a fine camel's-hair brush and India ink mark them off with precision at regular intervals of one or two millimeters, then place each in the same place and position from which it was taken. It will be found that only their tips grow; the marks above the tips remaining the same distance apart.

Put a thermometer in the sawdust in order to observe the temperature, upon which it will be found the rate of growth depends. Place the seedlings near the stove or over a register where the temperature of the sawdust can be gradually raised to from 28° to 30° C. Having previously measured and noted the exact length of the radicle of each plant, observe its increase, while the temperature remains constant, for a given period of say from five to ten hours. Next place the case containing the seedlings in an improvised ice-chest (any box which can be well closed will answer), and when the temperature has been reduced to 10° C., or nearly that, measure the roots carefully again. Hold this degree of cold as nearly constant as possible for five or ten hours, whichever may have been the period of time in the first case. Compare the growth in the two periods and note the difference.

SECOND SERIES. — SPECIAL EXPERIMENTS.

I. Diffusion.

Place a tumbler containing an inch or two of pure water upon a firm shelf where it will not be subject to any jarring, and put in it a vial filled to the brim with some colored liquid, for instance blue or purple ink. Then by means of a tube or "thistle-funnel" resting on the bottom of the tumbler pour into the tumbler water enough to come up to the mouth of the vial, and very cautiously add more until the mouth is covered to a depth of about an inch. If the pouring has been skilfully done, there will be scarcely any of the ink mixed with the surrounding water. Let the apparatus stand undisturbed for a week or so, and note any changes in the color which may be observed from day to day.

Try the same experiment with a saturated solution of common salt in place of the ink, and at intervals of three days cautiously remove a little of the water from the bottom of the tumbler by means of a small tube or pipette, and test it for chlorides.

II. Osmose. Diffusion through a Membrane.

Scoop out a small cavity in a fleshy root, for instance that of a carrot, and carefully dry it with a cloth. Then fill it with fine sugar, and let the root stand in some place where it will not be disturbed. Note any changes which take place in the sugar and in the condition of the root. By comparative examinations of the tissues removed and those remaining, ascertain whether any of the sugar has entered the cells.

Tie a thin, sound piece of parchment paper (or, better still, parchment) over the mouth of a thistle-funnel, and fill the bulb of the funnel with a strong solution of common salt. Then suspend the funnel in pure water, so that the level of the water outside corresponds to that of the brine inside, and keep the apparatus in a warm place, noting any change of level of the liquid in the funnel tube. Try other substances in the tube; for instance, dilute potassic hydrate, concentrated potassic hydrate, syrup, and dry powdered gum-arabic.

Carefully examine the upper surface of the leaf of Lilac, Oleander, or Echeveria for the presence of stomata, and if none are found, make the following trial with a good, sound, young leaf, being careful to see that the plant is well watered. Put a drop of water on the upper surface of the leaf, and dust upon it either finely powdered sugar or salt, until the drop has taken up all it can, and the mass looks nearly dry; then blow off the residue, and cover the leaf or plant with a bell-jar. Keep it in a warm place and water well. Observe in the course of a few hours, and at frequent intervals during the next four or five days, any changes which the spot of sugar undergoes. It is a good plan to prepare several such spots with different substances.

III. Pellicle Precipitates. — Traube's Artificial Cell.

Dissolve 5 grams of pure potassic ferrocyanide in 100 cubic centimeters of pure water. Place some of the solution in a test-tube having a foot, and drop into the tube a small fragment of moist chloride of copper. Observe the changes which take place in the shape of the film which instantly forms around the fragment. Try the same experiment with a saturated solution of potassic ferrocyanide, and afterwards with solutions containing respectively 1 and 10 per cent of the ferrocyanide.

What effects are produced when a solution of potassic ferrocyanide is shaken up with a solution of copper chloride?

The pellicle precipitates can be further examined as directed on page 226. Calcic chloride and sodic carbonate can be employed in the examination instead of the substances there mentioned.

IV. Pfeffer's Artificial Cell.

Repeat Pfeffer's experiments (page 227), with all the precautions there advised.

In every case where a manometer, or pressure-gauge, is to be used, corrections must be made for temperature and for barometric pressure according to the directions given in such works as Bunsen's "Gasometry."

V. Absorption of Water.

Moisten one side of a perfectly flat, thin piece of hard wood, for instance the holly-wood used for scroll-sawing, and note any change of form which occurs. What effect is produced by moistening, in the same way, the other side of the wood?

Fill a strong stone bottle with large dry seeds of known weight, for instance beans, and put it in a pail of water so that the water can pass into its mouth. If the bottle should break in a few hours, remove quickly with blotting-paper all the outside moisture from the seeds, and determine their increase in weight due to absorption of water.

Place a thermometer bulb in a tumbler half full of dry starch; slowly add to this water of exactly the same temperature, and note any change of temperature which accompanies the absorption of the water by the starch.

Weigh a fleshy root, and carefully dry it in a water-bath, to determine the amount of water which can be expelled at 100° C. Then raise the temperature of the root to somewhat above 100° C., by carefully heating it in a sand-bath, and observe any loss of weight. Determine also the amount of water contained in a fibrous root of Indian corn, a small woody stem, "dry" wood, leaves of Indian corn, Begonia, and Sedum, the pulp of an apple, grains of wheat.

After the above substances have been thoroughly dried and weighed, immerse them in water for one hour, wipe them as dry as possible by means of blotting-paper, and weigh again. How much water can each absorb in one hour? In like manner ascertain how much they will absorb in ten hours and in twenty-four hours.

VI. Root-Absorption.

Repeat the following experiments by Ohlert: —

Cut off the so-called spongioles, the very tips of the roots of sound seedlings which have been cultivated for a few days upon moist sand or sponge (or, better still, with all the roots in water), and cover the wounds with asphalt-varnish. The wounded end of the root must be quickly dried with blotting-paper before the varnish is applied. Then put the roots of the plant again upon their moist support or in water, and endeavor to answer by careful observation the question: Does or does not the plant absorb enough water for its needs without the "spongioles"?

Cultivate seedlings of one or two plants, for instance radish and wheat, upon (1) rather dry sand; (2) moist sand; (3) wet sand, or upon blotting-paper of these three degrees of moisture, and notice if there is any appreciable difference in the number of root-hairs produced. Can the development of the hairs be increased by increasing slightly the temperature of the support?

VII. Root Pressure.

Cut off squarely the stem of a young dahlia or sunflower well rooted in a flower-pot of moderate size, and to the stump fasten immediately a T-tube, with its pressure-gauge as directed on page 264. Ascertain the pressure shown by the mercurial gauge at intervals of an hour, and determine also the effect of changing the temperature of the soil in the flower-pot.

VIII. Stem Pressure.

Apply a pressure-gauge to the cut stem of some woody plant well established in a flower-pot (for instance, a strong rose), and ascertain the amount of pressure exerted by the sap.

In the winter time or early spring try the experiments referred to on pages 264–267.

IX. Transfer of Water through Stems.

Repeat De Vries's experiments described on page 263. For these, stems of sunflower and tobacco answer very well, while those of heliotrope are not very good. Ascertain the height to which a color (as anilin red) will rise in the cut stem of a young woody plant under different conditions of warmth, exposure of the leaves to light, etc. Repeat the experiment with a strip of blotting-paper, described on page 260. Try the foregoing with the substitution of a salt of lithium for the dye, and determine the rate of ascent.

It will be well for the student at this point to review carefully the principal facts regarding the amount of moisture which the atmosphere can take up at different temperatures. In all transpiration experiments he should determine the percentage of moisture in the atmosphere to which the leaves of the plants are exposed, and for this purpose the well-known Hygrodeik, or Hygrophant, may be employed. But if only the simple wet and dry thermometer bulbs are at hand, the student can find all necessary data for his calculations in the tables published by the Smithsonian Institution.

Place in a watch-glass under the microscope water containing finely powdered indigo, and immerse in it the clean-cut surface of a leafy shoot. Observe in which direction the indigo particles move.

X. Transpiration, or Exhalation.

Repeat the following experiment devised by Henslow: "Take six or eight of the largest, healthiest leaves you can find, two tumblers filled to within an inch of the top with water, two empty dry tumblers, and two pieces of card each large enough to cover the mouth of the tumbler. In the middle of each card bore three or four small holes just wide enough to allow the petiole of a leaf to pass through. Let the petioles hang sufficiently deep in the water when the cards are put upon the tumblers containing it. Having arranged matters thus, turn the empty tumblers upside down, one over each card, so as to cover the blade of the leaves. Place one pair of tumblers in the sunshine, the other pair in a shady place. In five or ten minutes examine the inverted tumblers."

Tie a piece of thin rubber-cloth around the flower-pot and lower part of the stem of any young leafy plant, and weigh the whole upon a common balance capable of turning with a decigram, under a lead of two or three kilograms. If nothing better can be procured, one of the best forms of small platform balance will answer. A thistle-funnel should be tied up with the stem, so that water can be supplied to the plant as required. Ascertain the amount of transpiration from the foliage of the plant during twenty-four hours under the following conditions: (1) at a temperature not falling below 60° F. (about 16° C.); (2) at a temperature not rising above 40° F. (about 4° C.).

What is the loss of moisture in one hour under direct exposure to the brightest sunlight? Note temperature and moisture in the air. What is the effect upon transpiration of placing the flower-pot in some crushed ice, the temperature of the air remaining about the same as before?

Determine the minimum, maximum, and optimum temperature for transpiration of any suitable herbaceous plant, for example, a Pelargonium (House Geranium).

XI. Extravasation from Leaves.

Cover a young healthy plant of Indian corn or wheat with a bell-jar, being careful to keep it warm. If, after a little time, a drop of water should appear at the tip of any of the leaves, remove it by blotting-paper, and replace the bell-jar. What is the lowest temperature at which water is thus given off by young leaves of the above plants?

If a young Caladium is at hand, examine the tip of the leaf for the jet of water (page 268) which can sometimes be seen. If the plant is a suitable one, and the jet can be seen at all, ascertain the lowest temperature at which it is ejected.

XII. Incombustible Matters in the Plant.

Burn upon platinum foil (free access of air being permitted), known weights of the following substances, and weigh the ash left in each case: (1) oak-wood, (2) pine-wood, (3) a young leaf of any plant, (4) a much older leaf of the same plant (for instance raspberry), and (5) some grains of Indian corn.

If no platinum foil is at hand, burn the substance in a hard glass tube open at both ends and held slightly inclined in the flame of an alcohol lamp or of a Bunsen burner. If the glass tube is used instead of platinum foil, weigh the tube and the substance together before heating, and afterwards weigh tube and ash together to obtain the difference in weight.

XIII. Examination of the Ash of Plants.

If the student has facilities for conducting qualitative chemical analyses, he would do well to examine the ash of the following plants: Sugar-beet, Buckwheat, and Oat.

If he has had sufficient practice in quantitative chemical analysis to warrant it, an examination of the ash of some one of the plants which have been spoken of in 664 and 665 would form a useful exercise. The investigation of the ash of a single species at different seasons is recommended.

XIV. Water-Culture.

In the study of water-culture no plants can be more easily managed than buckwheat and Indian corn. Secure good seedlings, and treat them as described in 669. After the plants have become well established in their new surroundings, use for the nutrient liquid the following solutions in a fixed order, and with the precautions laid down on page 249.

1. Well-water, or other drinking-water.
2. Distilled water with potassic nitrate.
3. “ “ “ “ chloride.
4. “ “ “ magnesic sulphate.
5. “ “ “ calcic chloride.
6. “ “ “ “ sulphate.
7. “ “ “ potassic phosphate.
8. Nutrient solution I. (672).
9. “ “ II. (673).
10. Distilled water alone.

XV. Assimilation Proper.

Chlorophyll and other coloring-matters. Make a solution of the pigment by placing bruised leaves of grass in strong alcohol for a few hours, and keeping them from the light. It is well to prepare at least ten ounces of the strong extract, which can be used in all the following experiments.

Examine the color of about an ounce of the above extract held in a small vial. What is its color by transmitted and by reflected light? In the latter examination it is better to throw a strong light from a burning-glass or double convex lens upon the surface of the liquid. How long will the liquid keep its color in the strong light?

Treat, as directed in 774, one ounce of the extract which has not been exposed to light, and place the turbid mixture aside in a dark place until it becomes clear. What are the colors of the upper and the lower layer into which it separates?

If a microspectroscope is available, make on paper projections of the spectra of the following substances: (1) Chlorophyll solution, (2) the upper layer of the liquid just mentioned, and (3) the lower layer of the liquid. Examine also the spectrum of a thin green leaf.

If possible, examine the colors of autumnal leaves, and of alcoholic extracts from colored flowers and colored fruits.

Place a few red sea-weeds in pure water, and let them remain there for ten hours. What is the color of the water by (1) transmitted light? (2) by reflected light? Extract the coloring-matter of red sea-weeds by means of alcohol, and compare the alcoholic with the aqueous solution.

What is the color of an alcoholic extract of the bruised tissues of Monotropa uniflora?

Etiolation. Keep seedlings in a warm, dark place until they have lost their green color, and then, having removed some of their leaves for immediate examination, place the plants, with the remaining leaves attached, in the light. Make alcoholic extracts of the blanched leaves and of the green ones, comparing them from all points of view.

Examine pine seedlings grown in complete darkness, and ascertain the nature of the pigment which their green cells contain.

Carbonic acid and assimilation. Compare at the end of two or three weeks the dry weights of two seedlings grown under the following conditions: Both the seedlings have furnished to them exactly the same kind and amount of soil, and are provided with equal amounts of nutrient solutions at corresponding times; both are placed under tubulated bell-jars, and have the same amount of moisture in the atmosphere to which they are exposed. The seedling in one bell-jar obtains a supply of carbonic acid gas, since there is an opening in the jar through which the enclosed air communicates with that outside containing its normal proportion of carbonic acid. The seedling in the other jar has no carbonic acid supplied, since a cup which contains potassic hydrate deprives the air already in the jar of all its carbonic acid, and an open receptacle, filled with pumice-stone saturated with potassic hydrate, removes all carbonic acid from any air entering the jar. One plant is thus furnished with enough available carbonic acid, the other is in an atmosphere wholly free from it.

In a modification of the foregoing experiment, supply a known quantity of carbonic acid in aqueous solution to the *soil* of the second plant, being careful to prevent by means of a cover of rubber-cloth any escape of the carbonic acid from the soil of the flower-pot into the air of the jar, and after a few days compare the weights of the plants as before.

Can a water plant derive its carbonic acid from water containing a small amount of sodic bicarbonate in solution?

Add to the normal air contained in a freshly filled bell-jar, in which a seedling is growing, a known quantity of pure carbonic acid.[1] Later, double and quadruple the quantity added, and observe the effect produced upon the plant. Experiment with different species of ferns and club mosses in the same manner. Observe in another series of experiments the effect of sunlight in modifying the influence of an excess of carbonic acid gas in the atmosphere.

The measure of assimilative activity is to be found either in the amount of pure oxygen evolved in assimilation, or in the amount of carbonic acid decomposed in it.

1. Determinations depending upon the amount of oxygen evolved: The gas which is given off during assimilation, especially by water plants, is never absolutely pure oxygen; but since it contains so small a proportion of other matters under most circumstances which the student is likely to meet, the amount of it evolved may be taken safely as the *approximate* measure of assimilation. The method of measurement by counting bubbles emitted by water plants in water (see 814) is always practicable and easy of execution. The evolved gas can be easily collected in any convenient inverted receptacle. If the gas collected and measured is analyzed eudiometrically, as directed in Bunsen's "Gasometry," the determination leaves little to be desired.

2. Determinations depending upon the amount of carbonic acid decomposed. To the air contained in a glass vessel inverted over mercury a known quantity of carbonic acid is added. The plant previously placed in the receptacle decomposes a part of this, and after a given time the amount decomposed is ascertained by measurement of the carbonic acid that remains.

Effects of different gases upon assimilation. A few plants and two or three small Wardian cases, or, better, capacious bell-jars, will answer for this study. Select only sound plants for examination, and be careful to have those in one bell-jar as nearly as possible of the same size and strength as those in the others. Let the air in one of the jars be ordinary atmospheric air; to that in the others add a known but small quantity of one of the following gases; namely, (1) common coal gas; (2) sulphurous acid; (3) chlorine. Compare the growth and vigor of the plants from time to time, and observe whether insolation makes any difference in the appearance of the plants exposed to the gases mentioned.

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[1] In all cases where an additional amount of gas is introduced into a bell-jar, allowance must be made in some way for the possible increase of pressure. For the necessary correction in these cases, and for other details regarding the management of gases, consult Bunsen's "Gasometry."

XVI. RESPIRATION.

The measure of this process is usually found in the amount of carbonic acid given off by plants. The methods of determination of this amount are, although apparently simple, open to some objections; but by the exercise of great care in the management of the simple appliances, their results are in general trustworthy.

The carbonic acid which is given off by the plant may be measured in one of the two following ways: (1) A current of air freed from all its carbonic acid by means of wash-bottles containing potassic hydrate is allowed to pass into a receptacle in which are confined the plants to be examined. The air withdrawn from this receptacle passes slowly through Liebig's potash bulbs in which are held a known amount of potassic hydrate. At the conclusion of the observation the amount of carbonic acid which has been given off by the plants and been taken up by the potassic hydrate in the bulbs can be accurately determined. (2) The current of air which is withdrawn from the receptacle containing the plant is permitted to pass very slowly through a long slightly inclined tube in which is held a solution of pure baric hydrate. As the bubbles of gas pass through this liquid and give up their carbonic acid, they cause an abundant precipitation of baric carbonate in it. The second method, which is essentially that of Pettenkofer, yields uniform results, and is in general to be preferred to the first. It is better applicable to observations upon intramolecular respiration; in which, as pointed out in 981, some gas like nitrogen or hydrogen, wholly free from any trace of oxygen, is allowed to come in contact with plants or parts of plants, and the amount of carbonic acid given off is determined as in the former case. Interesting results are obtained by placing in the receptacle very young seedlings, or buds which have just begun to unfold.

XVII. GROWTH.

The measurement of growth. Growth can be satisfactorily measured in the three following ways, each of which is adapted to particular instances: —

1. *Direct measurement.* Determine the place and rate of growth of young internodes of any rapidly developing plant, for instance Morning Glory, by marking the whole space of the internodes into equal intervals, and subsequently determining

the actual increase in distance between any two or more lines. In all cases mark the part under examination with good India-ink, making clear, narrow lines. To avoid any possible error caused by influence of lines marked only on one side, make lines on both sides of a part whenever possible. To measure the growth of leaves, use the method spoken of on page 156.

2. *Measurement by a micrometer eye-piece.* With the tube of the microscope kept perfectly horizontal, examine the position of a line of India-ink, upon a perianth leaf of Crocus, or upon the root-cap of Windsor bean. Observe the space which the image of the line appears to pass through in a given time, and refer this to the previously determined values of the spaces of the micrometer.

3. *Measurement by an index.* (*a*) On a simple arc. For this use the simple and admirable modification of Sachs's auxanometer, devised by Bessey (American Naturalist).

(*b*) On a recording drum. A slender brass or steel shaft is attached to the hour-spindle of a cheap clock, and from the shaft is suspended firmly a stiff pasteboard drum of about the same size. This revolves with the spindle, and if well made is carried without any appreciable vibration. A piece of glazed paper of the size of the drum is moistened, and a little mucilage placed on one edge, so that when the paper is rolled around the drum, its edges can be firmly fastened together. Be careful to have the seam in the paper so placed as to avoid any catching of the needle index attached to the plant. When the paper on the drum is dry, it is smoked lightly and evenly over a smoky turpentine flame. The needle at the tip of the index is now placed against the smoked paper so as to press lightly upon it, and, as the drum revolves, leave a clean mark. When a sufficiently long record has been registered, the paper is carefully removed and dipped in (not brushed with) a solution of common rosin in alcohol, which upon drying prevents any of the lamp-black from coming off.

Two corrections are necessary with this simple apparatus: (1) for the curve of the descending needle at the end of the radius; (2) for any changes in the position of the needle caused by the varying amount of moisture in the air.

For recording temperature, it is possible to use a metallic thermometer with a long index, and have the two records side by side. It is well, however, to have the needle for the thermometer give a different mark in order to prevent any subsequent confusion.

The proper methods of examining the formation of new cells in a simple case are indicated in the studies upon a stamen-hair of Tradescantia noted on page 380.

XVIII. Movements of Plants.

The student is advised to select some one plant in a vigorous condition and make a thorough examination of all the phenomena of movement which it presents. The plants named below are among the best for such an examination, and they can be made to grow even under rather unfavorable conditions, like those afforded by schoolrooms.

Spontaneous movements. Desmodium gyrans, the Morning Glory, or Hop, may be used. The first requires a high temperature and a fair amount of moisture in the air in order to exhibit its peculiar movements satisfactorily.

Movements following shock. The Sensitive plant (Mimosa pudica) should be observed. It can be experimented upon with various kinds of irritants, both mechanical and chemical, at various temperatures, and under the influence of anæsthetics. For the experiments with anæsthetics only very young plants are suitable, and they cannot well be used afterwards for other investigations.

In the case of all of the above plants note any changes which the leaves undergo during the day and at the approach of night.

The details given in 1045 suffice to indicate the general method of exaggerating by means of slender glass threads the slow and slight movements of plants, and do not need further treatment here. For observations with such threads, the following plants are very useful: seedlings of the Morning Glory, clover, cress, cabbage, and sunflower.

XIX. Tension of Tissues.

Make sections of young internodes as directed in 1025, securing in every case accurate measurements of all the parts, both before and after their separation. It will be well to examine in like manner a large number of young roots, stems, leaves, and parts of flowers, noting in all cases the age of the part examined.

XX. Insectivorous Plants.

In the study of these plants the student is advised to read carefully Mr. Darwin's work on the subject, and verify, by means of good specimens of Drosera rotundifolia, the facts there recorded. Students are reminded that Mr. Darwin's observations were made with the simplest appliances, and with a degree of care never excelled.

For independent study abundant material may be found in the common Sarracenias of the North and South, in regard to which very much still remains to be learned.

XXI. Cross-Fertilization.

For this study, repeat the observations of Darwin as they are given in his work on Cross and Self Fertilization; or if that is not at hand, as they are briefly stated in the abstract in the present volume, pages 448–450.

XXII. Hybridizing.

With the precautions given on page 456 the student should be able to undertake experiments in hybridizing species of the following common genera, all of which lend themselves readily to this process: Nicotiana, Verbascum, Lilium, etc. Be careful to exclude foreign pollen in all cases.

XXIII. The Ripening of Fruits and Seeds.

Good material for this study is afforded by the following plants: Solanum, Impatiens, Pyrus, Prunus, and Tecoma.

XXIV. Germination.

Select sound seeds of some common plant, for instance beans or Indian corn, and test with them the truth of the following statements: (1) Water is essential to germination. (2) Germination cannot begin without access of free oxygen. (3) Seeds of the plants selected require the same temperature for the beginning of germination. (4) When the process of germination has once begun, light is necessary to any increase of the plant in dry substance (compare experiment Series 1, No. II.). (5) Carbonic acid is constantly given off during germination. (6) In some cases carbonic acid will continue to be evolved even when no more oxygen is supplied (compare intramolecular respiration). (7) The temperature of germinating seeds is higher than that of the surrounding atmosphere (compare respiration).

What is the optimum amount of water required for the speedy germination of the following seeds, — Windsor beans, peas, clover, squash, and sunflower?

What is the optimum amount of oxygen required?
What is the optimum temperature required?
Compare the precocity of unripe and ripe seeds of any plant.

XXV. Effects of frost.

Wrap up a leaf of Begonia in thin rubber-cloth, to protect it from moisture, and place it in a freezing mixture of powdered ice and salt. After an hour examine the tissues of the leaf with special reference to any mechanical injury which they may have sustained. Having completed this preliminary study, proceed to the examination of any well-developed seedlings, and note in every case (1) the effect produced upon the parts which have been quickly thawed; (2) the effect where thawing has been allowed to go on very slowly.

Freeze any strong seedlings and after a time thaw them slowly. Place them then under favorable conditions for growth, in order to ascertain whether their vitality has been destroyed. In cases where death of the part or plant ensues, does it appear to come from the freezing or from the thawing?

Measures of Length.

	Inches.
Meter	39.37079
Millimeter	0.03937
Micro-millimeter (μ) the unit of microscopic measurement	0.000039

Measures of Capacity.

	Pints.	Cubic Inches.
Liter	1.761	61.02705
Cubic centimeter or milliter	.00176	0.06103

Measure of Weight.

	Grains.
Gram	15.43235

Measures of Temperature.

Centigrade, or Celsius.	Fahrenheit.	Réamur.	Centigrade, or Celsius.	Fahrenheit.	Réamur.
°	°	°	°	°	°
+100	+212	+80	+16	+60.8	+12.8
90	194	72	15	59	12
80	176	64	14	57.2	11.2
70	158	56	13	55.4	10.4
60	140	48	12	53.6	9.6
50	122	40.	11	51.8	8.8
49	120.2	39.2	10	50	8
48	118.4	38.4	9	48.2	7.2
47	116.6	37.6	8	46.4	6.4
46	114.8	36.8	7	44.6	5.6
45	113	36	6	42.8	4.8
44	111.2	35.2	5	41	4
43	109.4	34.4	4	39.2	3.2
42	107.6	33.6	3	37.4	2.4
41	105.8	32.8	2	35.6	1.6
40	104	32	+1	+33.8	+0.8
39	102.2	31.2	0	+32	0
38	100.4	30.4	—1	+30.2	—0.8
37	98.6	29.6	2	28.4	1.6
36	96.8	28.8	3	26.6	2.4
35	95	28	4	24.8	3.2
34	93.2	27.2	5	23	4
33	91.4	26.4	6	21.2	4.8
32	89.6	25.6	7	19.4	5.6
31	87.8	24.8	8	17.6	6.4
30	86	24	9	15.8	7.2
29	84.2	23.2	10	14	8
28	82.4	22.4	11	12.2	8.8
27	80.6	21.6	12	10.4	9.6
26	78.8	20.8	13	8.6	10.4
25	77	20	14	6.8	11.2
24	75.2	19.2	15	5.	12
23	73.4	18.4	16	3.2	12.8
22	71.6	17.6	17	1.4	13.6
21	69.8	16.8	18	—0.4	14.4
20	68	16	19	2.2	15.2
19	66.2	15.2	20	4	16
18	64.4	14.4	30	22	24
17	62.6	13.6	—40	—40	—32