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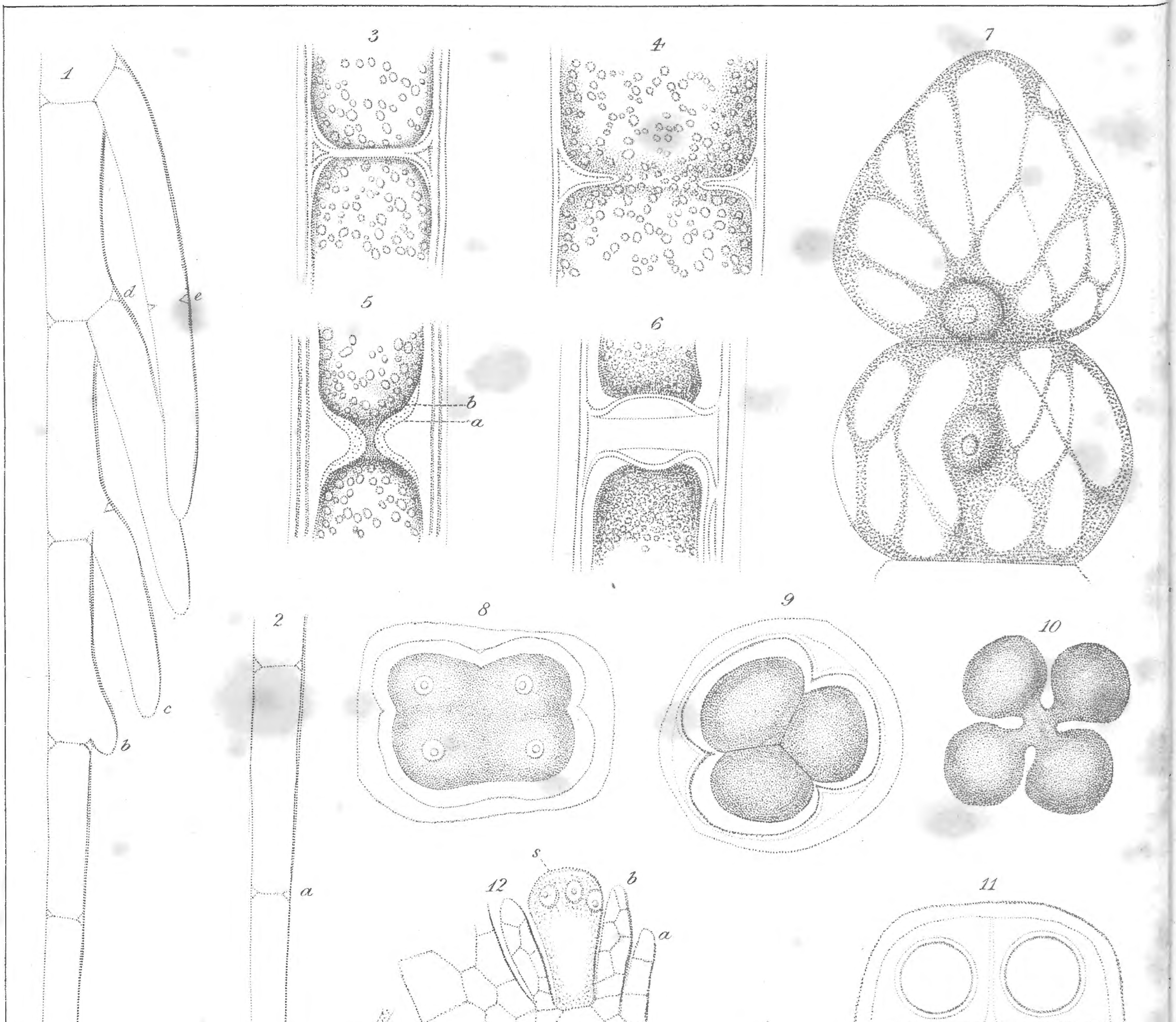
ANATOMY & PHYSIOLOGY OF THE VEGETABLE CELL.



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PRINCIPLES
OF THE
ANATOMY AND PHYSIOLOGY
OF
THE VEGETABLE CELL.

BY
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TRANSLATED
(With the Author's permission)
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With an Illustrative Plate and numerous Woodcuts.

LONDON:
JOHN VAN VOORST, PATERNOSTER ROW.
MDCCCLII.

LONDON
T. E. METCALF, PRINTER, 63, SNOW HILL.

AUTHOR'S PREFACE

TO THE

ENGLISH TRANSLATION.

Mr. Arthur Henfrey having informed me that he intends publishing an English translation of the present treatise, I take this opportunity of making known to the English reader the purpose I had in view in the preparation of the book. The following pages were not originally intended to appear as an independent work, or to give a summary of the wide subject of the Anatomy and Physiology of Plants, but appeared as an article, in the "Cyclopædia of Physiology" published by Dr. Rudolph Wagner, of Göttingen, drawn up to furnish students of Animal Physiology, and more particularly the Medical Profession, with a review of the Anatomical and Physiological conditions of Vegetables (of the Cell), in order to enable them to form a definite judgment upon the analogies which might be drawn between the structure and vital functions of animals and plants. This intention, together with the circumstance, that I was compelled to crowd the whole exposition into the space of a few sheets, rendered it necessary to direct especial attention to the individual cell, as the fundamental organ of the Vegetable Organism. Since, however, the cell only presents itself in anatomical and physiological independence in the lowest plants, and since, in the more highly organized plants, both the structure and the physiological functions of the individual cells become subject to greater dependence upon the other parts of the plant, in proportion as the collective organization of the vegetable is more complex; moreover, since functions then present themselves, of which no trace can be found in the lower plants, it became requisite to take account of the plants of higher rank, and of the various organs which these possess. The treatise, therefore, contains, if an imperfect, still in many respects, a more extensive *resumé* of Vegetable Physiology, than might be conjectured from the title.

Unhappily, the Physiology of Plants is a science which yet lies in its earliest infancy. Few of its dogmas can be regarded as settled beyond doubt; at every step we meet with imperfect observations, and consequently with the most contradictory views; thus, for example, opinions are still quite divided regarding the doctrines of the development of the cell, of the origin of the embryo, and of the existence of an impregnation in the higher Cryptogams. Both in these and in other cases, the small compass of the present treatise forbids a more extensive detail of the researches upon which the opposing views are founded; I hope, however, that I have succeeded in making clearly prominent, the chief points upon which these contests turn, and thus, in facilitating the formation of a judgment by the reader; and, I have never neglected to indicate the literature from which further instruction is to be derived.

HUGO VON MOHL.

Tübingen, *October 19th*, 1851.

CONTENTS.

EXPLANATION OF THE PLATE.

Figs. 1—6. *Conferva glomerata.*

Fig. 1. The growing points of the plant.—*a*, Terminal cell; *b*. Ramification of a cell, beginning; *c*, Ramification further advanced, with the commencement of the formation of a septum at its base; *d*, a perfect septum; *e*, Prolongation of a branch-cell twice the length of the cells in general, with the commencement of the formation of a septum in the middle.

„ 2. Terminal cell grown to the double length, with an imperfect septum in the middle.

„ 3. Constriction of the cell-contents by the half-completed septum.

„ 4. A half-completed septum, in which a considerable deposition of cellulose membrane has already taken place.

„ 5. A septum in progress of formation after the action of an acid, which has caused contraction both of the primordial utricle (*a*) and the cell-contents (*b*).

„ 6. Complete septum split into two lamellæ by the action of an acid.

„ 7. The two uppermost cells of a hair from the filament of *Tradescantia Sellowii*, with nuclei and currents of protoplasm.

Figs. 8—11. *Formation of the Pollen in* Althæa rosea.

„ 8. Four nuclei in the contents of the parent-cell, with the commencement of the formation of four septa. The primordial utricle and cell-contents contracted from the action of alcohol.

„ 9. Farther advanced development of the septa of the parent-cell.

„ 10. The primordial utricle removed from the parent-cell, not yet completely divided into four parts.

„ 11. Completed division of the parent-cell.

FIGS. 12—18. *Formation of the embryo in* Orchis Morio (from Hofmeister).

Fig. 12. The ovule, a considerable time before fertilization. *a*, the outer coat; *b*, the inner coat; *s*, the embryo-sac; *c*, the funiculus. Three nuclei have been formed in the micropyle end of the embryo-sac.

„ 13. The internal parts of the ovule a short time before fertilization. *a*, inner coat of the ovule; *s*, embryo-sac; *b*, germinal vesicle.

„ 14. The ovule at the moment of fertilization, *a*, *b*, *s*, as in the preceding figure; *p*, the pollen-tube; *f*, a few cells which have made their appearance at the chalazal end of the embryo-sac.

„ 15. Further development of the impregnated germinal vesicle. It contains two nuclei which lead to its division into two cells.

„ 16. The embryo-sac with a pollen-tube adherent. The germinal vesicle is parted into two by division into an upper (*a*) and a lower (*b*) cell.

„ 17. The pro-embryo (*Vorkeim*). Its superior portion (*a*), the suspensor, has originated through the division of the cell *a* of Fig. 16; its inferior portion, the rudiment of the embryo (*b*) through the division of the cell *b* of Fig. 16.

„ 18. An embryo (*b*), with its suspensor (*a*), in a farther advanced stage of development.

FIGS. 19—22. *Spores of Prolifera rivularis* (from Thuret).

„ 19. Moving spore possessing a circle of ciliæ.

„ 20—22. Various stages of the germination.

„ 23. Two ciliated spores of *Conferva glomerata* (from Thuret).

„ 24. Germination of the same (from Thuret).

„ 25. Seminal filaments (*Samenfaden, spermatozoids*) of *Chara* (from Thuret).

„ 26. Two cells from the antheridium of *Sphagnum*, with seminal filaments (from Unger).

„ 27. An isolated seminal filament (from Unger).

„ 28. A seminal filament with two ciliæ treated with iodine.

„ 29. Seminal filament of *Pteris serrulata* (from Leszcyc-Suminski).

ANATOMY AND PHYSIOLOGY

OF THE

VEGETABLE CELL.

INTRODUCTORY REMARKS.

IF we examine the texture of plants with a powerful microscope, we find that it does not consist, as appears to the naked eye or under slight magnifying power, of a homogeneous substance perforated by a greater or less abundance of cavities, but is composed of minute portions, of definite form and organization, separable from each other (the *elementary organs).*

Observ. Universal as the agreement among phytotomists has been for some thirty or forty years on this fundamental proposition of vegetable anatomy, it was a long time before it acquired general recognition. The very founders of the anatomy of plants, Leeuwenhoek, Malpighi, and Grew, were, indeed, led by their researches to the detection and distinction of the elementary organs as organized parts, but the real conditions were again misconceived throughout the whole of the eighteenth century. On the one hand, Ludwig and Böhmer, seeking an analogy with animal cellular tissue, described vegetable cellular tissue as a mass of irregular fibres and lamellæ interwoven together; on the other hand, C. F. Wolff *(theoria generationis)* described vegetable substance as a homogeneous mass hollowed into holes and canals, a view which still found an active defender during the first ten years of the present century, in Brisseau de Mirbel, and is even now held by him to be the condition in the earliest stage of development of vegetable tissue, if not that of the subsequent stages. More correct views were first substantiated by German phytotomists of the present century.

The primary form of the elementary organ of plants is that of a completely closed, globular, or elongated vesicle, composed of a solid membrane, and containing a fluid (utricle, *utriculus).* If this remains still closed after its development is completed, it is called a cell, *cellula;* but if a row of utricles arranged in a line become combined, during the course of their development, into a tube with an uninterrupted cavity, through the absorption of their cross walls, a compound elementary organ is produced,—the *vessel (spiroid* of Link).

Observ. The tracing back of the whole of the elementary organs to the primary form of the utricle, has been accomplished only quite recently. The earlier phytotomists, who took the elongated cells for long tubes, overlooked their analogy with the short cells, believing that they were rather to be compared with the vessels, and they described them as a special anatomical system under different denominations (fibres, lymphatic vessels, &c.), in which error they were followed even by Treviranus

(“*Physiolog.*” i. 64), although Sprengel, Rudolphi, Link, and Kieser had already recognized that they all were modifications of the cell. Far less than this was the true nature of the vessels perceived by the earlier phytotomists; and I believe that I was the first to detect their origin from rows of closed cells (“*Memoirs of the Acad. of Munich,*” i. 445. *De structura palmarum*, § 26—29). No sharply defined line can be drawn between vessels and cells, for reasons which will be hereafter discussed. Whether the milk-vessels, which indeed occur only in a comparatively small portion of plants, and play a very subordinate part both in anatomical and physiological relations, originate in an analogous manner from rows of cells, or are to be regarded as a system essentially different from the rest of the elementary organs, is a question upon which no opinion has yet acquired an universal acceptance. Unger asserts the former (“*Annals of the Vienna Museum,*” ii. 11); but it is more than doubtful whether his observations were accurate, and it seems that the milk-vessels ought to be regarded as membranous linings of passages which appear between the cells. (*See* an anonymous memoir in the “*Botanische Zeitung,*” 1846, 833, entitled “The Milk-vessels: their Origin, &c.”)

The basis of the substance of all vegetables consists of the cells, since even in the most highly developed plants all the organs are in the youngest condition composed of cells alone, and the vessels only appear during the subsequent development. In the lower plants (Fungi, Algæ, Lichens, Liver-mosses and Mosses) all the elementary organs persist in the organization of the cell.

Observ. The circumstances, that a plant is composed of cells alone, or also possesses vessels, have not that importance either in a systematic or a physiological point of view which De Candolle attributed to them, when he used them for the primary division of the vegetable kingdom, into Cellular and Vascular plants, for these conditions do not run parallel with the total organization of plants, since there exist both Cryptogamic and Phanerogamic plants with and without vessels.

I. THE ANATOMICAL CONDITION OF THE CELL.

A. FORM OF CELLS.

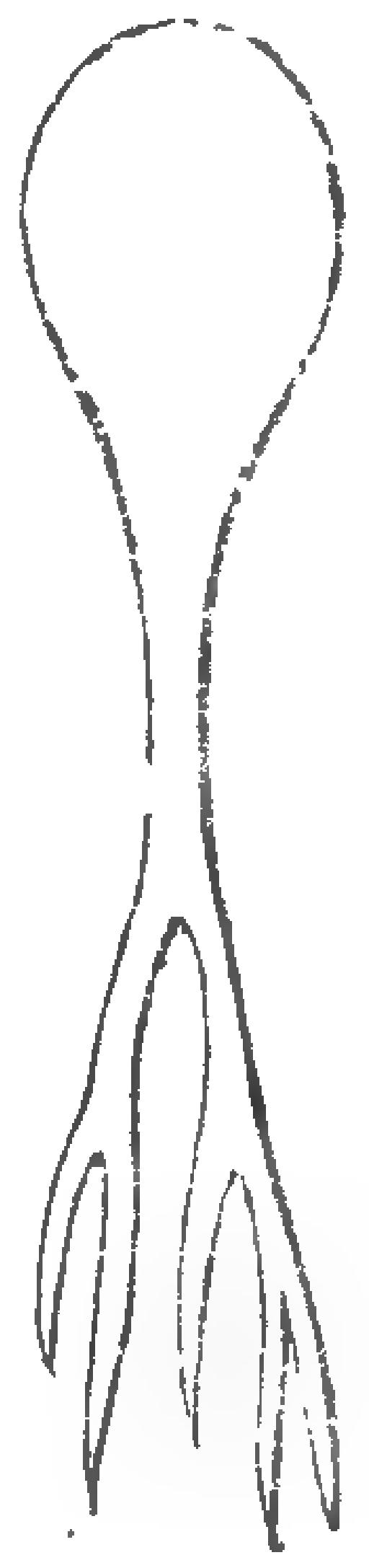
The forms under which cells present themselves are so manifold, that a special examination of all would occupy a far greater space than can be devoted to it in this place; I therefore confine myself to a few observations.

In the first place, in examining the form of the cell, we have to take notice that it depends upon two circumstances. On one hand the form of the cells is determined, like that of every organic body, by its indwelling laws of development; on the other hand, the individual cell, in the far greater majority of cases, cannot follow those laws uninterruptedly, because it forms part of a compound tissue, and is compelled by its intimate connexion with the surrounding elementary organs, to accommodate itself to the space thus determined for it, and in consequence of the pressure to which it is exposed laterally from the surrounding elementary organs, to assume forms which would be foreign to it under conditions of free, unrestrained development.

The sphere must be regarded as the fundamental form, in which every freely developed cell first appears. Although this form occurs not unfrequently with great regularity in very young cells, this is more rarely the case in full-grown cells. For in most instances the growth of cells is by no means uniform; sometimes one diameter remains short and the cell assumes the form of a flattened ellipsoid; but far more often one of the diameters becomes more or less elongated, and the cell passes into the form of an elongated ellipsoid, or, by farther extension, into that of a cylinder. Roundish forms are found more or less regularly developed in many lower Algæ, *e.g.*, in *Protococcus*, in the yeast plant, in completely or almost wholly isolated cells of higher plants, as in spores and pollen-grains, in the knob-shaped ends of many hairs of plants, &c. The cylindrical or attenuated conical forms are likewise frequent in the lower orders of the vegetable kingdom, in hairs, and the like.

The frequently occurring form of the elongated ellipsoid, and still more the cylindrical shape, point to the innate tendency of the vegetable cell towards an unequal growth, in which an opposition manifests itself between the longitudinal axis and the transverse axes, between the upper and lower ends, and the lateral faces of the cell; but in many other cases a still greater deviation from the primary form is met with, where particular points exhibit an isolated growth, giving rise to papillary elevations and gradual development of these into cylindrical processes, and thus to a ramification of the cell. The phenomenon is very common; it occurs, for instance, in the formation of the pollen-tubes upon the stigma, in the germination of most spores, and in the most striking degree in many Algæ. In these last the ramifications produced at the lower end of the cell frequently form a contrast to the upper end, since they fulfil the functions of root fibrils, *e. g.*, in *Botrydium* (fig. 1), in germinating *Confervæ*, &c., while the protrusions sprouting out from the upper end form the foundation of abundant, often very regular, ramifications of the plant, *e. g.*, in *Vaucheria*, *Bryopsis*, &c. This phenomenon is seen most distinctly in unicellular Algæ, as in the genera just named; but in most cases this process of ramification is combined with cell-division, which renders the detection of it difficult, and the uni-cellular becomes converted into a many-celled plant, *e. g.*, in *Conferva glomerata* (pl. 1, figs. 1—6).

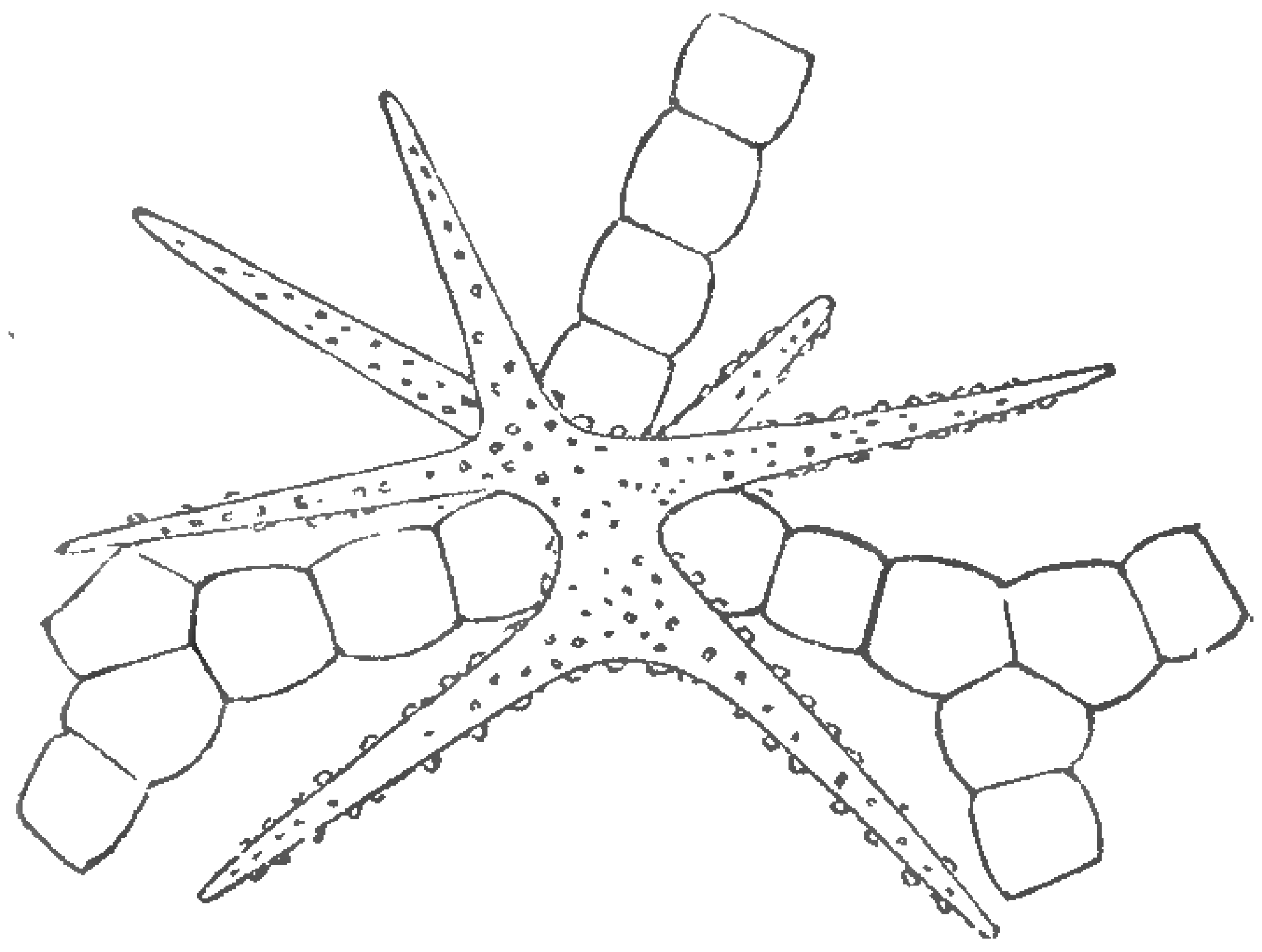
Fig. 1.



Botrydium granulatum.

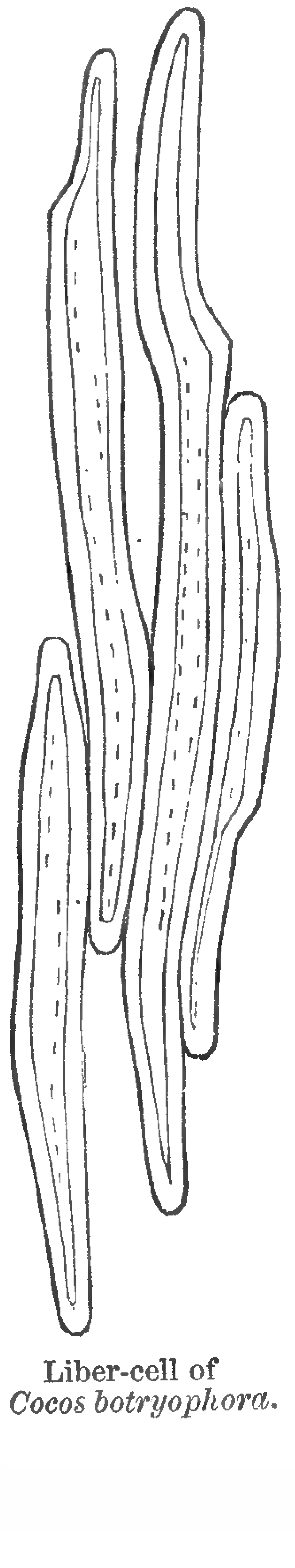
Those cells which have grown together with other cells or with vascular utricles, into a tissue, exhibit much slighter differences of form than the freely developed cells. It is true that in this case even a greater complication of form may arise from the growing out of particular places through unequal development, when one side of a cell lies free upon the external surface of a plant or in one of its internal air-cavities, as is evident in many hair-structures, and in the star-shaped cells of the air-cavities of the *Nymphææ* (fig.2); but in most cases such irregular growth of individual cells is rendered impossible, simply by the mechanical conditions in which they are placed. It is a general rule, that cells combined into a tissue are bounded by a number of plane surfaces, instead of possessing a rounded external form, since that part of a cell by which it is adherent to another cell becomes flattened, and only the free parts of the cell-wall can follow the original tendency to become rounded. The form of such cells depends, therefore, principally upon their relative position, and their more or less crowded condition; and the further modification of the form depends upon whether the dimensions of the cell in different directions are pretty nearly equal, or one dimension considerably exceeds the rest.

Fig. 2.



Stellate hair from the leaf-stalk of *Nymphæa advena.*

Fig. 3.



Liber-cell of *Cocos botryophora.*

Taking into consideration, in the first place, the latter condition, we can divide cells combined into a tissue, by no means, however, very strictly, into the short and the elongated.

The short cells, developed pretty uniformly in all directions, form the elements of the structure of all higher plants, since all their organs are formed, in their earliest stages, of these alone, and even in full-grown plants the bark and pith of the stem, as well as the soft parts of the leaves and the organs of fructification in general, are composed of cells of this form. During the development of the individual organs, fibrous strings are formed in the cellular mass constituting their ground-work, and these fibrous strings, which are composed of elongated cells and usually also of vessels, which lie among the elongated cells, receive in this case the name of *vascular bundles,* and taken collectively constitute the *wood* of the plant. The mass composed of short cells, in which the vascular bundles are imbedded, is named, in contradistinction to the latter, the *parenchyma.*

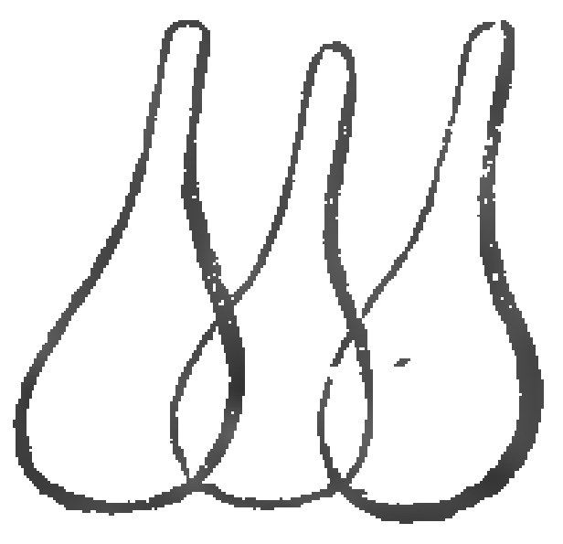
The elongated cells of the vascular bundles (fig. 3) are, as a rule, distinguished from the short parenchymatous cells, not only by their elongated, often fibrous shape, but also by the two ends being attenuated to points. In this case they are not arranged end to end in lines, but their attenuated extremities are interposed between the lateral surfaces of the cells situated above and below them; while the parenchyma cells, if, as is usual, they are arranged in lines, stand one upon another with flattened ends, their cavities being thus separated by partitions directed at right angles to their longitudinal axes. Link founded upon this difference of the ends the distinction between parenchymatous and prosenchymatous cells, a distinction which is indeed well grounded when we compare extreme forms, but which is by no means to be carried through, since the most manifold transitions occur from parenchymatous cells, with more or less oblique cross-walls, to perfect prosenchymatous cells.

In many Thallophytes, especially in many Fungi *(e. g., Boletus igniarius)* and Lichens *(e. g.,* in *Evernia)*, isolated portions of the substance are found of fibre-shaped, frequently irregularly interwoven cells *(irregular cellular tissue* of Kieser). Gradual transitions also occur from this form of cell to the form of the parenchymatous cell.

The form of the parenchymatous cells is most intimately connected with their relative position.

The simplest condition is afforded by such cells as lie one above another in a simple row, as the cells of the *Confervæ* (pl. 1, fig. 1), articulated hairs, &c. Here the cells become flattened on the surfaces of contact, while the side-walls retain their natural curvature. Accordingly as these possess a cylindrical curvature, or one more approximating to a globe, does the entire cellular filament obtain a cylindrical or beaded shape.

Fig. 4.

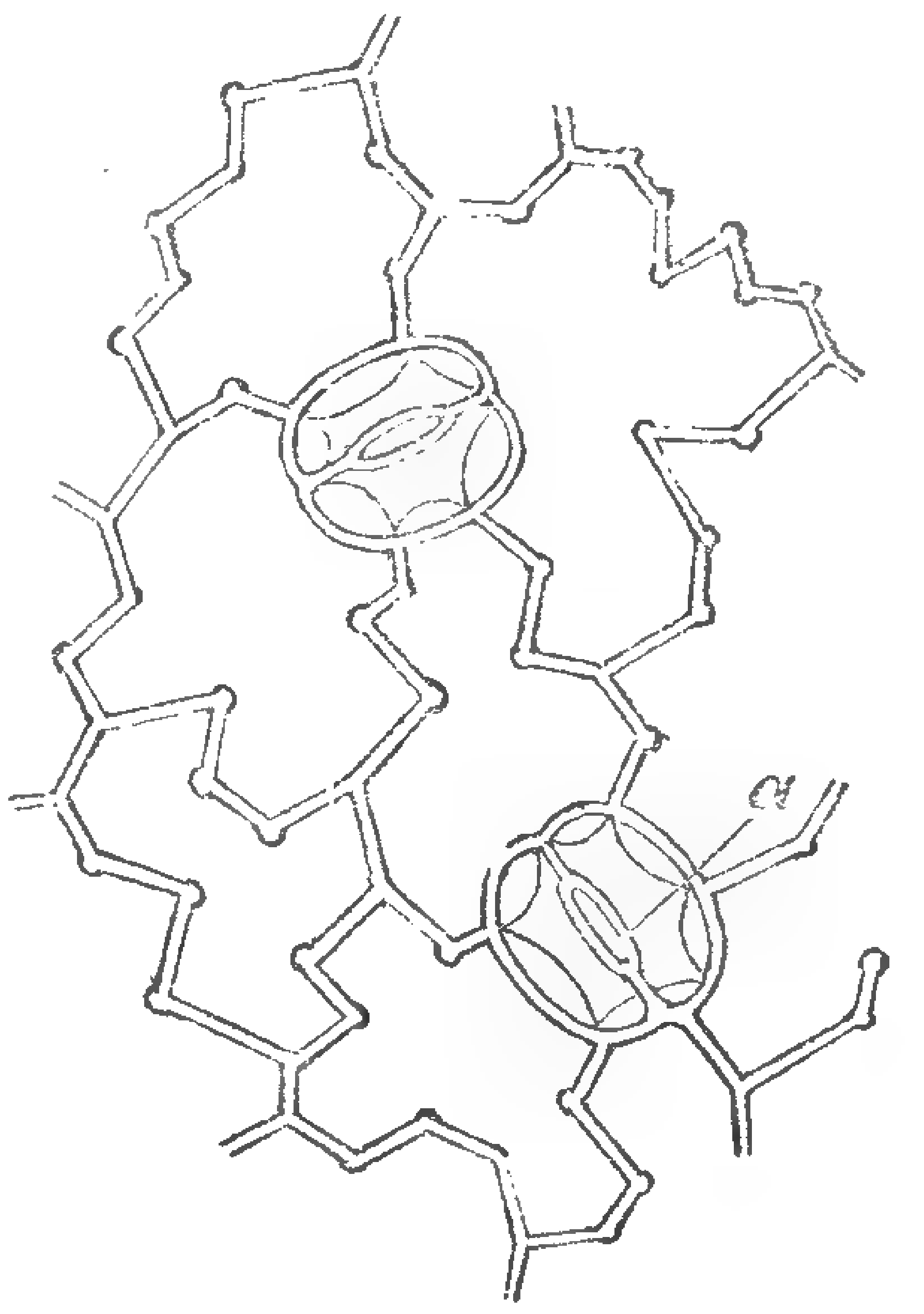


Cells of the epidermis of the petal of *Dianthus barbatus.*

When parenchymatous cells lie side by side in a simple layer, as is the case in the leaves of most Mosses and *Jungermanniæ*, and in the epidermis of the higher plants, their lateral surfaces, by which they are coherent together, become flattened; while the lower and upper free sides are either more or less convex, conically elongated (fig. 4), or quite flattened like the rest. Taken as a whole, such cells exhibit the form of many-angled plates or prisms, the shapes of which again present modifications, accordingly as the growth of the cells in the direction of the surface, which they combine to form, is uniform or irregular. The lateral faces of tabular cells are usually perfectly flat. Yet it sometimes happens, for instance in the anthers of *Chara*, and in the epidermal cells of many leaves (fig. 5), that the side-walls are curved into waving lines, or zigzagged in sharp angles.

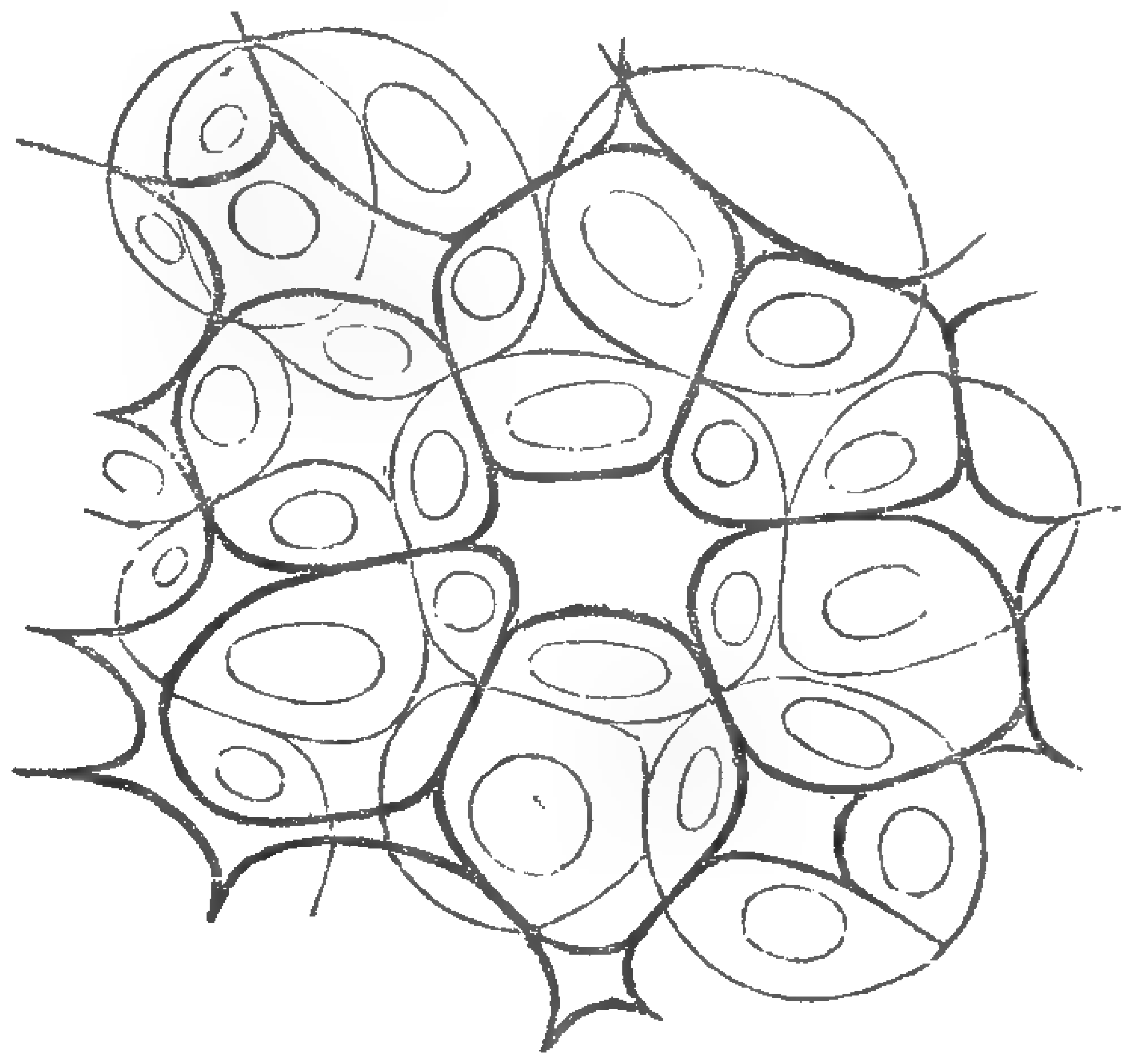
It is not so easy to define the form of the parenchymatous cells when they are collected together in masses (fig. 6), as is the rule in the internal substance of organs, for instance in pith, in bark, &c., for here every cell is surrounded on all sides by other cells, and exhibits as many flattened surfaces as there are cells standing in connexion with it. Kieser ("*Grundz. der Anatomie der Pflanzen*," § 127) sought to demonstrate, that the form of the cell must necessarily be that of a rhombic dodecahedron under such circumstances, since this form encloses the greatest space within the smallest amount of limits, and that their form is usually that of a rhombric dodecahedron elongated in a perpendicular direction, because the primary form of the vegetable cell is not the sphere but the ellipsoid. This proposition may be admitted theoretically, but it would be a vain labour to seek actually to observe the form of the rhombic dodecahedron in a cell in nature, since the contiguous cells are always far too unequal in size for them to become moulded into regular mathematical forms by their reciprocal pressure. So that in cross sections of a parenchymatous tissue the cells are found certainly of many-angled but of irregular forms; and the faces of transverse slices of the individual cells have a very variable number of sides (usually from five to eight). It is therefore more suitable to call such cells *polyhedral* instead of *dodecahedral*.

Fig. 5.



Epidermis of the lower face of the leaf of *Helleborus fœtidus.*

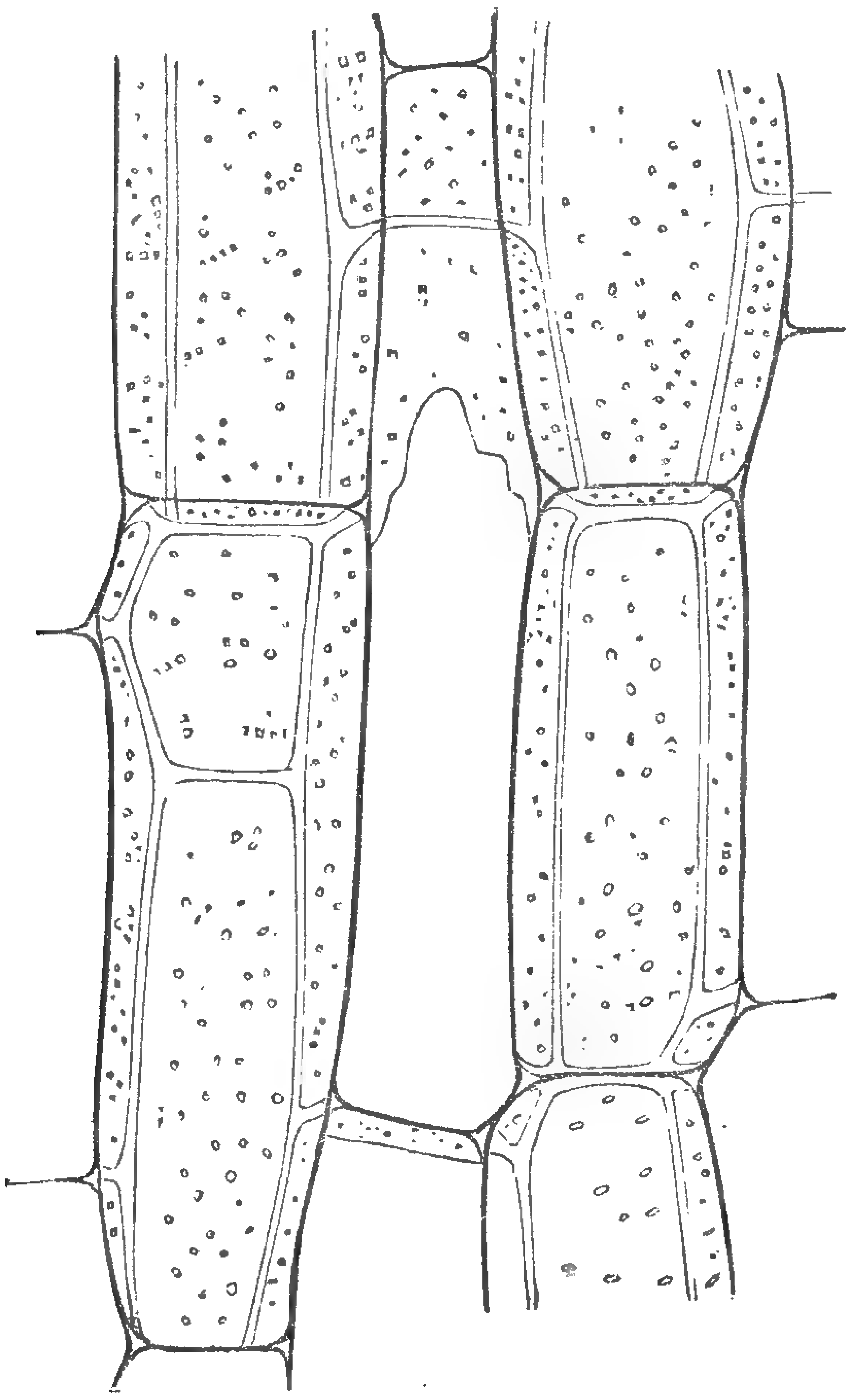
Fig. 6.



Parenchymatous cells from the bark of *Euphorbia canariensis.*

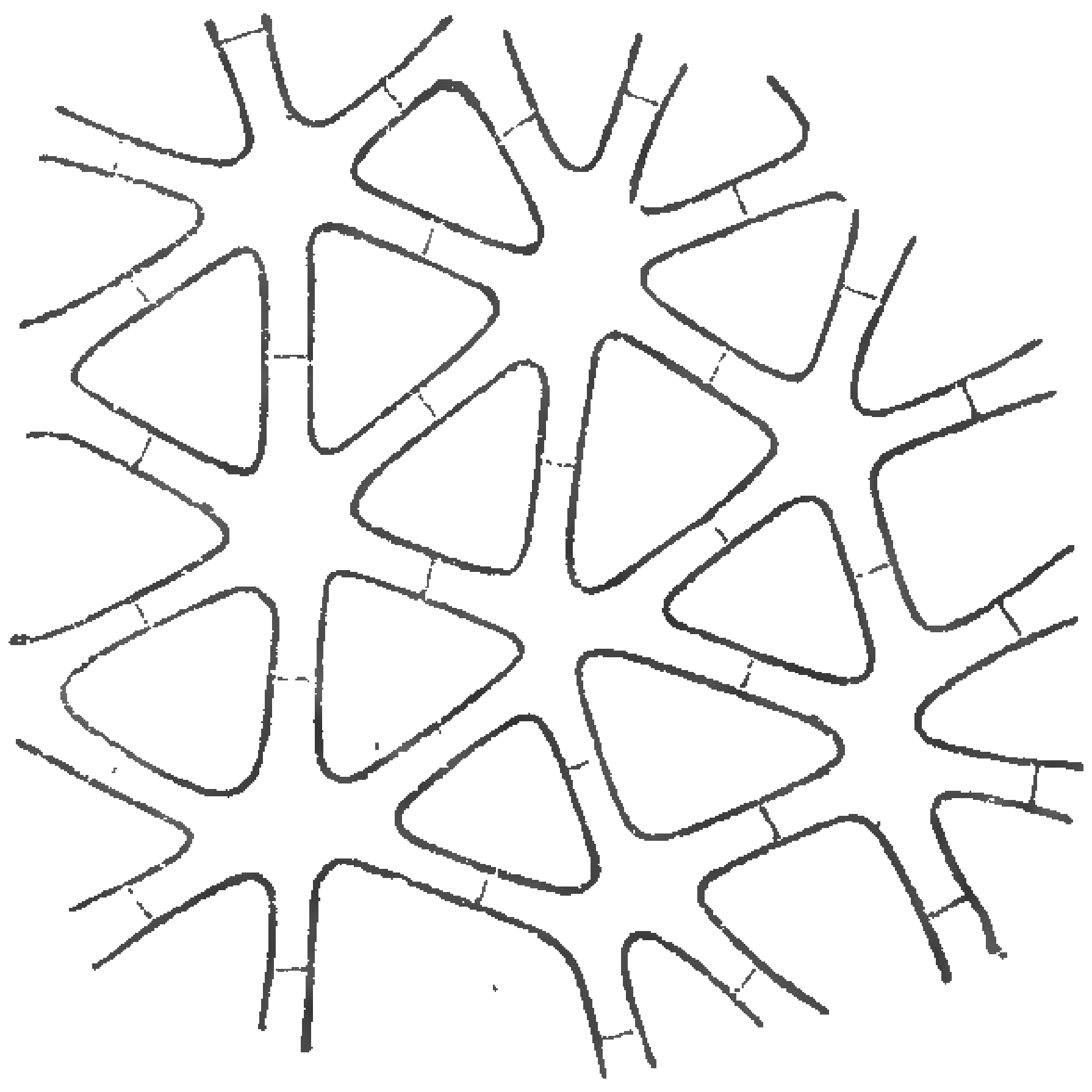
On the more or less crowded arrangement of the cells it depends whether the plane surfaces of these meet at acute angles (fig. 7); or whether, when the cells are more loosely aggregated, the surfaces of contact are but small (fig. 6), and large portions of the cell-walls between them remain unconnected with the neighbouring cells. In the latter case, the free portions of the cells retain their natural rounded form. In particular cases, however, the portion of the cell-wall immediately surrounding a plane surface in contact with another cell, grows out in a tubular form, so that when several such processes are formed, the cell acquires a star-like appearance. When in such cases the cells are arranged in one plane, as occurs in the cross-walls of the air-canals of many water-plants, all the rays of the star lie in one plane (figs. 8, 9); when, on the other hand, the cells are heaped together in masses, as in the pith of *Juncus effusus*, the rays project from all sides of the cell.

Fig. 7.



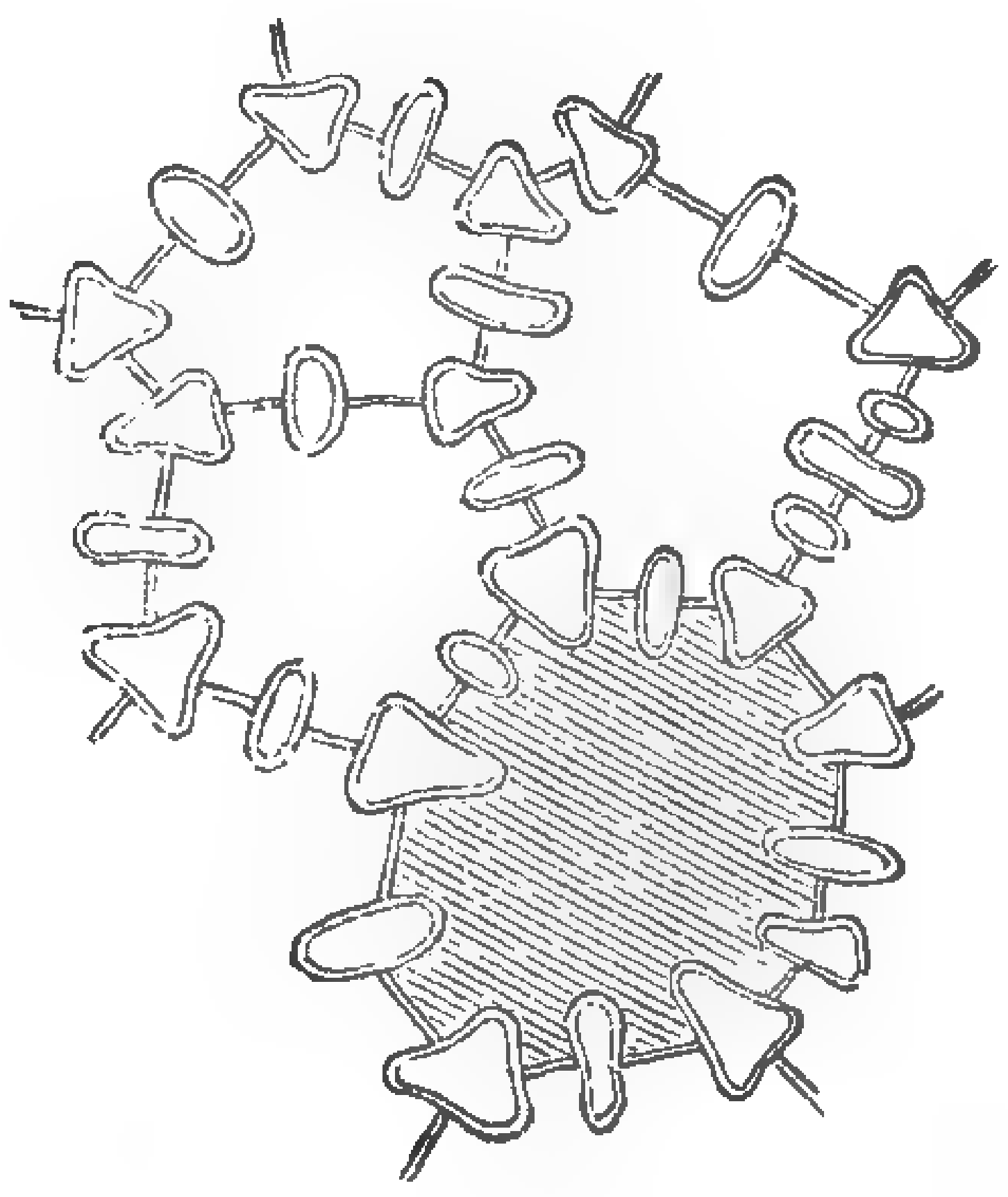
Cells of the pith of *Acanthus mollis*.

Fig. 8.



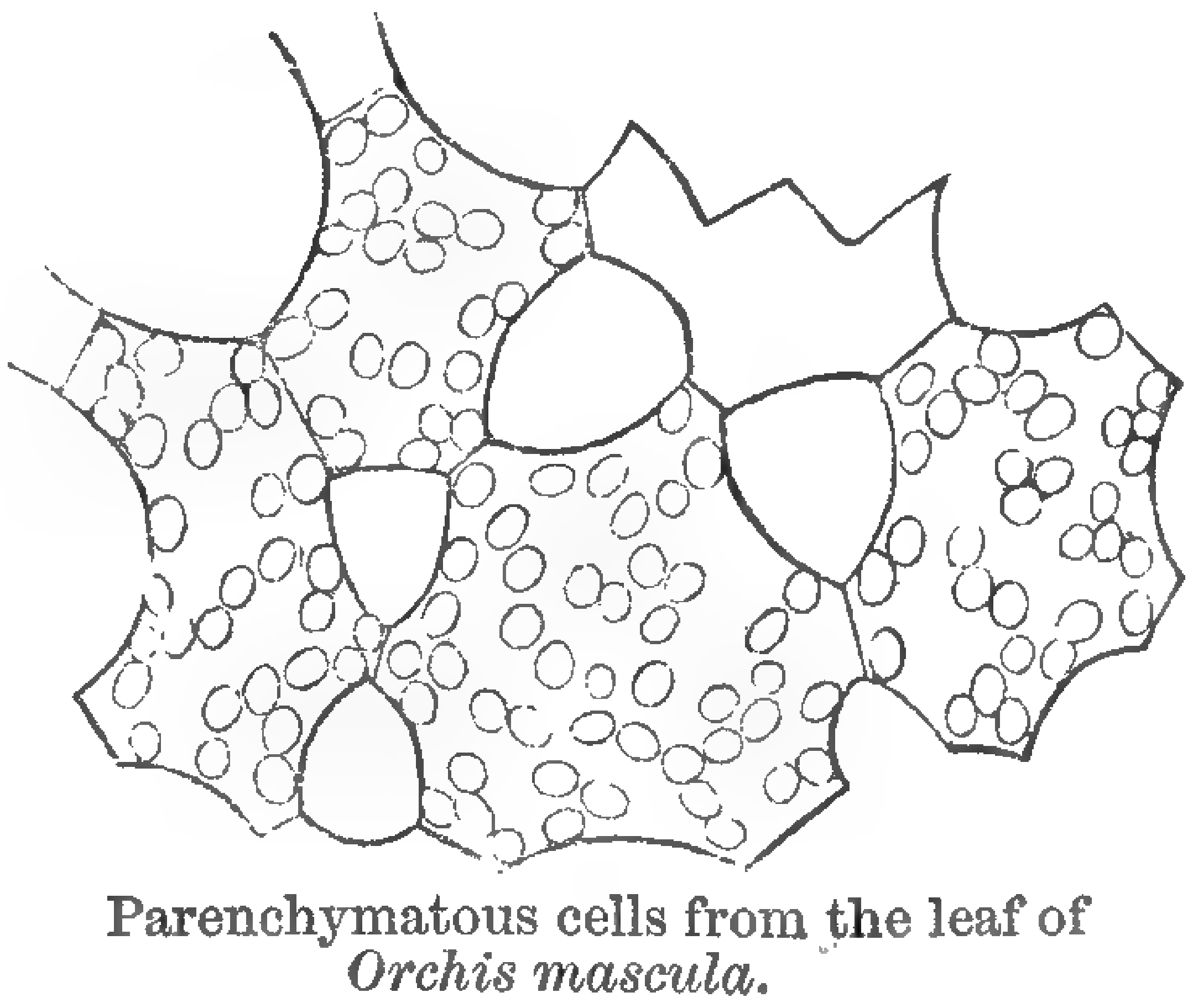
Stellate cellular tissue from the leaf-stalk of *Musa*.

Fig. 9.



Partition bounding an air-canal in the leaf-stalk of *Sagittaria sagittifolia*.

Fig. 10.



Parenchymatous cells from the leaf of *Orchis mascula*.

Far more frequent than such regularly branched cells, are those of a roundish form, exhibiting a shorter projection at one or more points, and so having a moderately irregular form; the parenchyma of the lower side of the leaves of most plants is composed of such cells (fig. 10).

Observ. Some phytotomists have distinguished a greater number of tissues according to the forms of the cells, applying particular names to them, especially Hayne ("*Flora*" 1827, ii. 601), Meyen ("*Phytotomie*" 57, "*Physiologie*" i, 12), and Morren ("*Bulletin de l'Acad de Bruxelles,*" *V. No.* 3). The arrangement of Hayne, which did not attract the least notice, I may pass over here. Meyen distinguished: 1, *Merenchyma*—tissue composed of spherical cells, the cells only partially in contact; 2, *Parenchyma;* 3, *Prosenchyma*—this name was applied by Meyen to the woody tissue of the Coniferæ; 4, *Pleurenchyma,* which was the name by which he distinguished the prosenchyma of all other plants. The division of merenchyma from parenchyma was superfluous, and cannot be carried out, because there are so many transitional forms; the alteration of the established term prosenchyma into pleurenchyma was altogether inconvenient, and was not adopted. But the wilderness of botanical terminology would have been increased beyond all reasonable measure by Morren, had not his subdivisions been passed over unregarded; for he divided the parenchyma alone into no less than eight tissues, which he named, *merenchyma, conenchyma, ovenchyma, atractenchyma, cylindrenchyma, colpenchyma, cladenchyma,* and *prismenchyma.* All such far-fetched subdivisions of the cellular tissue are wholly valueless, because no exact connexion exists between form and function, and frequently enough the same organ is formed of cells differing considerably in form,—in two closely allied plants.

B. SIZE OF THE CELL.

Important as the accurate determination of the size of the individual elementary organ is, in many special researches, particularly those relating to the history of development, yet in general the knowledge of the size of cells is of very subordinate value; and this the more that not only do the cells of the same organ exhibit extraordinarily great variations in respect to their size, but the contiguous cells of one and the same organ not unfrequently differ considerably from each other. Pollen grains afford a very striking example of the former; their dimensions are tolerably constant in each species of plant; but their diameter varies from 1-300th of a line in *Myosotis* to 1-15th of a line and more in *Cucurbita, Strelitzia, &c.* The cells of a single organ often differ to the extent of some being twice or thrice as large as others.

The diameter of the cells of parenchyma may be stated at a general average of from 1-20th to 1-100th of a line; but in particular cases (*e. g.*, in the spores of many Fungi, in the yeast cells) it falls to less than 1-500th, and in other instances it rises, *e. g.*, in succulent parts, in the pith of the elder, &c., to 1-10th of a line and more; so that in such cases the individual cells are actually visible to the naked eye, which is not generally the case.

The dimensions of many elongated cells form a striking contrast with this small magnitude of the majority of parenchymatous cells, since while the transverse diameter of the former is usually considerably smaller than the diameter of the parenchymatous cells, the longitudinal extension is very remarkable. In regard to the majority of elongated cells, especially the prosenchymatous cells of the wood and *bast* or liber of most plants, we should be very much deceived if we deduced from the fibrous structure of these organs a great length of the constituent cells; yet, on the other hand, cases do occur when particular cells exhibit an astonishing length. The prosenchymatous cells of wood generally exhibit only a length of 1-3rd to one line, exceeding this last dimension but seldom; as a rule, the bast cells attain about the same length; yet in some cases they occur of far more considerable length, for I found them 1·6 to 2·6 lines long in a Palm (a species of *Astrocaryum*). The bast cells of flax and hemp are considerably longer, but difficult to measure, since it is often impossible to ascertain the commencement and termination of a cell. Many hairs formed of simple cells also exhibit a very considerable length, especially cotton, the longest fibres of which do not, however, exceed one to two inches. Among the cells of the higher plants the pollen grains are the most striking for their great longitudinal growth, the filiform prolongation penetrating into the style attaining in long-styled plants like *Mirabilis longiflora, Cactus grandiflorus, &c.*, a length of three inches and more.

The most striking examples of large cells are found in the family of the Algæ, in many uni-cellular plants, as in *Vaucheria*, *Bryopsis*, and especially in *Chara*, in the larger species of which the great cells forming the interior of the stem attain the length of several inches, and a diameter of 1-3rd of a line and more.

C. THE CELL-MEMBRANE.

a. Physical Properties.

In most cases the membrane of cells possess a considerable degree of stiffness and solidity. But in this respect extreme differences occur between the cells of different plants and of their different organs; and, moreover, this condition may exhibit extreme variations at different periods of the growth of the same cell. The membrane of young cells, also the cells of many lower plants, for example of most Algæ, Fungi, Lichens, and the cells of fleshy leaves and fruits are very soft; while the cells of many woods, *e. g.*, in Palms and Tree Ferns, and those of the albumen of many fruits, exhibit a bony hardness; and finally, the cells of the epidermis of *Equisetum* and *Calamus* possess such solidity, that it scratches metal, and strikes fire with steel.

All membranes are readily penetrated by water, and in the operation become more or less softened and swollen up. The latter phenomenon occurs in a higher degree the younger and softer the cell is; whether, however, as Schleiden states, the membranes of nascent cells are actually soluble in water, is more than doubtful to me. The swelling up occurs strongly in many thick-walled cells which in a dry condition have a horny consistence, as in Lichens, Fucoideæ, and in certain gelatinously soft cells (the so-called collenchyma cells) lying beneath the epidermis of herbaceous plants. In the short parenchymatous cells no great difference appears to occur in the strength of the expansion in the different directions; but in the elongated cells of the bast and wood, the swelling up resulting from moistening takes place principally in the direction of the breadth, and only in a very small degree in the longitudinal direction.

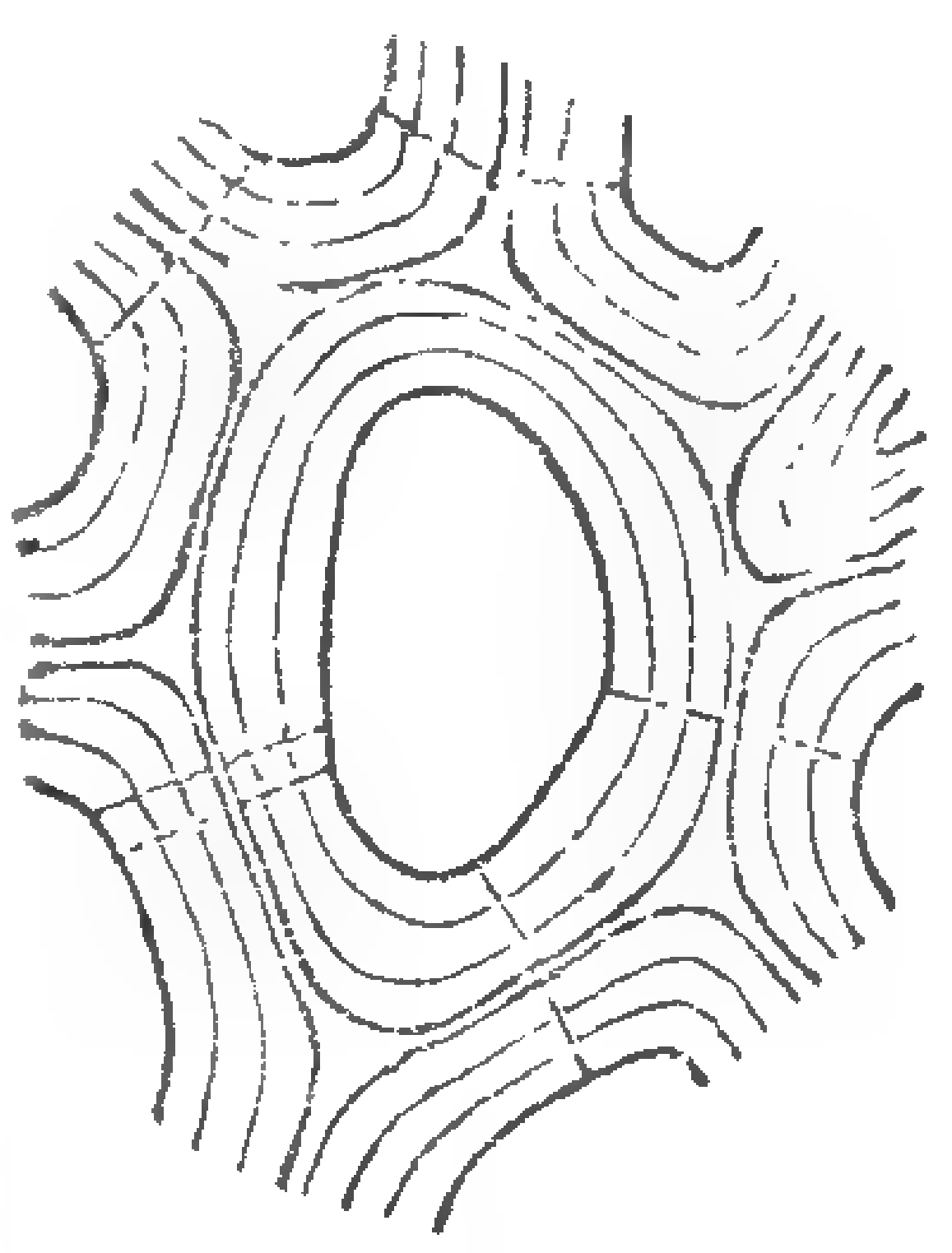
The cell-membrane of young cells is completely colourless and transparent; in full-grown cells it is frequently imbued with yellow, red, or brown colouring matters, whereby in many cases the transparency is importantly interfered with. This alteration is very striking in the change of the sap-wood into heart-wood, for in many trees, *e. g.*, in the ebony and yew, the white is converted into a more or less dark colour, without the cell-membrane increasing in thickness, while at the same time it acquires a far more considerable solidity and independence of the influence of moisture.

Observ. It is difficult to conceive how some phytotomists (Link, "*Element. Phil. Bot.*" 1824, p. 366; Meyen, "*Physiol.*" i. 30) came to the opinion that cells contract in the direction of their length when moistened, and again expand when dried, since, on the contrary, all cells expand in every direction when moistened. In the elongated cells of the wood the contraction by drying in the direction of the length is, of course, but small, yet it occurs constantly. In wood of Dicotyledons the longitudinal contraction from the wet to the perfectly air-dried condition amounts to only 0·072 to 0·4 per cent., while the contraction in the direction of the breadth is as much as 4 to 9 per cent. According to Schleiden's experiments, the bast-cells of flax expand only about 0·0005 to 0·0006; but he considers it possible that there was an important error here (*Beiträge*, i. 69). According to the researches of Ernest Meyer, the Manilla hemp *(Phormium ?)* expands, when wetted, about 1-50th of its length, while the increase of breadth amounts to 1-5th.

b. Structure.

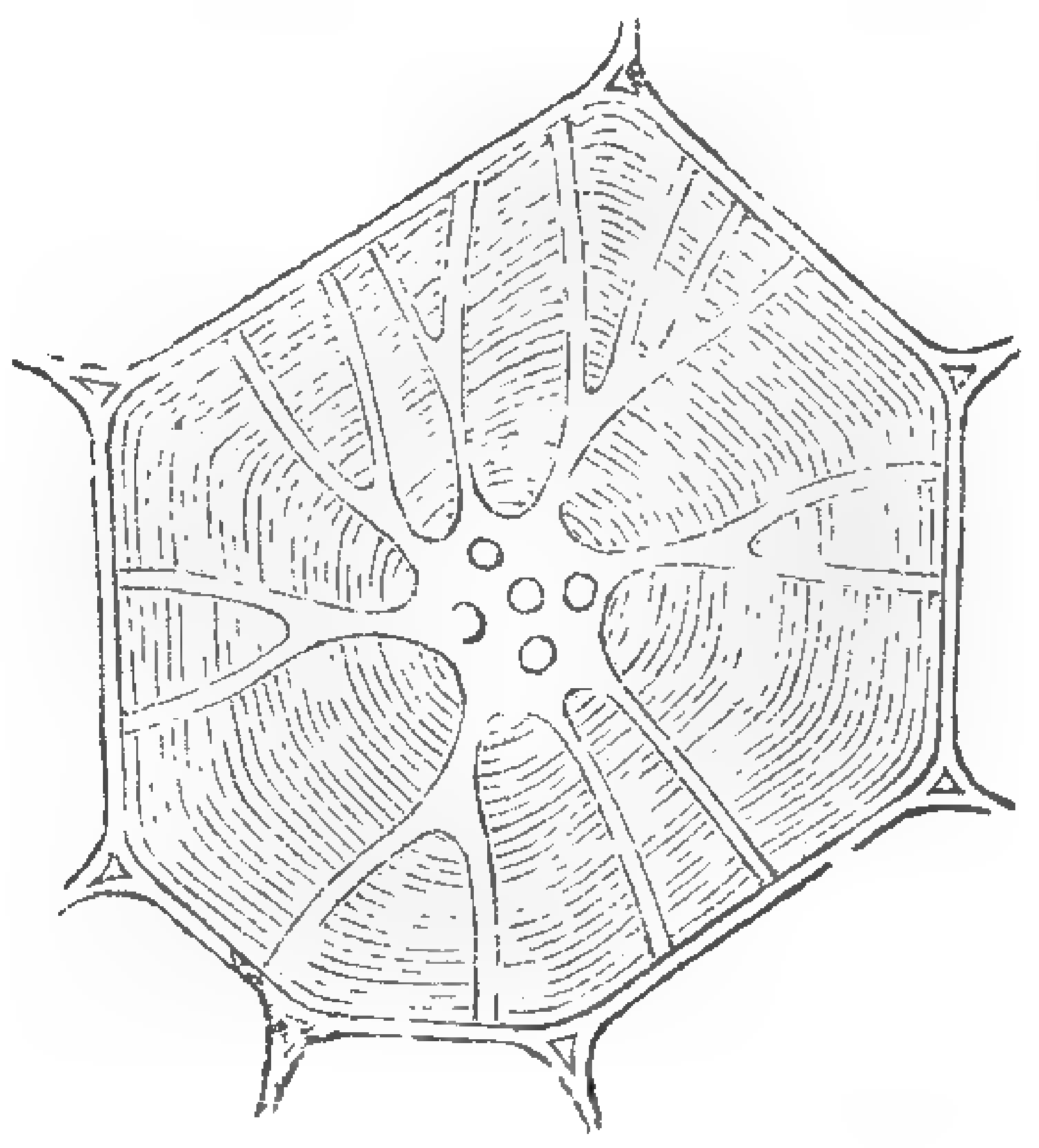
In examining a transverse section of a thick walled cell, *e. g.*, of wood-cells of *Clematis Vitalba*, the bast-cells of Palms, (fig. 11), or the thick walled pith-cells of *Hoya carnosa*, (fig. 12) we find by strongly magnifying, that the cell-membrane is not homogeneous, but composed of numerous super-incumbent layers concentrically surrounding the cavity of the cell. By the action of a mineral acid of proper

Fig. 11.



Transverse section through the liber-cells of *Cocos botryophora.*

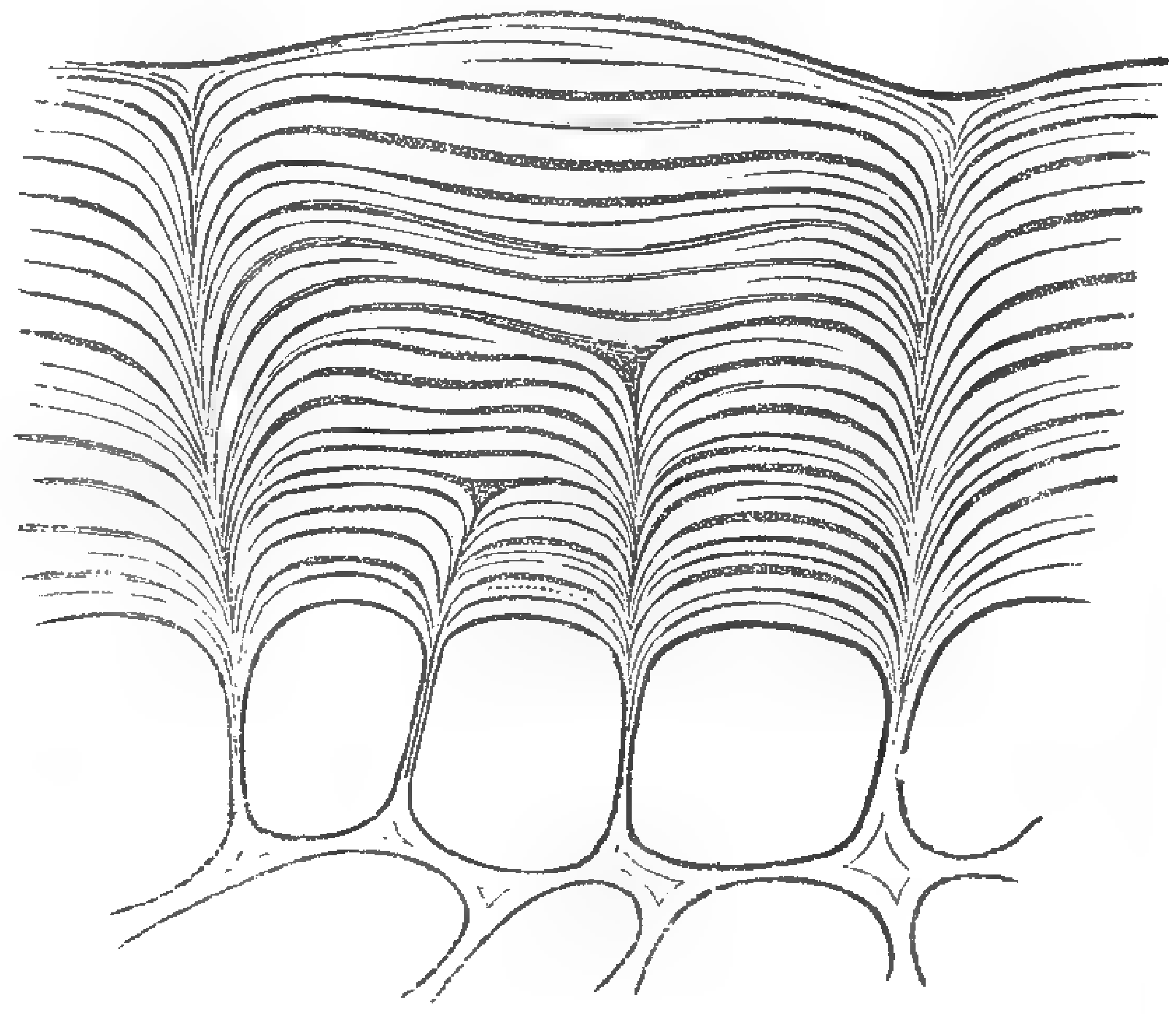
Fig. 12.



Transverse section through a thick walled cell of the pith of *Hoya carnosa.*

degree of concentration the membrane is caused to swell up, its lamellar structure becomes very much more distinct, and a great number (often fifty) of separate layers may be detected. By this means the lamellar structure may be demonstrated even in those cases in which the unaltered membrane appeared completely homogeneous; for instance, in the horny cells of the albumen of *Phytelephas*. Usually the wall of the cell is of equal thickness on all sides; in this case the layers run uninterruptedly round the cavity and form perfect cells encased one within another. In many cases (*e. g.*, very frequently in the epidermis-cells—fig. 13—and in the brown cells which surround the vascular bundles of the Ferns) the different sides of the cell possess, on the contrary, a very different thickness; in this case the layers of the thicker portion of the wall are not continued over the thin sides, but are bevelled gradually off.

Fig. 13.



Cells of the Epidermis of the stem of *Viscum album.*

This condition alone allows us to conclude with great probability, that the growth of the cell-membrane in thickness does not depend upon the thin membrane of the young cell itself growing thicker by the absorption of new cellulose, but that it arises from a periodical deposition of new membranes upon the already completely developed wall. But the complete confirmation and more accurate knowledge of this process are only obtained through the circumstances next to be mentioned.

The wall of young cells having yet very thin membranes, appears perfectly smooth and uniform; but if the tissue of the same organ is examined at a later period, the walls of its cells are found to have become thickened; these walls are almost without exception found to be covered with a greater or smaller number of porelike points or slits, which are distinguished by the name of dots (tüpfel or *pits*). A more minute examination of the cross-section of the cells (figs. 11, 12) reveals that these spots are formed by canals which open freely into the cavity of the cell, but are closed externally by the outermost thin membrane of the cell. When all these circumstances are taken together, it becomes most indubitably evident, that the primary membrane of the cell is completely closed and not possessed of visible pores; that the subsequent deposits, on the contrary, have the form of perforated membranes, and that the deposition of these secondary membranes takes place in the direction from without inwards upon the inside of the primary membrane.

Observ. It is now no longer worth while to give an historical review of the opinions that had been expressed as to the structure of the cell-wall and of the spots, before the appearance of my essay "On the Pores of Vegetable Cellular Tissue," in 1828. But it is necessary to advert to the objections which have recently been advanced by Harting and Mulder against my doctrine of the structure of cells, and of the gradual and successive deposition of the secondary layers from without inwards. *(See* Harting *"Mikrochem. Onderzoekingen,"* &c., in the *"Tidshrift voor naturlijke geschiedenis,"* XI.*)* (translated in the *Linnæa* XIX. Harting : *"Letter to H. v. Mohl,"—Bot. Zeitung*, 1847, 337.—Mulder *"Physiological Chemistry."*—Mohl *"On the Growth of Cell Membranes,"—Bot. Zeitung*, 1846, 337.) I believe I may safely leave unnoticed the objections advanced by Hartig. *("Beiträge zur Entwickelungsgesch. der Pflanzen,"* 1843; *"Das Leben der Pflanzenzelle.")*

Mulder and Harting attack my theory on both anatomical and chemical grounds, and seek to demonstrate that the cell-membrane increases in thickness in the direction from within outwards by the deposition of layers upon the outside of the original membrane, which process of growth is followed, in some cases, by a deposition in the interior of the cavity of the cell, while in particular instances (in the cells of horny albumen) the membrane itself grows thicker by the interpenetration of foreign matter. In the first place, my opponents deny that the thin membranes of the young cell are imperforate, and that only the subsequently internally deposited layers are porous, since they, on the contrary, believe, that they found the membrane of young cells to be perforated like a sieve, while a perfectly closed membrane is deposited subsequently on the outside of these closed cells. It is, of course, not for me to decide who observed most correctly, I or Harting; but I must stand by the facts I have stated, and do not believe that Harting would have been deceived in the manner he has, if, instead of selecting only cells having small pits for his observations, he had extended his researches also to cells with large pits, between which the secondary membranes appear in the form of narrow fibres; and had properly regarded the analogy which exists between the structure of the vascular utricles and cells. Harting finds a second reason for his view of the external growth in his micrometrical measurements of young and of thickened cells (*Linnæa,* 1846, 552), by which he arrived at the conclusion that the cavity of the wood-cells expands during the increase of thickness of a shoot, in exactly the same proportion as the unlignified cells, whence he argued that the thickening of their walls is to be ascribed to a deposition taking place upon the outside of their primary membrane. On the other hand, I consider that I have demonstrated by my measurements (*"Bot. Zeitung,"* 1846, 358) that exactly the contrary occurs, and that the thickening of the walls is combined with a narrowing of the cavity of the cell.—Mulder and Harting deduce a third counter-evidence from the chemical reaction of the cell-wall (which will be spoken of hereafter). The membrane of young cells is coloured blue by the action of iodine and sulphuric acid; in full-grown cells this very often happens only to the innermost layers, while the intermediate acquire a green or yellow, and the outermost membrane a brown, colour, altogether withstanding the solvent power of sulphuric acid, which is not the case with the intermediate and inner layers. From this my opponents draw the conclusion that the membrane of the young cell and likewise the inmost layers of full grown cells are composed of cellulose, the intermediate and outermost layers, on the contrary, of other compounds, which are subsequently formed and deposited on the outside of the cellulose membrane. Against this I have shewn (*"Botanische Zeitung"* 1847,497) that the chemical researches by which their deductions are supported, were imperfect; that the outermost layers of cell-membrane are composed in like manner of cellulose, but are infiltrated with foreign compounds, which prevent the reaction of iodine and sulphuric acid; that the date of origin of a layer must not be deduced from the chemical reaction, since both the inner and outer layers may undergo a chemical metamorphosis, which does not stand in any connexion with the time of its origin; and that therefore anatomical grounds alone can serve for the decision of the order in which different layers have been developed.—Lastly, in reference to the statement that the thick walled cells of the albumen of *Phytelephas, Iris,* &c. (figs. 14, 15), and the so-called collenchyma cells (fig. 16) possess uniform, and not lamellated, walls, and that consequently their primary membrane itself has increased in thickness; this assertion depends simply upon imperfect investigation. If the authors had treated these cells with sulphuric acid of the proper degree of concentration, they would have found the lamellation.—In short, the researches which I was caused to undertake by the objections of Harting and Mulder, served only to strengthen the grounds on which I had built my theory of the growth of cell-membranes.

Fig. 14.

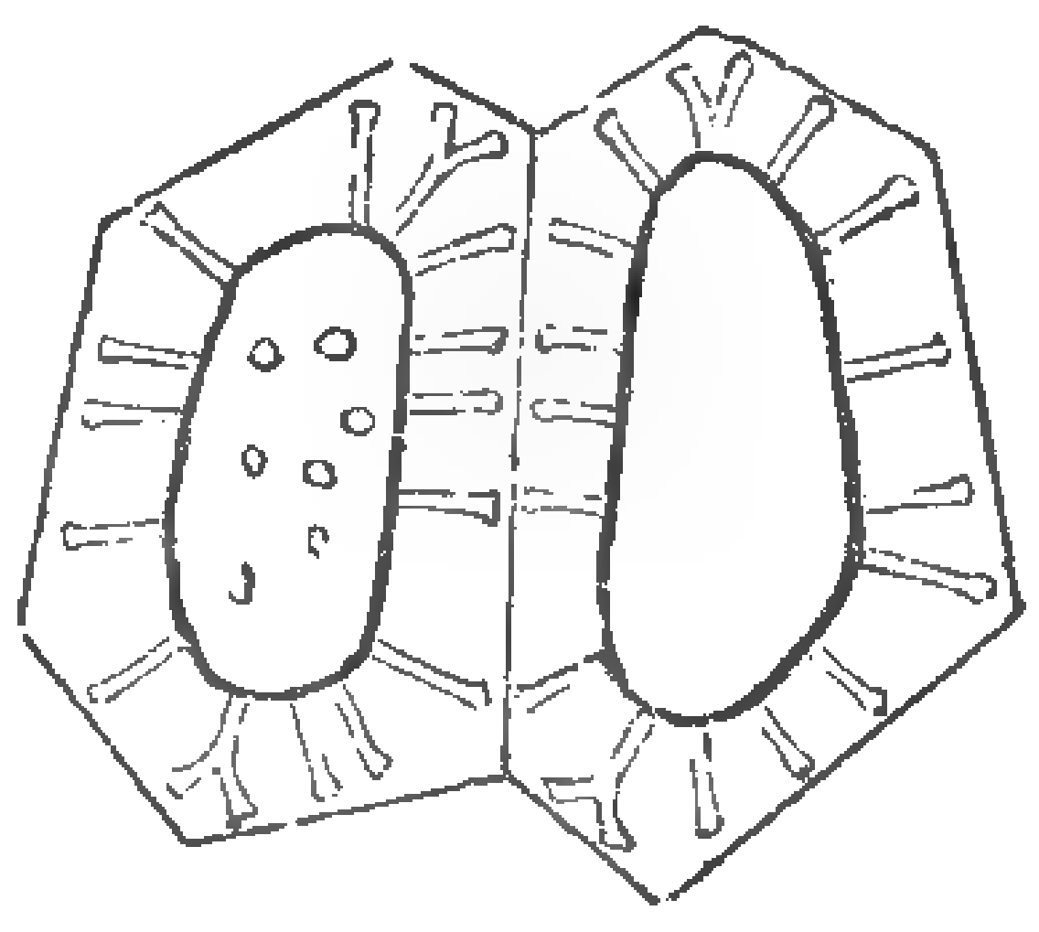
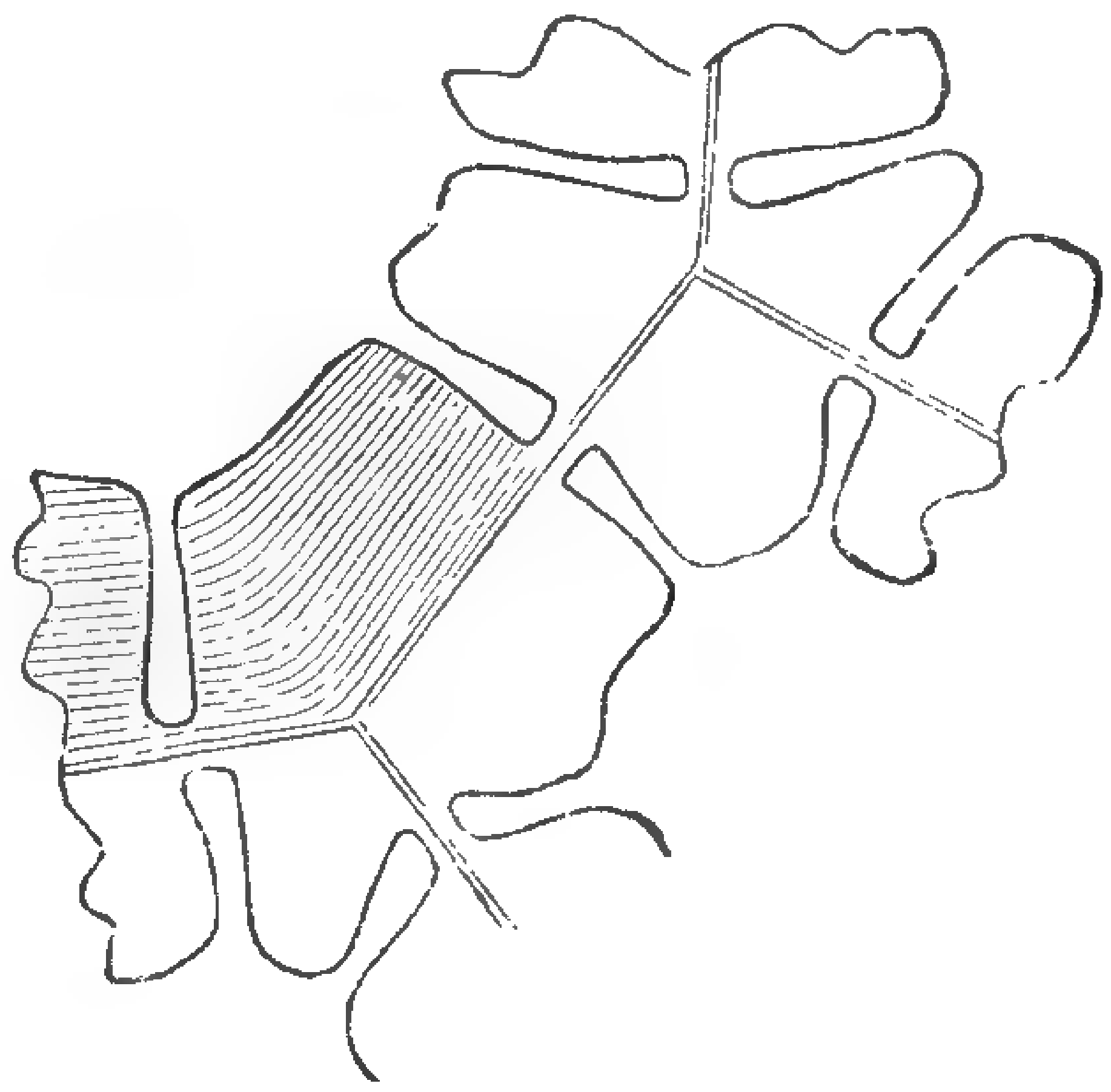
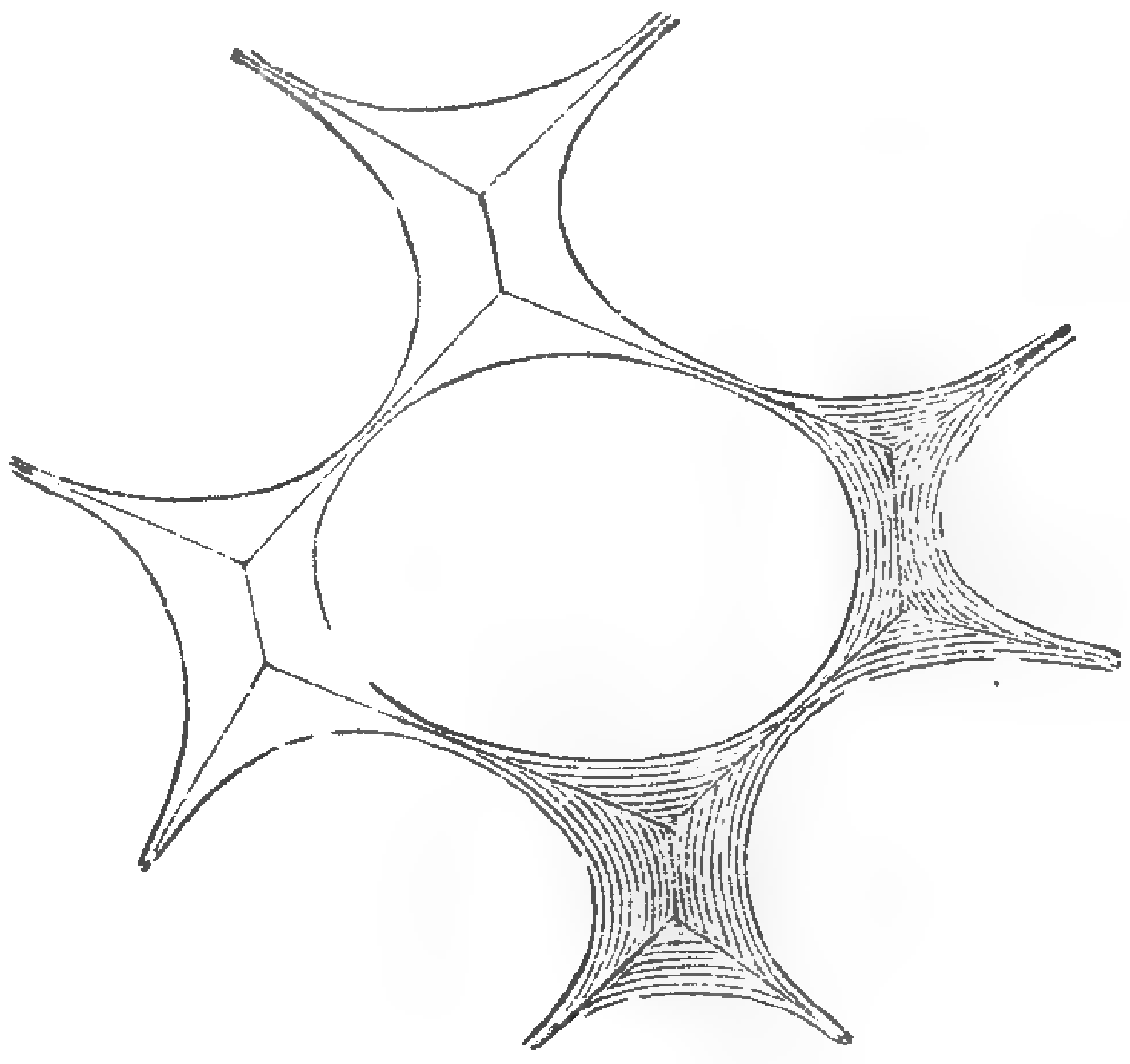


Fig. 15.



Cells of the albumen of *Sagus tædigera.*

Fig. 16.

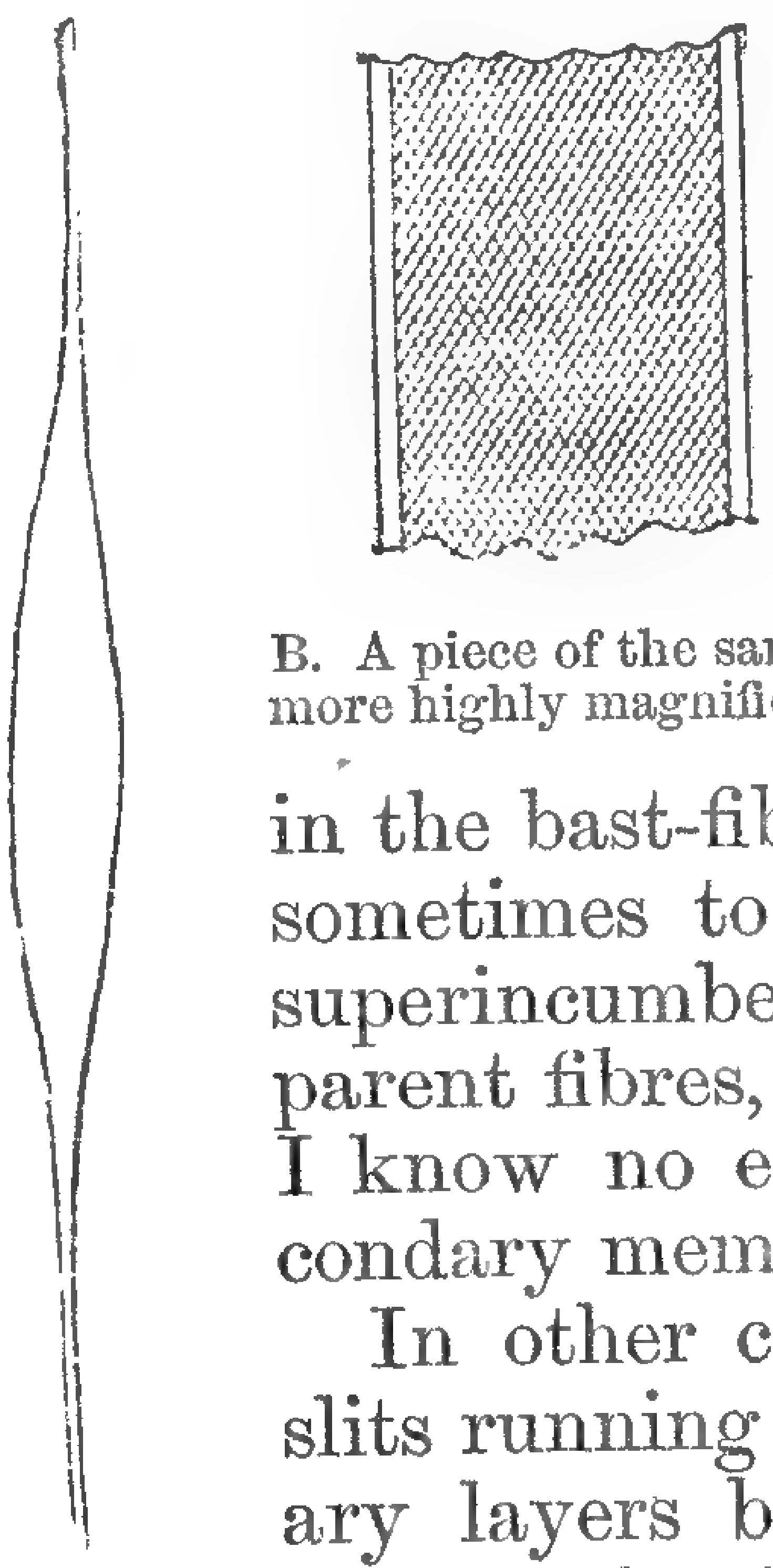


Cells from the leafstalk of *Nymphæa alba.*

The secondary cell-membranes deserve a separate mention. Taken altogether, it is seldom that they appear to the eye, as the primary membrane does, in the form of an uniform smooth pellicle, as it were a hardened mucilage, for example in the *Confervæ* and in many hairs. Whether in such a case they are really devoid of special structure, is doubtful, for such cells, when drawn out lengthways, sometimes tear in an oblique direction, so that they may be more or less perfectly drawn out into a spirally wound band. This phenomenon, together with the visible conditions of structure, to be spoken of directly, appear to me to indicate that the secondary cell-membranes, without being composed of actual primitive fibres (which cannot in any way be demonstrated), possess indeed a fibrous structure, since their molecules are connected more firmly in the direction of a spiral than in any other direction. (See "*On the Structure of Vegetable Membrane,*" in my "*Vermischte Schriften.*")

Next to these cells, appearing perfectly homogeneous to the eye, come such as exhibit a very fine spiral streaking of their membrane, as is the case in the cells of many woods, *e.g.*, in *Pinus sylvestris*, and in a very striking degree in the bast-tubes of the Apocyneæ and Asclepiadeæ, *e.g.*, in *Vinca* (fig. 17), *Nerium*, *Ceropegia*, and *Hoya*. Although in many of these cases also the membrane has the aspect of being composed of separate fibres lying very close together, yet this appears actually not to be the fact, but the streaking to be dependant upon the unequal thickness or density of the different parts of a connected membrane. In favour of this is, in particular, the circumstance, that in the bast-fibres of the Apocyneæ, the spiral is wound sometimes to the right, sometimes to the left, in the superincumbent layers of the same membrane; the apparent fibres, therefore, then cross, a condition of which I know no example in the actual division of the secondary membrane into fibres.

Fig. 17.

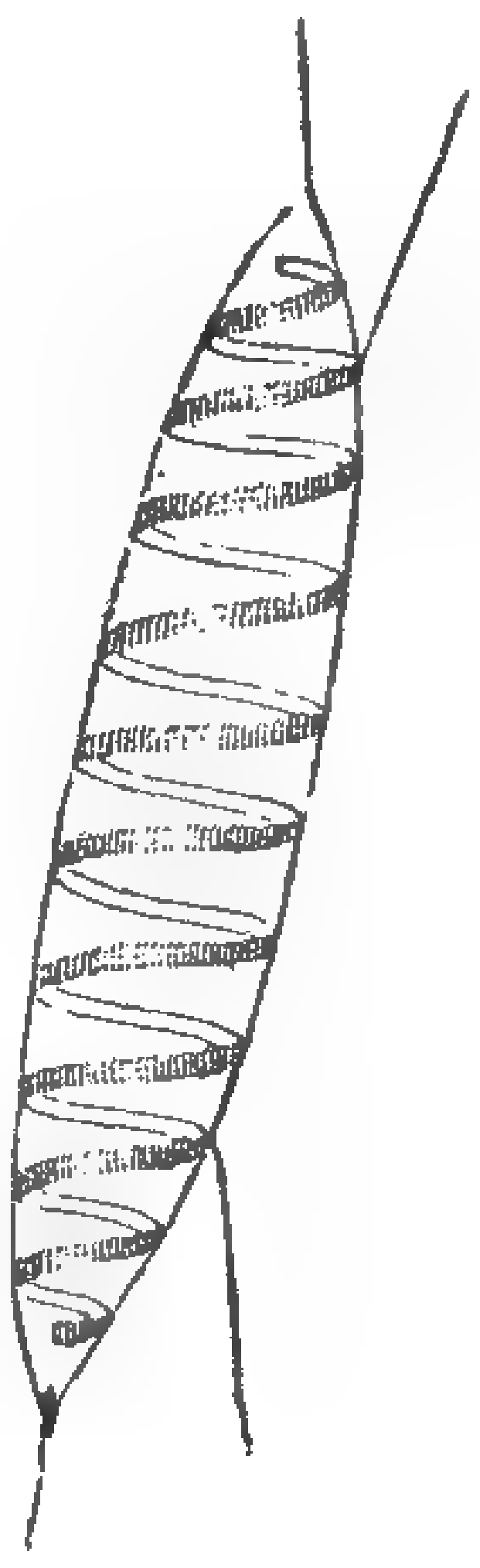


B. A piece of the same, more highly magnified.

A. Liber-cell of *Vinca major.*

In other cases occur, instead of the streaks, perfect slits running in a spiral direction, by which the secondary layers become divided into broader or narrower bands (fibres), running parallel with each other. The direction of the spiral in which the fibres run is, as a rule, the same in all the cells of a tissue; therefore the fibres of two contiguous cells cross upon their two coherent walls. In the overwhelming majority of cases the fibres are wound to the right (in a botanical sense, *i.e.*, therefore in the manner of a left-handed screw). Instances of the contrary do certainly occur, sometimes merely as isolated cases in particular elementary organs, sometimes regularly in particular specimens of a plant. Such spiral fibres occur in rarer cases in the common parenchymatous cells of the stem and leaf-stalk; for example, to a very remarkable extent in various species of *Nepenthes*, in many Orchideæ; on the other hand, they are more frequently confined to special organs, for instance to the elaters of the Hepaticæ, the cells of the sporangium in *Equisetum* (fig. 18), a portion of the cells of the leaf and the cells of the cortical layer in *Sphagnum*, the hairs in the Cactaceæ, particular layers of the seed-coat in *Casuarina, Salvia*, many Polemoniaceæ, &c., and in many plants to the anther-cells. Particular organs composed of such fibrous cells, not unfrequently possess a spongy, soft consistence, *e. g.*, the outer rind of the root of many tropical Orchidaceæ and Aroideæ, the sepals of *Illecebrum verticillatum*, the pericarp of *Cachrys Morisoni, C. odontalgica*, the ribs of the fruit of *Œthusa Cynapium.*

Fig. 18.

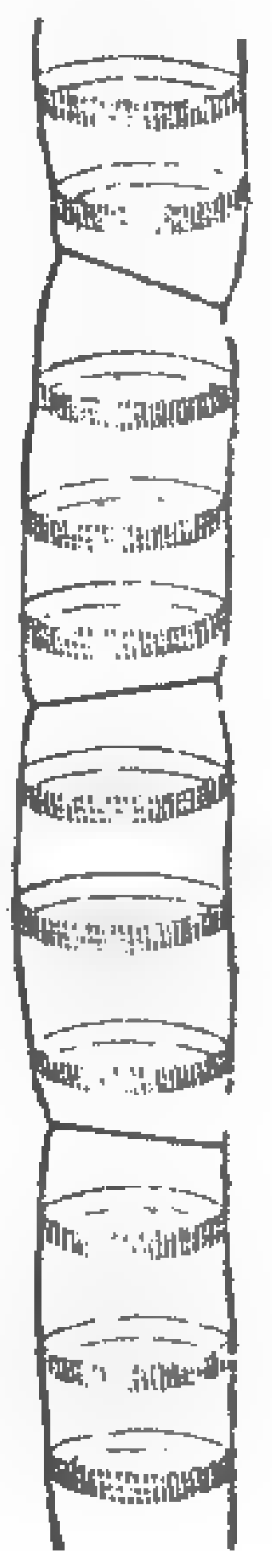


Cell from the sporangium of *Equisetum arvense.*

The annular fibre (fig. 19) which runs in a transverse direction on the cell-wall, crossing the longitudinal axis of the cell at right angles, is to be regarded as a slight modification of the spiral fibre. It not unfrequently occurs alternating with the spiral fibres in the same cells as the latter, *e. g.*, in the cells of many anthers, in the sporangium of the Jungermanniæ, and in the leaves of *Sphagnum.* It may be regarded as a middle form between the right and left wound spiral fibres.

The reticulated structure of the secondary membranes occurs infinitely more frequently than the regular spiral formation, and scarcely a plant can be found, from the Mosses upward, in which this structure cannot be more or less clearly distinguished in the majority of its cells. Sometimes, but in comparatively rare cases, the secondary membranes of the reticulated cell resembles those of the spiral-fibrous cell, in that they are likewise divided by closely adjacent pits into narrow fibres, which fibres, however, do not run in a spiral direction, but are connected into a more or less regular net, with narrower or wider, roundish or angular meshes, *e. g.*, in the cells of the wing of the seed in *Swietenia*, of the pericarp of *Picridium tingitanum, P. vulgare*, in the seed-coat of *Cucurbita Pepo*, of the parenchyma of the leaf of *Sanseviera guineensis* (fig. 20), in isolated cells of the pith of *Rubus odoratus, Erythrina Corallodendron.* But in the great majority of cases the secondary membrane is perforated by comparatively small orifices at few points only, and therefore does not appear under the form of a net-work of narrow fibres, but as a connected membrane perforated like a sieve. Since this is the usual condition, which occurs in almost all cells (*see* fig. 7), it will be unnecessary to cite examples; yet it may be permitted to name some particularly characteristic cases, the investigation of which prepares the way to a comprehension of less distinct structures, *e.g.*, the parenchymatous cells of the leaf-stalk of *Cycas revoluta*, the thick walled pith-cells of *Hoya carnosa* (fig. 12), the cells which form the stony concre-

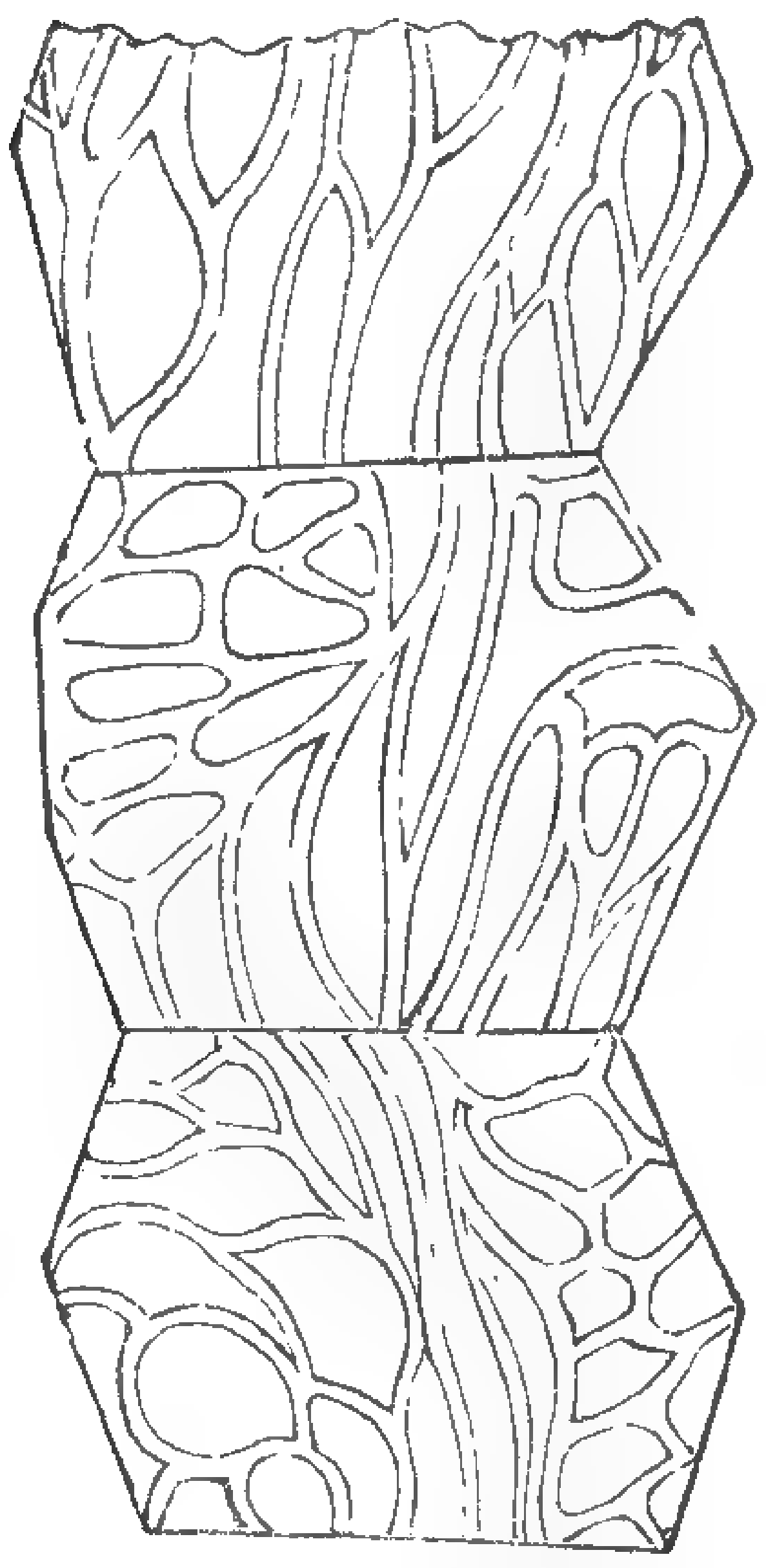
Fig. 19.



Cells from the sporangium of *Marchantia polymorpha.*

tions in the flesh of pears and quinces, the horny albumen of *Phytelephas,* of many Palms (fig. 14), and of the Rubiaceæ. These smaller orifices in the secondary membrane are denominated pits, the cells themselves pitted cells. The numerous transitions from this form of cell into the form of those having a net-work of narrow fibres, and from these into the spiral-fibrous cells, furnish the evidence that the fibres are not, as earlier phytotomists believed, to be considered as a peculiarly organized elementary portion, but that they are nothing else but narrow sections of the secondary membrane lying between elongated pits; that between fibre and membrane there exists a distinction in form, but none in essential nature.

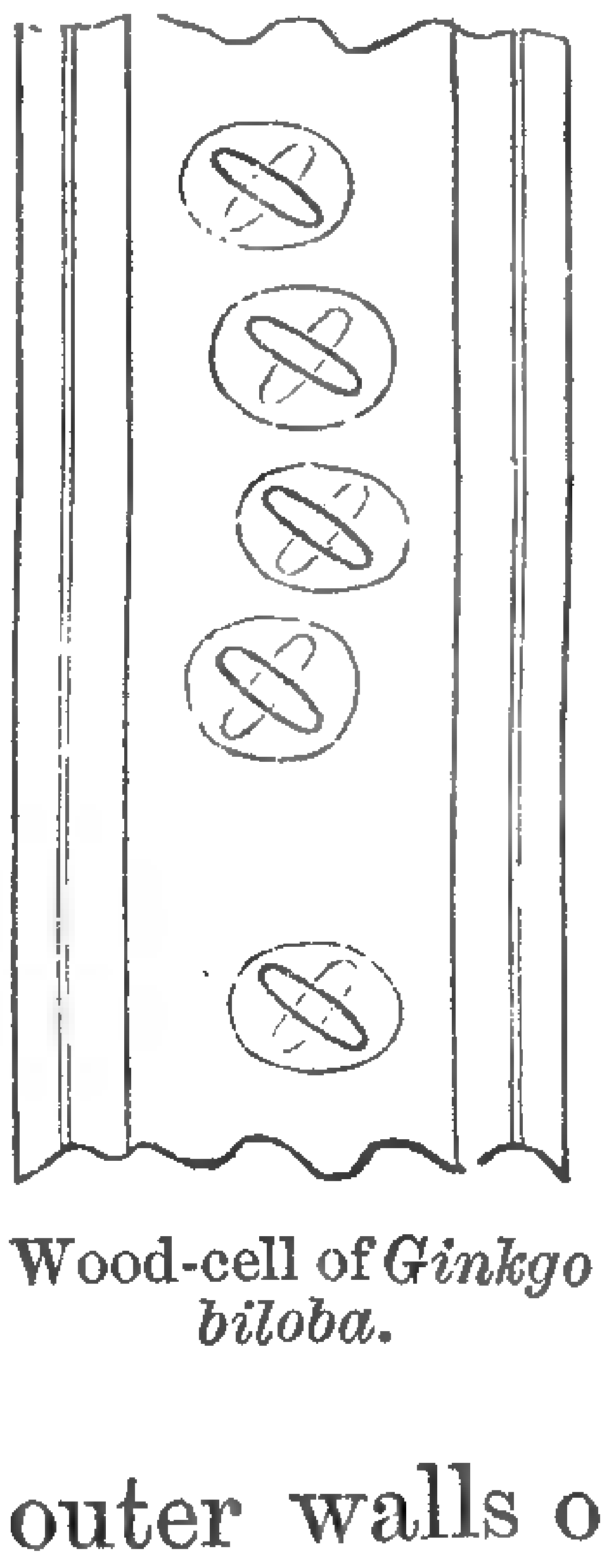
Fig. 20.



Cells of the leaf of *Sanseviera guineensis.*

The distribution of the pits upon the cell is usually altogether irregular, especially upon the horizontal transverse walls of the parenchymatous cells. On the other hand, it is common, and especially in elongated cells, for the pits upon the lateral walls of the cells so far to exhibit regularity in their position, that they stand more or less exactly in the direction of a spiral, and are frequently drawn out lengthways in this direction (fig. 21), so that they appear as short slits. Sometimes also a certain rule may be met with in reference to the places on which pits exist or are deficient. Thus in the wood-cells of most Coniferæ they are found on the side-walls, turned towards the medullary rays; thus in loosely connected parenchymatous cells they not unfrequently occur on the flattened parts of the walls by which the cells are coherent together, while they are absent from the surfaces which bound the inter-cellular passages, as occurs frequently in the cortical cells of Dicotyledons; or, if they occur on the inter-cellular passages, they differ in size and form from those situated on the side-walls of the cells, *e. g.*, in *Cycas,* in the wings of the seeds of *Swietenia.* The pits are moreover usually wanting to the outer walls of the epidermal cells, but they may also occur here; as, for example, on the leaves of *Cycas.*

Fig. 21.



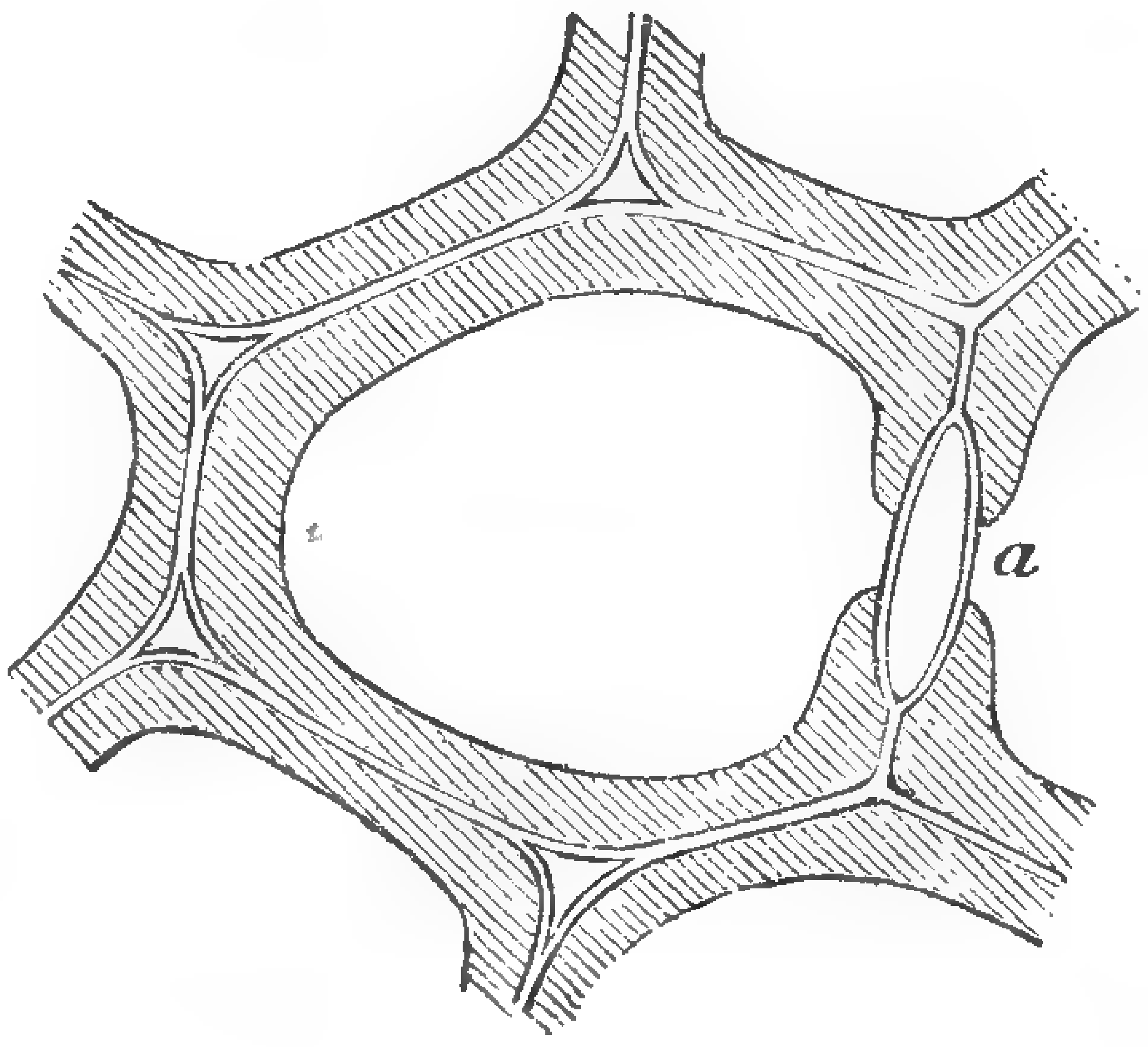
Wood-cell of *Ginkgo biloba.*

The pits of one cell are most intimately connected in regard to form and position with those of the contiguous cell; and it is a general law, that when two pitted cells are coherent together, the pits of the two cells lie exactly opposite to each other; so that in very thick walled cells the cavities of the two cells are only separated from each other, in the canals of the pits, by the primary walls, which form a very thin partition (figs. 11, 14, 15). This dependence of the structure of one cell upon that of its neighbours, becomes the more prominent the more the reticulated formation prevails in the secondary membranes, and it disappears in proportion as the spiral structure becomes more distinctly evident. Therefore where the pits are scattered irregularly they correspond accurately in form and position; where they are arranged in a spiral direction, and present the appearance of short elliptical slits, they correspond in position but no longer in form, since being situated obliquely in the opposite direction, they cross and only correspond at their central portion (fig. 21). Finally, when the pits are extended into long spiral slits, surrounding the cell, the relation to the contiguous cells has altogether disappeared.

In thick walled cells the pits usually form cylindrical canals, which, however, frequently open into the cavity of the cell by a funnel-shaped opening at their inner extremity; and sometimes the outer blind end is somewhat enlarged. Not unfrequently two or more pit-canals unite into one common passage, opening into the cavity of the cell (fig. 12).

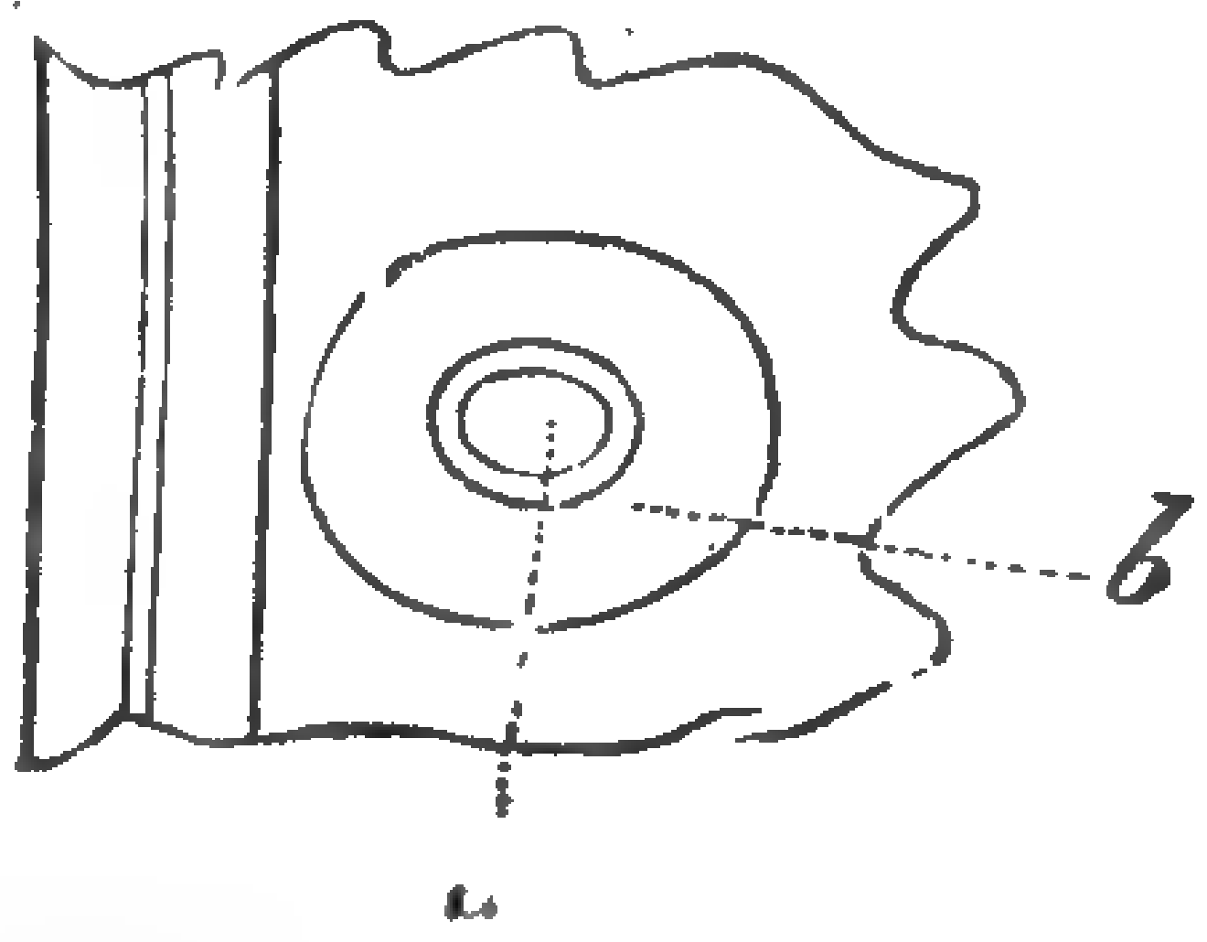
In many cases the primary walls of two contiguous cells separate from each other at the spots where the pits lie and leave a lenticular cavity between them, which has a rather larger circumference than the pit itself (fig. 22) and then appears like a ring surrounding the pit (fig. 23). I am only acquainted with this structure in elongated cells; it is most distinct in the wood-cells of the Coniferæ and Cycadeæ, but it occurs in the wood-cells of many Dicotyledonous trees. These cavities are not yet existent in very young cells, but they are found before the deposition of the secondary membranes, and the formation of pits arising out of this. Schleiden's assertion that these cavities arise from the secretion of a bubble of air between the previously blended cell-walls is incorrect; they are filled with sap in the young condition of the cells.

Fig. 22.



Transverse section through a *pit (a)* of *Pinus Pinea.*

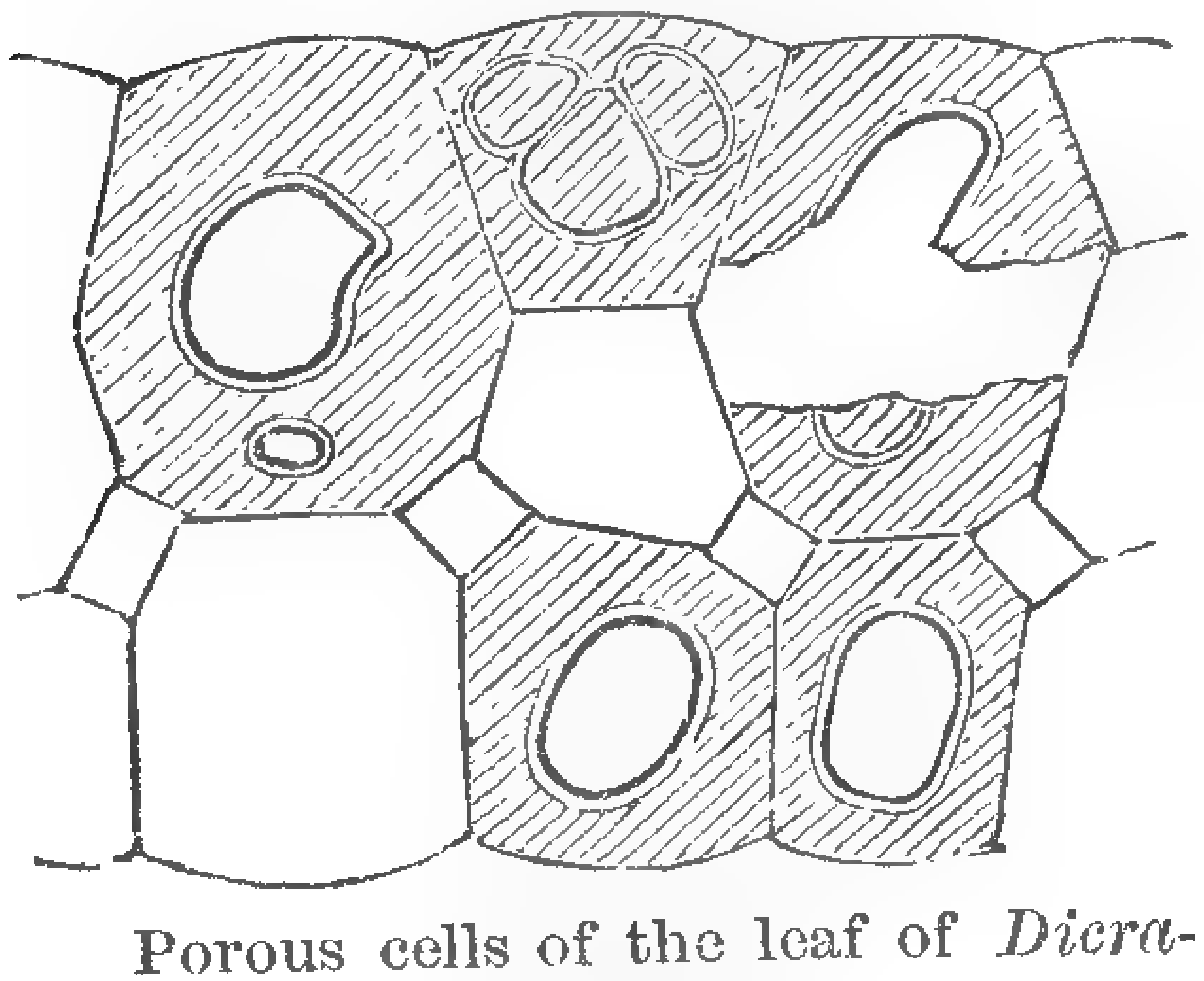
Fig. 23.



The *pit* of *Pinus Pinea* seen in face; *a*, canal of the pit; *b*, border.

In isolated, but very rare, cases, the primary membrane which is stretched across the pits as a partition, becomes absorbed after the completion of the development, whereby the pitted cells become converted into porous cells. This occurs most remarkably in certain Mosses, especially in the fibrous cells of *Sphagnum*, the leaf-cells of *Dicranum glaucum* (fig. 24), and *Octoblepharum albidum*, &c. (See "*Anatomical researches on the Porous Cells of Sphagnum*" in my "*Vermischte Schriften,*" 294; also Schleiden, "*Beiträge,*" i. 71.) This phenomenon is very rare in the Phanerogamia; I found it decidedly in fibrous-cells, *e. g.*, in the rind of the root of *Epidendrum elongatum*, in the seed-coat of *Martynia*, &c., &c. Whether it occurs normally in the wood-cells of *Pinus*, as Unger asserts, is yet a matter of doubt to me.

Fig. 24.

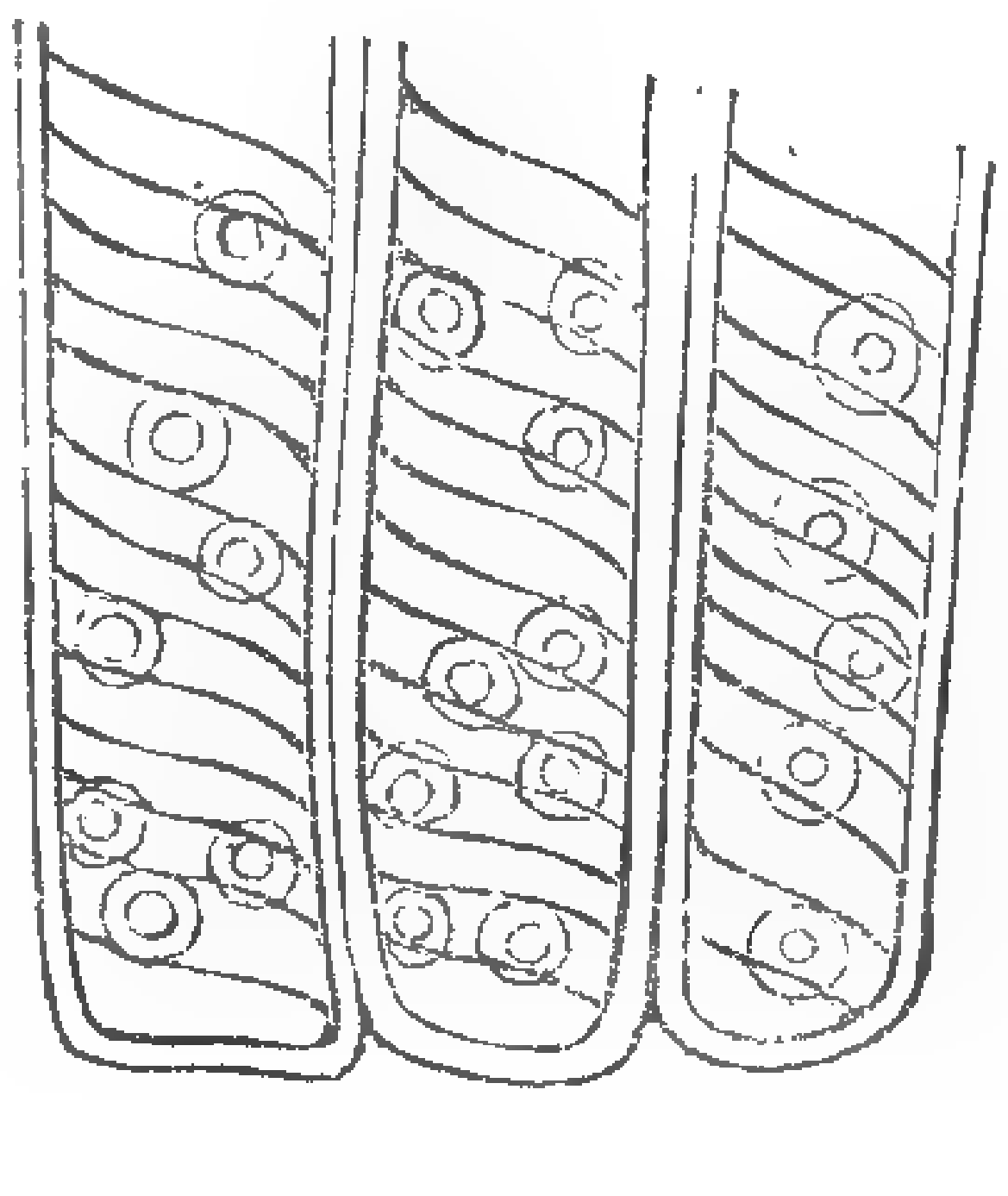


Porous cells of the leaf of *Dicranum glaucum.*

In the generality of cases, all the layers deposited on the inside of the primary membrane agree completely in their form, so that there is no reason why we should adopt a further division of the layers than that into primary and secondary membrane. But in particular cases, the secondary membrane consists of two layers of strikingly different structure, so that it becomes necessary to distinguish between primary, secondary, and tertiary membranes.

To what extent such a distinction into secondary and tertiary membrane exists, cannot be stated in the present state of our knowledge. I must, therefore, confine myself to the mention of certain examples in which the existence of the tertiary membrane may be demonstrated with certainty. To these belong the wood cells of *Taxus* and *Torreya*, the primary and secondary membranes of which are formed exactly as in the wood-cells of *Pinus*, but their cavity is lined with an inner membrane, which is covered with a fibre-like thickening running in regular spiral lines (fig. 25). The same structure is repeated in the wood-cells of certain Dicotyledonous trees, *e.g.*, in *Viburnum Lantana*.

Fig. 25.



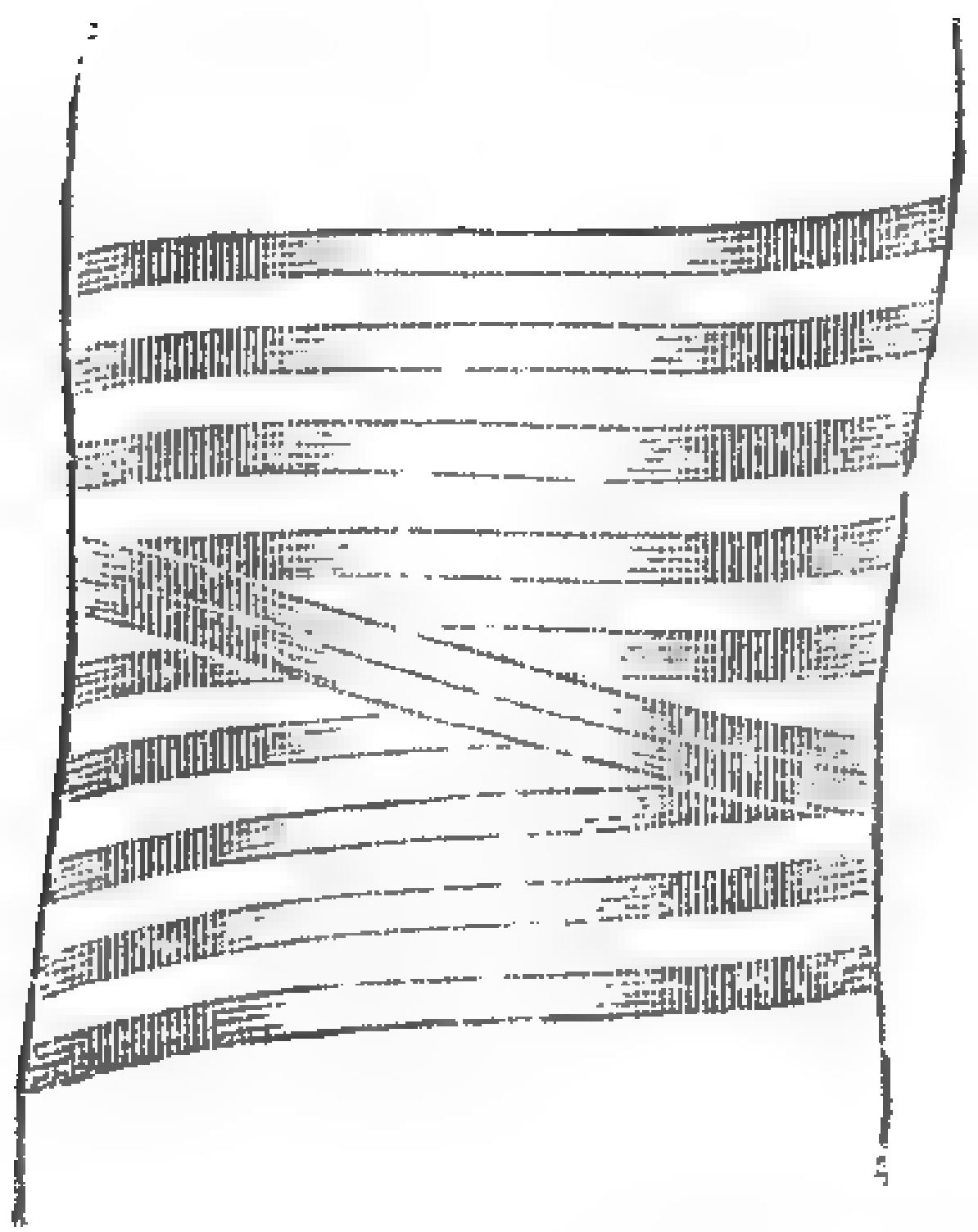
Wood-cells of *Taxus baccata.*

The contrast between the secondary and tertiary membranes is most striking in cells which occur in the coats of the seeds of very various plants, and in which one of the inner membranes is split into spiral fibres; while the other consists of homogeneous layers, which when wetted with water swell up so strongly that they burst the primary membrane. This property is generally found in the secondary layers, while the tertiary membrane appears as a spiral fibre, *e.g.*, in the outer cells of the seed-coat of *Collomia* and other Polemoniaceæ, of the pericarp of *Salvia*, in the hairs of the fruit of *Senecio vulgaris*, &c.; in other cases the secondary membrane is formed of spiral fibres, and the tertiary layers consist of the substance capable of swelling up, *e. g.*, in the hairs of the seed of *Ruellia strepitans.*

Observ. 1. Hartig, who first discovered that the tertiary membrane in *Taxus* possessed the form of a connected pellicle and was not composed of fibres, propounded the doctrine ("*Beiträge zur Entwicklungsgesch. der Pflanzen,*" 1843): that such an inner coat, which he called the *ptychode*, occurred in all cells. He thought that this membrane was distinguishable from the intermediate layer (his *Astathe*) by definite chemical characters, since it was not coloured blue by iodine and sulphuric acid, like the latter, and agreed in this character with the outermost coat of the cell (which he called the *Eustathe*). Hartig considered this inner layer as the oldest, the outermost the youngest, of the cell-membranes. The whole of this doctrine depends upon very imperfect observations. The tertiary membrane of *Taxus* is composed of cellulose, it is therefore a true cell-membrane; but Hartig seems, in many other cases, to have taken the *primordial utricle* (subsequently to be described) for a layer of cell-membrane, and thus to have classed together structures which have nothing at all in common.

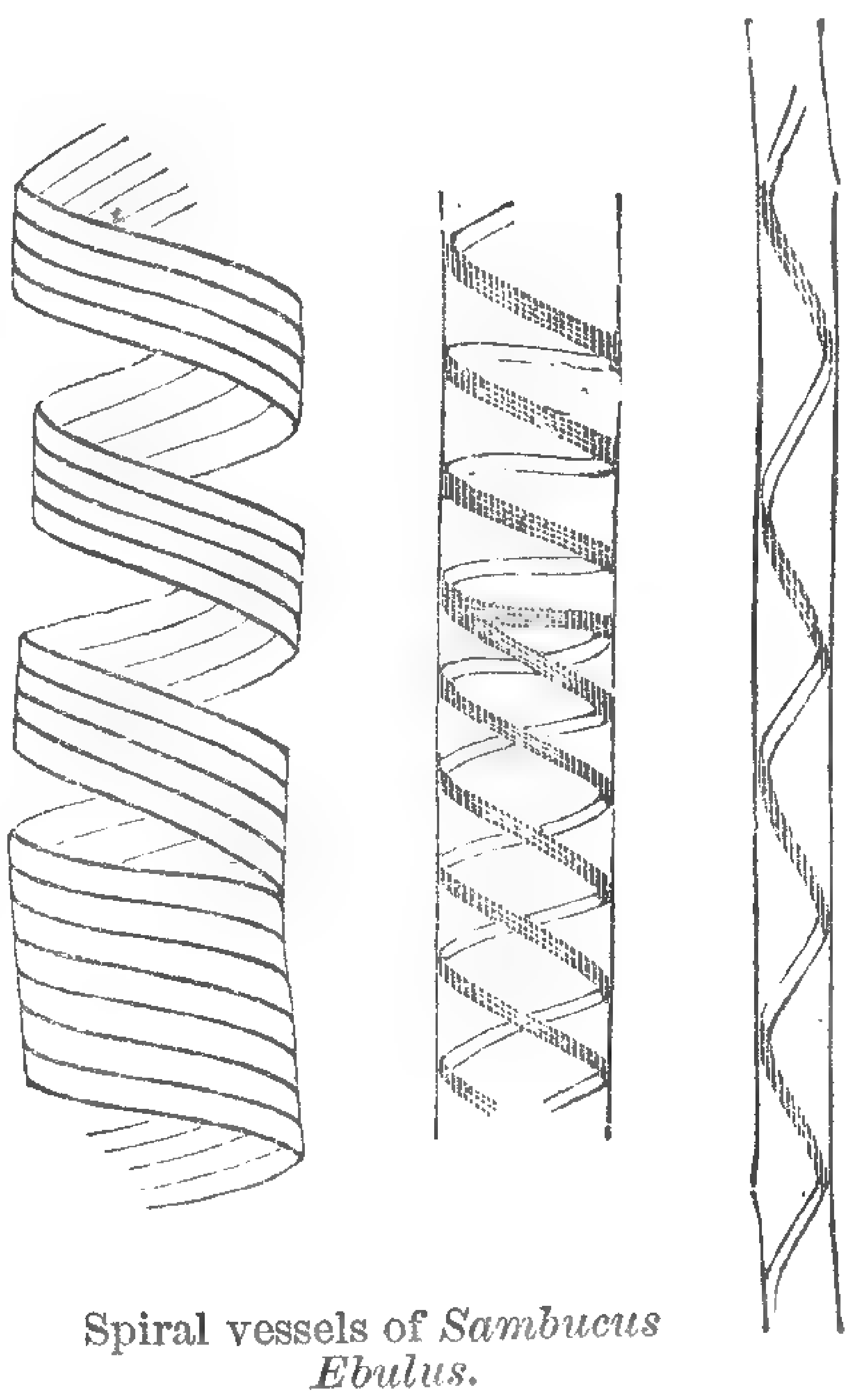
Observ. 2. It may not be out of place, after this exposition of the structure of the secondary membranes, to cast a glance at the structure of the vascular utricle, since the different modifications of the structure of the cell-wall are met with again in the vessels, and, indeed, in many cases displayed much more distinctly than in the cells, so that these conditions were observed in the vessels long before they were known in the cells, albeit much that was incorrect was stated of them. The vessels were divided according to the modifications of the structure of their secondary layers, into spiral, annular, reticulated, dotted vessels, &c.

Fig. 26.



Spiral vessel of *Impatiens parviflora.*

Fig. 27. *Fig.* 28. *Fig.* 29.

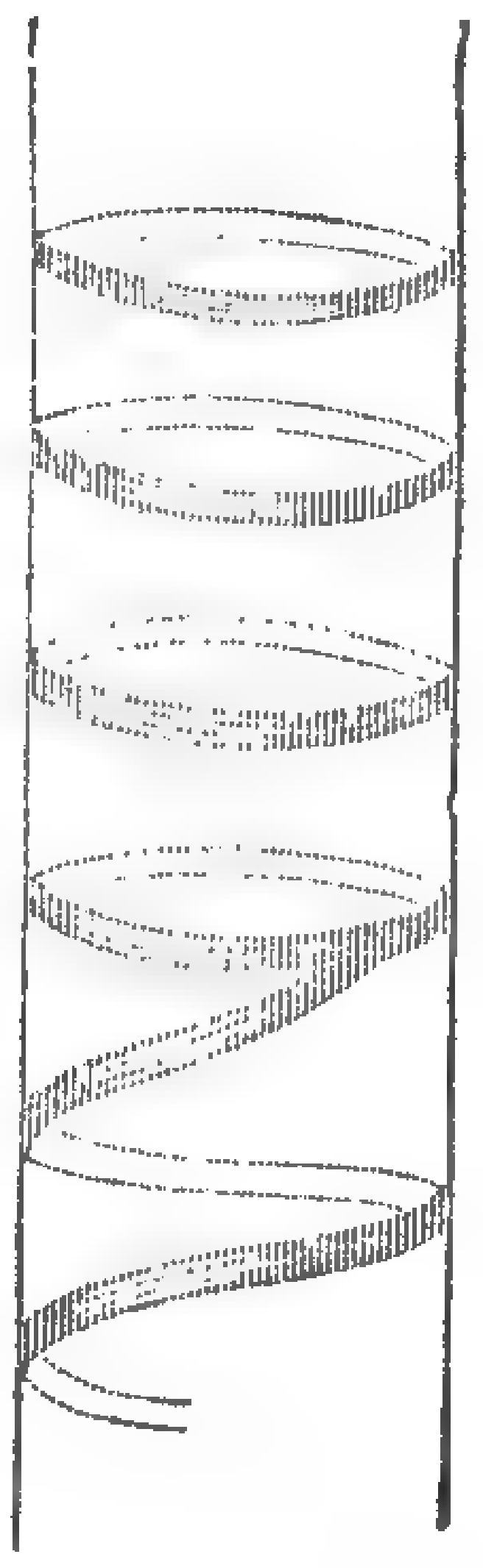


Spiral vessels of *Sambucus Ebulus.*

The most widely distributed form is the *spiral vessel,* for this occurs in all plants which possess vessels; and particularly, in most organs the first vessels which appear belong to this form, so that they are met with in the hindmost parts next the pith, of the vascular bundles of the stem. The secondary membrane of these vessels is divided into one or more (in *Musa* as many as 20) parallel *spiral* fibres, which as a rule terminate in an annular fibre at the upper and lower ends of the vascular utricle. If the vessel is developed in an organ which has already completed its longitudinal growth, the turns of the spiral fibre lie close together (fig. 27); but if the organ undergoes elongation after the completion of the development of the vessel, the turns of the fibre are drawn far apart (figs. 28, 29), 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.

The *annular vessels* (fig. 30) form a slight modification of the spiral vessels, for in many cases a series of vascular utricles containing spiral fibres are regularly found followed in the same vessel by a series of utricles which contain annular fibres, or spiral fibres and annular fibres alternate without any definite rule, often in the same vessel.

Fig. 30.

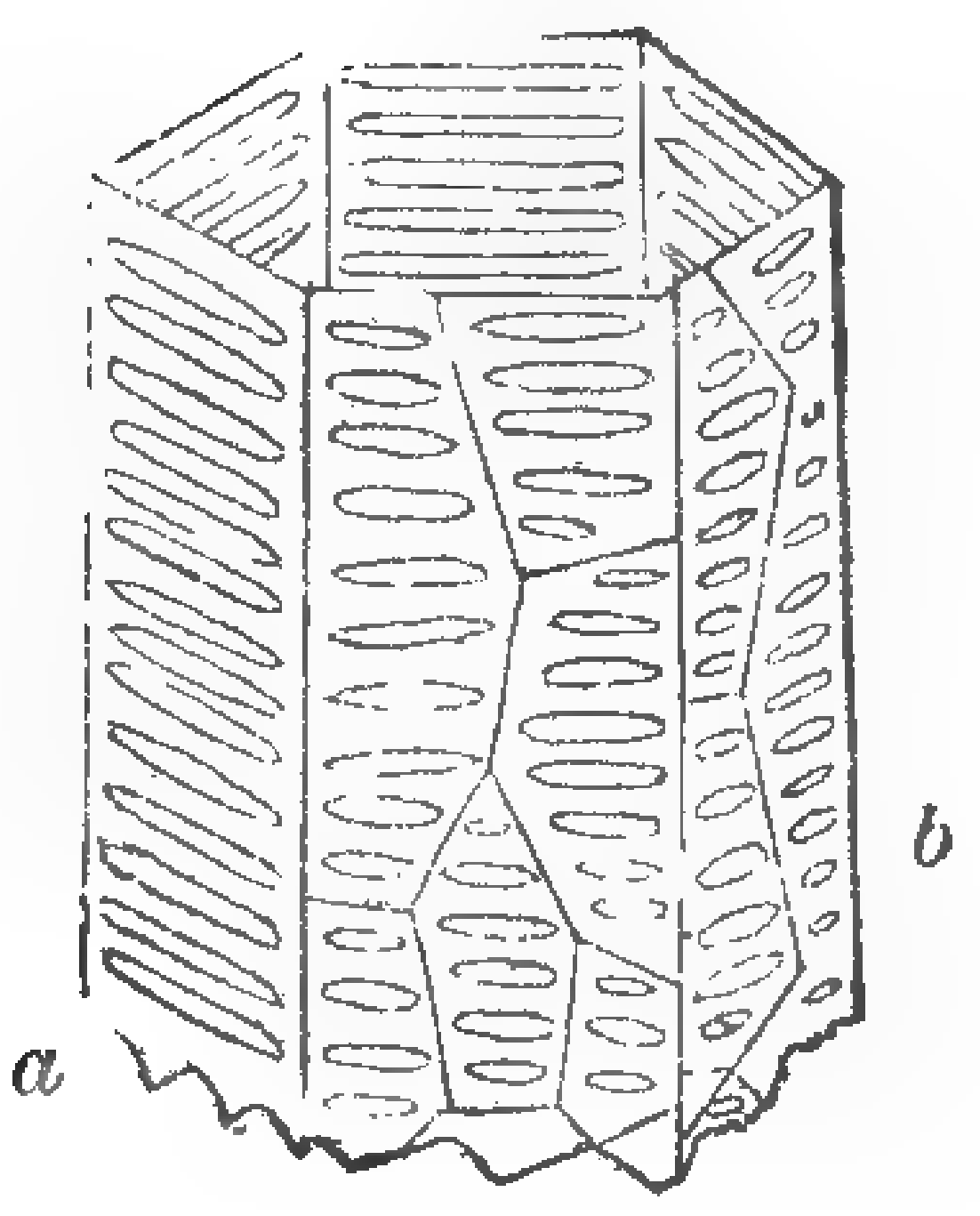


Vessel from the stem of a Gourd, containing both rings and a spiral fibre.

The *reticulated vessels* occur in manifold modifications, in particular among the vascular Cryptogamia, and in the outer youngest parts of the vascular bundles of the Monocotyledons. In these occurs a dependence of the form and distribution of the pits upon the formation of the adjacent parts, similar to that which we have found in the pitted cells. When several vessels lie immediately upon one another, the walls by which they are coherent together (fig. 31, *a*) are covered with transverse pits, separated by narrow fibres, and these pits occupy the whole breadth of such a side-wall, but are not continued over the angles at which the several lateral faces of the vessel meet. To this form is applied the term *scalariform ducts.* But if the wall of such a vessel is in contact with cells by a large or small surface (fig. 31, *b*) its pits exhibit the elliptical or rounded form of the pit of the cells, and are sometimes distributed quite irregularly, sometimes arranged in a spiral direction, and the vessel retains the name of *reticulated.* Very frequently the same vessel exhibits both these modifications of structure at different points.

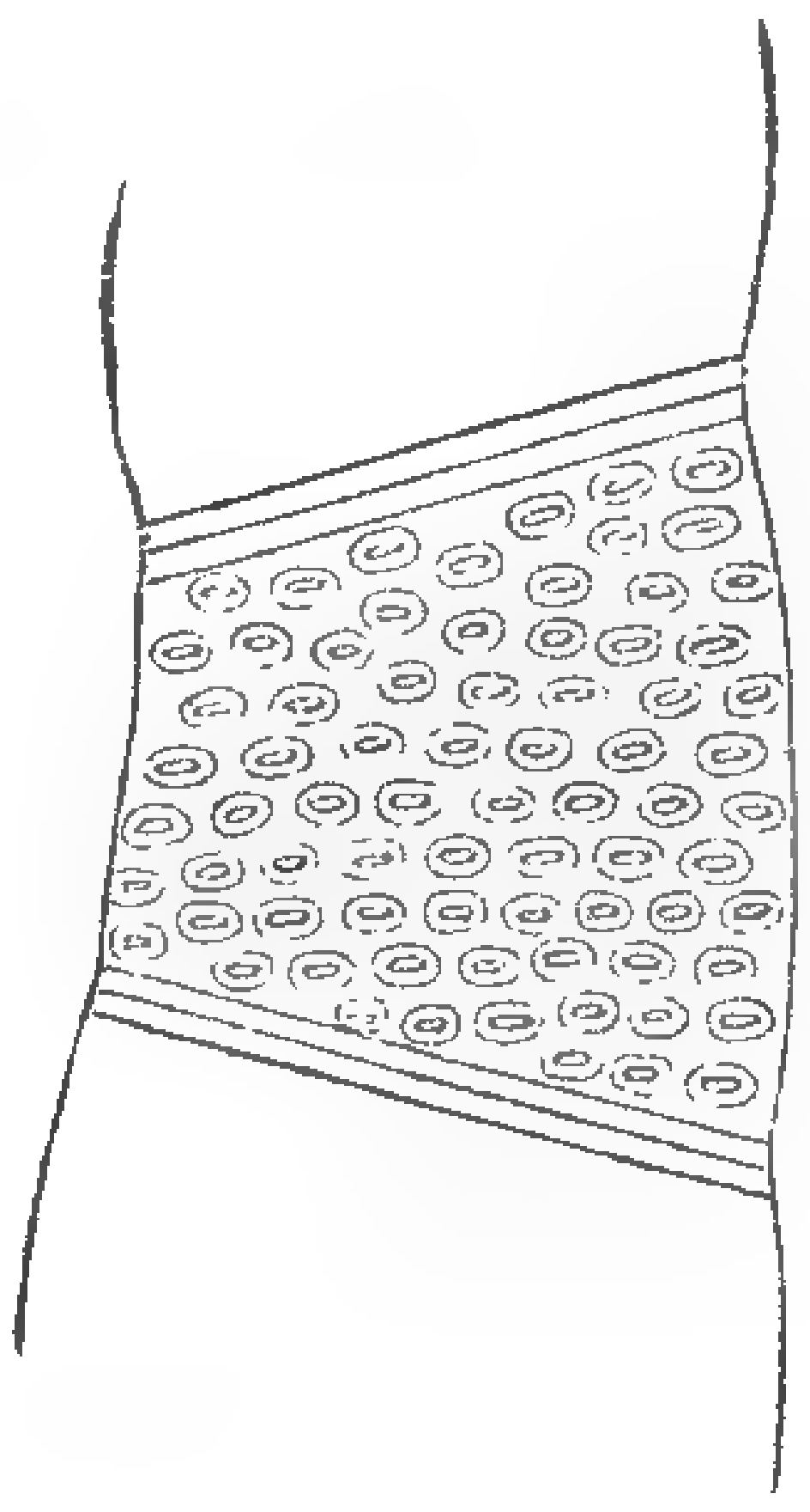
Lastly, the *pitted vessels* (fig. 32) which occur in the wood of Dicotyledons (with the exception of its oldest parts, in contact with the pith) exhibit on those points of their walls by which they are in contact with a second vessel, a more or less abundant quantity of pits surrounded by a line, while the walls bordering on cells present the form of reticulated vessels, *i. e.*, possess pits without a boundary line, or are quite devoid of them. In some cases, for example in the Lime, a tertiary membrane occurs in the pitted vessels, which appears in the form of fibres running between the pits.

Fig. 31.



Reticulated vessel from a tree Fern.

Fig. 32.

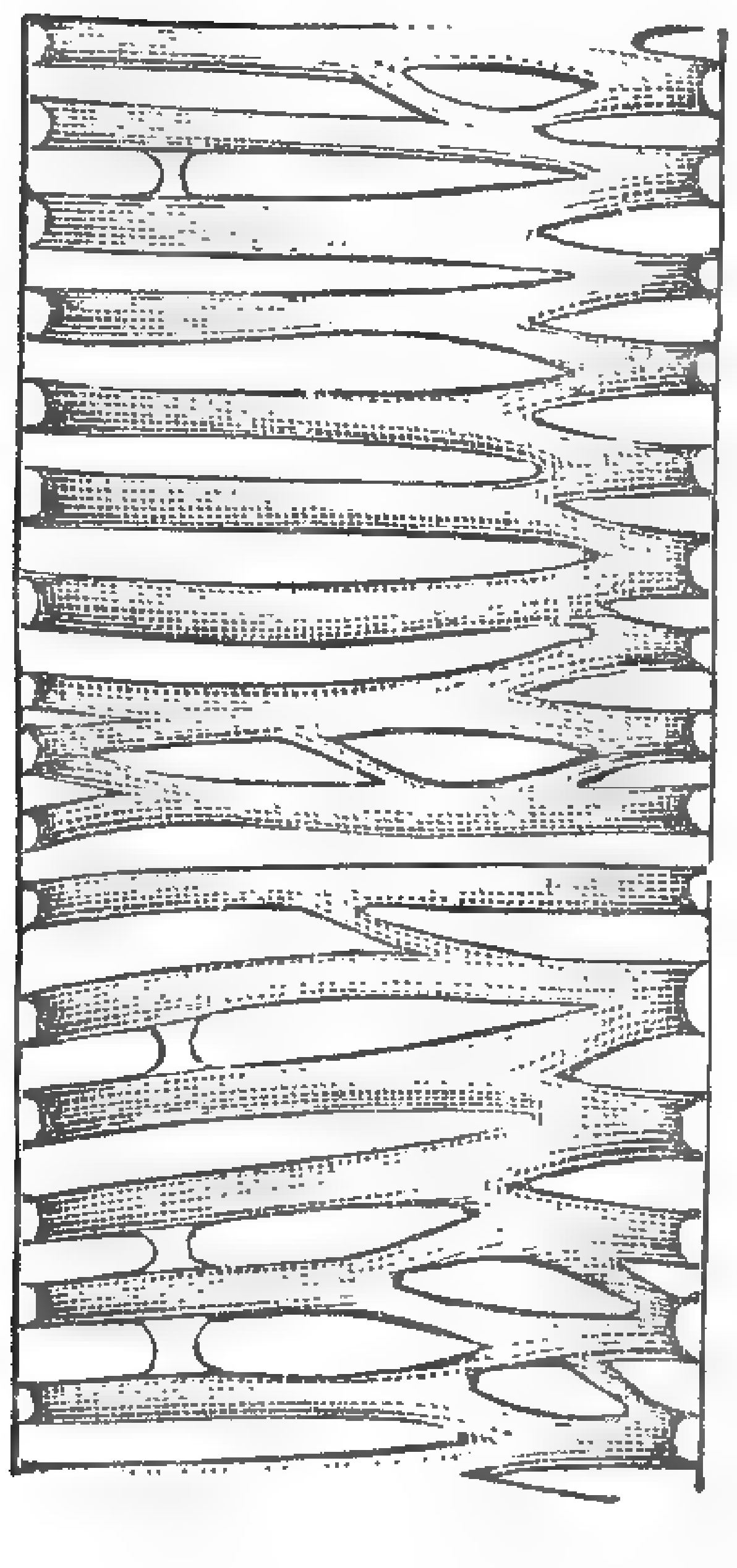


Pitted vessel from *Laurus Sassafras*

The septa between the vascular utricles do not always become perfectly absorbed; but in the reticulated, and especially often in the pitted vessels, secondary layers are deposited in the form of a net-work, or of parallel cross fibres on the transverse or oblique partitions of the vascular utricles, while the primary membrane is regularly absorbed between these fibres, so that the open communication between the vascular utricles is not interrupted.

Observ. 3. In the description of the structure of the cells and vessels, I have mentioned the spiral and reticulated course of the fibres as two distinct modifications of the structure of the secondary membrane. Since transitions between the two structures frequently occur (fig. 33), and since when the fibre is reticulated the pits are arranged more or less distinctly in spiral lines; since, moreover, the pits scattered over an uniform membrane frequently have a longish form, and their long diameter likewise situated in an oblique spiral direction, the thought readily presents itself that spiral structures form the basis of secondary membranes of all cells and vessels, and that the other forms owe their origin to subsequent transformation of the spiral cell and spiral vessel. The view has been expressed by most phytotomists in reference to the vessels; but the conceptions that have been formed of the processes occurring in this metamorphosis were for the most part of rather a rough character. Thus the notion was extensively embraced, that the spiral fibre could not follow the expansion which the vessel underwent during its growth, and tore up into fragments, which 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.*"

Fig. 33.



Reticulated vessel from the leaf-stalk of *Rheum hybridum.*

Schleiden ("*On the Spiral Structures in the Vegetable Cell,*" *Flora,* 1839) sought to explain the origin of the annular vessels from the spiral vessels in a manner less easy to refute, assuming that in each case two turns of a spiral fibre grew together into a ring, while the rest of the fibre, running between these rings was subsequently dissolved. My own observations ("*On the Structure of the Annular Vessels,*" in my "*Vermischte Schriften,*" 285) compel me to declare most decidedly against this explanation, since they demonstrated the rings to be primæval, original structures, from their very first appearance, and the seeming transitional stages from spiral vessels into annular vessels to be permanent intermediate forms between the two kinds of vessels.

The idea that the reticulated vessels are produced from spiral vessels has been more extensively defended, and especially lately by Schleiden and Unger (*Linnæa,* 1841, 394). Nothing appeared simpler than the assumption that cross fibres were formed between the convolutions of the spiral fibre, and that the spiral was thus converted into a reticulated vessel. But two circumstances lead me to reject this notion most decidedly. In the first place, observation of the vessels in which the secondary layers have just begun to be formed, gives evidence that the delicate fibres first deposited are already connected into a net-work, as is especially seen in the examination of the young roots of the Palms. On the other hand, this conception of the transition of a spiral vessel into a reticulated vessel is incompatible with the mechanical condition of the fibre. When two spiral vessels lie upon one another their fibres must cross, since in the majority of cases the fibres of the two vessels run in the same direction (homodromous); but we find that when two reticulated vessels lie against one another, the fibres in the two vessels are placed transversely, and correspond accurately together in position; which could only result from the fibres of the two vascular utricles losing their original spiral directions, and one being pressed down to the right, the other to the left, until their situations should exactly correspond. Who will believe in such a motion of fibres, which are not free but adherent to the vascular utricles, themselves coherent together? and who has seen anything of the kind? A process of this kind might be held to be possible so long as we were ignorant of the true structure of the vessel, and believed that the fibre lay free in the cavity of the vessel, an error which formerly prevailed extensively, and which one would not have expected to have still met with in a writing of Schleiden's ("*Beiträge*," i. 188). And if the incredible statement, that the fibre performed such a journey over one side of the vessel, were actually assumed to be true, how should the prolongations of it over the other sides of the vessel behave? Would these tear away or be pulled backwards and forwards, to restore by their more oblique position what was lost in their spiral course over the other side? Instead of the confusion which must necessarily arise from this, we meet with the most beautiful order. If the lateral walls of the vessel are in contact with cells, we find its pits corresponding with those of the cells; if one part of a vessel is connected with another vessel we meet with horizontal, slit-like pits. Thus we see clearly that one elementary organ influences the organization of an adjacent one in a definite manner, but we are nowhere able to observe, that an organ already developed to a certain extent allows its already organized parts to perform movements in order to place themselves opposite the parts of the neighbouring organs. Since none of these matters can be seen, the processes are referred back by Schleiden to a time at which the observation is impossible. Thus he says ("*Grundz. der wiss. Botanik*," i. 228), it seems to him very probable that the spiral is in existence long before it is visible under our optical instruments, since it is composed at first of a substance which does not differ optically from the cell-wall and cell-contents; hence, many forms might be referred to the spiral only at that epoch, if we assume that the intermediate stages were run through before the structure was yet visible. I readily allow the author to speculate as to the course of fibres which cannot be seen, but I must be excused from following him into this region. Valentin, indeed, who originated the theory of the expansion of the spiral fibres in all directions ("*Rep. f. Anat. and Phys.*" i. 88), believed that this could be demonstrated by observed facts, for he stated that he had found the secondary membrane making its first appearance in the form of a granular substance, the granules of which at first exhibited no definite order, but were subsequently arranged into spirals, and became connected into the spiral lines which might be distinguished on the completely formed membrane; a view which has not acquired confirmation from any subsequent observer.

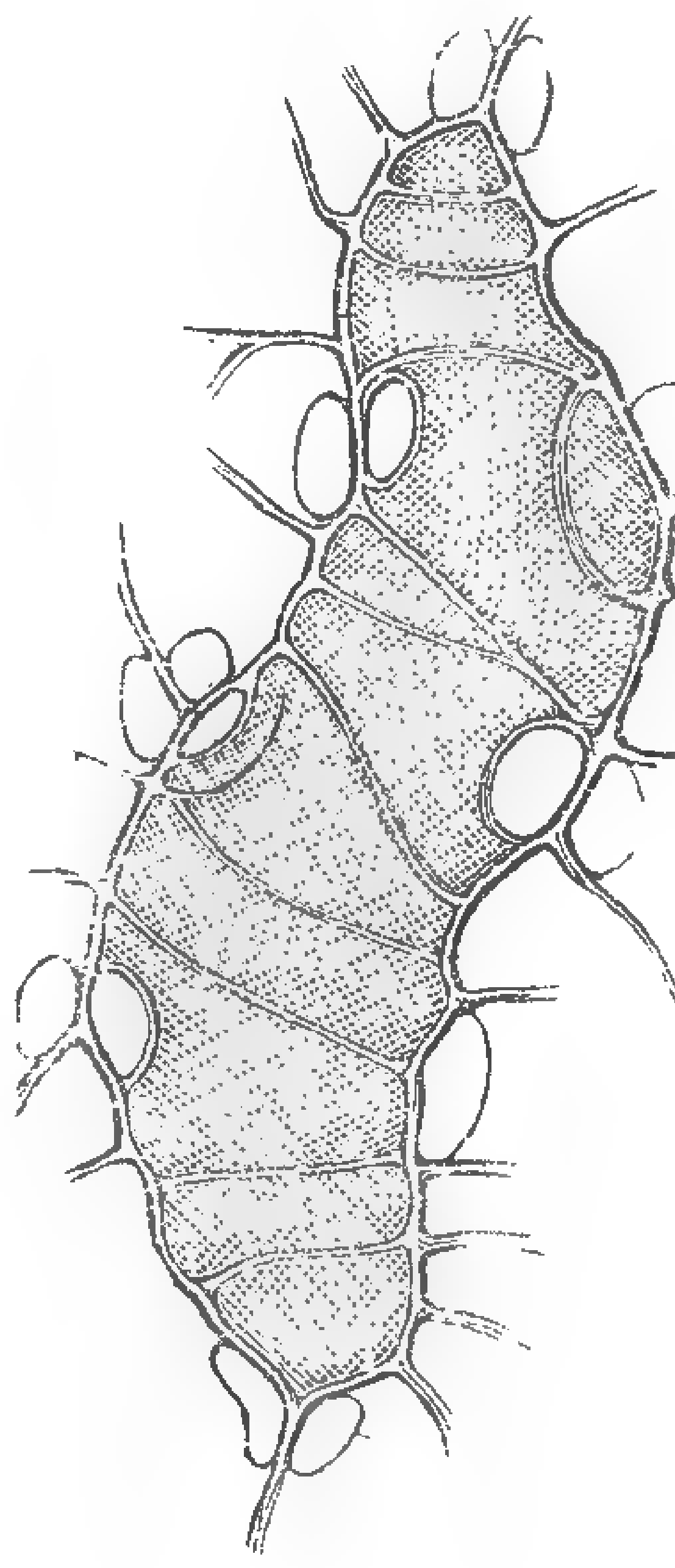
It is scarcely worth mentioning that, Meyen ("*Physiologie*," i. 45) set up the theory that not only the secondary layers, but also the primary membrane was composed of distinct spiral fibres grown together. He was led to this opinion principally by the cells containing a very fine spiral fibre, of a *Stelis* gathered by him in Manilla, the structure of which he completely misapprehended, since he imagined that the fibres formed the primary membrane, while they belonged to the secondary.

In conclusion, it may be remarked that Schleiden's hypothesis ("*Beiträge*," i. 187), that in the formation of the secondary layers there exist at first, at least, two spiral bands, one corresponding to the ascending current, the other to the descending current of the mucilaginous formative substance, the two extremities coalescing at the ends of the cell, and that in most cases these become blended together at a very early period, is simply to be banished into the region of dreams.

The opinion which formerly prevailed widely, and which Link ("*Phil. Botan.*" 1837, i. 177) still defends, that the pits of the scalariform ducts and pitted vessels are the remnants of the fibres of spiral vessels broken up into fragments, requires no further refutation. Holes in a membrane can scarcely be considered as elevations.

Observ. 4. In the preceding I have spoken of cells and vessels as clearly separated organs, because in most plants the fully-developed cell differs in a marked manner from the fully-developed vessel; but it must not be forgotten that transitional structures occur. One form, the porous cells, has already been mentioned; these come near to the vessels in the large open pores, by which they communicate with each other, but they are distinguished from those by the fact, that they form a parenchymatous tissue in the manner of cells, lie upon the surface of organs, and, in part, in *Sphagnum* (fig. 33, B), open even to the external air; while the vascular utricles are always combined into tubes, which run among the cells in the interior of plants. Another intermediate structure occurs in the vascular Cryptogamia, particularly in the *Lycopodia* and Ferns, as well as in the Coniferæ and Cycadeæ. In these plants we meet with the peculiar condition that the wood is not composed of a mixture of elongated cells and vessels, but of elementary organs of one kind, which resemble prosenchymatous cells in their form, and vessels in the structure of their walls, and give evidence of their near relation to the latter, in the fact that the prolongations of the vascular bundles of the stem entering into the leaves, contain perfectly developed vessels; as also in the fact, that in the stems of Coniferæ and Cycadeæ, the innermost elementary organs, bordering on the pith are perfect spiral vessels, and that in *Ephedra* particular wood-cells become united into perfect pitted ducts.

Fig. 33, B.



Porous cell furnished with annular fibres from the leaf of *Sphagnum cymbifolium*.

Observ. 5. Perhaps it is not altogether superfluous, in reference to the terminology of the pitted cells and vessels, to remark that since the structure of the pits *(tüpfel)* and their distinction from actual holes have been understood, it is the more general custom to apply the term pit *(tüpfel)* to the canals perforating the secondary layers, and closed externally by the outer membrane of the utricle, and the term *pore* to the same canals when the primary membrane has been absorbed and the orifices of the utricles open freely into each other. Schleiden, on the contrary, uses the name of *porous* instead of pitted (getüpfelten) cells, calls the pits pores, and the pores holes (löcher), because ("*Beiträge,*" i. 189) according to Adelung and Heinsius, the word *tüpfel (dot)* means a shallow depression, or a slightly elevated spot upon a surface. I will not enter into any etymological controversy against such authorities, but keep simply to my Swabian German, and am consequently of opinion that a panther's skin is *getüpft* (spotted or dotted), although its spots are neither depressed nor elevated.*

c. Chemical Conditions.

The basis of the membranes of all the elementary organs of vegetables consists of neutral hydro-carbons; in almost all cases, and perhaps without exception, of cellulose.

Cellulose is colourless, insoluble in cold and boiling water, alcohol, ether, and dilute acids, almost insoluble in weak alkaline solutions, soluble in concentrated sulphuric acid; it is converted into dextrine by dilute sulphuric acid at a boiling heat. When imbued with iodine it becomes coloured indigo blue if wetted with water, this colour appears more readily under the conjoined influence of water, sulphuric acid, and iodine. According to Payen, the formula of its composition is $C_{12}\,H_{20}\,O_{10}$.

Cellulose probably does not occur in a pure condition in any cell-membrane, since a series of both organic and inorganic compounds are deposited within it; in which fact is to be sought the explanation of the manifold physical and chemical differences which are exhibited by the membranes of the same cell at different periods of their age, as well as by the cells of different plants.

The combination of cell-membrane with inorganic substances is a very general condition, for the only examples of exception to this which have as yet been met with, are a few species of Mould Fungus (Mulder), into which, however, ammonia might still have entered as a substitute for the fixed bases. In all other plants a skeleton (the ash), corresponding to the form of the membrane, and composed of the alkalies, earths, and metallic oxides which had been deposited in it, remains behind after the cell has been burnt. The younger an elementary organ is, the more abundant, in general, the alkalies appear to be; the older it is, the more exclusively the earths and metallic oxides seem to be combined

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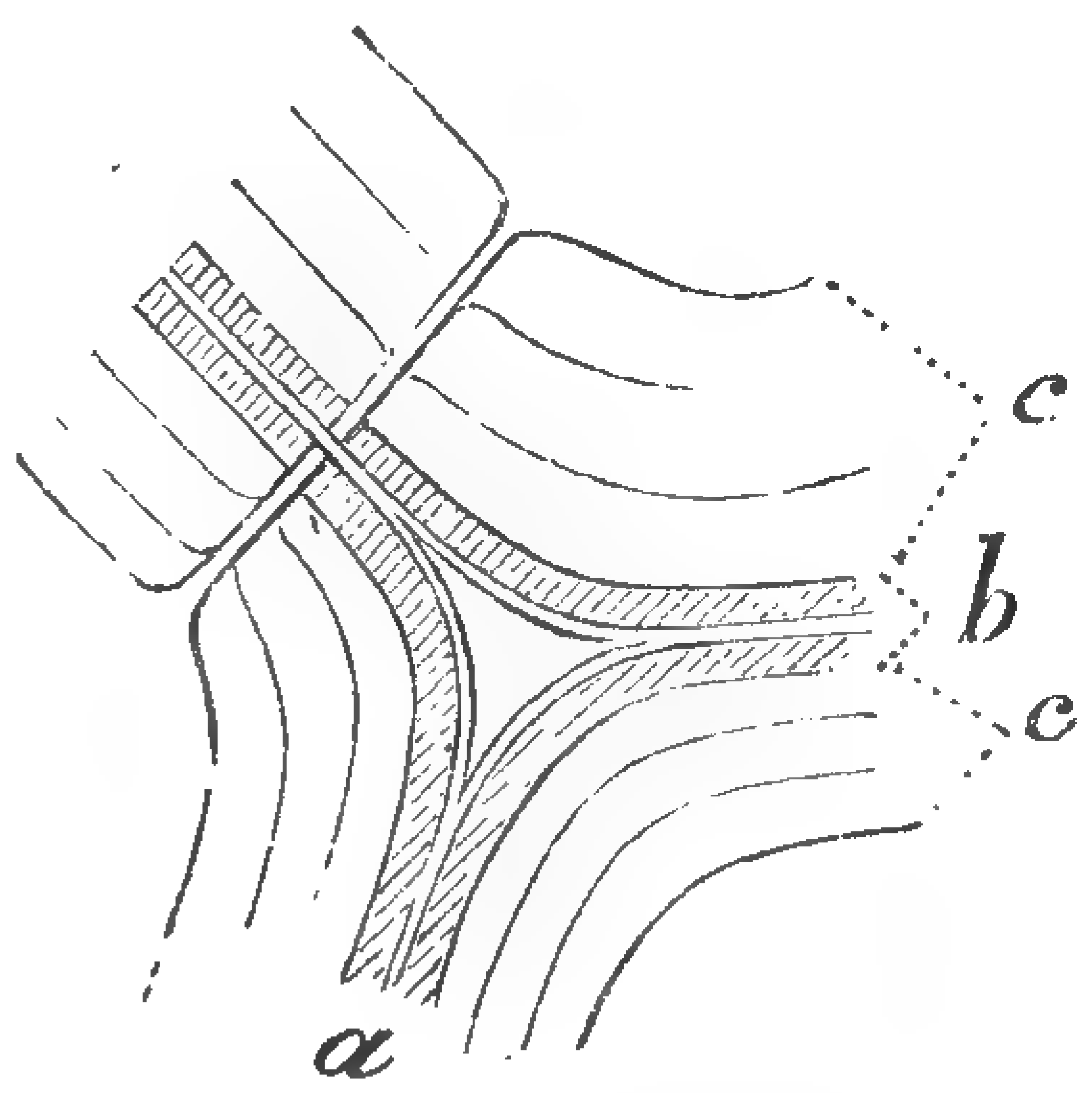
* Some confusion exists also in our English terminology, the terms *dotted* and *pitted* tissues are indifferently applied to these structures, called by the Germans *getüpfelt.* I have used the word *pitted* throughout this translation to express this term, because it indicates the true structure. —A. H.

with its substance. The higher the degree in which the latter occurs, the harder the membrane becomes, as is shewn by the relation of the heart-wood to the sap-wood, and in a still greater measure in many seed-coats of a bony consistence, *e. g.*, the pericarp of *Lithospermum*, which contains much lime, the epidermis of *Equisetum* and *Calamus*, in which a great quantity of silica is deposited. However, we are without any accurate knowledge of these conditions, in spite of the countless analyses of ashes which we possess, for these give the product of ash of the cell-contents and cell-membrane together.

The deposition of organic substances is not less general than that of inorganic compounds, at least in particular layers of cell-membrane. Among these the nitrogenous compounds are certainly the most widely distributed. They 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 scarcely a full-grown cell is met with in which this is not the case. That these nitrogenous compounds belong, in many instances, and especially in the cells of the wood, to the series of proteine compounds, we have evidence (as Mulder pointed out) in the violet colour which hydrochloric acid produces after long operation, and in the yellow colour which ammonia produces after a previous action of nitric acid. The presence of these compounds explains how, according to Chevandier's analysis, wood contains 0·67 to 1·52 per cent. of nitrogen. The darker yellow a cell-membrane is coloured by nitrogen, the more firmly it withstands the action of sulphuric acid, and the more difficult it is to obtain the blue colour by the combination of this and iodine. In most parenchymatous cells, especially in the thin walled, this blue colour usually appears so intensely that the original yellow tint totally disappears; in the thick walled cells, on the contrary, especially those of wood, the strong yellow colour is not altogether overcome, and the colour assumes a dirty green tint; lastly, in others no blue colour is produced at all, and the membrane offers such resistance, even to concentrated sulphuric acid, that it either only swells up slightly or remains quite unaltered, only becoming coloured deep brown; as is the case particularly in external layers of epidermis-cells and the outermost layers of almost all full-grown cells, especially those of wood. This outermost layer may readily be taken for the primary membrane of the cell; but as a rule it is composed of several super-imposed layers, and frequently contains the outer ends of the pit canals (fig. 34), whence

Fig. 34.



Liber-cell of *Cocos botryophora*. *a*, Primitive membrane; *b*, secondary, strongly incrusted layers; *c c*, the rest of the secondary layers.

it is quite clear that in an anatomical sense it is not a well-defined membrane, but that it is composed of the primary membrane, and a few layers which belong to the secondary deposits, and which have undergone the same chemical changes as the primary membrane itself.

Besides the nitrogenous compounds and the colouring matters which are diffused through many cells, especially those of the wood, the membranes of a great number of cells also afford a series of compounds devoid of nitrogen, which sometimes have a different composition from cellulose, sometimes are isomerous with it. Compounds of the first kind in which carbon, and, still more, hydrogen, are contained in relatively greater quantity than in cellulose, occur in the cell-membranes of fully developed wood, on which account all the earlier elementary analyses of wood give a false result, since the mixture of different compounds forming the cells of the wood was taken for a simple combination (the so-called woody fibre).

While it is beyond doubt that all the compounds differing from cellulose in composition, form interstitial deposits in the cell-membrane composed of cellulose, entering into it subsequently to its first production, it is on the other hand doubtful whether the compounds which are composed, like cellulose, of carbon and the constituents of water, and which are either isomerous with cellulose, or differ from it perhaps only in containing a smaller amount of water, are to be regarded in like manner as depositions in the cellulose, or whether they replace cellulose and form the cell-membrane itself, or at least some of the layers of it. Doubts in reference to this point are raised, especially by the cells of many of the lower plants, *e. g.*, the cells of many Lichens, as of *Cetraria islandica*, which are partially soluble in hot water, and yield a substance similar to starch; also the cells of many Algæ, as *Sphærococcus crispus*, which yield a mucilage by boiling, and of which Kützing *("Phycologia generalis")* assumed that they were composed of a peculiar compound, named by him *phytogelin*. In none of these cases can we state with any certainty whether, or what share, cellulose takes in the formation of these membranes; and as little whether or not inorganic compounds, which might modify the characters of the cell-membrane by their action, are combined with it. We labour under the same uncertainty in regard to the differences which distinguish young cells from those in older conditions. Thus the membrane of the former swells up strongly in water, and is not coloured blue by iodine alone (but only by iodine and sulphuric acid). We have not at present any definite facts to enable us to express a decided opinion whether we are to assume that the compound of which the young cell-membrane is formed is essentially different from cellulose, and during the progressive development of the cell undergoes a chemical metamorphosis, a change of arrangement of its constituents or the like, or that this compound is replaced by cellulose, or that both are to be regarded as the same compound only distinguishable by slight differences in their conditions of aggregation; or that the differences are caused by the interstitial deposition of various foreign compounds. The same occurs in reference to the substance of those cells which are coloured blue with the same facility as starch, by the action of a weak tincture of iodine, but differ from starch by their behaviour to warm water, as is the case in the horny albumen of many plants, *e. g.*, of *Cyclamen*, in the cells of the embryo of *Schotia*, &c. (See "*On the Blue Colouring of Vegetable Cell-membrane by Iodine*," in my "*Vermischte Schriften*," 335.)

Observ. 1. The credit is due to Payen ("*Memoires sur les developpements des vegetaux*," 1844) of having demonstrated that the substance of all cells, from the highest plants down to the Fungi, when purified from foreign deposits, exhibits the same composition, and assumes the blue colour of cellulose on treatment with iodine and sulphuric acid. According to his views the cellulose occurs in a tolerably pure condition in very young cells, while the membranes of older cells are combined more or less with foreign organic or inorganic compounds (which he called incrusting substances), through the presence of which the physical and chemical properties of the cell-membrane undergo alterations. These incrusting substances may be more or less completely extracted by treating the cellulose tissue with acids, ammonia, alcohol, ether, &c. Thus, according to his statement, nitrogenous substances and silica occur in the cuticle, pectate and pectinate of lime and of the alkalies in the thick walled epidermal cells of the *Cacteæ*, inuline in the cells of the Lichens and Algæ, and in the hard cells of wood capable of being polished three or four compounds, designated by Payen *lignose*, *lignone*, *lignine*, and *ligninose*, substances which are richer than cellulose in carbon and hydrogen.

Observ. 2. We owe to Mulder ("*Physiological Chem.*") very extensive researches on the chemical conditions of the walls of the elementary organs. He also, like Payen, arrived at the result, that the membrane of all young organs consists of cellulose in almost a pure condition (the formula of which he determined as C_{24}, H_{42}, O_{21}); but in reference to the alterations which the membranes undergo in the course of time, he propounded totally different views. He here starts from the fundamental doctrine that a given layer of an elementary organ which is not coloured blue by iodine and sulphuric acid, does not contain cellulose; that therefore, when the same layer can be demonstrated to consist of cellulose in the earliest periods of the growth of the elementary organ, the cellulose must have been displaced by other compounds, or that if this origin from a layer of cellulose cannot be demonstrated, it is a later formation, and has been composed of other compounds from the first. In this way he arrives at the conclusion, that the membrane of the elementary organs increases in thickness in three ways:—1, By the deposition of younger layers upon the inside of the membrane; this occurs in the vessels and in a doubtful manner in the thickened pith-cells of *Hoya carnosa*. 2, By the deposition of layers upon the outside of the elementary organs, which occurs generally in cells; in parenchymatous cells layers of the same kind alone are generally deposited; in wood-cells, on the contrary, first an outer coat is formed, and then subsequently intermediate layers of considerable thickness are formed between this and the inner primary membrane. 3, The new substances are deposited *in* the cell-wall of many cells (in the horny albumen of *Phytelephas, Iris,* and the so-called collenchymatous cells), and therefore the wall does not exhibit lamellation. The constitution of these different deposits is described as very varied. Proteine is shewn to be merely an infiltrated matter, taking no part in the formation of the cell-wall, and is wholly wanting, or only just traceable in very young cell-membranes; but it occurs in the intermediate substance of all old wood-cells, and most old pith-cells, but not in bark-cells or collenchymatous cells. The following compounds are particularly noticed as forming definite layers of the elementary organs. *Intermediate wood-substance* (the formula of which is stated at C_{40}, H_{56}, O_{26}), a compound which is coloured yellow by iodine and sulphuric acid, swells up in weak acid and dissolves in stronger; it gradually displaces the cellulose more or less perfectly in the secondary layer of vessels, forms the outer layers of pith-cells and the intermediate of the wood-cells, in which it becomes the more intimately combined with the cellulose the further the layers lie toward the inside. *External wood-substance,* which is coloured brown by iodine and sulphuric acid, and does not dissolve in the latter; it is stated as probable that this is isomerous with the intermediate wood-substance, but (as in the woody matter of the putamen of hard fruits) is distinguished from it by containing *ulmin.* It forms the outer layer of wood-cells, scalariform ducts, and pitted vessels. Besides these more generally distributed compounds, there occur other peculiar, less extensively prevalent, compounds not yet fully characterized, one of which forms the cuticle; another the cells of cork; another the cells of the horny albumen of *Iris* and *Alstrœmeria.* The following are regarded as incrusting compounds, penetrating into the substance of the cell-wall: *pectose* in the cells of the collenchyma, of the Apple, &c.; *starch* in *Cetraria islandica; vegetable mucilage* in *Sphœrococcus crispus;* and a peculiar substance isomerous with cellulose, in the cells of the albumen of *Phytelephas.*

My own investigations (*"Investigation of the question 'Does cellulose form the basis of all vegetable membranes?'"—Botan. Zeit.* 1847, 497) compel me to declare most distinctly against the view of Mulder's, that a great proportion of the layers composing the membranes are from the first composed of compounds different from cellulose; and also against his opinion as to the relative ages of the layers, deduced from these propositions (which I have already discussed above under an anatomical point of view). I found that the application of iodine and sulphuric acid, in which Mulder places such unconditional trust, is a means in the highest degree unsafe for deciding whether a membrane contains cellulose or not. 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. The first proved to be most effective in the cells forming the surfaces of plants (such as epidermal cells, periderm and cork); a maceration for twenty-four to forty-eight hours in strong solution of potash, at common temperatures, caused iodine to produce a pure blue colour in all these cells. The application of potash is not so effective in the cells situated in the interior of the plant, but that of nitric acid always answers the purpose completely, either when the preparation is left to macerate for a length of time in dilute acid, or is boiled in acid of moderate strength until the yellow colour which it assumes at first has disappeared again. 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. After these experiments there cannot be any doubt, that cellulose forms the basis of all the membranes of the higher plants, that the greater or less resistance of many membranes to the combined action of iodine and sulphuric acid, is caused by infiltrated foreign compounds, and that the "substance" of cuticle, of cork, and the "outer and middle wood-substance," regarded by Mulder as peculiar compounds, are combinations of cellulose with foreign infiltrated deposits. Of what nature these deposits are, which interfere with the reaction of cellulose, future researches of chemists must decide.

Observ. 3. Schleiden takes up quite a different point of view. (*"On Amyloid." Beiträge*, i. 168. *"Some remarks on the substance of vegetable membranes." Beiträge* i. 172.) Without regarding that the cell-walls are not composed of one chemical compound, but that they have a series of substances deposited in them, possibly exerting an influence upon their properties,—he considers the differences which are observed in the cell-membranes as unconditional proofs of difference in the substances of which they are formed, and believes that the compounds distinguished by chemists, forming the series of hydrates of carbon, are but a very sparing selection from the infinite multiplicity of compounds belonging to this series, occurring in plants. According to his views, the plant forms a fundamental substance, which remains the same in reference to its elementary composition, but is capable of infinite modifications by internal imperceptible changes, and also, in part by the increase or diminution of chemically combined water: forming a series, the adjoining members of which differ imperceptibly to us, sugar being the lowest, and the substance of perfectly developed membrane the highest, of the members, which become more and more insoluble in water from below upward. Three compounds, in particular, of this series, forming cell-membranes, are minutely characterized according to their behaviour to iodine and water: 1, *Cellulose*, of which it is stated that it is not coloured blue by iodine, when in a pure condition (*"Grundz. der wiss. Botanik*," 3rd ed., i. 172), which is decidedly untrue. 2, *Amyloid*;—Schleiden used this name to signify the substance, announced by himself and Vogel, composing the horny cells of the cotyledons of *Schotia*, *Hy-*

menœa, Mucuna, and *Tamarindus,* which are readily coloured blue by iodine. According to his account amyloid dissolves in boiling water, and its compounds with iodine are dissolved in water with a golden yellow colour. The latter is decidedly incorrect, and in regard to the former, Schleiden himself says ("*Beiträge,*" i. 167), only the intermediate layers were dissolved even after twelve hours boiling, and all the cellulose tissue remained. 3, *Vegetable Jelly;*—under this name Schleiden comprised a series of compounds, which chemists mention under different names *(Bassorin, Cerasin, Pectin, Gelin, &c.),* but which he united on account of their property of swelling up strongly in water and not becoming coloured by iodine. He ascribed to this substance the property of gradually becoming diffused in cold water, and believed many vegetable cells to be composed of this substance, transitions from it existing on the one hand (through the cells of the Fucaceæ) into cellulose, and on the other (by many kinds of horny albumen) into amyloid. Excepting the statements that cellulose is not coloured by iodine, and that there exist cells soluble in water, there is no doubt of the correctness of the anatomical foundations on which this theory rests. But on the other hand, there is just as little doubt that the whole of this representation of the infinite multiplicity of neutral hydrates of carbon and the distinction between them according to their greater or less expansion in water, and more or less facility with which they are coloured by iodine, could only be considered as established, when it was proved that the substance of vegetable cells possessed this property in its pure condition, and that these differences were not caused by foreign deposits. Since not only is this proof wanting, but, on the contrary, the most definite evidence exists that the chemical and physical properties of vegetable membranes can be modified in the greatest degree by infiltrated matters, Schleiden's view is devoid of any solid foundation.

D. CELLS IN THEIR RECIPROCAL CONNEXION.

Leaving out of view the lowest plants, and the spores and pollen-grains of the more highly organized, cells do not occur isolated, but grown together in great numbers in connected masses; in this manner they form the so-called *cellular tissue, contextus cellulosus* (parenchyma or prosenchyma, according as it is composed of parenchymatous or prosenchymatous cells).

From the structure of the cell, as a closed vesicle formed of a special membrane, it follows that in cellular tissue the partitions between any two cell-cavities must necessarily be composed of a double membrane, and this may be readily observed in reference to the secondary layers, in all thick walled cells, by means of the microscope, for it is clearly seen, that the individual layers of the membranes surround the cavities of the cells concentrically, and that the secondary layers of the several cells are separated from each other by the primary membrane.

Observ. It is by no means so simple an affair as it seems at first sight to determine the limit between two cells. Formerly, when observers were restricted to weaker and less perfect magnifying instruments, the surface of the cross section of the primary membrane appeared as so narrow a line, that it was taken for the boundary line between two neighbouring cells, and was drawn as such. Subsequently, when the knowledge of cellulose structure had progressed further, the primary membrane was distinguished from the secondary layers, and the outermost layer of cell-membrane was seen under stronger microscopes to have a clearly visible breadth (or thickness), the idea remained of an easily distinguishable boundary line between the two coherent cells, and such a line was even figured. This, as Hartig correctly observed, was untrue, for our microscopes do not shew any boundary line between the two coherent primary membranes (*see* figs. 21, 22, 25, 32, 44). When Hartig drew from this the general conclusion that no limit exists, and that the outer membrane of the two cells is common to both, his induction was too hasty. The impossibility of seeing a line of demarcation with our microscopes, warrants, *à priori*, nothing more than the conjecture that our present instruments are not yet sufficiently perfect for the purpose. It is self-evident under these circumstances that nothing has been accurately made out as to the manner in which cells are connected.

The cells cohering together may be separated from each other; in very succulent tissues, as in the parenchyma of many juicy fruits, a slight pressure suffices for this; in somewhat firmer tissues the connexion of the cells may often be so loosened by boiling in water or by freezing, as to become easily separable; while in very solid tissues a long maceration in water or a short boiling in nitric acid is necessary. It might be imagined that the double nature of the outer membrane could be readily demonstrated by this separation of the cells, but wrongly, for I found that the outer membrane, when distinctly perceptible, was not split into two layers in such cases, but torn into pieces, some adhering to one and some to the other cell, so that the separated cells were composed chiefly of secondary layers.*

It has been remarked already, in the description of the form of cells, that the flat faces of cells meet at sharp angles in comparatively few cases, since the corners and edges are generally rounded off. It follows necessarily from this condition, that the cells are not, for the most part, coherent together by their whole surfaces, but leave empty spaces between them, which run along the edges of the cells in the form of triangular canals having no special walls of their own, opening into each other at the corners of the cells, and so forming a net-work of narrow and wide tubes branching throughout the whole plant, to which the name of *intercellular passages* has been applied (*see* figs. 6, 7). In living plants they are, with few exceptions, filled with air.

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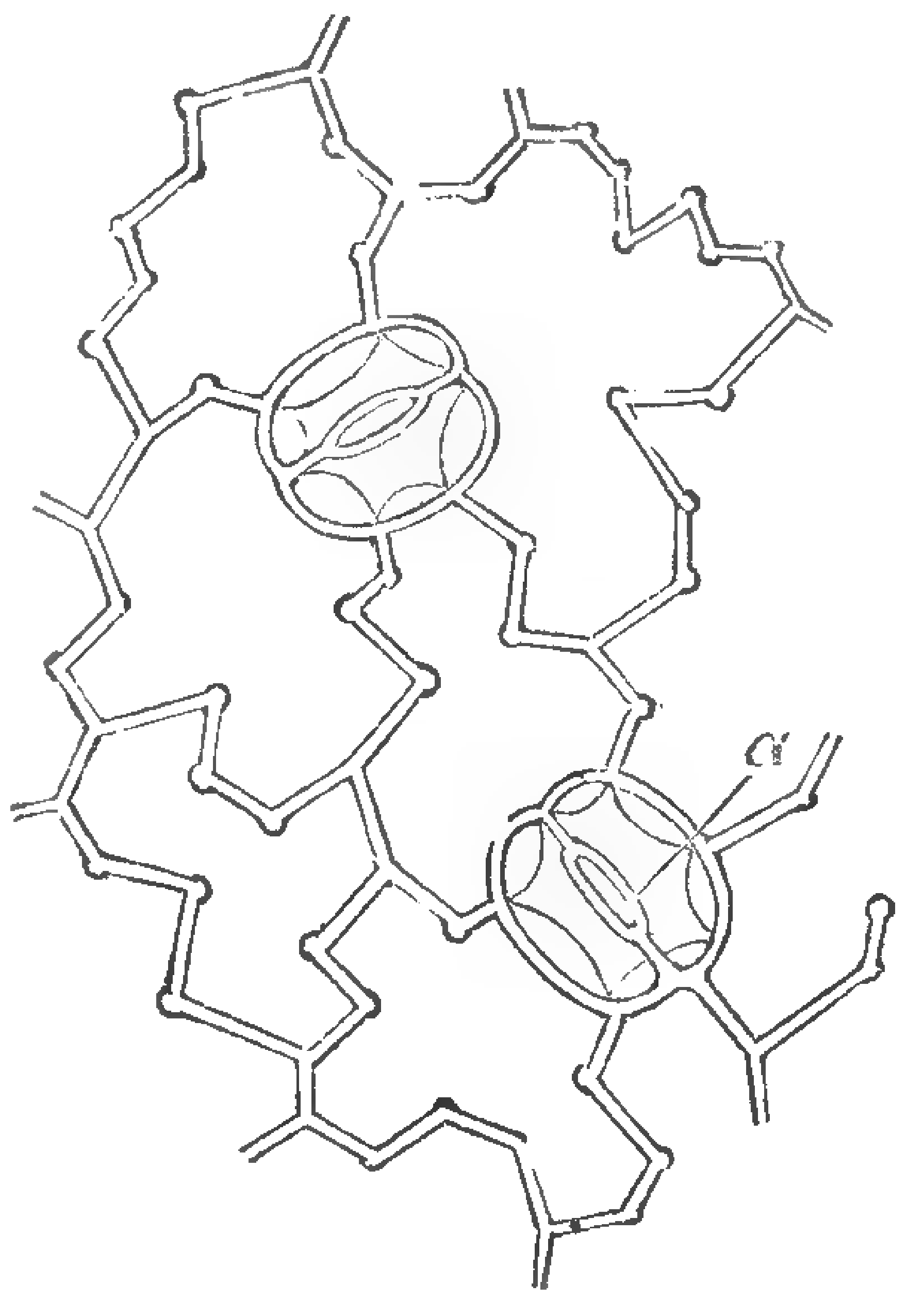
* Schultz has lately made known a process for isolating the conjoined cells even of woody tissues. It consists in boiling them for a short time with chlorate of potash in nitric acid. It is not clear, however, that this does not *dissolve* the outer membranes.—A. H.

Intercellular passages occur mostly between parenchymatous cells; they are frequently absent from prosenchyma, or when present, are, at least, very narrow. They are closed in most places at the surface of the plant, since the parenchymatous cells which form the outermost layer of the plant are, in general, and in all parts growing under ground or in water without exception, accurately in contact at their angles; on the other hand, on most organs exposed to the air, especially on the lower sides of leaves, there occur little orifices bounded by crescent-shaped, curved cells, *stomates* or *stomata* (fig. 35), which allow a free communication between the air contained in the intercellular passages and the atmosphere.

Fig. 35.



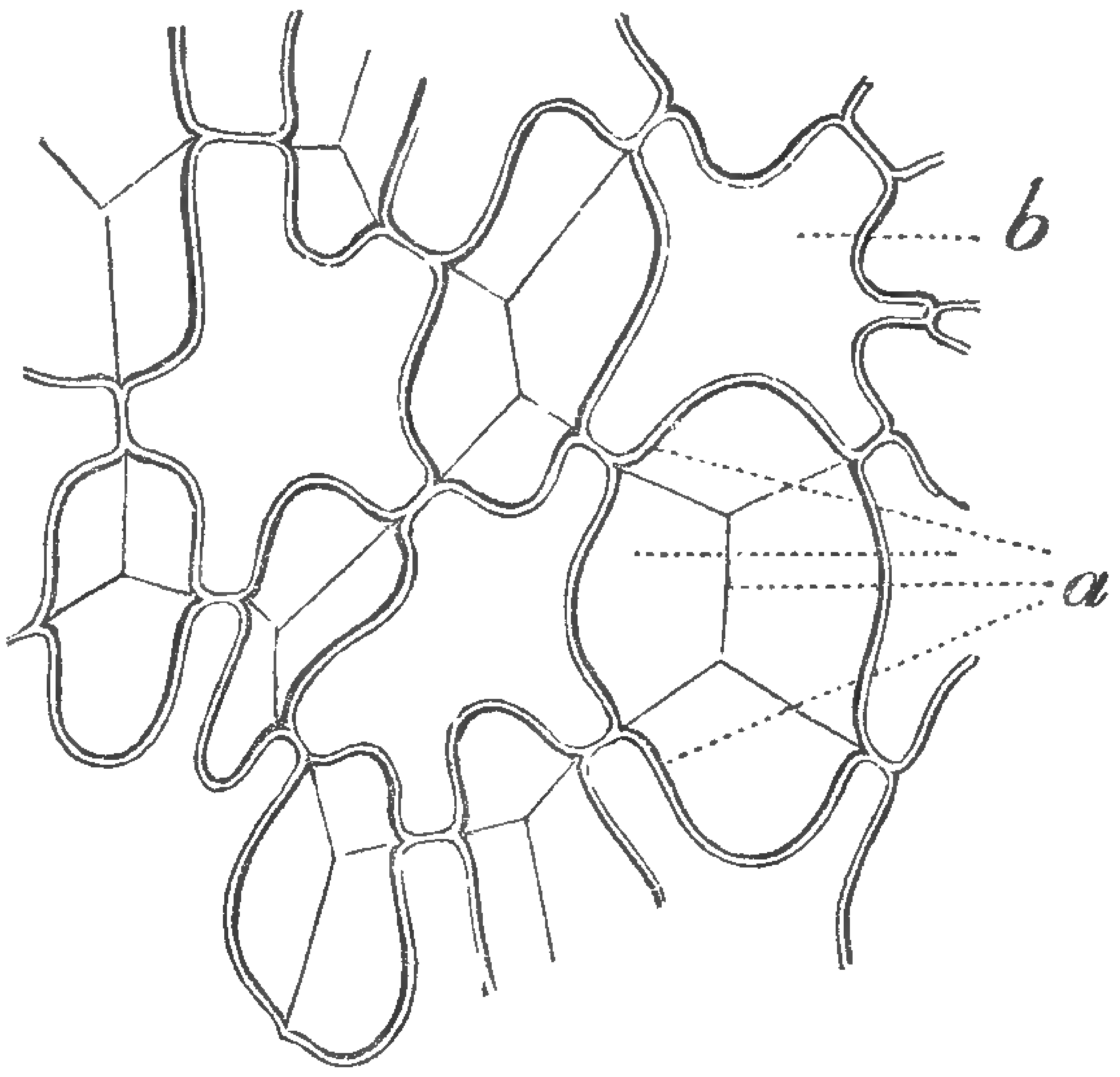
Epidermis of the lower face of *Helleborus fœtidus*. *a*, stomate.

The more regularly polyhedral the cells are, the more do the intercellular passages take the form of regular, narrow canals (*see* fig. 7); on the other hand, the more globular the shape of the cells (fig. 6), and in a still higher degree, the more an unequal growth has caused them to approach the form of the stellate cell (fig. 10), the more do the intercellular passages take the form of irregular cavities, and the more spongy becomes the tissue of the organ formed of such cells, since the space occupied by the intercellular passages then becomes more equal to, or in extreme cases, many times surpasses, that filled by the cells. The lower side of leaves and corollas are formed of such tissue, moderately spongy, the pith of *Juncus effusus* gives a very highly developed example.

In other cases the intercellular passages lying between regular polyhedral cells become expanded at particular points into larger cavities, or into long canals, which latter are frequently interrupted at certain distances by partitions composed of stellate cells. This is the case in the stem and in the leaf-stalk of many water- and marsh-plants, in which the wide, regular air-canals are often separated from each only by a single layer of parenchymatous cells; there also exists a roundish air-cavity (breathing-cavity, *Athmungshöhle*) beneath each stomate. Canals and cavities of this kind serve in other cases as reservoirs for peculiar fluids secreted by the neighbouring cells, *e.g.*, for balsams in the Coniferæ, for etherial oils in the Umbelliferæ, Aurantiaceæ, &c., for gum in the Limes, Cycadeæ, and for milk-sap in *Rhus*.

In many cases the spaces between the cells are filled up with a solid matter, the *intercellular substance*, which is secreted by the cells upon the outer surface, and sometimes only imperfectly fills the intercellular passages, but usually forms a dense mass in it and quite obliterates its cavity. This occurs in remarkable quantity in the tissue of many Algæ, especially of the Fucoideæ, the Nostochineæ, in the cortical layer of many Lichens, in the Albumen of many Leguminosæ, *e. g.*, *Sophora japonica* (fig. 36), *Gleditschia*, &c. It is found in smaller quantity, and therefore less readily perceptible, in the intercellular passages of wood, *e. g.*, of *Pinus* (fig. 22) and *Buxus*, as well as in the intercellular substance of bark. The mass composing the intercellular substance usually resembles so much the substance of the cell-walls between which it lies, that the application of re-agents, as of iodine and sulphuric acid, does not afford any certain means of accurately distinguishing it from cell-membrane; in other cases the boundary line between them is very sharply defined.

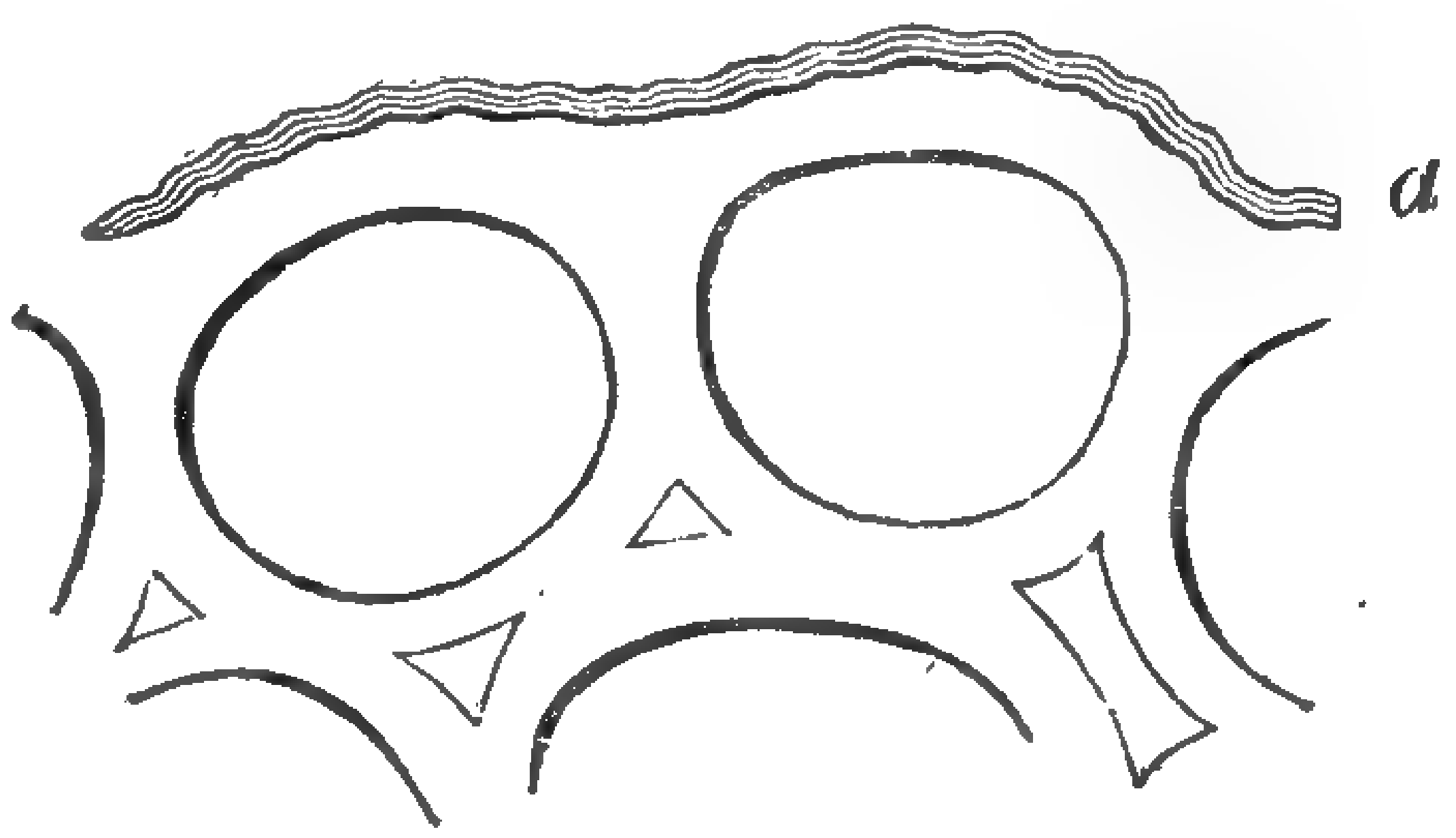
Fig. 36.



Transverse section through the albumen of *Sophora japonica*; *a*, intercellular substance; *b*, cavity of the cells.

An analogous secreted layer, appearing in the form of a membrane, occurs upon the surface of freely exposed cells; it possesses, like the outermost membrane of wood-cells, the property of resisting obstinately the solvent power of sulphuric acid. To this belong the outer membrane of spores and pollen-grains and the cuticle (fig. 37, *a*), which invests the whole of the surface exposed to the air of the higher plants, in the form of a connected membrane.

Fig. 37.

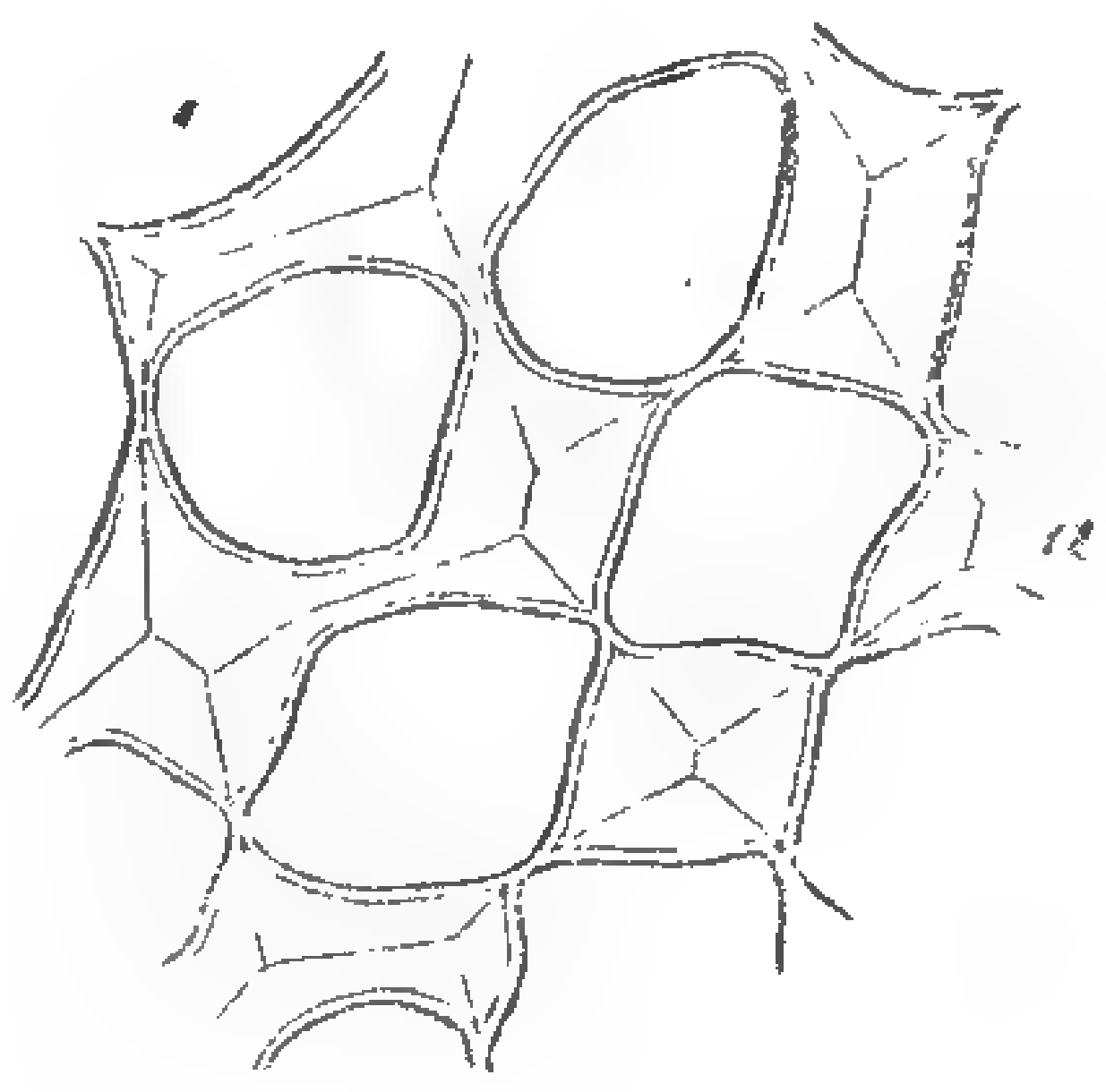


Cells of the epidermis of the leaf of *Helleborus fœtidus*. *a*, cuticle.

Observ. When I propounded the theory of the intercellular substance ("*Illustrations and Defence of my View of the Structure of Vegetable Substance*," 1836), this appeared to me to possess a far greater importance in the vegetable organism, than it proved to have subsequently on more accurate investigation of this substance itself and more minute research into the development of cells. I did not perceive that the intercellular substance is a product of the cell, and thought I had discovered in it an universally distributed mass, in which the cells are imbedded, and which, in many cases, exists before the formation of the cells. The real condition is in most cases decidedly the reverse; but it is not yet, however, clearly made out whether or not, in certain cases, for instance in the albumen of *Schizolobium excelsum* (*see* Schleiden on "*Albumen*" in the "*Nova act. Natur. Curios.*" xix. p. 11, pl. xliii, fig. 55), cells and intercellular substance originate together; but nothing can be decidedly determined about this, since we are altogether without observations on the development.

In very many cases it is extraordinarily difficult to distinguish the intercellular substance from the cell-wall. In regard to this, my opinions differ in many cases from those of many other observers; for instance, of Schleiden, especially in relation to the structure of the cells which swell up in a jelly-like manner in water (the so-called collenchyma-cells), which occur in the outer layer of the rind in many plants; for example, in *Cucurbita Pepo*, and *Beta vulgaris* (fig. 38), in which, according to my view, the parts swelling up *(a)* belong to the cell-membrane, and are formed of secondary layers deposited in the angles of the cells; while, according to the opinion I formerly expressed, still defended by Schleiden, the cells possess walls of uniform thickness, and the laminated mass lying between their angles is to be regarded as intercellular substance. In such difficult cases it is best to allow the cells to swell up in nitric acid, to render the stratification of their membrane more distinct, and thus to make out the position of the primary membrane (fig. 39).

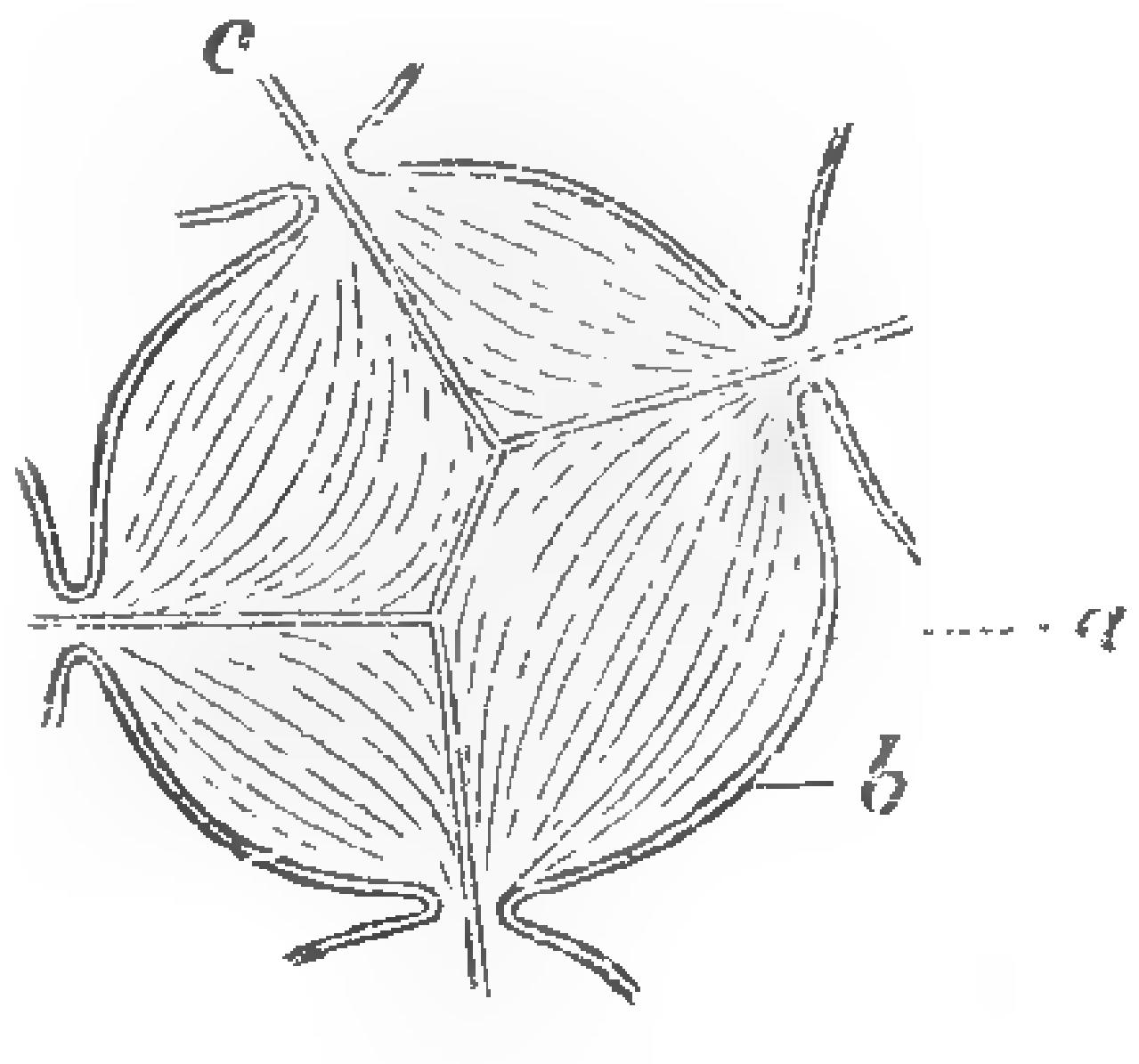
Fig. 38.



Collenchyma-cells from the stem of *Beta vulgaris*. In the angles of the cells the substance of their membrane *(a)* is very hygroscopic, and swells up gelatinously in water.

Unger ("*Botan. Zeitung*," 1847, 289) has recently sought to demonstrate that the origin of the intercellular substance and of the cells is simultaneous. The reasons advanced by him do not seem to me convincing. In the present state of our knowledge, however, we can say very little about this; the whole theory of the intercellular substance requires a thoroughly new investigation.

Fig. 39.

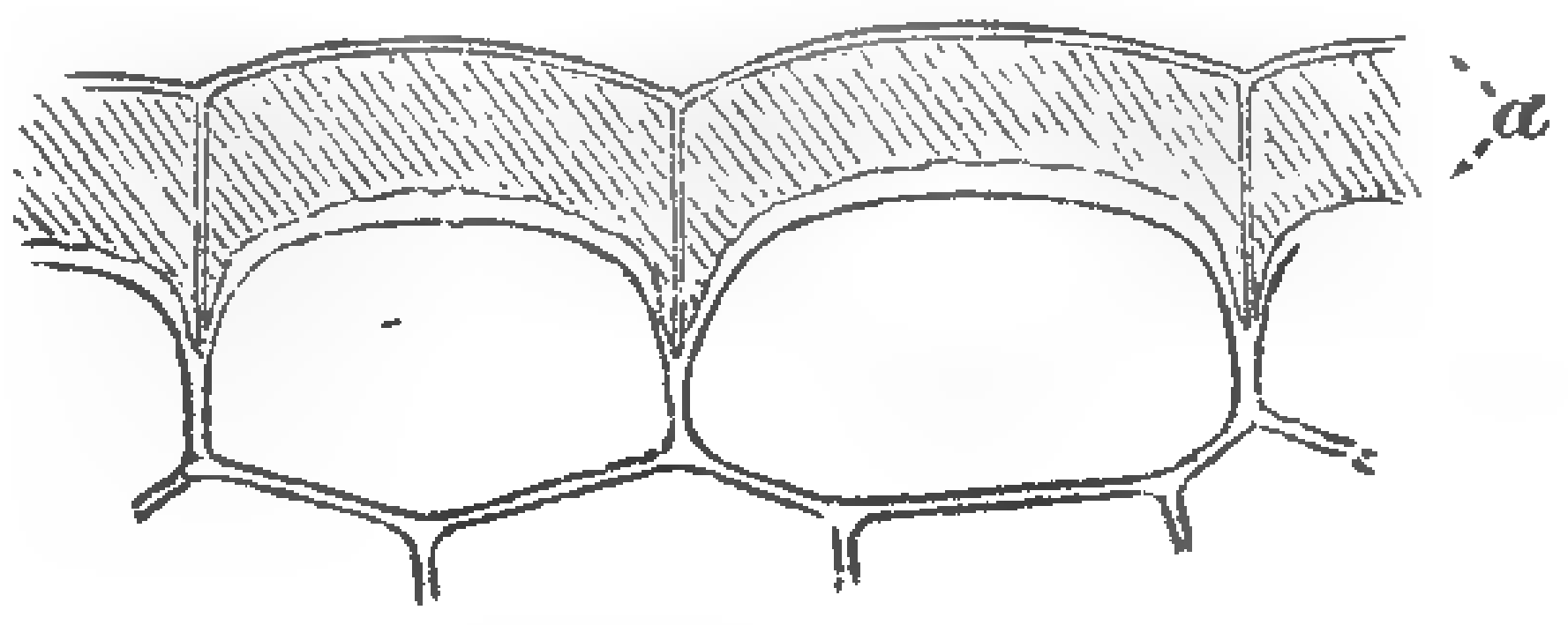


The point of union of four cells of *Beta* swollen up in hydrochloric acid. It shews the uniform dense tertiary layer *(b)*; the gelatinous secondary layers *(a)*; and the primary membrane *(c)*.

The membrane secreted upon the surface of cells exhibits most remarkable conditions, since no internal organization or composition from different layers can be detected in it, while it is yet very frequently clothed in an extremely complicated manner with reticulated projecting ridges, straight or waving lines, or granular or spiny projections, as is seen in the most varied and elegant manner on many spores and pollen-grains. Linear projections also occur frequently upon the cuticle, and these are by no means arranged in correspondence with the subjacent cells. It is not at present known of what chemical compound these membranes are composed; cellulose is not found in them.

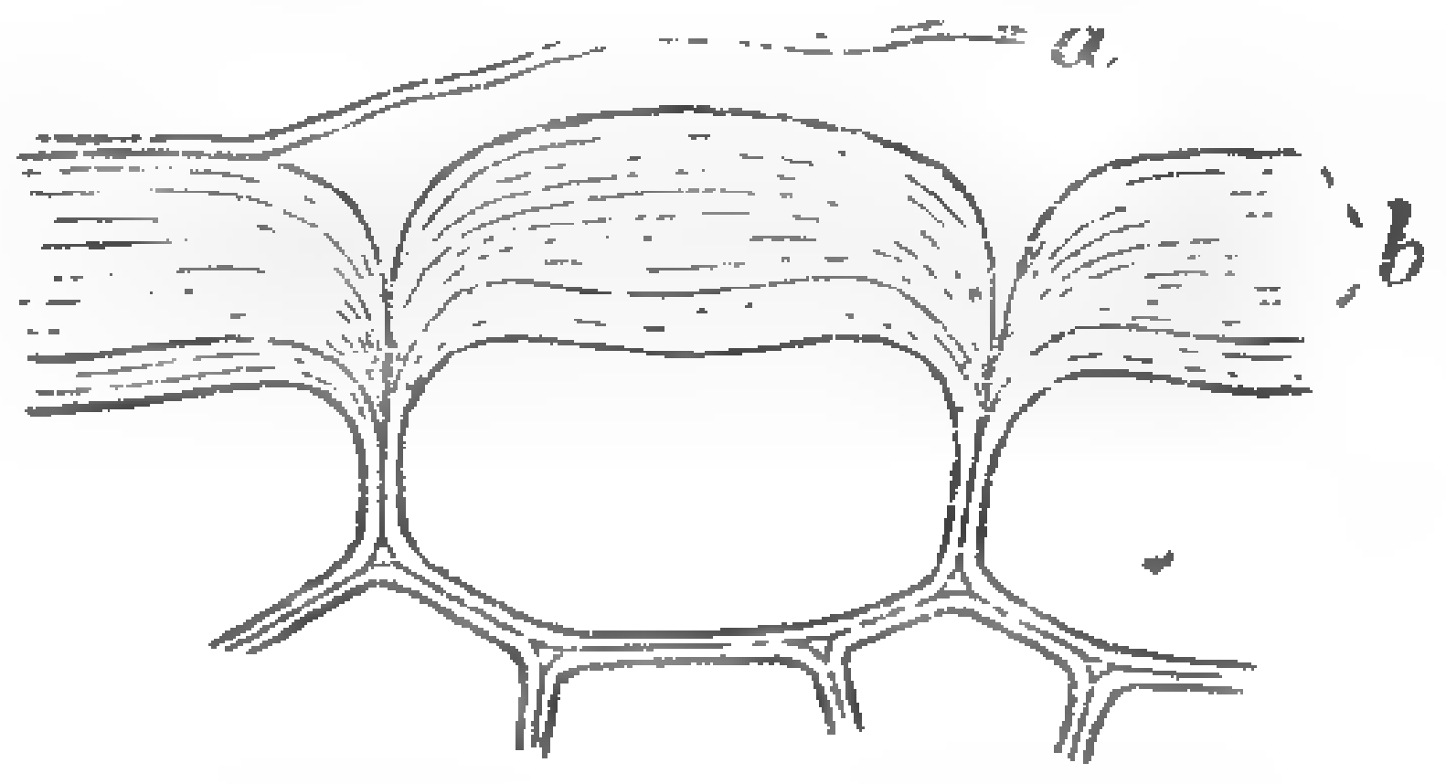
The structure and origin of the cuticle, and the epidermis-cells lying beneath it, have been the subjects of manifold discussions. When an epidermis, especially one from the upper side of a leathery leaf, is sliced transversely, the walls of its cells turned outwards are seen to be much thicker than the rest. Iodine and sulphuric acid either colour the whole of this outer wall dark yellow, and sulphuric acid does not dissolve it, or, the outer wall exhibits these properties down to a certain depth, so that a layer (fig. 40, *a*) is thus formed, which is most strikingly distinct from the subjacent cells, and when the latter have been dissolved in sulphuric acid, remains behind as a continuous and apparently homogeneous membrane. Since Ad. Brongniart ("*Ann. des Sc. Nat. Sér.*," § i, 65) had discovered that a continuous membrane, not composed of cells, called by him cuticula, might be separated by maceration from the outer surface of the epidermis, it appeared natural to suppose that the layer just spoken of, which is frequently very thick and is coloured brown by iodine and sulphuric acid, was this *cuticula*, and to ascribe its origin to a secretion upon the outside of the epidermis-cells, a process of which Schleiden even gave a detailed description ("*Grundz. der wiss. Bot.*," 1st ed. i, 288). This view, however, proposed by Treviranus, and defended by Unger, Harting, Mulder, and others, is in great part wrong. The so-called cuticle consists, with the exception of a layer extremely thin in most plants (fig. 41, *a*), of the thickened walls of the cells, which are infiltrated with a substance coloured brown by iodine, to which they owe their power of resisting the action of sulphuric acid. When this substance is removed by caustic potash, not only is the composition out of cell-membranes evident, since the separate layers of these become visible, but iodine now very readily produces a blue colour ("*Bot. Zeitung,*" 1847, 592). This composition of the so-called cuticle, of cell-membranes, is seen beyond all doubt in the epidermis of an old stem of *Viscum album* (fig. 42); 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 (H. v. Mohl, "*On the Epidermis of Viscum album,*" —*Bot. Zeitung*, 1849). I call these layers belonging to the epidermal cells the *cuticular layers of the epidermis*, to distinguish them from the mass secreted on the outside of the cells, the true *cuticle*, which is soluble in caustic potash, in most cases forms but a very thin coating over the epidermal cells, and only rarely, as in the shoots of *Ephedra*, and the upper surface of the leaves of *Cycas*, forms

Fig. 40.



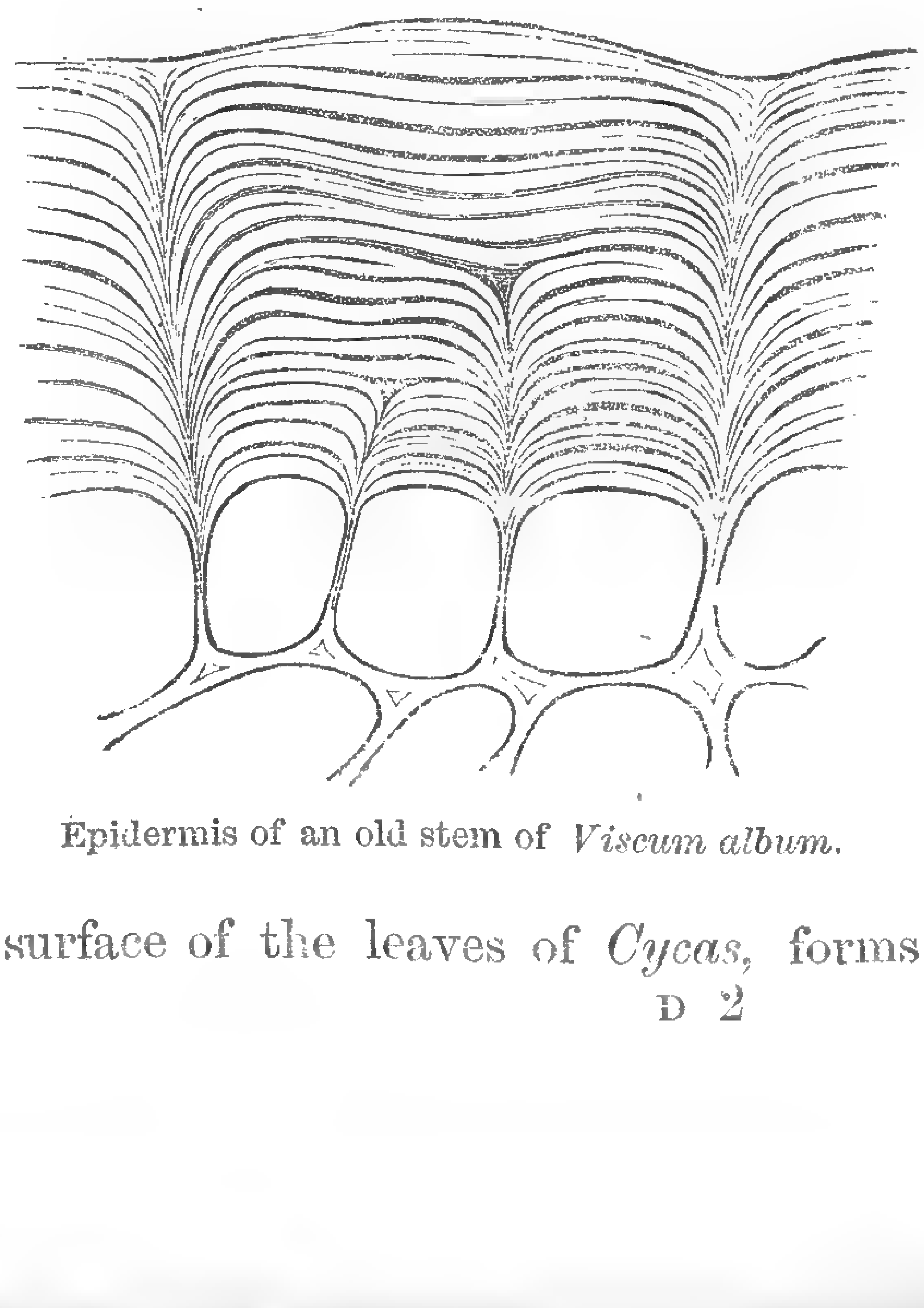
Cells of the epidermis of the upper face of the leaf of *Hoya carnosa*. *a*, the portion of their walls acquiring a yellow colour with iodine.

Fig. 41.



The epidermis of the upper side of the leaf of *Hoya carnosa* treated with caustic alkali. *a*, the cuticle separating; *b*, the swollen, laminated cuticular layers of the epidermal cells.

Fig. 42.



Epidermis of an old stem of *Viscum album*.

a layer of considerable thickness, and in which no cellular has yet been shewn to exist.

E. CONTENTS OF CELLS.

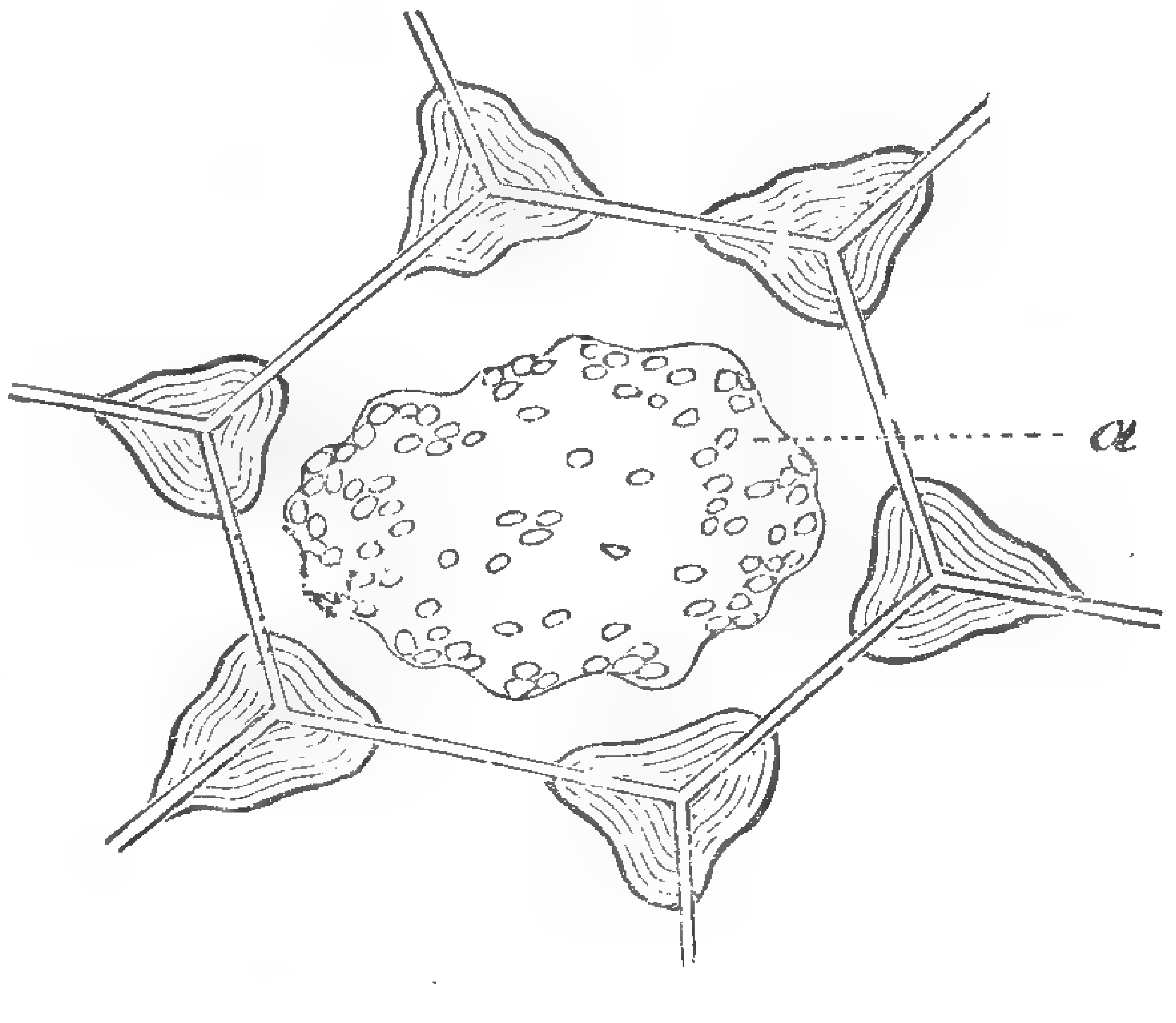
In the present state of our knowledge it is an impossibility to give even a tolerably complete description of the contents of cells, since of the large number of organic compounds produced by the vegetative processes, almost all of which occur in the cells, only a very small number can be demonstrated at present in the plant itself by means of the microscope, since most of them occur in solution in the cell-sap and in too small quantity for them to be rendered visible by re-agents. I must, therefore, confine myself to the mention of the organized productions found in cells, and the universally diffused substances.

a. Primordial Utricle, Protoplasm and Nucleus.

In all young cells, whatever their subsequent contents may be, whether they persist in the stage of cells or become changed into vascular utricles, a series of formations are met with, which disappear again more or less perfectly in the subsequent periods of life, and which stand in the closest relation to the origin and growth of the young cell, but only in particular cases in relation to their later functions.

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 cells, 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 (fig. 43, *a*) the *primordial utricle* (*primordialschlauch*) (H. v. Mohl, "*Remarks on the Structure of the Vegetable Cell,*"—*Bot. Zeitung,* 1844, 273. *Transl. in Taylor's Scientific Memoirs,* vol. iv. p. 91). Iodine colours it yellow, and it is therefore probably always nitrogenous. According to Mulder, proteine may be detected in it in many, but not all, cases, by nitric acid. Cellulose cannot be found in it, and the compound of which it is composed is as yet unknown.

Fig. 43.



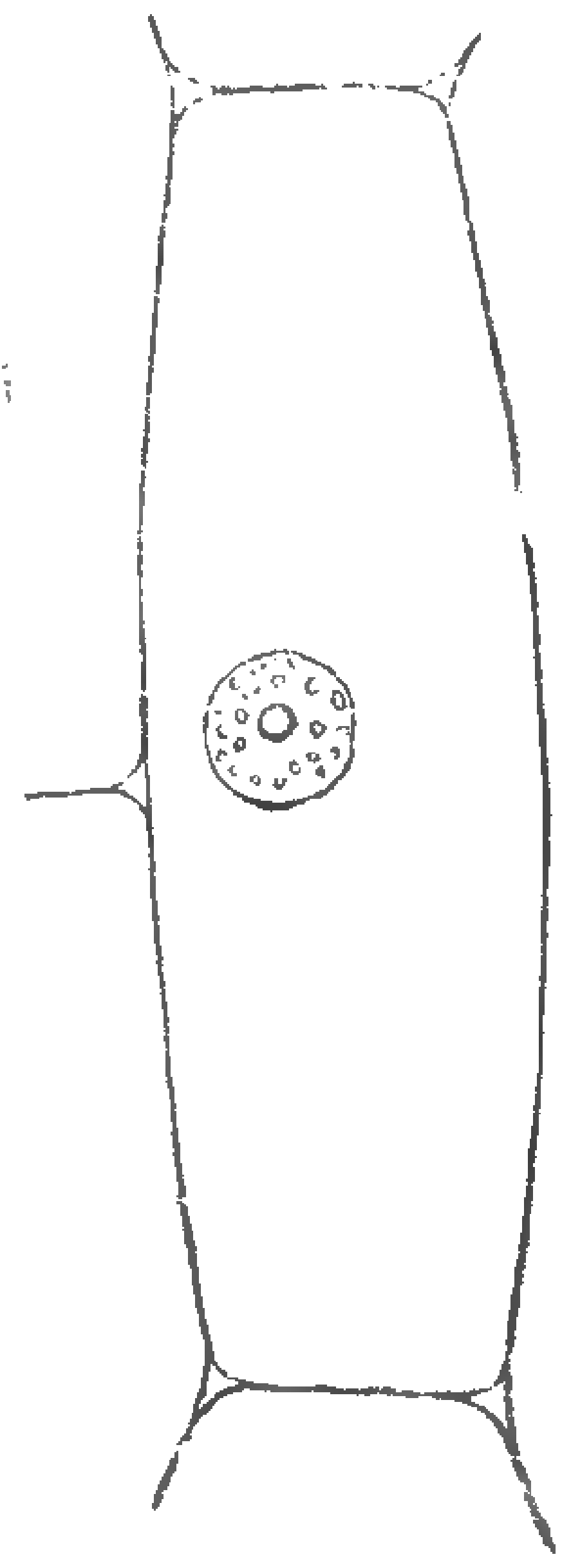
Cell of the leaf of *Jungermannia Taylori.* *a*, the primordial utricle separated by the action of iodine.

The primordial utricle disappears again with the thickening of the walls of the vessels, the cells of the wood, of the pith, of the inner part of the petiole, and of thick leaves. It usually adheres firmly to the cell-wall, and can be discovered even at first in the form of a thin granular coat, coloured yellow by iodine, when the cell-wall is dissolved in sulphuric acid; in particular cases it appeared to me not to be so firmly connected, but to be dissolved and to assume before it vanished the form of an irregular net of fibre-like streaks. On the other hand, the primordial utricle retains its complete integrity throughout the whole life of those cells which contain chlorophyll, thus especially in the cells of leaves, and in those of the fleshy rind of the Cacteæ, *Euphorbiæ*, &c., and in like manner in the cells of many Cellular plants, particularly of the Algæ.

Observ. It was natural enough that the primordial utricle should have been seen by others before I called attention to its existence as an universally prevailing structure; in particular, Kützing (*Linnæa*, 1841, 546, "*Phycologia generalis*," 38) had discovered it in the Algæ, and described it as a special coat of the cell under the name of the *Amylid-cell*. He applied this unsuitable name under the idea that its substance was changed into starch by the action of potash, which is not the case. Karsten had described the same in his "*Dissertatio de cella Vitali*," but attributed import to it quite different from that I have, since he considered it to be a secondary cell. Nägeli ("*Zeitschrift f. wiss. Botan.*" i. 96) had detected it in the Algæ, but taken it not for a membrane, but a layer of mucilage,—a view in which Schleiden appears to participate. I must declare against this opinion *in toto*. No fixed limit can, of course, be indicated between a soft membrane and a compact layer of mucilage, but a layer from which (as will be described more minutely further on) folds grow out and cause constriction of the contents of the cell, certainly must be regarded as a membrane, and not a layer of fluid mucilage.

In the centre of the young cell (fig. 44), with rare exceptions, lies the so-called *nucleus cellulæ* of Rob. Brown ("*Zellen-kern;*" "*Cytoblast*" of Schleiden); the origin of this will be treated more minutely hereafter in the description of the origin of cells; it is usually of very considerable size in proportion to the magnitude of the young cell, so that in particular cases, *e. g.*, in the cells of jointed hairs, it almost fills up the cavity. The remainder of the cell is more or less densely filled with an opake, viscid fluid of a white colour, having granules intermingled in it, which fluid I call *protoplasm* ("*On the Movement of Sap in the Interior of the Cell*,"—*Bot. Zeitung*, 1846, 73). This fluid is coloured yellow by iodine, coagulated by alcohol and acids, and contains albumen in abundance, whence young organs are always very rich in nitrogen.

Fig. 44.



Cell from the stem of *Orchis mascula*, with a nucleus.

As the cell increases in size, its membrane grows in much greater proportion than the nucleus, which certainly frequently enlarges for a certain time, but becomes smaller in proportion to the cell. During the growth of the cell irregularly scattered cavities are formed in the protoplasm; these are originally isolated, and very frequently present a most deceptive resemblance to cavities of delicate-walled cells, subsequently, however, they become blended together in many directions; the protoplasm is then accumulated at one side, in the vicinity of the nucleus; on the other side it coats the inside of the primordial utricle, and these two collections are connected together by thread-like processes which are sometimes simple and sometimes branched, so that the nucleus appears suspended, as in a spider's web, in the centre of the cell.* An internal movement in the protoplasm now begins to be visible. Originally no definite arrangement can be perceived in it; but the more the protoplasm changes from the uniform mass which it originally formed, into the condition of threads, the more distinctly it may be seen that each of these threads represents a thinner or thicker stream, which in one thread flows from the nucleus to the periphery, turns round there, and flows back again in another thread. The thickness, the position, and the number of these threads are subject to constant change, which shews, beyond a doubt, that the currents move freely through the watery cell-sap, and are not enclosed in membranous canals. In most cases the nucleus does not appear to take any part in this movement; but the motion may easily be overlooked on account of its slowness, since I found in *Tradescantia virginica*, in which I saw the nucleus move slowly up and down, that this only passed over the distance of 1-45,000th of a line in a second, which is naturally much too little to allow of the movement being seen directly, even by the application of the strongest magnifying powers. The nucleus retains its central position in many cases even when the cell is fully developed, *e. g.*, in *Zygnema*, but it mostly becomes gradually withdrawn towards one side of the wall of the cell, where it becomes attached by its viscid investment to the primordial utricle, but always forms the centre of the currents of sap. The circulation of the protoplasm is very slow; I determined it in the hairs of the filaments of *Tradescantia* at an average of 1-500th of a line per second, in the stinging hairs of *Urtica baccifera* 1-750th, in the hairs of *Cucurbita Pepo* at 1-1857th, &c. ("*Bot. Zeitung.*" 1846, 92.)

In most cells this phenomenon is transitory, for not only is the nucleus itself dissolved in time in the majority of cases, but the protoplasm also becomes more and more diminished in quantity, or at least frequently appears motionless, as appears in all proba-

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* Pl. 1, fig. 7. The end cell of a hair of the filament of *Tradescantia Sellowii.*

bility to be the case in the cells of many succulent fruits, in which the nucleus frequently remains perfect up to the time of the maturation of the fruit. In one series of cases, however, the circulation is persistent in the full-grown cell, *e.g.*, in the stinging hairs of nettles and *Loasœ*, in the hairs of Cucurbitaceous plants, in the hairs of the filaments of *Tradescantia*, in the hairs of the corolla of *Campanula Medium*, in the cells of the leaves of *Sagittaria sagittifolia, Stratiotes aloides.* In some plants the protoplasm is not distributed in isolated reticularly arranged currents, but flows along the cell-wall in a broad stream, returning back upon itself in a circular direction at one side of the top of the cell, and flowing down upon the other side, the nucleus following the current. This form of the circulation is displayed very beautifully in the cells of the leaves of *Vallisneria spiralis*, and in the cells of *Chara*, the inside of which is clothed with spirally arranged rows of chlorophyll granules, which the current accurately follows.

Observ. 1. The wonderful phenomenon of the movement of the protoplasm is usually designated by the most unsuitable name of "rotation of the cell-sap." Although described by Corti in 1774, the phenomenon was altogether forgotten till discovered a second time by Treviranus in *Chara*, in 1807. For a long time it was supposed to be a peculiarity belonging to a few water plants (*Chara, Hydrocharis, Vallisneria, Caulinia*), until the researches of recent times shewed that it was an universal phenomenon. The cause of the motion is altogether unknown; the explanation of Amici, that in *Chara* the rows of chlorophyll granules which clothe the walls of the cells, and which the current of sap follows, exercise a galvanic action upon the sap, and thus give rise to the motion, cannot be considered applicable, since these granules are absent in all other plants and even in the roots of *Chara*. The description of the phenomenon in question, by Schultz, furnishes a pattern of imperfect observation and unfortunate conclusions; he regards the currents of protoplasm as composed of milk-sap, flowing in a branched vascular system, having its origin in the vessels of the milk-sap, and penetrating the walls of the cells ("*Die Cyclosis des Lebensaftes in der Pflanze*," 293).

Observ. 2. According to Schleiden's statement ("*Grundz*," i. 211, pl. 1, fig. 6), it sometimes happens that a secondary cell-membrane becomes deposited over the nucleus as it lies upon the wall of the cell, so that it is enclosed in the substance of the cell-membrane and protected from further change. This account is altogether incorrect. The nucleus, like all the rest of the contents of the cell, lies in the cavity of the primordial utricle, and the cell-membranes are formed over the outside of the latter. The conditions which determine the early solution of the nucleus or its persistence in the full-grown cell, are altogether unknown. It vanishes very soon in vascular utricles and in wood-cells; it has likewise very often disappeared from full-grown parenchyma-cells, especially in those of the middle layers of the stem, while it is very frequently found quite perfect in spores, pollen-grains, in the cells of jointed hairs, in the cells of berries, and in the boundary cells of stomates; the cellular tissue of many Orchideæ and Commelynaceæ is remarkable for the long retention of the nucleus.

Observ. 3. It has already been remarked that the cavities in the protoplasm, filled with watery cell-sap, sometimes deceptively resemble cells. This is the case in a much less degree as long as the protoplasm is only hollowed into distinct isolated cavities, but the similarity becomes very great when the hollows have so increased in number or size, that the layers of protoplasm between them have assumed the form of thin partitions. In this case the cavities acquire the shape of polyhedral parenchymatous cells; and those lying on the surface of the mass of protoplasm become rounded off on their free sides, as cells would in such a case; in short, the resemblance to a delicate-walled cellular tissue could not be greater. Yet if we reflect that the protoplasm is a viscid fluid, which, as its delicate currents shew most distinctly, does not mix with the watery cell-sap, this appearance becomes comprehensible enough; the protoplasm bears the same relation to the cell-sap as a frothing fluid does to the air contained in its bubbles. The unceasing flow and continued transformation of the mass of the protoplasm, furnish most distinct proof that we have to do with a fluid, and not with an organized structure. We must keep in view this condition of the protoplasm of the young cells, if we would avoid being deceived by the forms which it frequently presents in full-grown cells, especially in those of succulent fruits, *e. g.*, of Grapes. In these it forms not only, in part, a connected frothing mass, but a portion of it occurs in isolated globular masses, which usually contain in their interior one or more cavities filled with cell-sap, and consequently possess the form of vesicles. These are met with in every gradation of size, from scarcely perceptible vesicles to bodies like cells, some 1-100th of an inch in diameter. No more movement in the substance of the protoplasm can be detected in these cases; on the contrary, the walls of these vesicles exhibit a tolerable degree of firmness, so that the comparison of them with cell-like structures is not at all far-fetched. Nevertheless, such a comparison seems to me out of place; since none of our means,—for instance, application of the compressor, or treatment of iodine,—will enable us to discover on these vesicles a membrane which would form a contrast with the contents. Under these circumstances, I can only regard as a mistake Karsten's view ("*Creation*," *Die Urzeugung.—Bot. Zeitung*, 1848, 457; "*Contributions to the Knowledge of Cell-life.*" —*Bot. Zeit.* 1848, 361), according to which these utricles are the rudiments of cells.

b. Cell-sap.

In full-grown cells the protoplasm usually forms but a very subordinate part, as to mass, of the contents of the cell; while the watery cell-sap, which at first appeared only in isolated cavities, formed by degrees in the protoplasm, fills the whole cavity of the cell The quantity of it is subject to variation, according as the plant has absorbed or evaporated more water; the decrease, however, cannot descend below a certain limit in the cells of most organs of the higher plants, without destroying the life of the cell.

Although the cell-sap always contains in solution a series of organic and inorganic compounds, as a general rule it appears to the eye like pure water, since it is but rarely that colouring matters (usually red or blue) are dissolved in it; and still more rarely is the quantity of the uncoloured substances, such as gum, dissolved in it, so great as to increase in a striking manner its power of refracting light.

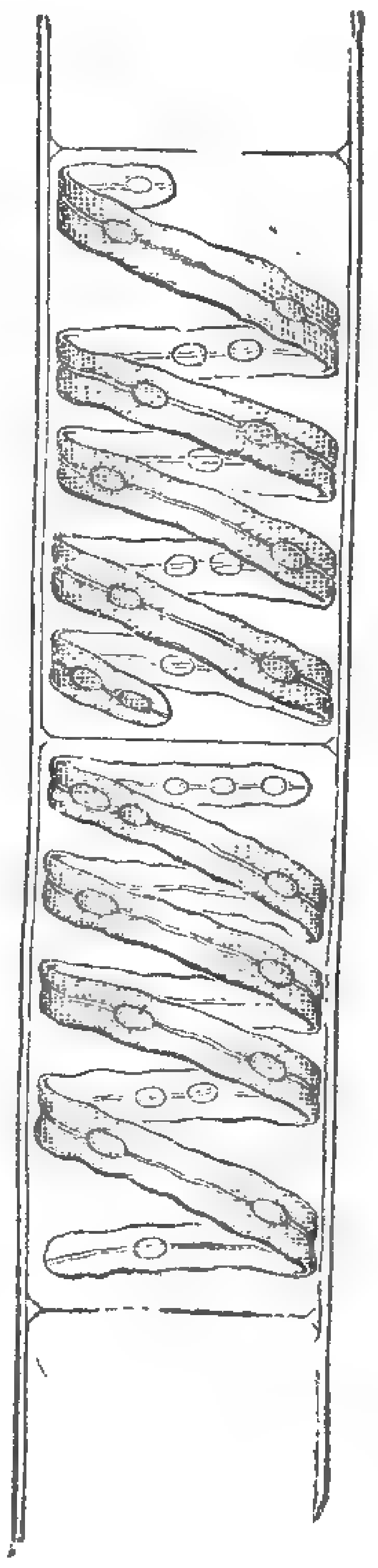
In many, yet comparatively rare, cases, the cell-sap of particular cells becomes wholly displaced by compounds which the cell itself prepares, *e. g.*, etherial oils.

Observ. Among the organs of the higher plants, ripe seeds alone bear to be perfectly dried without being killed; the older wood of trees may also lose a great quantity of its sap without death; the limit to which this is possible is as yet unknown. The rest of the organs, particularly the leaves, do not bear any considerable loss of water. It is different in many lower plants, especially the Mosses, Lichens, and many Algæ, *e. g.*, in *Nostoc,* which may be completely dried up without injury.

c. Granular structures.

In the majority of parenchymatous cells, organic structures—usually of granular form—are met with, at all events at certain periods of the life, swimming in the cell-sap or slightly adherent to the walls. Two of these, the chlorophyll granules and starch are very generally diffused.

Fig. 45.



Zygnema.

Chlorophyll (leaf-green), on the presence of which depends the green colour of plants, never occurs dissolved in the sap, but always in the form of a softish mass of definite or indefinite shape; many phytotomists have asserted the existence of a green-coloured cell-sap, but I have never been able to find it.

Amorphous chlorophyll forming patches or threads which adheres to the cell-wall and the granules contained in the cell, is of comparatively rare occurrence, yet it occurs here and there in the Phanerogamia, in the same cells with the chlorophyll granules. Usually chlorophyll possesses a sharply defined form. In certain Algæ it presents itself in the form of flat bands, in *Conferva zonata, Draparnaldia plumosa,* &c., in each cell as a transverse annular band; in *Zygnema* (fig. 45), in the form of a spirally wound band; in *Mougeotia,* in the form of a flat or curved plate lying in the interior of the cell, &c. In the great majority of plants, however (*see* fig. 10), it possesses the form of globules, which sometimes lie upon the wall of the cell (where they are usually irregularly scattered, but in *Chara* arranged in rows), sometimes swim in the cell-sap, and sometimes surround the nucleus.

But a very small portion both of the band-shaped masses in

Zygnema, &c., and of the chlorophyll globules consists of the green colouring matter; so that in pieces of plants from which the colour has been extracted by alcohol, they are found little altered in size, as softish masses which are coloured yellow by iodine, therefore contain nitrogen. Whether this is simply albumen, as Treviranus states, remains to be proved; but it is probable that it is a proteine compound.

Even in the matter extracted by ether, the true green colouring substance forms but an extremely small portion, according to Mulder's researches ("*Physiological Chemistry*," 275), since the great mass of that which is soluble in ether consists of wax. The chemical composition of chlorophyll is not yet made out with certainty; Mulder's analysis gave $C_{18}\,H_{18}\,N_2\,O_3$, but requires repetition. From his researches it would appear that chlorophyll is allied to the indigo-like bodies, and Mulder considers it probable that uncoloured chlorophyll exists in all parts of the plant, capable of conversion into green by free oxygen; a conjecture, however, against which speaks the circumstance that neither the expressed sap, nor any tissue whatever of plants, acquires a green colour by exposure to the influence of the air.

Starch granules are very frequently enclosed in the chlorophyll granules. (See "*On the Anatomical Condition of Chlorophyll*," in my "*Vermischte Schrift.*") and not only in the band-shaped strips of *Zygnema*, but in an extraordinary number of cases in the chlorophyll granules of the most varied plants, and especially distinctly in those of *Chara*. Sometimes only one starch granule exists in the chlorophyll grain, sometimes several, but usually not more than three or four; in *Anthoceros* alone I found from 50 to 100 starch granules in each of them. These starch granules are usually of very small size; the longest I determined at 1–300th of a line, the smallest, acquiring a distinct blue colour with iodine, 1–2000th of a line, and it still remains uncertain whether or not still smaller granules, which occur in many cases in chlorophyll, consist also of starch. The history of the development of chlorophyll is still involved in obscurity. So far as I have traced the matter, it stands in the closest connexion with protoplasm at its first appearance in uncoloured organs which have been developed in the dark, when the formation of chlorophyll is brought about in these by the influence of light; for on the first appearance of the green colour, isolated portions of the protoplasm are seen to assume a greenish tint, exhibiting the form of granular patches of mucilage having no definite outline. Subsequently, the starch granules, where such occur in the cells, *e.g.*, in the potato, or any young leaves, become clothed by a more or less thick coat of chlorophyll presenting a distinct boundary line; while in other cells chlorophyll granules are met with which contain no starch. In other cases in which the very young organs contain no starch, *e.g.*, in the vegetating points of *Conferva glomerata*, granules of it appear at a later period in the perfect chlorophyll globules, and increase in size with the age of the plant. Thus it seems to me that starch does not stand in any causal and necessary connexion with chlorophyll, but that the proteine substance combined with chlorophyll sometimes assumes the definite form of globules, bands, &c., and sometimes, when starch granules are present, becomes deposited on these as upon a nucleus.

Observ. The relation of chlorophyll to starch is viewed in an essentially different way by Mulder, who rests upon my description of the former. He assumes that the chlorophyll granules are always produced from starch granules, since the latter become partly or wholly converted into the wax connected with the green colouring matter, and in so doing either assume the form of globules or become blended together, and produce amorphous chlorophyll. This transformation of starch into wax must be accompanied by an abundant evolution of oxygen gas; and Mulder therefore believes that plants do not exhale this gas because they are green, but while they are becoming green. I cannot accept this theory on account of anatomical reasons, for in many young organs we find chlorophyll but not starch, which should precede it, and in the *Confervæ* particularly, in which the chlorophyll occurs in the form of bands and plates, as in *Zygnema*, &c., these structures never consist of a substance having any resemblance to starch, but, on the contrary, the starch granules occurring in this chlorophyll increases in size with the age of the plant.

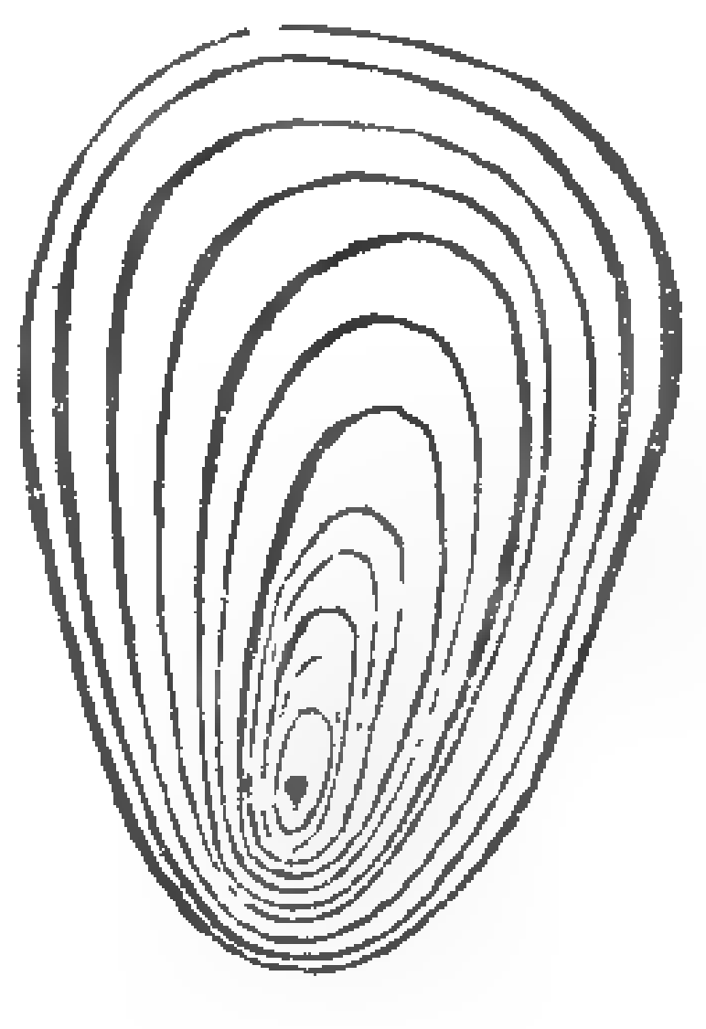
Observ. 2. I have described the chlorophyll granules as a softish, homogeneous substance, and not as utricular structures, such as they were formerly stated to be by Sprengel, Meyen, Agardh, Turpin, and others, for I never could succeed in discovering upon them an enveloping membrane distinct from the contents. Their utricular nature has, however, been defended in recent times by Nägeli. ("*Zeitschr. f. wiss. Botan.*" iii. 110); according to his statements, a whitish membrane and green contents may be clearly distinguished in the large chlorophyll granules of the Algæ, Charæ, and Mosses. Also Göppert and Cohn ("*Bot. Zeit.*" 1849, 665) say that in *Nitella* they saw the chlorophyll granules expand by absorption of water into vesicles composed of a thin translucent membrane, which finally burst. I am not in a position at the present moment to test these statements respecting the chlorophyll granules of *Nitella;* but I have formerly frequently examined them and detected the occurrence of starch granules in the chlorophyll, but could never find a membrane upon the latter. Nägeli believes, moreover, not only that he has seen a membrane in many cases, but that he has found proof of a complete analogy of these vesicles, with cells, in the phenomena of their vegetation. In this he is not warranted by a single fact; for that the chlorophyll granules may grow, and during growth alter in form, is no proof at all of the cellular nature, any more than is the circumstance that their number may be multiplied by division as in *Nitella.* Division might occur in globules devoid of a membrane; but that it depends on the formation of secondary vesicles inside the chlorophyll vesicles, is an hypothesis devoid of all foundation.

Observ. 3. We know very little as yet of the anatomical conditions of the other colouring matters of plants. The reds and blues are usually dissolved in the cell-sap ; in particular the red colouring matter of leaves, which acquire this colour in autumn, that of most flowers and red fruits ; and in like manner the blue colouring matter of most blue flowers. Only in very rare cases do we find the red and blue colouring matter of flower in the form of globules, *e. g.*, the red of *Salvia splendens* and the blue of *Strelitzia reginæ.* Whether the pigment is here as in chlorophyll connected with a foreign matter forming the globules, or itself alone constitutes these is unknown. The yellow colour of leaves which are bleached in autumn consists of altered chlorophyll (Xanthophyll) ; in flowers the yellow pigment usually occurs in the form of globules ; but in other cases diffused uniformly in the cell-sap ; in the yellow perigonial leaves of *Strelitzia* it has the form of slender, crescentically curved and irregularly wound fibres, which swim in the cell-sap. In the red coloured Algæ, the chlorophyll seems, at first sight, to be replaced by red colouring matter, but according to the researches of Kützing ("*Phycologia generalis,*" 21), green chlorophyll granules are also present, only their colour is hidden by the red colouring matter which accompanies them.

Starch (*Amylum*) is still more widely diffused than chlorophyll, since perhaps no plants except the Fungi are without it. Whether or not starch occurs in an amorphous condition is still doubtful. Schleiden ("*Grundzüge*" i. 181) believes that he found it in this state in *Sarsaparilla,* in the rhizome of *Carex arenaria,* and in the seeds of *Cardamomum minus.* It is likewise doubtful if it occurs in a state of solution, for I have repeatedly seen the sap of particular cells, particularly of *Zygnema,* but also of Phanerogamia, *e. g.*, of the Potato, acquires a wine-red colour with iodine ; but this colour is no certain sign that we have to do with starch. The form in which starch occurs universally is that of small, colourless, transparent granules, which are accumulated in the cells without definite arrangement and in variable number, sometimes swimming freely in the sap, sometimes slightly adherent to the wall. Their size varies from an immeasurably small diameter to a magnitude visible even to the naked eye (according to Payen from 2-1000ths of a millimetre in *Chenopodium Quinoa,* to 185-1000ths in the Potato) ; granules of very different diameter occur together in the same cell, but the maximum size of the granules of each plant is tolerably definite.

Like the size, the form of the granules varies extremely in different plants, and is sometimes so characteristic, that in many instances we can determine with tolerable certainly, by the microscope, the source where a starch has been obtained. Small granules are mostly regularly globular ; but the larger full-grown granules exhibit very irregular forms in many plants, being sometimes elongated into the shape of rods, sometimes flattened, sometimes made to assume angular form by mutual pressure, and mostly possessing irregular projections. (*See* the figures by *Fritzsche* in "*Poggend. Ann.*" part 32; of Payen in "*Mem. sur les Developpements des Vegetaux,*" and of Schleiden in his "*Grundzüge.*")

Fig. 46.



Starch granule of the Potato.

The starch granules of different shape agree in the circumstance that they are not composed of one uniform mass, but of super-imposed layers of varying density, whence they derive a pretty appearance with polarized light, each granule exhibiting a coloured cross. These layers are usually much thicker on one side of the granule than on the other (fig. 46), so that the organic centre is far removed from the middle point, and often closely approximated to the surface. In fresh granules there is no cavity in the centre, but one is readily produced by dessication and by the contraction this produces of the internal softer substances. This process may be traced very beautifully under the microscope, by removing a part of the water, by strong alcohol, from fresh starch granules taken from the Potato. In this case a little globular cavity is first formed, and then radiating fissures soon run out in all directions, traversing the layers of the granule at right angles. This undoubtedly results from the middle layers being softer, and more swollen up by water than the outer. But the firmness is still so great that the starch granules may be broken up into angular pieces by pressure. Cold water does not exert any solvent power over them, even when the granules are cut into thin slices, so as to allow the water to come immediately in contact with their inner layers. In boiling water they swell very much, even a hundred times their original volume, without actual solution. The same effect is produced by the action of strong acids and caustic alkalies. When iodine and water act simultaneously either in the swollen or unswollen granules, these are coloured, according to the amount of iodine they absorb, wine-red, indigo-blue, and up to the deepest black blue, without undergoing any alteration, for when the iodine is removed again by alcohol, they again possess their original properties.

In all vegetable cells starch is a transitory product, destined to be re-dissolved at a later period, and applied to various purposes of nutrition. Thus the starch disappears from the albumen of the seeds of Palms about the period of maturation, and in its place appears a fixed oil, for which it undoubtedly furnishes the material; thus it disappears in the elaters of the Liverworts when the spiral fibre is developed in them; and it vanishes during the germination of seeds and bulbs, serving for the nutriment of the young plants, &c. It is unknown at present in what way the solution of the starch granules takes place in these cases; when artificially converted into dextrine and sugar, by diastase or sulphuric acid, a swelling up of the granules precedes its transformation; but this does not happen in the living plant, for the substance of the granule remains solid, and is corroded and dissolved layer by layer from without inwards.

Observ. 1. Observation has not yet taught us anything concerning the development of starch granules. That they are originally small and roundish, is decided, and the laminated structure proves that the increase of size does not depend on the expansion in all directions of the original granule, but on gradual deposition of layers produced successively. As to the order of the succession nothing is known. We may, with Payen and Münter ("*Bot. Zeitung,*" 1845, 193), conclude, from inner layers being softest and richest in water, that the innermost layer is the youngest; when we follow this hypothesis we must naturally assume that simultaneously with the deposition of each new layer, or rather of a new central nucleus which is by subsequent growth to be converted into a layer, all the old layers expand, and exhibit an increase of thickness, the more irregular the older they grow, since the eccentricity of the organic centre increases with the size of the granule. Or we may conclude, on the contrary, with Fritzsche and Schleiden, from the young starch granules being globular, and the innermost layers of full-grown granules also possessing a globular form, while the outer layers exhibit an irregular thickness on their different sides,—further from two starch granules lying side by side, being sometimes enclosed in a common external layer,—that the outermost layer is the youngest.

Observ. 2. Most recent researches upon starch indicate that all the layers of the granules are composed of one and the same substance, and that there is no enveloping membrane contrasting with the contents. But the latter is likewise asserted in many hands. Several German phytotomists, especially Sprengel, had already regarded the granular structures occurring in cells as vesicles and as the rudiments of cells, but Turpin ("*Organographie vègètale,*" *Mem. du Museum,* xiv.) and Raspail ("*Systeme de la Chimie organique*") were the authors who especially developed and disseminated this theory. Turpin regarded the granular structures which occur in cells (therefore starch and chlorophyll in particular), comprehended by him under the general name of *globuline,* as vesicles which sprouted from the cell-walls, were attached by an umbilicus (for which he took the hilum of starch granules), and grew into cells by subsequent enlargement. These views obtained greater diffusion in regard to the starch granule through Raspail, and much credit was given to his statement that it was composed of an outer membrane resisting the action of water, and inner contents soluble in water and consisting of gum. All this has been, very properly, long since forgotten, for all these statements rest upon the most wretched observations; but the utricular nature of the starch grain has been again defended recently by Nägeli ("*Zeitschr. f. wiss. Bot.*" iii., 117, *Ray Society's Publications,* 1849, p. 183). According to him, the starch grain consists of a membrane and fluid contents; concentric layers are deposited on the inside of the membrane, as in lignifying cells, thus the cavity of the vesicle is reduced to the smallest possible size, being, however, always filled with fluid. Evidence for these statements is sought for in vain, even in the plants named by Nägeli, in which he affirms that he found the outer membrane tolerably thick and uncolourable by iodine; wholly derived from his imagination is the further statement that the granules rendered angular by mutual pressure originate together inside a chlorophyll granule; for granules of this kind are met with in subterraneous parts, in which no trace of chlorophyll occurs, as in the rhizome of *Gloriosa superba.*

In many plants the starch is replaced by *inuline*, in many parts, especially in the roots; *e. g.*, in the tubers of the Dahlias, of *Helianthus annuus*, &c. Since we possess no re-agent for it this substance still escapes from microscopic investigation, even if Schleiden's statement, that it occurs in the form of small granules, is well founded. Thus nothing is known respecting its diffusion in the Vegetable Kingdom.

Observ. According to Mulder's statement, inuline is coloured yellow by iodine, this was the case with an inuline prepared from *Taraxacum* by Mulder, which I had an opportunity of examining. Other inuline, which Prof. Chr. Gmelin prepared for me from the Dahlia, was not coloured in the least by iodine, even when I added tincture of iodine to the hot solution, before the inuline was precipitated from it.

d. Compounds dissolved in the cell-sap.

Certain compounds, most closely allied to starch and inuline, escape from microscopic observation almost under all circumstances, notwithstanding their wide distribution in the Vegetable Kingdom, because they are dissolved in the cell-sap, and there are no means of detecting small quantities of them; these are dextrine, gum, and sugar.

Dextrine seems to occur in all organs which are the seat of an active process of nutrition, but can only be discovered in the expressed saps, not by microscopic observation.

Other kinds of gum, gum arabic, cherry-gum, tragacanth, the mucilage of the seeds of Quinces, of Linseed, &c., playing a comparatively subordinate part, being diffused through but a small part of the Vegetable Kingdom, are mostly to be considered as secretion in the plants in which they do occur, and frequently are only met with in isolated parenchymatous cells, as in *Cactus*, or in the cells of particular organs, such as the seed-coats, or in cavities and canals which lie between the cells, as in the Cycadeæ. When such kinds of gum completely fill the cells or canals in which they occur, they may be detected by the dense, slimy mass which they form with water, or by the coagulation caused by alcohol; in many cases, for instance in the cells of the seed-coat of *Cydonia*, it is doubtful whether the gum is to be regarded as a substance secreted in the cavity of the cell or as forming secondary layers in it. In any case the substance of which many cell-membranes swelling up strongly in water are composed, such as the secondary layers of the cells of the seed coat of *Collomia* and of the pericarp of *Salvia*, seems to be closely allied to these kinds of gum. So long as these mucilaginous substances remain so loosely characterized by chemists, and no re-agents for them have been made out, vegetable anatomists are not in a position to make out their distribution in the Vegetable Kingdom, or their importance to the plant.

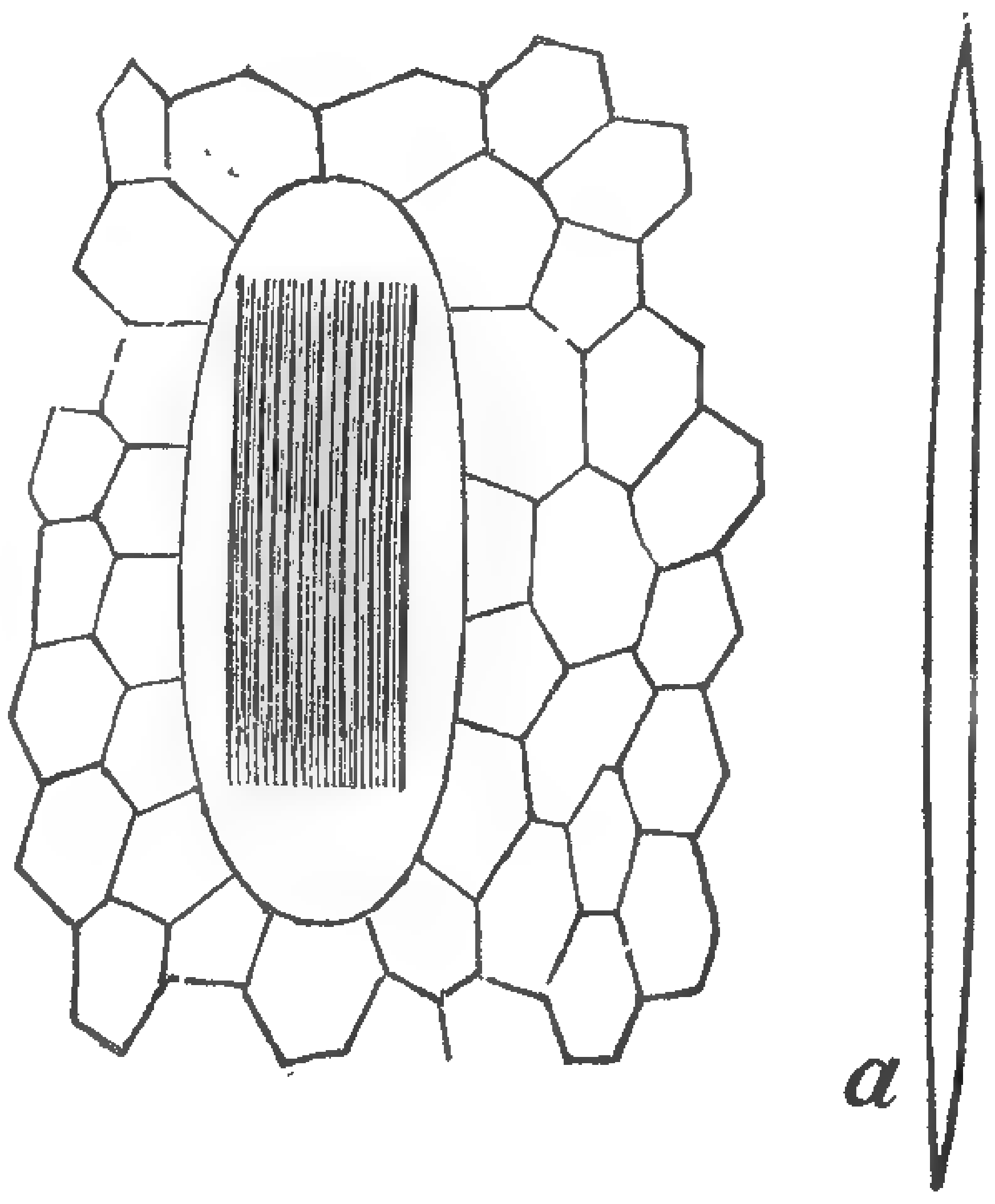
Sugar is very widely distributed, especially cane-sugar, since it not only replaces starch in many plants at the time just preceding flowering, as in the Sugar-cane, the Beet, &c., but still more frequently precedes the deposition of starch in an organ, and is also formed at the solution of the starch as in trees in Spring, in germinating seeds, &c. Neither Cane nor any other sugars (grape-sugar, fruit-sugar, mannite, &c.) are objects for microscopic observation, since they are dissolved in the cell-sap, and we are without re-agents for them.

Although occurring in a fluid form, the *fixed oils* are readily detected by their refusal to mix with water, and by their strong refracting power, when they occur in abundance, as they do principally in the seeds of many plants, more rarely in the coats of the fruit (in Olives, many Palms, &c.), still more rarely in the organs of vegetation (tubers of *Cyperus esculentus*). But when they exist only in smaller quantities, as is the case in a great number of plants, they escape observation by the microscope, since they are not then separated as clearly visible drops floating in the cell-sap, but are combined with the proteine substances. The essential oils, when produced in large quantity, usually completely fill isolated cells, or groups of cells and cavities which lie between cells, and then are easily discovered; on the other hand, in very many cases they seem to exist in such small quantities, that they are wholly dissolved in the cell-sap; at all events they cannot be visibly demonstrated in the greater number of petals.

All plants prepare a more or less abundant quantity of organic acids (oxalic, malic, citric, tartaric acid, &c.), which are found only in exceptional cases in a free condition, usually combining with bases into acid-salts dissolved in the cell-sap; and many of the inorganic acids, which the plants receive from without, remain undecomposed. The greater part of these salts, especially those of the alkaline bases, escape microscopic examination by their solution in the cell-sap; but there is scarcely one of the higher plants in which some organ or other does not secrete in the cavities of its cells insoluble salts of the earths with organic or inorganic acids, in the form of crystals. This usually takes place in cells which contain no granular organic structures; but crystals, and chlorophyll granules, and the like, do not necessarily exclude one another. In particular cells situated at the upper sides of the leaves of many Urticaceæ, *e. g.*, in *Morus*, *Ficus elastica*, &c., is found what appears to be a peculiar organic structure (a conical projecting process of the internal wall of the cell, formed of cellulose), upon which crystals are agglomerated as upon a nucleus.

Crystals occur sometimes singly in a cell, or in numbers irregularly scattered, combined into star-shaped groups, or laid side by side in the form of a bundle. The last condition (fig. 47) is the most frequent, for there can scarcely exist a plant in which have not been found in some organs, for instance the anther, or in the bark, such bundles of very fine, needle-like four-sided crystals, terminating at each end in four-sided pyramids (De Candolle's "*Raphides*"). The composition of these needle-like crystals is variously given; according to Payen and Schmidt, they are composed of oxalate of lime; according to Buchner and Trinchinetti of phosphate of lime; according to Nees von Esenbeck of a double salt of lime and magnesia with phosphoric acid. In very many plants, *e. g.*, very beautifully in the Rhubarb-root, occur four-sided rather obtusely pointed prisms of oxalate of lime; and moreover very frequently mulberry-like agglomerations of rhombohedrons, which are composed of carbonate of lime, more rarely of tartrate of lime (in old Cacteæ), and sulphate of lime (in the Musaceæ). (*See* "Unger on "*The Formation of Crystals in Vegetable Cells*," in the "*Ann. of the Vienna Mus.*" Th. ii.—Payen "*Memoires sur les Developpement des Vegetaux*,"—Schmidt "*Sketch of a General Method of Investigating the juices and excretions of the Animal Organism.*")

Fig. 47.



Needle-shaped crystals, from the bulb of *Polyanthes tuberosa*. *a* One of the crystals strongly magnified.

F. ORIGIN OF THE CELL.

It is an universal law in the development of cells that the contents are formed before the cell-membrane, and that the organization of the nitrogenous structures precedes that of the membrane composed of cellulose. In plants, the formation of cells occurs only in the cavity of older cells, and not between or upon them.

The formation of the cells takes place in two different ways: 1, through division of older cells; 2, through the formation of secondary cells *(tochter-zellen)* lying free in the cavity of a cell.

Observ. It would be superfluous to give an account of the older theories of cell-formation which had existed up to the appearance of my dissertation on the multiplication of vegetable cells by division, in the year 1835, since none of them were based on any secure foundation. Actual origination of cells had been observed only in pollen-grains and spores, but the connexion of the formation of these with cell-formation in general was altogether overlooked, and the emptiest conjectures had been ventured as to the origin of cells from chlorophyll and starch-granules, from the globules of the milk-sap, from cavities appearing in a homogeneous cambium, &c. Brisseau de Mirbel was the only one who sought to solve the problem of cell-formation by careful observation of the development of *Marchantia*, but he did not succeed in finding out the mode of development of the single cell; he believed that he discovered three modes of formation of cells: *a*, between other cells (*développement inter-utriculaire*); *b*, on the surface of other cells (*dévél. super-utriculaire*); *c*, in the cavity of other cells (*dévél. intra-utriculaire*). But all more recent observations speak decidedly against the existence of the first two modes of development described by Mirbel. It is true that Kützing ("*Phycologia generalis*," 64) has assumed the formation of cells in the intercellular substance, and, in like manner, Unger ("*Grundz. der Anatomie*," 45) attributes this process to the Phanerogamia. Neither of them, however, have any adequate evidence for the support of their views. In the dissertation just spoken of, I sought to demonstrate in the Cryptogamic water-plants, that the earlier notion of the necessity of cells originating under the form of very small vesicles was false, and that division of the cells takes place by the formation of partitions, which cut off the contents of the parent-cells into separate portions; but it was not until I had discovered the primordial utricle that I was able to trace accurately the processes in the formation of this septum. (*See* the revised edition of this paper in my "*Vermischt. Schrift.*" 1845.) Before this had happened Schleiden ("*Beiträge zur Phytogenesis*," in "*Müller's Archiv.*" 1838, Transl. in "Taylor's Scientific Memoirs," vol. ii.) had discovered the free cell-formation, and declared it to be the sole mode of formation of cells, whereby the whole theory of the development of cells was pushed into a false direction, from which it has been chiefly brought back into the right path by Unger and Nägeli, who demonstrated the great prevalence of the process of cell-division.

a. Division of the Cell.

The multiplication of cells by division commences by changes undergone by the primordial utricle of the dividing cell, in consequence of which partitions are developed, growing gradually inwards from the periphery of the cell, and dividing the cavity of the cell into two or more separate compartments. This process is preceded in almost all cases by a formation of as many nuclei as there are to be compartments in the mother-cell; in rare cases this process does not occur, and the changes of the cell-contents are limited to the phenomena which present themselves in the primordial utricle.

I investigated the second simple process chiefly in *Conferva glomerata* ("*Verm. Schrift.*" 623). This *Conferva* (pl. 1, fig. 1) exhibits growth and cell-multiplication at two places. The principal trunk of it consists of a row of cylindrical cells of pretty nearly equal length; the end cell of these *(a)* becomes elongated to twice the length of a cell (fig. 2), and then divided in the middle (fig. 2 *a*), by a cross-partition, into two cells of the usual length, of which the lower remains unaltered, while the upper undergoes the same changes as the previous terminal cell, &c.

While the filament is becoming longer in this way, the membranes of many of the older cells of the filament become protruded out sideways at the upper end (fig. 1, *b*), the process growing gradually into a cylindrical branch (fig. 1, *c*) as large as a cell, which then becomes shut off at the base from the stem-cell, by a partition (fig. 1, *d*); then it presents the same elongation and the same division in the middle (fig. 1, *e*) as the end cell of the stem exhibits, thus producing a branch, which is capable of ramifying again in like manner.

So that consequently, there are never any small cells, which would be required to grow, formed in these plants, but every cell possesses from the first very nearly the dimensions to which it is subsequently fixed, only a slight growth in width occurring in it.

The process of the formation of the septum is as follows: the cells are lined by a primordial utricle, on the inside of which lies a layer of chlorophyll granules (pl. 1, figs. 5, 6), which by the action of substances injurious to the life of the plant, such as alcohol, acids, &c., are separated from the primordial utricle (fig. 5 *a*), while this also under the same circumstances becomes detached from the cell-wall. At the place where the partition is to be formed, an annular fold grows inwards, gradually contracting and parting off more completely the chlorophyll layer, which is detached from the primordial utricle for some distance (fig. 5). During this time a cellulose membrane is deposited all over the outside of the primordial utricle (figs. 3, 4); so far as this lies between the outer surface of the primordial utricle and the inner surface of the dividing cell, it constitutes the youngest and innermost of the secondary membranes of the latter; but at the point at which the primordial utricle forms the fold just described this cellulose layer is continued into the duplicature of the fold, and thus forms an annular, thin, imperfect septum composed of two layers. This annular fold, and the cellulose membrane lying in it, contract more and more upon the central orifice until this disappears, the chlorophyll layer and the primordial utricle are cut off into two portions, and the cellulose membrane presents itself as a perfect partition (fig. 6). Thus, without important disturbance of the contents of the mother-cell, two secondary cells are formed in it, which receive within them the whole contents, and the membranes of which so far as they are in contact with the membrane of the parent-cell serve as layers of thickening to it, while where the secondary cells touch they appear as a partition of the parent-cell.

Observ. 1. I have given a somewhat detailed account of these processes, because I believe that I have traced them more minutely than others have done. Nägeli ("*Zeitschrift.*" i. 98) thinks that my description of the parting off of the cell-contents by a fold growing inwards in the cell, is incorrect; he denies to the primordial utricle the characters of a membrane, and contends that it is a layer of mucilage, not sharply defined internally, and to the interior of which the chlorophyll granules adhere; he further assumes of the chlorophyll mass, that it is not separated gradually from without inward, into two parts, but at once across the whole cavity, and at this point the mass of mucilage at the same time, and suddenly, forms a double layer as a cross wall, which secretes the true cell-membrane. These statements do not all agree with nature; the formation of the septum is gradual, the time required for its formation amounts, according to Mitscherlich ("*Monatsber. d. Akad. zu Berlin,*" *Nov.* 1847) to 4—5 hours.

Observ. 2. The division of cells without previous formation of a nucleus appears to occur only in cellular plants and especially in the Algæ. It has been observed by Nägeli in Oscillatoriæ, Nostochineæ and Diatomeæ. It has been extended to the Phanerogamia by Unger, who thought he saw nuclei first appear in already formed cells in many cases, a statement which certainly depends on error of observation.

The division of the cells of the Desmidieæ takes place in a manner differing somewhat from the mode described in *Conferva glomerata.* (See "*Folke, Physiol. Studien.*" 1 *Heft; Ralfs's* "*British Desmidieœ,*" 5.) In these unicellular Algæ the cell consists of two symmetrical halves, the boundary between which is sometimes indicated only by a line (*e.g.*, in *Closterium*), and sometimes lies hidden in an often very considerable constriction (*c.g., Euastrum, Cosmarium*). When the cell divides, these two halves of the cell separate from each other, while a new portion is developed between them, consisting of a very delicate pellicle forming a continuation of the cell-membrane, and this new portion becoming divided into two parts in the middle by a septum, the original cell is separated into two, each of which is composed of half of the original full-grown cell, and one of the very small rudiments of a second half. This second half grows until it equals the older half in size and shape, whereupon the subdivision begins again. It is doubtful whether, as Ralfs assumes, the same process occurs also in the division of the cells of the Nostochineæ, *Zygnemeœ* and many *Confervœ.*

In all cases of the division of cells in plants having a stem and leaf, and likewise in many cases among the Thallophytes, the formation of the septa is preceded by the development of as many nuclei as there are subdivisions formed in the cell. The mode of origin of these nuclei is two-fold: either they are formed anew, or an existing nucleus separates, by division, into several.

When nuclei are formed anew in a cell, masses of protoplasm, not sharply defined outside and increasing in density inwards, become accumulated at the points where the nuclei are to appear. Later on, especially by treating with iodine, we may observe in the middle of each of these masses a globular body formed of mucilaginous granular substance, more homogenous and frequently far more transparent than the surrounding protoplasm, often clearly defined externally, and almost without exception containing one or more sharply circumscribed round granules (the *nucleoli, Kernkörperchen)*; the large round bodies are called the nuclei *(zellen-kern)* or cytoblasts. The nuclei are usually smaller at their first appearance than they are afterwards, so that their growth is unmistakable. The surface of perfect nuclei appears smooth and clearly defined, but it cannot be decided with certainty whether we ought to distinguish an enveloping membrane and contents distinct from this, or to ascribe the membranous aspect of the outer layer to a somewhat greater density; the nucleoli always appear solid at first; they often become hollowed out into vesicles subsequently. The substances both of the nucleus and of the nucleolus are coloured yellow by iodine.

Observ. Opinions differ very much as to the mode in which the nucleus is formed from the granular protoplasm. Schleiden was the first to discover the import of the nucleus and to trace its development. According to his views (" *Grundzüge*," 3 *ed.* i, 208) they originate by the formation of large granules in the protoplasm (afterwards the nucleoli) and other granules becoming heaped up around these, and the whole becoming more or less blended together and united into the nucleus. According to Nägeli's views (" *Zeitschrift. f. wiss. Bot. III.* 100, *Ray Society's Publications*," 1849, p. 166), the nucleus is not formed by the union of a considerable mass at once, but appears first as a very minute structure, for the rudiments of the nuclear body may be distinguished while they are yet little larger than the globules of the protoplasm. He also assumes that the nucleolus is formed first, and then a layer of protoplasm is deposited around it, which again becomes enclosed in a gelatinous membrane not coloured by iodine; Hofmeister (" *Entwick. d. Pollens*," in "*Bot. Zeit.*" 1848. "*Die Enstehung des Embryo*," 1849, 62) declares distinctly against both these opinions. According to his researches, the formation of the nucleus is not preceded by the origin of nucleoli, but the nucleus presents itself first under the form of a globular drop of a mucilaginous fluid, which becomes coated by a membrane over its outer surface. In many cases no trace of a nucleolus can be seen in the nucleus at first, and one or more (up to twenty) are subsequently formed in it, while in other cases one or more granules of a more solid substance swim in the fluid of the nucleus from the very first, but not all of these are necessarily developed into nucleoli, for only some of them can increase considerably in size and acquire a membranous coat, the others becoming dissolved. Leaving out of the question the membrane of the nucleus and of the nucleoli, the existence of which I never could satisfy myself, this latter view appears to me the more correct; that of Nägeli decidedly wrong.

The second mode of origin of a nucleus, by division of a nucleus already existing in the parent-cell, seems to be much rarer than the new production of them, for as yet it has been observed only in few cases, in the parent-cells of the spores of *Anthoceros*, in the formation of the stomates, in the hairs of the filaments of *Tradescantia*, &c., by myself, Nägeli, and Hofmeister; but it is possible that this process prevails very widely, since, as the preceding statements shew, we know very little yet respecting the origin of nuclei. Nägeli thinks that the process is similar to that in cell-division, the membrane of the nucleus forming a partition, and the two portions separating in the form of two distinct cells. I was quite as unable to see such a membranous septum and a membrane on nuclei generally, and the division appeared to me to take place by gradual constriction. According to Hofmeister's description ("*Enstehung des Embryo,*" 7) the membrane of the nucleus dissolves, but its substance remains in the midst of the cell; a mass of granular mucilage accumulates around it; this parts, without being invested by a membrane, into two masses, and these afterwards become clothed with membranes and appear as two secondary nuclei *(tochter-kerne).*

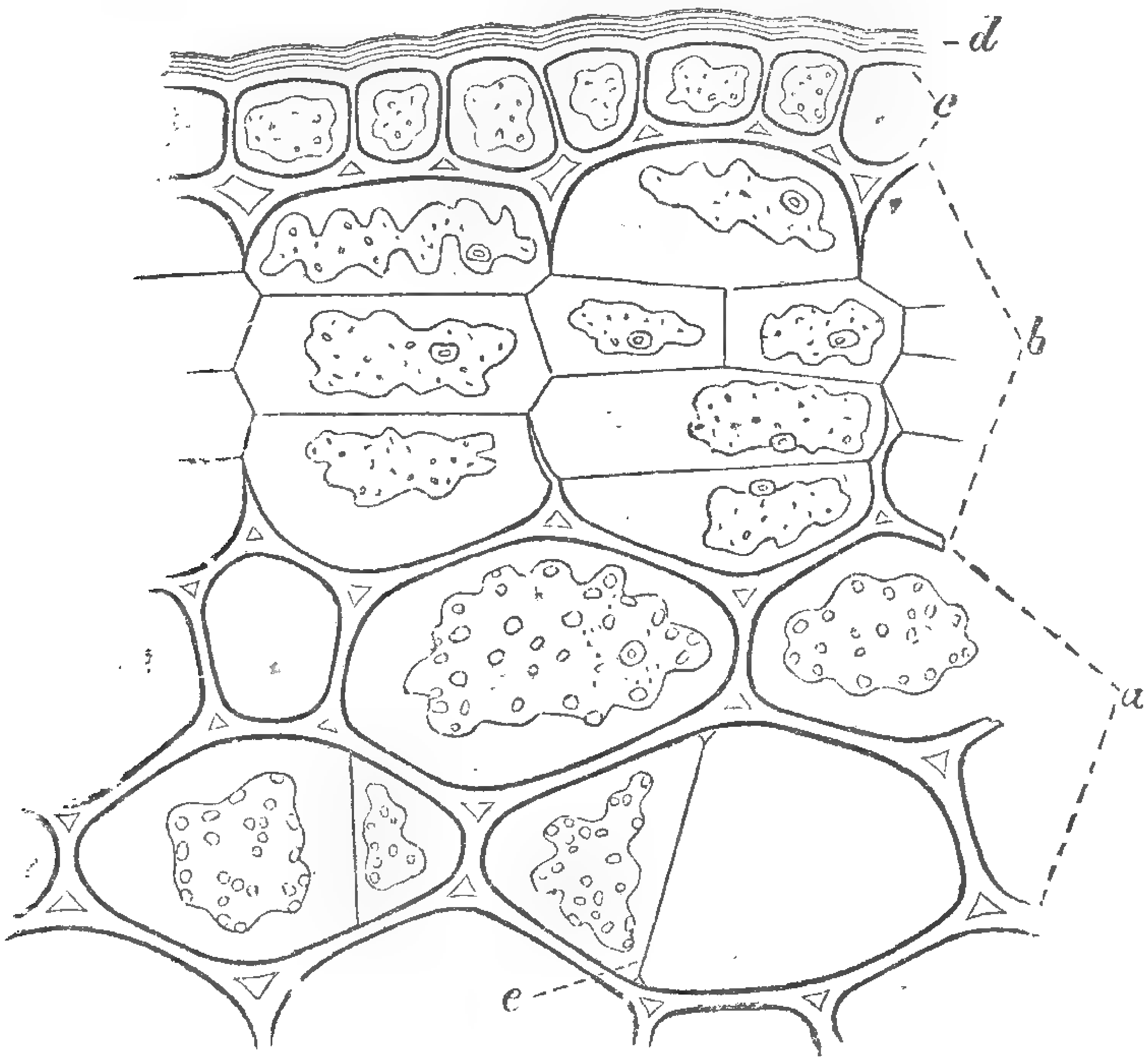
It is still an unsolved question how often the process of division of the nuclei can be repeated, whether it continues indefinitely, or whether after one or more divisions it becomes extinct, and the formation of a new nucleus becomes necessary. In the spores of *Anthoceros* I found a second division, for in the parent-cell of these a mass was formed, which first parted into two subdivisions, and then each of these divided into two nuclei. Wimmel found the same in the development of pollen-grains ("*Zur Entwickelungsgesch d. Pollens.*"—*Bot. Zeit.*, 1850, 225). In these cases, therefore, a twofold division occurred. But, according to Wimmel, the case is different in the formation of the parent-cell itself, for when one of these cells is about to divide, a new nucleus is formed in it, which becomes divided and gives rise to the development of two secondary cells. When one of these secondary cells is to be divided again, its nucleus takes no part in it but becomes absorbed, a new nucleus being formed which divides, &c., so that here each nucleus is capable only of one division.

The number of nuclei that are formed in a cell varies very much; in most cases there are two, as in the formation of parenchymatous cells in the bark and the pith, in the formation of wood-cells in the cambium; but in elongated cells, particularly in hairs which become articulated, half a dozen or more nuclei are often found lying in a row. In like manner varies the proportion of the size of the nucleus to the cavity of the cell; in the parenchymatous cells of wood, in the cells of bark, and of the suberous layer of the Dicotyledons, I found the nucleus relatively very small; but in the hairs, in the cells of very small organs still contained within the bud, as in the young leaves, in the cells of the apex of the root, in which organs the cells divide while they are still very small, the nuclei occupy a very considerable portion of the cavity of the cell.

The formation of nuclei is soon followed by that of septa between every two of the former, which is effected by the primordial utricle becoming folded inwards in the same manner as described above of *Conferva glomerata*, till a partition is formed reaching to the centre of the cell, and by the deposition of cellulose membranes on the outside of the primordial utricles during this process, which membranes form secondary layers to the parent-cell where in contact with its walls, and laminæ of a partition dividing the parent-cell where in contact at the point of junction of the two secondary cells. The number and direction of their septa depend altogether on the number and position of the nuclei, since each of these becomes the centre of a secondary cell. The secondary cells accurately fill the cavity of the parent-cell, so that there is no trace of inter-cellular passages running between them, and the entire contents of the parent-cell are taken into the cavities of the secondary cells.

Since the membrane of the secondary cells deposited during the formation of the partition is immeasurably thin, while the membrane of the parent-cell usually possesses, before the division, a perceptible, often considerable, thickness, we naturally find, on examining a cellular tissue shortly after the division of the cells (fig. 48), a very considerable difference in the thickness of the different sides of the cells composing it, for some of the walls consist of the blended membranes of the secondary cells, others of these united to the membranes of the parent-cells. This condition is in a high degree striking in the investigation of many organs in which the development has just begun, *e.g.*, in the formation of a periderm in the outer cells of the bark, where most of the newly-formed and thin septa run parallel with the epidermis; in cam-

Fig. 48.



External layers of the rind of *Cereus peruvianus.*—*a*, cells of the rind with contracted primordial utricles contracted, in part containing newly-formed septa *(e)*. *a*, Cork-cells; *b*, the outer layers of the rind-cells, newly-formed by the division of the latter; *c*, cells of the epidermis; *d*, cuticle.

bium, where the septa lie parallel with the bark; in jointed hairs, &c. When the secondary cells exhibit no more, or but very little growth, this condition of the thickness of the walls is permanent, and it is possible, when the membranes of the secondary cells have been thickened by the deposition of layers, to distinguish their membranes clearly, in their whole course, from the membrane of the parent-cell, *e.g.*, in the pith of *Taxodium distichum.* On the other hand, when, as is usually the case, the secondary cells increase much in size after their production, this condition is changed. In these cases the membrane of the parent-cell must naturally share in the expansion of the secondary cells, and become thinner in proportion to this expansion; in consequence of this the membrane of the parent-cell mostly vanishes completely from the eye, especially when the division and with it the expansion of the secondary cells is repeated.

It has already been observed that the secondary cells completely fill the cavity of the parent-cell at their first origin. Thus, no traces of intercellular passages can be found in tissues in the first stages of their development. The passages are formed subsequently by the separation of the cell-membranes at the angles of the cells, and are not, as is usually represented, the remains of free open spaces between globular cells which have been compressed together in consequence of growth. In like manner the stomatal pores are produced by the separation of two cells formed by the division of a parent-cell.

Observ. That the formation of cells in all the organs of plants (excepting the cells originating in the embryo-sac) depends upon the division of older cells, an opinion which could not, for a long time past, be opposed by any careful observer, unless he were misled by preconceived notions. Even Meyen ("*Physiologie,*" ii. 334) declares this process of cell-formation to be very general; but Unger ("*Linnæa,*" 1841, 402; "*Bot. Zeit.,*" 1844, 489), who subsequently applied to this process the term *merismatic cell-formation;* and Nägeli ("*Zeitschr. f. wiss. Bot.,*" iii. 49, 1846), who used the expression *parietal cell-formation,* more especially asserted the general occurrence of this process of formation; the former declaring to be the usual mode, the latter ascribing to it the production of all vegetative cells.

But circumstances occurring in the division of the cells were interpreted in a different way from what I have done. Meyen assumed that the cell-membrane itself became folded inwards, and in this way formed the partition, which is decidedly incorrect. Unger thought the septum to be originally simple, splitting afterwards into two lamellæ; Nägeli denied that the septum is formed gradually from without inwards, assuming that the membrane of the secondary cell is formed simultaneously all round its cavity, whence it would of course result, that the septum composed of the membranes of two contiguous secondary cells would be formed at once across through the cavity of the parent-cell.

In reference to this latter point, I, of course, readily admit that one seldom succeeds in observing the gradual development of the septum in consequence of the folding inward of the primordial utricle, but in particular cases I have seen this process most distinctly. The description given above rests chiefly on observations which I instituted upon the parent-cells of pollen-grains, and in the cells which separate from each other in the pore-cells of stomates. Mirbel ("*Recherches sur le Marchantia*") detected, in 1833, that the parent-cells of the pollen-grains divide by septa which grow from without inward; but the correctness of this statement was denied by Nägeli ("*Entwickelungsgesch. d. Pollens,*" 1849), who asserted that secondary cells (which he called special parent-cells) were formed in the interior of the parent-cells, and that the seeming septa were nothing else than the coherent walls of these cells, which were not formed in the direction from without inwards, but simultaneously all over the contents,—a view which was shared also by Hofmeister ("*Entw. d. Pollens.*"—*Bot. Zeit.* 1848, 654). That these representations are incorrect, and that the septa grow from without inwards (*see* pl. 1, fig. 8—11, which represent different stages of development of the parent-cells of the pollen-grain of *Althœa rosea*), was already stated by Unger ("*Ueb merismatisch. Zellenbildung bei der Entwick. der Pollenkörper.*"—"*Bericht. der Ver. der Naturforsch. zu Gratz.*"), and no doubt remained in my mind, since I succeeded in bursting parent-cells of pollen-grains, the septa of which were but half-formed, and pressing free the primordial utricle (pl. 1, fig. 10), which was half constricted by folds passing inwards, into four globular subdivisions connected together into a common cavity in the centre. I have elsewhere ("*Verm. Schrift.,*" 252) sought to demonstrate that in like manner in the formation of stomates, there is no production of secondary cells in the parent-cell, with an intercellular space running between them, as Nägeli states. The observations of Henfrey ("*Annals of Nat. History,*" vol. xviii, 364) are in exact accordance with mine. Of course one does not succeed in the vast majority of cases of the examination of a tissue where the cells are in course of development, in observing the gradual growth of the septa from without inwards, and when I assume that this process occurs universally, I certainly rest upon the analogy to the few cases in which I have traced their gradual development; but it seems to me more logically correct to lay the main stress upon a few accurately investigated cases, than to disregard such observations, and to use as the basis of the theory of the development of cells, the imperfect, though numerous, observations in which the gradual growing in of the septum was not seen, but the mode in which it really was formed was not perceived at all.

b. Free Cell-formation.

In free cell-formation, the cell-membrane is developed over the surface of a mass of nitrogenous substance swimming in a fluid which contains formative matter, without the co-operation of a parent-cell. In the regular course of vegetation this process of cell-formation occurs only in the interior of cells; it may occur independently of the life of the parent plant in the creation of parasitic Fungi, Yeast cells, &c., both in the decomposing fluid of cells and in the excreted or expressed juices. In normal free cell-formation the secondary cells usually possess but a very small size in comparison with the parent-cell, and stand in no connexion, or, at least, not a necessary one, with the walls of the latter.

In the Phanerogamia, free cell-formation occurs only in the embryo-sac, in which both the rudiment of the embryo (the embryonal vesicle) and the cells of the endosperm originate in this way; in the Cryptogamia it occurs only in the formation of spores in the Lichens, and some of the Algæ and Fungi.

The formation of free cells is usually preceded by the production of nuclei. In this case more or less abundant accumulation of protoplasm in the parent-cell forms the first sign of the secondary cells. This sometimes fills up the cavity of the parent-cell, *e.g.*, in the parent-cells of the spores of the Lichens, *Pezizæ*, &c., sometimes it occurs in relatively small quantity under the form of cloudy masses not sharply defined, and of currents, as is usual in the embryo-sac (pl. 1, fig. 12, *s*). In this protoplasm are formed isolated points of concentration in the form of more or less transparent nuclei, around which accumulates a variable portion of the surrounding protoplasm, originally exhibiting no decided outline, subsequently clearly defined by the formation of a primordial utricle over the surface, which is rapidly followed by the production of a cellulose membrane enclosing the whole nitrogenous contents (pl. 1, figs. 13, *b*; 14, *b*).

Observ. To Schleiden belongs the merit of discovering free cell-formation and the dependance in which the origin of a cell stands to the formation of a nucleus; but he was led by this discovery to the misconception that this was the only mode of formation of the cell occurring in nature. In accordance with this hypothesis, the cells which were formed in other cells would always be much smaller than the parent-cells, and would gradually expand until they filled up the cavity of the parent-cells, and their walls came into contact. But as the whole process could not take place in cells which contain granular structures, such as chlorophyll or starch granules, or the like, without the displacement of these structures, and yet in a cell of that kind in which division occurs, all these structures are still present after the division, Schleiden invented an hypothesis to explain the circumstance, namely, that these structures in the cavity of the parent-cell were dissolved outside the secondary cell, and formed a-new inside it. But as nothing of this process can be observed in nature, it alone suffices to refute the doctrine of the universality of free cell-formation. Even when quite recently, in consequence of Nägeli's observations, Schleiden ("*Grundz.*" 3rd ed. i. 213) can no longer deny that a division of cells does occur, still he is far from acknowledging the universal diffusion of this process, since he only refers to the older notion, retracted by Nägeli himself, that this mode of formation occurs in the Phanerogamia or in the special parent-cells of the pollen-grains, and altogether ignores the fact that Nägeli and others have shewn this to be the mode of formation of all cells except those originating in the embryo-sac; consequently, Schleiden still ascribes to free cell-formation an influence on the development of the plant which by no means belongs to it. When he states that the cells are developed in this way in the embryonal vesicle, this is decidedly false, for all recent observations agree in shewing that the embryo originates from the germinal vesicle by cell-division; not less incorrect is it, that free cell-formation may be traced in jointed hairs, and just as little does it accord with the mode of formation of other plants that, as is stated ("*Grundz.*" i. 211), cells are formed in cells, and the parent-cells absorbed, in the points of the roots and shoots of the stem of *Cypripedium.* The entire representation proves that Schleiden has never once observed the division of a cell.

The first account given by Schleiden ("*Beitr. zur Phytogenesis, Muller's Archiv.*" 1848) of the process of cell-formation, was faulty in many respects. He altogether overlooked the important circumstance that the nitrogenous substances were the originators of the formation of the nuclei and the cell, for he believed the granules of protoplasm, which he denominated mucilage (*schleim*), to be identical with the granules of gum, and thought that the protoplasm might be replaced by starch, and go through similar metamorphoses; for he expressly mentions that starch, or the granular mucilage replacing it, is present in the pollen-tubes, but those substances are soon dissolved or change into sugar or gum. In the formation of a nucleus those little mucilaginous granules were produced in the protoplasm, then a few larger granules, and soon afterwards the nuclei shewed themselves. When a cell was formed, it had at first the form of a segment of a sphere, the plane side formed by the cytoblast, the convex side by the cell-membrane. Originally the cell-membrane was soluble in water, but it soon expanded more and more, and acquired greater consistence; and its walls, with the exception of the cytoblast, which always formed part of the wall, were composed of gelatine. The cell now soon became so large that the cytoblast appeared only as a little body enclosed in the lateral wall. The cytoblast might go through the whole vital process with a cell, if it were not dissolved and absorbed in cells destined to higher development, either in its place or after it has been cast off like an useless member, in the cavity of the cell.—The whole of this account of the relation of the nucleus to the cell-membrane is incorrect. The nucleus is not connected with the cell-membrane under any circumstances, for it is enclosed, with all the rest of the contents of the cell, in the primordial utricle. Its position in the newly originating cell is, as appears to me, always central, and its form mostly globular; it does certainly often lie upon the wall of the cell subsequently, and becomes flattened. The distinction which Nägeli tries to carry out between central and parietal nuclei is not founded in nature.

In Schleiden's more recent writings the above views are partially modified. It has been recognized that the supposed gum is a nitrogenous substance, but the name mucilage (*schleim*) has been retained; and it is stated of the young cell, that in many cases, after one side of it had become elevated like a vesicle from the surface of the nucleus, a second layer is deposited upon the free side of the latter, protecting it from solution; the special statement that all cells are formed in this way is more and more extended to all organs of plants, even to the cambium-layer of the Dicotyledons ("*Anatomie der Cacteen,*" 35).

Although it is a rule, which has no exception in the normal development of the cells of all the higher plants, that nuclei make their appearance in the nitrogenous substances which give rise to the formation of a free cell, yet this is not a necessary condition, for it appears that every globular mass wholly or partly composed of proteine compounds is capable of undertaking the function of a nucleus, clothing itself with a membrane, and thus producing a cell. This state of things is of very frequent occurrence in the formation of the spores of the Algæ, where the whole contents of an entire cell, *e. g.*, in *Vaucheria*, of two copulated cells, *e. g.*, in *Zygnema*, become balled together into a globular mass, and coated by a membrane. But it is not always such large masses, composed of starch and chlorophyll granules and protoplasm, which give rise to the formation of a spore; in very many cases smaller globular masses of the green contents, produced by the union of a a few chlorophyll granules, and undoubtedly also single granules of chlorophyll, may assume this function whence Kützing called the granules lying in the cells of Algæ—*gonidia.* This occurs in the most striking manner in *Hydrodictyon*, in every cell of which the sporidia produced from chlorophyll granules arrange themselves in a net-work over the whole of the inner surface of the parent-cell, become converted into cells which grow together at their angles, and thus collectively form a new plant.

Pollen-grains and the spores of the higher Cryptogamia exhibit a peculiar mode of formation which connects the division of cells with free cell-formation. After the development of four nuclei, produced by the division of a single nucleus, accompanied simultaneously by the absorption of that nucleus which had given origin to the parent-cell, the latter becomes divided into four compartments (Nägeli's special parent-cells) by the folding inward of its primordial utricle and the gradual formation of septa (which are four or six in number, according to the relative position of the nuclei, or, it is first divided into two segments, which are again divided into two chambers (Nägeli's special parent-cells of the second degree). These secondary cells are adherent to the wall of the parent-cell wherever in contact with it, therefore up to this epoch only the common process of cell-division occurs (pl. 1, figs 8, 9, 11). But the contents of each one of these four subdivisions now become clothed by a new membrane (the inner pollen or spore-coat), which, although in accurate apposition with the membrane of the cell in the cavity of which it lies, does not adhere to it, and subsequently secretes the outer pollen- or spore-coat. The formation of this inner pollen-cell only resembles free cell-formation in the circumstance that its membrane is produced in the cavity of another cell, around a primordial utricle which contains a nucleus, without adhering to the parent-cell and forming one of its secondary layers; it is distinguished from free cell-formation by the fact that the nucleus and the primordial utricle around which the new cell-coat is produced, belonged previously to the parent-cell, and had caused the origin of this itself, and had not been newly-formed for the secondary cell.

II. THE PHYSIOLOGICAL CONDITIONS OF THE CELL.

Even as in anatomical respects the cell appears, on the one hand as an independent organism, self-contained, and following its own proper laws of formation in its development, and again, on the other hand, in the great majority of plants, does not appear isolated, but forming part of a greater whole, with which it is not merely mechanically connected, but by the influence of which its organic development is modified, so that its form, the position of its pits, &c., are dependant on the condition of the neighbouring cells,—so, in like manner, is the physiological activity of the cell, on one hand independent of, and on the other dependant on, and ruled by, the vital activity of the entire plant.

The vital functions of plants are separable into two great classes, into those of *nutrition* and those of *propagation.* Both are committed to the cells. The share which the individual cell takes in one or both of these functions varies extremely according to the degree of elevation of the organization of the plant.

In the lowest plants, whether, as in *Protococcus,* they consist of a single cell, or as in the Confervas of rows of cells united into a thread, each cell is capable of an independent existence. It absorbs fluid from the surrounding medium, respires, assimilates the absorbed substances, &c.; in short, the simple vesicle suffices for the accomplishment of all the various functions which must cooperate in the nutritive processes of the plant. The more highly organized a plant is, the more these various functions are committed to particular organs, the offices of which in this way become special and one-sided, thus being reduced to a dependance on the functions of the other organs. The function of absorption is committed to the root; that of breathing and the elaboration of the absorbed substances to the cells of the leaf, &c. With the combination of many cells into a whole, leading a common life, comes the necessity of a passage of the sap from one organ to another, a circulation of the fluids, which the simply formed plant can wholly dispense with. This movement of the sap is in great part committed to particular cells, which take but a subordinate part in the real business of nutrition.

Analogous to the more independent condition of the cell as an organ of nutrition, in proportion as the organization of a plant is simpler, the greater is its activity as an organ of propagation. In the lowest plants the same cell is an organ of vegetation in the earlier period, and an organ of fructification in the later period of its life, germinal granules *(keim-körner)* being formed in its interior. In the higher plants, on the contrary, these two functions are committed to different cells, in which case, at first, as in the

Lichens, all the organs of fructification are alike, while in the more highly developed plants a contrast between these appears, a male and female sex, the conjunction of which is necessary for the origin of a new plant.

Thus, the more complicated the structure of the entire plant becomes, the more manifold the vital phenomena of the whole display themselves, the more do we see the functions of the fundamental organs of the vegetable become restricted to an activity continually becoming more special. The question here presents itself: In what connexion does the more manifold or more special activity of the cells stand with their organization? To this question we have no answer. The organization of cells, the substances of which their membranes are composed, are so uniform throughout the whole vegetable kingdom, and all the organs of the particular plant, that as yet the connexion which must exist between the form and organization, and the function of the cell, is altogether unknown.

The function of nutrition and that of propagation form a striking contrast in all the cases in which the propagation is by spores and seeds, since the reproduction in these, through the germination of an organ furnishing a new plant, always causes the death of the organ of propagation, and in many cases of the whole plant. But there is another kind of multiplication; the propagation by buds, which depends on the common laws of growth, and has its origin in the organs of vegetation. This mode of increase is based on the peculiar growth of the plant. Leaving out of view the simplest forms of the vegetable kingdom, the plant does not consist of a fixed number of organs, developed together and attaining the full-growth at the same time, so as to form a completed whole, and to suffer a common death; but the organs of the plant are developed successively in an unlimited series; every fresh shoot has the strength of youth, and is capable, under favourable circumstances, of entering on an independent life separately from the other parts, and of growing into a new plant. When even all the parts of a plant do lead a common life, they do not collectively form *one* individual, but separate individuals growing out of each other, and blended together in consequence of their growth. It depends on the degree of organization of a plant what part we are to regard as a special individual. When an uni-cellular plant divides into two cells we must regard each cell as an individual, *e.g.*, in the Diatomeæ; in the Thallophytes, for instance in the Lichens, each lobe of the thallus can carry on an independent life when separated from the rest of the plant; in the higher plants each branch forms a repetition of the stem which grew from the seed, and a ramified plant is looked upon as a collection of as many individuals as there are branches upon it. In this manner a branched plant (when not exhausted by the production of seed) is ever young in its fresh shoots, although one part after another grows old and dies; new, active individuals sprout annually from the old ones, and there is no natural termination to the life of the whole. At the same time, the possibility is given for a plant, in consequence of this unceasing production of shoots, to become separated into an unlimited number of distinct plants, in a natural way by spontaneous, or by artificial, division. From this peculiarity of the unlimited growth of a shoot has the German language derived the expressive terms *gewächs* (a vegetable, from *wachsen* to grow).

Observ. The peculiarity of their organization, and the unlimited power of growth of plants, offer many difficulties to the definition of the duration of plants, and have given rise to many incorrect theories. Every individual cell, and every individual organ has a determinate end to its life, but the entire plant has not, since the individual shoots run through their periods of development quite independently, and only share in the weakness of age of the older organs when these are no longer able to convey to the young shoots the needful amount of nourishment, in which case the latter do not die from deficiency of vital energy, but are starved. It therefore depends wholly upon the mode of growth of a plant whether this occurs or not. When a plant possesses a thallus spreading horizontally by the growth of its circumference, it can annually extend itself into a larger circle, after the old parts in the centre have been long decayed, as is seen in old specimens of crustaceous Lichens, in the fairy rings caused by Fungi, &c. In like manner when a higher plant has a creeping stem, and possesses the power of sending out lateral roots near the vegetating points, and in this way conveys nourishment directly to the young terminal shoots, the latter are wholly independent of the death of the older parts of the stem and of the primary roots, and there exists no internal cause for death in such a plant. It is truly a different plant every new year and vegetates in a new place, but there is no definite boundary between it and its predecessors; such a plant is like a wave rolling over the surface of a sheet of water, it is every moment another, and yet always the same. Thousands of inconspicuous plants, of Mosses, Grasses, Rushes, &c., have vegetated in this manner upon peat bogs and similar localities perhaps for thousands of years. Plants with upright stems are placed in much more unfavourable circumstances. It has been declared of these also, and particularly of the Dicotyledonous trees (De Candolle, "*Physiologie Vegetate,*" ii. 984), that they have no internal cause for death, but I believe incorrectly. Examples of very old trees, such as De Candolle collected (*e. g.*, *Taxus* 3000, *Adansonia* 5000, *Taxodium* 6000 years old, &c.), only prove, naturally, that death occurs at a very late period in many plants placed in favourable circumstances, but not that it does not necessarily happen. To me there appears to exist in all trees, whether they belong to the Dicotyledons, or, like the Palms, to the Monocotyledons, an internal cause which must produce death in time—namely, the increasing difficulty of conveying the necessary quantity of nourishment to the vegetating point, resulting from the elongation of the trunk from year to year. Even when the force which carries the sap up suffices to raise it to 200 feet or more (many Palms, as *Ceroxylon andicola*, *Areca oleracea*, attain a height of 150—180 feet; some Coniferæ, *e. g.*, *Pinus Lambertii; Abies Douglasii,* of more than 200 feet), yet a maximum is reached there, and the terminal shoot is less perfectly nourished every succeeding year, becomes stunted more and more, and the tree at length dies.

Thousands of experiments have shewn that the young shoots of old trees, when used as grafts, slips, &c., furnish as strong plants as the shoots of young trees; even in the Palms *(Phœnix dactylifera)* experiment has shewn that the apex of the stem, when its vegetation begins to slacken in an old tree, grows again into a strong tree when cut off and planted in the earth. Not one single experiment speaks in favour of the opinion promulgated by Knight, that all parts of a tree have a common end to their life, and that the different trees which have been raised from one and the same tree by grafts, decay about the same time as the parent plant. A whole series of cultivated plants (I will only mention the Vine, the Hop, the Italian Poplar, and the Weeping Willow) are propagated by division, without any decreased power of vegetation ever being seen. Nothing was in greater contradiction to the laws of vegetable life, than the frequently expressed opinion, that the Potato disease of recent years was to be ascribed to a degeneration of the Potato plant, arising from the unceasing propagation by tubers.

If we are surprised at the intensity of the vegetative force of individual plants, in consequence of which it re-appears with new, unweakened energy in every bud, so must we marvel at the force committed to so simple an organ as a cell is, if we reflect what an influence it exerts upon the total economy of nature, as one of the grandest of phenomena. The plant lives almost solely upon inorganic substances; its cells are chemical laboratories in which these are combined into organic compounds. The plant prepares in this way not only the nutriment required for its own development, but also the food on which the entire animal kingdom depends. But plants not only nourish animals, they maintain the air in a fit state for their respiration, since their breathing process removes carbonic acid from the atmosphere and replaces it by oxygen gas.

In all these functions the plant is throughly dependant upon the outer world; its food is brought to it without its own co-operation, by water and air; its respiration takes place without activity of its own, through a penetration of its substance by gases with which it is in contact, in consequence of a physical law; not even does its internal circulation of juices depend on a mechanical activity of a circulating system; thus every necessity for motion is removed. It is true we here and there meet with movements in this or that organ, but these, occurring isolated in the vegetable kingdom, are also altogether of subordinate kind in the individual plant. They also are committed to the cells.

A. THE CELL AS AN ORGAN OF NUTRITION.

A. ABSORPTION OF WATERY FLUIDS.

In all plants the fluid nutriment is taken up by absorption through cells. As the cell-membrane has no orifices, only such matters as are actually dissolved, can be absorbed into the cell with the water which penetrates the cell-membrane; in like manner, in all the higher plants, a mechanical penetration of solid substances, even when suspended in water in the finest state of division, between the cells into the interior of the plant, is impossible, since the cells which form the surface of the plant are accurately fitted together, leaving no orifices between, except the stomates, which never occur upon roots or parts growing under water.

Gaseous fluids, by which the cell-walls are also readily penetrable, may in like manner be taken up by the cells situated at the surface; but they can moreover penetrate between the cells, into the interior of plants, through the stomates.

Observ. The Thallophytes possess no proper organ of absorption, but the whole of their surface is adapted for it, and when, as in many Algæ and Lichens, they have root-like processes, these are only organs of attachment and not special organs of absorption. In many Fungi and Lichens the substance of the thallus is composed of such loosely connected cells, that fluids which come in contact with them penetrate between the cells into the substance of the thallus, so that the absorption is not confined to the superficial cells here. Even in the Mosses the root does not make any considerable figure as an absorbing organ, their freely penetrable leaves being the chief agents of the absorption of water. In the higher plants absorption is committed to the root alone, since the epidermis of the leaves and the periderm of the other parts are much too difficult of penetration by water, to be capable of taking up a sufficient quantity of it. This obstruction occurs even in the root except at the young parts situated near the points. Consequently, if a plant be placed in water in such a manner that its younger roots are curved up above the surface, it dries up, while it keeps fresh when only the younger roots (not however the extreme points, known by the name of spongioles, alone) are immersed in water. The parts, however, the leaves particularly, protected against the entrance of fluid water, are readily penetrable by watery vapour, and plants can in this way appropriate water from very moist air, as is clear from the increase of weight of entire plants or cut twigs; this explains the great use of dew to the vegetation of dry, hot regions.

It has long been decided, that solid substances, insoluble in water, no matter how finely they are powdered, *e. g.*, the charcoal of gunpowder, cannot pass into plants; but this may be doubtful of the colouring matter of Phytolacca, of decoction of log-wood, of infusion of saffron, &c., since many observers, *e. g.*, De Candolle, have seen such colouring matters pass into living plants. But all accurate observations indicate that this does not happen in uninjured roots, but only occurs when the coloured fluid comes in contact with wounds of the plants.

Since the discovery of endosmose, most vegetable physiologists have assumed it as an axiom that the absorption by cells depends wholly and solely upon the laws of endosmose, none of the peculiar forces of the living cell co-operating. All the conditions to bring about strong endosmose do really exist in the living vegetable cell, namely, a membrane freely penetrable by watery fluids; on the one side of this the cell-sap which contains proteine substances, dextrine, sugar, &c., in solution, on the other side the water occurring in nature, in the state of an extremely diluted saline solution. This renders it readily explicable how cells which are laid in water swell up rapidly, in many cases, if they contain a concentrated protoplasm and have not firm walls (*e. g.*, many pollen-grains), the powerful absorption of water causing them to burst; and how, on the other hand, if they are laid in a strong solution of sugar, gum, &c., they become emptied and collapse. Under these circumstances, the assumption that the absorption of the cells will be regulated by the laws of endosmose, is fully justified, yet special proofs of this can only be partially advanced, because on one side the phenomena of absorption are too little known in many respects, and on the other side the theory of endosmose is not yet perfect enough to allow of our making out in all cases the share it has in any given phenomenon.

According to the researches of Th. de Saussure ("*Recherch. chim. sur la Veget.*" 274), healthy and diseased roots behave very differently in reference to absorption, the latter taking up the substances dissolved in the water in far greater quantity than the healthy roots; the action of a poisonous substance (sulphate of copper) had the same result as disease of the roots, for it was not only taken up in relatively very much greater quantity, but also caused the absorption of other substances which were placed with it for absorption by the roots, in larger proportion than occurred in healthy roots. This condition alone would excite great doubts of the opinion of many physiologists, *e. g.*, of Treviranus, that the absorption is an expression of vital force, since it involves the contradiction that weakening and destruction of life are combined with an exaltation of an activity dependant on it; while it would not be at all striking for changes to occur in a diseased or dead cell, which would cause an alteration in the physical character of the cell and of the phenomena standing in connexion with it. If the roots are healthy, they take up different substances in very different quantity from solutions of like degree of concentration (Saussure experimented with solutions containing twelve grains of foreign matter in forty cubic inches of water), and they separate the fluid into a dilute solution which they absorb, and a more concentrated which they leave behind.

Observ. The distinctions which occur in solutions of different substances, are very considerable. Saussure in each case allowed half the solution to be absorbed, therefore fifty parts of the dissolved substance should have been absorbed, instead of which *Polygonum Persicaria* absorbed of,—

Chloride of Potassum	14·7	parts
„ Sodium	13	„
Nitrate of Lime	4	„
Sulphate of Lime	14·4	„
Chloride of Ammonium	12	„
Acetate of Lime	8	„
Sulphate of Copper	47	„
Gum	9	„
Sugar	29	„
Humous Extractive	5	„

Saussure tried to explain these differences in the absorption from physical differences in the solutions, especially by the assumption that the quantity of substance absorbed, depended on the greater or less degree of viscidity which it imparted to the water by its solution. He regarded, namely, the cell-membrane as a very fine filter, through which not only would a denser solution penetrate more slowly, but which was also capable of separating the solution into a more concentrated and a more diluted one. This explanation is certainly not sufficient, since we have no proof that the finest filter can effect such a separation of a fluid; and secondly, Trinchinetti found that the quantity of substances taken up by roots did not run parallel with the viscidity of their solutions. But there is nothing in the result of these experiments which would be in opposition to the laws of endosmose, in particular the separation into a thinner and a denser fluid stand in agreement with these, since many observations (of Jerichau, Brücke) have shewn, that in endosmose the fluid does not necessarily penetrate the septum *in toto*, but that in many cases a dilute fluid or merely water goes through. We are certainly not in a condition to state at present how one salt passes over in this, another in that, quantity; to do this it would be necessary to know the contents of the vegetable cells and the relation in which they stand to the cell-membrane and to the different solutions; but no contradiction exists between the phenomena referred to and endosmose. Formerly it might have been concluded from the different behaviour of diseased and healthy roots, that absorption was not a true physical process, but that the force of the living plant was to be considered in reference to it; but not to speak of the above-noticed contradiction that a vital act would be exalted in a dead cell, there occur in the disease and death of a cell, two alterations which cannot be without influence on the endosmose. In the first place the living cell exhibits a certain tension, which is lost in the dead cell; in the second place the primordial utricle is very readily detached from the inside of the cell-wall in diseased or dead cells; these two circumstances place the cell-wall in a condition essentially different from the normal one, and we may readily conceive that the endosmotic force of the cell-wall becomes essentially different, and that the dead cell-membrane is penetrated much more easily and quickly than the wall of the living cell. There are frequent opportunities of observing the more easy penetration of a diseased or dead cell, in microscopic investigations where tincture of iodine is applied; for, in the *Confervæ*, for example, where several cells lie near together, some healthy, others diseased, the latter are very much more quickly penetrated by the tincture of iodine.

An important question in absorption is this: are the different substances absorbed by different plants in equal relative quantity, or does one plant take up one substance, another a second in greater abundance? Saussure, who thought the latter condition not improbable, could not find any confirmation of it in his experiments, for the variations which he found in the absorption of different substances by different plants, were not more considerable than the variations which occurred in different experiments with the same plant. Trinchinetti *(Sulla facoltà assorbente delle radici)* made experiments on this question, by placing different species of plants in mixtures of two salts which do not decompose one another, whereby he shewed that certainly one plant absorbed one, another plant the other salt, in preference, from a mixture of nitrate of potass and common salt. Thus *Mercurialis annua* and *Chenopodium viride* absorbed much nitre and little salt, while *Satureia hortensis* and *Solanum Lycospersicum* took up much salt and little nitre, and from a mixture of sal-ammoniac and salt *Mercurialis* absorbed more sal-ammoniac, while *Vicia Faba* took more salt.

If, however, as there is every appearance, the result obtained by Trinchinetti be correct, we can by no means deduce from it the conclusion that the plant possesses the power of absorbing substances useful to it and excluding those which are injurious, for experience has amply demonstrated that it does not possess this latter power, that it can even, as Saussure's experiments with sulphate of copper shew, absorb injurious substances more easily than those which it applies to its nutrition, and we must assume that the cause of the differences in question is to be sought in the physical and chemical peculiarities of the particular substances, and their relation to the cell-membrane and the cell-contents.

Observ. It is a known fact that different species of plants which grow side by side in the same soil, to the roots of which the same nutriment is conveyed, shew by analysis of their ashes a very different composition of fixed constituents derived from the soil. This circumstance may be explained in two ways; either through the assumption that different species of plants take up different constituents in unequal quantity from the same solution, for which the experiments of Trinchinetti above-mentioned furnish positive evidence, or through the hypothesis defended by Liebig, that different plants take up equally, like a sponge, all that is dissolved in water, but again reject all superfluous or injurious substances. The first must be regarded as by far the more probable in the present state of our knowledge, since the second hypothesis, which is based upon Macaire-Princep's experiments, presently to be mentioned, that substances unfit for the plant can be again excreted by the roots, has not been confirmed by later researches. It is certainly not to be denied that plants possess in the fall of the leaves a means of removing a part of the substances taken up by their roots, but this means can only act in perennial plants, and not in annuals.

Since the roots undoubtedly possess the power of separating a saline solution into a dilute and a concentrated, and absorbing the thinner ; and since, according to Trinchinetti's experiments, certain plants absorb particular salts only in very small quantity, the question arises whether, in particular cases, the plants are in a condition to take up from a solution water alone, with the total exclusion of the dissolved substance. We have no definite experience on this point, but such a thing is not improbable. I may mention here that formation of Fungi has been observed even in arsenical solutions, for arsenic is a substance so hostile to vegetable life, that it can scarcely be supposed that any plant could maintain its existence when it contained arsenic in its sap. It was also observed by Vogel (Erdman and Marchand. "*Journ.*," Bd. 25, 209), that *Cereus variabilis* had taken up no copper after having been watered for ten weeks with solution of sulphate of copper, that the copper penetrated just as little into the leaves of *Stratiotes aloides,* and that *Chara vulgaris* vegetated for three weeks in a solution of sulphate of copper without taking up this metal.

If the experiments mentioned in the foregoing cannot be explained in every single detail through the laws of endosmose, yet there is a great probability that this will be possible in time. We must not forget, in considering this absorption, that in the majority of plants we have to do with an apparatus in which the laws of endosmose cannot display themselves clearly. These can only be seen undisturbed where no other force is acting upon the two fluids separated by a partition. But only the comparatively few plants growing totally under water occur in this condition, while the physical conditions in which the great majority of plants are placed, must give rise to important modifications in those of their phenomena depending upon endosmose. Since the leaves have a large surface with a comparatively small mass, and are provided with numerous stomates on the under side, they are fitted to evaporate a great quantity of water. This does occur in a surprising degree when external circumstances do not repress the formation of vapour; thus, for example, in Hales' experiments, a sun-flower 3½ feet high lost on an average a pound and four ounces of water daily in this way, the loss rising to a pound and fourteen ounces on a warm and dry day, from which Hales reckoned that in comparison of the surfaces, the evaporation was some three times as strong in this plant as in man, and in comparison of volume seventeen times as strong. So considerable a loss of water cannot remain without re-action upon the absorption of the root-cells. For since the sap in the cells of the leaves becomes so much more concentrated through the loss of water, their power of inducing endosmose will increase in proportion, they replace the water taken from them, from the cells of the stem, and so this action is continued through the whole tissue of the plant down to the roots, which strive to absorb water from without, in the same proportion as it is evaporated from the leaves. A proof that the evaporation of the leaf actually increases the absorption, is again furnished by the experiments of Hales, according to which the quantity of water that a shoot absorbs is in direct proportion to the number of its leaves, and the quantity of water absorbed sinks to one half when half the leaves are cut off the shoot; the experience also speaks in favour of it, that during winter the root of a plant standing in the open air, for instance, a vine or a hazel bush, begins to absorb if one of its shoots is introduced into a hot-house, and the unfolding of its leaves caused by the action of heat. Liebig ("*Researches on the Movement of the Juices in the Animal Organism.*" *Untersuch. über Saftbewegung, &c.*, 68) has also shewn the influence which is exerted by evaporation at one point even in apparatus artificially contrived, and which, when it is assisted by the pressure of the atmosphere, is capable of causing the fluid to flow through the membrane against the laws of endosmose. In plants, this influence not only suffices to increase the absorption, and cause it to commence under circumstances in which it did not otherwise occur, but is even powerful enough in plants which have been poisoned, to carry the poisoned fluid in great abundance upward through the already dead lower part of the plant.

Observ. I here refer to experiments which I have made both on Firs and Dicotyledonous trees in regard to the absorption of pyrolignite of iron, the diffusion of which through the plant is readily perceived by the dark colour. Young trees sawn off and placed with the cut surface in the fluid, became filled with it, when they had white wood like the Birch, in all their parts from below upwards, and continued to convey the fluid upwards in this way through the lower part of the stem, after all their cells were saturated with it and their cell-membranes were infiltrated with it through their entire thickness: under which circumstances we can certainly not imagine them to have retained a remnant of vitality.

a. Diffusion of the Sap in the Plant.

The mode in which the fluid taken up by the cells situated at the surface of the rind of the root becomes diffused in the plant, is a subject which lies in far deeper obscurity than the absorption of the cells in contact with watery nutriment. In the lower plants which are composed of single cells, as *Protococcus*, there can be no movement of the sap, and even in such as are composed of simple rows of cells, like the Confervas, each cell seems to elaborate independently the nutriment it takes up. In the Lichens we have already an indication in the different structure, and especially in the green colour of the internal layer, that here, where indeed no distinct organs exist, the different layers of the thallus are endowed with unlike physiological functions; we can scarcely imagine this without an exchange of the juices of the different layers, without a movement of the sap; but we are wholly ignorant of all that relates to this. The case is different with the Phanerogamia, in which the different processes connected with the nutrition are committed to different organs; here we at least know somewhat more accurately the course which the sap describes, at all events in the Dicotyledons.

A few simple experiments leave no doubt about this. The watery fluids are, as we have seen, absorbed by the cells lying at the surface of the rind of the root, they flow no further, however, in the rind, but pass into the wood, even in the small roots, and ascend in this through the stem and branches. The proof of this is furnished by two facts: if the bark of a plant, best of a tree, is cut through in a ring down to the wood, there is no interruption of the flow of sap to parts situated above the wound; but if the wood is cut through, the greatest care being taken to avoid injuring the bark, that portion of the plant above the wound dries up at once. From the wood of the stem and branches the sap flows onwards into the leaves, and in these into their parenchymatous tissues, as is proved by the powerful expiration of water vapour from them. Before the sap has reached the leaves it is incapable of being applied to the nutrition; consequently, the vegetation of a plant comes to a stand still when it is deprived of its leaves. The sap ascending from the root to the leaves is thence termed the crude sap. It undergoes a chemical change in the leaves, rendering it fit to be applied to the nutrition of the plant. To this end the sap flows backwards from the leaves through the bark, to the lower parts, as the following circumstances testify. If the bark is cut off the stem in a ring, the growth of that portion of the plant below the wound stands as it were still, the stem becomes no thicker, in the Potato plant no tubers are produced, &c.; but on the other hand, the growth above the wound is increased beyond the usual measure, very thick layers of wood are deposited, more fruit is perfected, these ripen sooner, &c. The deposition of starch which occurs in the cells of the medullary rays in Autumn, goes to prove that the portion of assimilated sap which is not used for nutrition on the way to the root, runs back to the wood through these horizontal medullary rays, and thus the sap describes a kind of circle, not, indeed, in determinate vessels, but in a definite path leading through the different parts of the plant.

Observ. It is difficult to conceive how in recent times the results of these experiments (for the details of which reference should be made especially to Duhamel's "*Physique des arbres*" and Cotta's "*Naturbeobachtungen üb. d. Bewegung des Saftes,*") could have been questioned, and the existence of the descending current of sap in the bark denied. Certainly it is no improvement on the theory cast aside, when the increased growth above the annular wound is explained by artificial interruption of the upward current of crude sap, in consequence of which the sap contained in the upper part of the plant, must soon become greatly concentrated and potential for development (Schleiden, "*Grundz.*" 2nd ed. II. 513). When we can succeed in fattening an animal by depriving it of a portion of its accustomed food, this explanation may be received as satisfactory.

Mulder also ("*Physiolog. Chem.*") denies that there exists a downward current of the sap, although he does not call in question the fact that the nutrient matters formed in the leaves do descend. That is to say, he assumes that the substances which the sap carries upwards are exchanged, according to the laws of endosmose acting in the ascending sap, with those substances which are elaborated in the leaves. If this were the case, the latter nutrient matters must descend in the same course and through the very cells in which the sap ascends, *i. e.*, through the wood; the above-mentioned experiments demonstrate that they certainly do not, but remain in the upper parts of the plant when this path is freely open to them.

The different layers of the wood do not convey the sap in equal quantity; the outermost, youngest layers, and in stems not more than two years old also the medullary sheath, principally preside over the conveyance of the sap. The older a tree becomes, and the harder the wood it possesses, the less share do the older layers take in the conveyance of sap; hence, trees with hard wood, like the Oak, where the sap wood exists in a circle round the stem, dry rapidly; while in trees with soft wood, like the Birch, the central layers of wood still carry sap, even in thick trunks.

When the question arises as to which elementary organs the sap ascends in, and by what force it is lifted upwards, we arrive at a region wherein all is still obscure, but in which so many the more hypotheses have been ventured.

In the first place, two views stand diametrically opposed to each other; according to one, the conveyance of the sap is committed to the vessels; according to the other, these carry air, and the sap flows in the cellular tissue. The adherents of the first opinion (to which belonged Malpighi, Duhamel, Treviranus, Link) chiefly depended upon the circumstance that when cut plants were placed in coloured fluids, these became diffused through all parts of the vascular system, a conclusion which, while referring to processes occurring in healthy plants, takes its stand on plants placed in most unnatural circumstances, and is now not considered valid by any one. In like manner, no great weight can be laid upon the phenomenon of the sap flowing from the cut vessels when trees such as the Birch, Maple, Vine, &c., are wounded in Spring; since these plants are in such different conditions before the unfolding of their leaves and in later periods of their vegetation, that a conclusion from one to the other must be regarded as inadmissible. More important to the theory of the conveyance of the sap are the experiments of Link ("*Ann. de sc. natur. XXIII.*" 144—"*Vorles üb. Kräuterkunde,*" i, 116), according to which, plants which have been watered for some days with a solution of ferro cyanide of potassium, and afterwards with a solution of sulphate of iron, had prussian blue precipitated in the vessels and not in the wood-cells. If this result proved constant, the experiment must be acknowledged as a conclusive evidence for the conveyance of the sap by the vessels, but although these experiments were confirmed by Rominger (" *Bot. Zeit.*" 1843, 177), and also have been made repeatedly by myself with the same results in many other cases, with Hoffman (*"üb. de Organe d. Saftbewegung,"—Bot. Zeit.* 1850 ; *Scient. Memoirs, Series 2, Vol. I.*), they furnished diametrically opposite results, without our being able at present to determine with certainty the cause of the difference, which possibly may have depended on accidental injuries in the plant where the saline solutions penetrated into the vessels.

The defenders of the idea that the vessels carry air, as the chief of whom in recent times Schleiden is to be named (" *Grundz,*" 2nd ed. II. 505), stand simply upon microscopic investigations, since in these air is always found in the vessels. This statement, special exceptions excluded, is undoubtedly correct.

In the first place, in regard to these exceptions, our woody plants furnish them during the time preceding the unfolding of the leaves in Spring. During the winter a portion of the cells of the wood are filled with sap, the vascular system with air. During the rising temperature of Spring the cells become gradually fuller and fuller of sap, and this subsequently enters the vessels also ; now the sap flows freely from wounds in the wood, which is not the case so long as this is contained in the cells alone; afterwards, when the unfolding of the leaves increases very much the evaporation of the plant, the wood is again partially emptied of its sap, and air re-enters more particularly into the vessels. This condition of a special fulness of sap, in which the vessels also convey it, seems to be a constant condition in certain tropical climbing plants, especially in *Phytocrene* and certain species of *Cissus* (*see* Gaudichaud, " *Observ. sur l'Ascension de la sève dans uns Liane;"—Ann. des. sc. nat.* 2nd ser. VI. 138—Poiteau, " *Sur la Liane des Voyageurs;"—Ann. des. sc. nat.* VII. 233). The sap is exposed to a more or less considerable pressure in the vessels, so that it mostly flows with force out of a wound ; the force with which this takes place was first determined by Hales, in his celebrated experiments on the Vine, which afterwards were fully confirmed by other experiments, more particularly by those of Brücke (" *Pogg Ann.*" 1844, No. 10). Hales found that the presence of the sap flowing out under favourable circumstances balanced a column of mercury twenty-six inches high. In the observations made by Gaudichaud on *Cissus hydrophora,* and by Poiteau on an unknown *Cissus,* the sap did not flow free from either the upper or lower piece of the cut stem, but only out of pieces of stem which were separated completely from the parent plants, so as to present two open ends ; here evidently the vessels were not over-filled with sap, and this was retained in the cut plant by the pressure of the atmosphere.

If we take into consideration that the vessels, save in the said exceptions, convey air, that in the Vine and other woody plants, before the bleeding begins, the cells are filled with sap, which is only afterwards taken up by the vessels, that after the unfolding of the leaves and the great evaporation resulting from this, the vessels are again emptied of sap, we cannot doubt that the cellular tissue of the plant is the primary and principal system to which the conveyance of the sap is committed, and that the vessels take part in the function only under special circumstances, when the plant is temporarily overfilled with sap, or in some very succulent plants perhaps throughout the whole period of vegetation.

All parts of the plant do not play an equally active part in the conveyance of the sap, for many experiments go to shew that the organs situated at the two ends of the plant are especially active at least in the ascent of the sap, the root fibres on the one hand driving sap upwards, and on the other hand the leaves attracting it.

That the ascent of the sap in Spring, before the unfolding of the leaves, is chiefly caused by the roots driving the sap upwards, might be partly deduced from the fact, that the force with which the sap flows from a wound in the stem of the Vine, is dependant on the temperature in which its roots are placed (Dassen, "*Froriep's Neuen Notizen,*" B. 39, p. 129), partly also from the fact that the sap does not flow merely from the cut stem of a bleeding Vine, but the same phenomenon is displayed in the roots down to their most slender ramifications. But that in many leafy plants, in which the attraction of the sap by the leaves is active as a second cause of the motion of the sap, the impulse exercised by the roots upon the mass of the sap is also frequently necessary, for the conveyance of a sufficient quantity of sap to the leaves, follows from the experiments of Dassen, according to which, in *Nymphæa alba* and other plants, the leaves dry up, when they, or the stems to which they belong, are placed with their cut surfaces in water, but they remain fresh, under similar surrounding conditions, when the fibrils of the roots are uninjured. Yet that the leaves, even when only a comparatively small number of them are left at the top of a plant, are in a condition to lift fluids to a very considerable height in the stem, independently of the influence of the root, follows from the experiments made by Boucherie ("*Compt. rendus,*" 1840, ii. 894) upon trees, in which a solution of pyrolignite of iron was applied to the lower ends of the sawn-off stems.

Observations on bleeding woody plants, especially on the Vine, prove that the activity of the roots is capable of causing the sap not only to ascend in the cells of the stem, but also to enter into the vessels. In like manner the activity of the leaves causes fluids, in which the open orifices of a cut stem dip, to ascend in its vessels.

At first sight it seems very easy to give an explanation of the ascent of the sap, both before the opening of the buds at the recommencement of vegetation, as well as during the period in which the plants are clothed with leaves. During the period of the rest of vegetation, the cells of a perennial plant are filled with a great quantity of organic compounds, under the form of proteine substances, sugar, gum, and more particularly of starch, which latter is converted into sugar at the re-commencement of vegetation. In consequence of this, the cell-sap becomes capable of setting up a powerful endosmose, and nothing seems more natural than that the cells of the roots should absorb the water which exists around them, and that the sap diluted by this should be taken up by the cells above, and so be carried gradually upwards from one cell to another, whence the notion that endosmose is the sole and sufficient cause of the motion of the sap, counts many adherents even in recent times. But on closer examination the matter appears less simple than it seemed at the first glance. The organic compounds, especially the starch, are not, for the most part, contained in the elongated cells of the wood, in which the sap ascends, but more particularly in the cells of the medullary rays and in those of the rind of the root, while in those Monocotyledons, which, like the Palms, lay up a store of sugar, gum, starch, &c., before the time of flowering, these substances are deposited in the parenchymatous cells of the stem. Thus the substances which cause the setting up of the endosmose, occur in cells which do not preside over the conveyance of the sap, while in the elongated cells of the wood, substances which would cause endosmose exist only in inconsiderable quantity, and in the vessels not at all. How then does the sap reach the wood-cells and vessels, and how is its motion imparted to it? I consider these questions as unsolved at present.

Brücke (l. c. 204) has indeed promised to demonstrate that this process depends on the laws of endosmose, that the parenchymatous cells first become densely filled with water by the help of the soluble and expansible substances contained within them, and then since they continually attract water, pour out that which they cannot make room for in their cavities, with a portion of the soluble substances, as sap, into the neighbouring vessels; but Brücke has not yet furnished the demonstration of this. But even if we would assume such an excretion from the cells causing the endosmose, to be founded on the laws of that phenomenon, it still would remain unexplained why this emptying of the parenchymatous cells does not take place by the most direct path, into the intercellular passages running between them, but into the wood-cells and vessels.

The influence which the leaves exert upon the ascent of the sap, is connected with the strong evaporation; this not only causes the sap within them to become more concentrated and thus more capable of attracting to itself, through endosmose, the sap contained in the cells of the stem (a property which the sap contained in the leaves acquires the more since its organic, especially gummy, compounds are formed out of inorganic substances), but, as Liebig has shewn, the evaporation from the superficial cells causes the flow of sap towards them by itself, and independently of the endosmose they exert. The ascent of the sap through the cells of the stem to the leaves is indeed explicable in this way; but in what way does the activity of the leaves cause fluids in which the open ends of the vessels of a cut stem dip, to be absorbed by the vessels and conveyed upwards in them? That endosmose has no share in this is self-evident, for all the conditions to induce it are wanting. Equally insufficient is the explanation given by L. W. Th. Bischoff (*"De verâ vasor. spiral. natur. et funct."* 62). According to his view, the air contained in the vessels is absorbed by the sap of the cells in the different parts of the plant, and used for the chemical transformation of their contents, consequently a fluid which is in contact with the open mouths of vessels must be driven into them by the pressure of the atmosphere. Were this correct, a shoot of which the end was cut off and its vessels thereby opened at their upper extremities, or a tree from which many branches have been cut off, so that the vessels are in communication with the external air in many places, could not absorb fluid into these vessels.

But in the ascent of the sap there occurs another phenomenon, which cannot be explained by the endosmose exercised by the cells; namely, the endeavour of the plant to carry up the sap more especially in a perpendicular direction. It is a well-known phenomenon that the bud which stands upon the end of a shoot receives the most sap; that it grows out into a stronger shoot than those situated lower down; that of two shoots of which one is brought into a vertical position, the other bent sideways or downwards, the growth of the former is favoured, and that of the other interfered with. The endosmotic force of its cells cannot be altered by this change of position, and yet the strength of the current of sap going to the shoot is altered.

All these explanations of the movement of the sap bear reference only to its ascent, not one of them applies at all to the descent of the elaborated nutrient sap. If the bark and the cambium layer attract the nutrient matter from the leaves because their cells contain a more concentrated sap than the cells of the leaves, it is not evident why they cannot draw the sap directly from the root and the wood, instead of by the long circuit through the leaves, and why the bark is wholly incapable of carrying sap upwards.

Gathering all these circumstances together it seems to me to follow from them, that the discovery of endosmose has not solved the problem which lies in the movement of the sap of plants, that in all probability it really does play an important, perhaps the principal, part in the absorption and carrying onward of the sap; but that as yet we have no definite experiments to enable us to determine accurately the share in the phenomenon which is to be ascribed to this force, and that a series of phenomena exist which are at all events at present inexplicable by endosmose.

c. Nutrient Matters.

The question, what substances serve for the food of plants, includes a two-fold one: 1, What elementary materials are made use of by the plant in the formation of its substance? and 2, What are the combinations in which those elementary materials are taken up by plants?

The number of elementary substances which occur in plants constantly, and, therefore, must be looked upon as necessary constituents, is very inconsiderable, viz.: 1, Oxygen; 2, Carbon; 3, Hydrogen; 4, Nitrogen; 5, Sulphur; 6, Phosphorus; 7, Chlorine; 8, Iodine; 9, Bromine; 10, Fluorine; 11, Potassium; 12, Sodium; 13, Calcium; 14, Magnesium; 15, Aluminium; 16, Silicium; 17 Iron; 18, Manganese.

Observ. These eighteen elements are not all combined in any one plant, for not only can one be substituted for another, which is chemically nearly allied, *e. g.*, potassium for sodium, magnesium for calcium, &c., but also particular of them, such as iodine and bromine occur only in certain plants, of which they certainly appear to be necessary constituents. Under these circumstances, these eighteen elementary substances are not all of equal importance; we must evidently lay the greatest weight upon those which occur in all plants, since these are to be regarded as the absolutely necessary constituents. In this respect the first four mentioned stand highest, since the principal mass of vegetable substance is composed of them, the first three furnish the material for the formation of cell-membrane, and nitrogen is a principal constituent of the proteine substances; sulphur and phosphorus, although contained in inconsiderable quantity in plants, play a most important part, since they in like manner appear to be necessary constituents for the formation of particular proteine compounds. It is different with the radicles of the alkalies and earths, for not only may one basic body be replaced by another in many cases, but even a substitution of ammonia for a fixed base is perhaps often possible. At all events, the latter appears to have been the case in certain Mould Fungi in which Mulder found no fixed basic substance; but yet in any case this condition must be regarded as a great exception, since alkalies and earths, and indeed particular earths, are necessary to the well-being of all other plants. The universally distributed chlorine is a necessary constituent of certain plants, while iodine and bromine play in general a very subordinate part. Silicium, iron, and manganese are very generally diffused, but in respect to their importance to the life of plants very little is known.

The questions, whether plants must take up from without the elementary substances which analysis discovers in them, or whether they have the power of transforming the elements one into another, to live upon pure water, &c., are no longer worth discussion in these days. Whether it be thought probable or not, that the elements of modern chemistry are actually elementary substances, it has been placed beyond doubt, from Saussure's researches onwards through all accurate subsequent observations, that no other substances occur in plants besides those which they take up from without (*see*, especially, Wiegmann and Polstorff "*Ueber d. anorgan. Bestandth. d. Pflanzen*").

Of all the elementary substances which enter into plants, oxygen is the only one that is taken up in a pure condition; plants can only appropriate the others out of chemical compounds, which they for the most part decompose. Here at once arises the question, whether the elementary substances when they are to serve as food for plants, must be already combined into organic compounds, or whether plants possess the power of feeding upon inorganic compounds? On no question of vegetable physiology has so active a strife existed as on this, especially since Liebig ("*Chemistry applied to Agriculture and Physiology*") appeared as a defender of one of the extreme answers to it.

No universally valid answer can be given to this question. It is beyond any doubt, that plants, if not as a whole, yet in an overwhelming majority, possess the power of forming organic out of inorganic substances, and that inorganic substances mostly play the principal part in the nutrition. This is evident, both from observations made on a large scale in free nature, and in small artificial experiments. It is a perfectly universal experience, repeated in the same manner in the primæval forests of the tropics, on the peat bogs, meadows, and heaths of temperate regions, and on the rocky soil of the Alps, that where the vegetation is left to itself upon a particular soil, and its products are not removed from the ground, masses of decaying organic substances are formed, in consequence of the death of the plants, accumulating from year to year, which can of course only be the case through each generation of plants producing a greater quantity of organic substances than it consumes. In a similar way, when an estate is cultivated on proper principles, a certain amount of organic substance is taken away, in the form of grain, cattle, &c., having its origin in the plants grown upon the estate, without the necessity of adding organic matters from elsewhere, and without diminishing the fruitfulness of the soil.

The experiments of Saussure also, which are above all to be depended on in questions relating to the nutrition of plants, shewed that plants which he grew with water, in a closed space, in an atmosphere rich in carbonic acid, increased their organic substance. He calculated in a manner which does not indeed admit of exactness, but still of an approximation to the true condition, that a plant which stands in a fruitful garden soil, cannot owe more than 1-20th of its weight to the absorption of organic substances (*"Recherches,"* 268). An abundance of experiments which have been made by the greatest variety of observers, have shewn that plants grown in sand which has been heated to redness, in metallic oxides, &c., all organic substances being excluded, exhibit growth, stunted though it be, and in many cases form flowers and fruit. It is not requisite to demonstrate more minutely how these circumstances shew the total error of the view, supported, indeed, less by vegetable physiologists than by agriculturists and foresters, that plants subsist solely on the mouldering remains of former plants and animals.

But on the other hand, it is not yet proved, 1, that all plants possess the power of living upon inorganic substances, and 2, that the inorganic substances are the sole food of plants; that the organic substances of humous only furnish a contribution to the food of plants, in so far as they are separated into inorganic substances by decomposition. This theory which, set up by Ingenhouss, has found its most active supporter of late years in Liebig, must in its one-sidedness be rejected in just the same way as the opposite.

In the first place, it is opposed by the no small number of parasitic plants, which are capable of using for food the sap of living plants, and indeed, in very many cases, only the sap of a particular one, or at all events of very nearly allied plants. A very large portion of the parasites (the Loranthaceæ) agree with common plants fully in their habit, colour, &c., another portion consist, on the contrary, of leafless plants not of a green colour, which bear the same relation to the plants which feed them, as the flowers and fruit of other plants do to their vegetative organs.

In the second place, there exists a very large number of plants, which in part resemble parasites in their exterior and in the want of the green colour, in part possess the usual aspect, and which derive their nourishment only from vegetable or animal substances in a state of decomposition. To these belong, besides the numerous class of the Fungi, many Orchideæ, bog-plants, &c.

Thirdly, the majority of other plants exhibit a stunted growth when raised in soil totally deprived of organic substances. In this respect, however, as the experience of agriculturists and foresters has proved, different plants manifest extraordinarily different necessities. While one plant, such as the fir, buckwheat, *Spergula, Sarothamus, Erica*, &c., flourish in a soil which contains only traces of organic substances, others, like the Cereals, require for their vigorous growth, a more or less abundant admixture of mouldering substances with the earth.

These circumstances indicate that different plants have a different behaviour in regard to their nutrition; that in some the power of living upon inorganic substances prevails, while others require a mixed food, and, finally, to the parasites are assigned solely the still undecomposed saps elaborated by other plants.

Observ. From such experiments made in the rough, of course no accurate scientific result can be deduced, these can be derived only from experiments carefully made upon a small scale. We are by no means without experiments on a small scale of this sort, but unfortunately most of them have been made in a manner which renders them incapable of furnishing any useful result. To these belong all earlier attempts to grow plants with distilled water, or water containing carbonic acid, in sand, pieces of marble, &c., in which plants of course would not flourish, but from which no conclusion can be drawn, since not merely the organic matters, but all the earths, salts, &c., which they required, were withdrawn from the plants. In order that these experiments should furnish any certain result, they would require to be made in such a way, that the same species of plant would be grown in a soil which contained organic substances, and in artificial mixtures which contained all the inorganic constituents of the fertile soil, without the admixture of any organic constituents. In respect to this, Wiegmann, at my suggestion, made experiments ("*Bot. Zeit.*," 1843, 801), according to which, plants raised in soil devoid of humous grew very poorly and mostly soon died. Mulder made a larger series of analogous experiments ("*Phys. Chem.*"), which likewise lead to the belief in the use of the organic substances contained in arable soil, as well as of the humic acid and ulmate of ammonia artificially added to it.

Even if these experiments were still far from having decided the question of the necessity of organic food in a definitive manner, the results are so very concordant with those of experience on a large scale, that there can be no doubt of their general correctness, the more, that these experiments made on the smallest scale, obtain a confirmation through the extraordinary small results which manuring with Liebig's solely inorganic manures has everywhere had, when comparative experiments have been made. Instead of reforming agriculture by his manures, Liebig has caused them to demonstrate the incorrectness of his theory of the nutrition of vegetables.

Yet the humous substances in vegetable mould, do not derive their importance to plants from an immediate applicability as food, but exercise their great influence on plants principally through their relations with the alkalies and earths, and especially with ammonia. I shall take the liberty of giving some of the principal results of Mulder's researches, since these open out a series of new points of view, which promise to become of the greatest importance to the theory of vegetable nutrition. According to these investigations, the substances beginning to undergo decomposition in the earth are gradually converted into a series of chemical compounds, first into ulmine, then into ulmic acid, humin, humic acid, geic acid, apocrenic, and finally into crenic acid. With the exception of the first and third, these compounds play the part of acids, and combine in the soil with its alkalies and earths. These acids, containing no nitrogen, possess a particularly strong affinity for ammonia, which is always met with, more or less abundantly, in combination with them. The compounds of these acids with alkalies are readily soluble in water, those with earths and metallic oxides little or not at all so. On the other hand, their compounds with the alkalies and ammonia readily form double salts with the earths and metallic oxides (apocrenic acid is penta-basic, crenic tetra-basic); the alkalies are therefore not only a means of rendering these acids readily soluble, but they assist in conveying the earths into plants by absorption.

Alumina plays a special part in reference to crenic and apocrenic acids, since it forms perfectly insoluble compounds with them, in which the acids are preserved from decomposition, and cannot be washed away by water; yet they are not thereby completely withheld from plants, since these compounds are capable of decomposition by ammonia, which is thus a means of conveying these compounds into plants very gradually, by continuous decomposition.

Most important as the above described relation of the humous acids to ammonia is, since their great affinity for it places them in a condition to attract this body, so important to vegetation, from the air and from the animal substances decomposing in the soil, and prepares them for absorption by the roots, yet they acquire still more importance from the fact that, according to Mulder's researches, the continuous decomposition of the humous substances is connected with formation of ammonia, since the oxygen of the air is used for the higher oxidation of the rest of their substance. The evidence that nitrogen is also conveyed to plants in this way, lies in an experiment of Mulder's ("*Phys. Chemistry*"), according to which, young Bean-plants which were raised in an atmosphere free from ammonia, in ulmic acid prepared from sugar free from ammonia, and in wood-coal, with water free from ammonia, yielded, on analysis, twice or thrice as much nitrogen as the seeds from which they were raised.

That the solutions of humous substances in water are absorbed by the roots as such, and not the products of their decomposition, it would certainly be difficult to prove, since these substances cannot be demonstrated to exist as such in the plant, but undergo a transformation directly they are absorbed. But in spite of the opposite results obtained by Hartig (Liebig's "*Agricultural Chemistry,*" 1 ed.) and Unger ("*Flora,*" 1842, 241), after Saussure's experiments (Liebig "*Annal.*" xlii. 275), Johnson ("*Mitth. d. Œcon. Ge'sells. zu Petersburg,*" 2 heft 162, extracted in Wolff's "*Chem. Forschungen,*" 202), and Trinchinetti's ("*Sul facolta assorbente della radici,*" 55), the assumption of such absorption is the less unsafe, that it has been long demonstrated, that roots have the power of absorbing dissolved vegetable substances, *e. g.*, tannic acid, narcotic extracts, &c. (*See* Mulder, "*Phys. Chem.*")

The inorganic compounds which are taken up by plants as food, and which furnish them with the four principal elementary bodies which they require for their formation, are *water*, *carbonic acid*, and *ammonia*.

As the absorption of watery fluids has already been discussed, I now turn to the consideration of *carbonic* acid. This, it is well known, exists universally diffused in atmospheric air and in water. Simple experiments prove that plants do not absorb the carbonic acid dissolved in water, with the latter, by means of their roots;

but that their green-coloured organs, consequently their leaves in particular, possess in a high degree, so long as they are exposed to light, the faculty of absorbing carbonic acid from the medium, be it air or water, in which they are placed, and of secreting oxygen gas in its place.

We owe the more accurate knowledge of this process especially to the admirable experiments of Saussure, which have been fully confirmed by later ones of Grischow, Boussingault, and others. The phenomena may be summed up in the following statements.

When green-coloured plants are exposed to the influence of sunlight, under water containing carbonic acid, they exhale oxygen gas. This exhalation of oxygen does not take place in boiled water.

When plants are exposed to the influence of sunlight in atmospheric air to which carbonic acid (up to 1-12th of its volume) has been added, they remove the carbonic acid and exhale oxygen in its place. This absorption of carbonic acid takes place very soon. Boussingault (" *Economie rurale,*" i. 66) placed a shoot of a Vine bearing twenty leaves in a glass globe, and while the sun shone upon the apparatus, drew through it in an hour fifteen litres of atmospheric air which contained ,0004 to ,00045 of carbonic acid, and at the exit of the air from the globe, the carbonic acid was diminished to ,0001 or ,0002. According to Chevandier's calculations, the trees of a forest, during the five summer months in which they bear leaves, withdraw from the column of air standing above the forest 1-9th of its contents of carbonic acid.

When a leafy shoot with its lower end dipping in water containing carbonic acid, is enclosed in a glass globe, its leaves exhale more oxygen than when its lower end is dipped in common water. A leafy shoot still connected with a tree, enclosed in a glass globe, increases the oxygen gas in the globe. Therefore in both cases the carbonic acid carried up with the ascending sap into the leaves is retained by the latter, and oxygen gas given off in proportion to it.

The exhaled carbonic acid is not contained in the plant in the form of gas, before its separation, for plants which contain no air, like *Confervæ,* or leaves from which the air has been exhausted by the air-pump, exhale oxygen in like manner. Pieces of torn leaves possess this function as well as entire leaves; leaves, on the contrary, which have had their organization destroyed by pressure, give off no carbonic acid, neither does the epidermis of the leaf. The quantity of oxygen gas which leaves give off depends upon their superficial extent and not on their mass.

The secretion of oxygen varies much in abundance under illumination by different rays of the solar spectrum. According to the researches of Draper (" *Treatise on the forces which produce the organization of plants,*" Appendix, 177), the following amounts of gas are set free: in red 0; in red and orange 24, 75; yellow and green 43, 75; green and blue 4, 10; blue 1, 0; indigo 0. The light here acts according to the intensity of its illuminating power; the chemical and heating rays of the spectrum are without effect.

Observ. The amount of oxygen given off is determined by the amount of carbonic acid furnished to the plant; the volume of the gas given off from the plant also corresponds to the carbonic acid taken up by it, but the gas exhaled does not consist of oxygen alone, a more or less considerable quantity of nitrogen being intermingled with it Draper (*l. c.* 180) obtained the following results:—

Pinus Tæda.

Experiment.	Oxygen.	Nitrogen.
1	16, 16	8, 34
2	27, 16	13, 84
3	22, 33	21, 67

Poa annua.

Experiment.	Oxygen.	Nitrogen.
1	90, 0	10, 0
2	77, 90	22, 10

When the experiments are made by exposing plants to the sun under spring-water, a part of the nitrogen is doubtless derived from the water, as well as another part from the air contained in the air-cavities of the plant; but these circumstances do not explain the exhalation of nitrogen completely, for according to Draper's experiments, it takes place when plants totally deprived of air by the air-pump are experimented on in water containing no nitrogen, and the quantity of nitrogen exhaled increases in proportion to the amount of oxygen during the experiment, while the reverse must occur if this intermixture depended on a diffusion taking place between the oxygen exhaled by the plant and the nitrogen contained in the water and in the plant. Draper draws from his experiments the conclusion that the exhalation of nitrogen, is a constant phenomenon, connected necessarily with the exhalation of oxygen, and conjectures that it is even the primary process which first sets in operation the decomposition of the carbonic acid, that it is to be ascribed to a decomposition of a nitrogenous substance in the leaf, which exercises the function of a ferment in the decomposition of the carbonic acid.

Boussingault ("*Economie Rurale,*" i. 5) drew the opposite conclusion from the results of Saussure's experiments, since in particular experiments the exhalation of nitrogen was so considerable, that the nitrogenous contents of the plant did not suffice for it; he therefore thought we could scarcely assume otherwise than that the nitrogen was derived from the air contained in the water and the plant. Under these circumstances, a trial of these conditions by accurate experiment is greatly required.

The reason that the quantity of oxygen gas given off by the plant is unequal to the carbonic acid taken up, is doubtless that a portion of the oxygen gas set free in the green parenchyma of the plant, enters into combination with oxidable substances contained in it. Many phenomena speak in favour of this. When cut leaves of water-plants, such as *Vallisneria, Potamogeton, Nymphæa, Hydrocharis*, &c., the tissue of which is traversed by wide air passages, are exposed to light under water, the oxygen does not flow from the surface of the leaves, but from the cut surfaces. It is therefore evident that the gas has to overcome a certain resistance to penetrate the epidermis, and we may fairly conclude that in many uninjured leaves, a portion of the oxygen excreted in the green substances is carried by the intercellular passages and vessels into the stem and roots of the plant, and consequently arrives at parts not green, which as will appear presently absorb oxygen; consequently a portion of the oxygen must be deficient, on the determination of the amount formed. For this process speaks Dutrochet's observation ("*Memoir*" i. 340), that in *Nymphæa lutea* the air contained in the interior of the plant contains less oxygen the further from the leaves it is taken; in the roots, eight per cent.; in the stem, sixteen per cent.; in the leaves, eighteen per cent. In accordance with this, stands the fact, that the vessels of the stem of the gourd contain 27·9 to 29·8 per cent. of oxygen by day (Bischoff "*de vera vas. spir. natura,*" 83), while by night no oxygen but much carbonic acid is formed in them (Focke, "*de respirat. veget.,*" 21).

It may be mentioned as a curiosity, that, according to Schultz's statements ("*Die Entdeckung der wahren Pflanzennahrung*"), the whole theory, that plants exhale oxygen in place of the carbonic acid taken up, rests upon an error, for the green parts of plants do indeed decompose vegetable acids, and salts of these acids, under the influence of light, but carbonic acid forms an exception to this. Wonderful to relate, hydro-chloric acid, which contains no oxygen, is named among the acids yielding most of it. It is unnecessary to remark that the repetition of the experiments by Boussingault, Grisebach, and Grischow, fully sustain the experimental skill of a Saussure against that of the Berlin physiologist.

The absorption of carbonic acid, and exhalation of oxygen by the green parts of plants, under the influence of light, are but a part of the complicated relations in which plants stand to atmospheric air. In order to form a conception of these, we must at the same time investigate the behaviour of the green parts in darkness, and of organs not of a green colour. Saussure is again the chief guide here.

As soon as green-coloured parts are withdrawn from the influence of light, their action upon the surrounding air is converted into the opposite, they now absorb oxygen, and exhale carbonic acid. The amount of oxygen taken up varies in the leaves of different plants: within twenty-four hours, from half to eight times the volume of the leaves. The volume of the carbonic acid exhaled, is somewhat smaller than the quantity of oxygen taken up; when the leaves are again brought to the light, they again exhale the oxygen which had disappeared.

All parts not coloured green (Fungi, roots, stems, flowers, &c.), whether exposed to light or not, take up oxygen and exhale carbonic acid.

It is usual to apply to this absorption and exhalation of particular kinds of gas, the term *respiration.* Many have regarded the term as inapt, because plants have no organ of respiration, and the like. Let us not contest words, but enquire in what relation these processes stand to each other and to the life of the plant.

Plants, from what has been said, have a double respiration, one consuming carbonic acid and exhaling oxygen by day in the green coloured organs, and one connected with a consumption of oxygen and a formation of carbonic acid in the green organs by night, and in those not green by day and night.

The question, which of these processes predominates, whether, on the whole, the plant consumes or forms a greater quantity of carbonic acid, whether consequently the respiration of plants is on the whole a deoxidating or an oxidating process, is again fully cleared up by Saussure's experiments.

When a plant is confined in a definite volume of air, the air is found unaltered in volume and composition after an equal number of days and nights; thus the plant has formed just as much carbonic acid by night as it has consumed in the day. But if carbonic acid is added to the atmospheric air in which the plant vegetates, or the plant is caused to absorb water containing carbonic acid, it exhales oxygen into the surrounding air.

There can be no doubt that plants in open air are in the same position as those in the last experiment. A very considerable quantity of carbonic acid is continually being added to the atmosphere through putrefaction, combustion, the respiration of animals, volcanic eruptions, mineral sources, &c.; this constant addition of carbonic acid above the usual amount, is again removed from the air by plants and replaced by oxygen. Consequently, plants do not purify the air by increasing the proportion of oxygen in it (if we do not take into account that carbonic acid which is not formed at the expense of oxygen of the air, such as that derived from volcanic sources), but by the removal of the carbonic acid constantly flowing into the atmosphere, formed at the expense of atmospheric oxygen.

In order to become acquainted with the influence which these two kinds of respiration exercise upon the vital operations of plants, we must investigate the phenomena that present themselves when one or other of these breathing processes is interrupted.

When plants are prevented, by keeping them from the light, from absorbing carbonic acid and exhaling oxygen, their nutrition suffers and they become etiolated. They do continue to form new shoots at the expense of the nutriment contained in their older parts; these are even larger than those developed under the influence of light, but weak and soft; the leaves remain small and do not become green, the normal qualities of the saps are not produced, bitter, milky plants remain sweet, &c. Some plants will exist for months in this sickly condition, but they cannot bear it permanently.

On the other hand, when the respiration connected with the consumption of carbonic acid is stimulated by affording to the plant, while exposed to light, an unusual quantity of carbonic acid, its nutrition is rendered more active. Even when nothing but water and carbonic acid are given, they are able to increase their organic substance, and the weight of this increase amounts to something like double that of the carbon which is contained in the absorbed carbonic acid.

Observ. In an experiment of Saussure's, little plants of *Vinca* appropriated 217 milligrammes of carbon from the carbonic acid absorbed, and their organic substance was increased about 531 milligrammes; two plants of *Mentha sativa* consumed 159 milligrammes of carbon and increased in weight about 318 milligrammes ("*Recherches,*" 226).

When the respiration of plants connected with absorption of oxygen and formation of carbonic acid, is interrupted by placing the entire plant in air containing no oxygen, for example in nitrogen, or by placing the plants under the air-pump, all their functions at once become paralyzed. The unfolding of the leaves and buds is checked and they rot, the leaves no longer turn towards the light; they no longer exhibit the alternate movements of waking and sleeping; sensitive leaves lose their irritability (Dutrochet, "*Mémoires,*" i, 361, 483); even single organs cut off from air decay while the rest live on: for instance, roots which are covered too deeply with earth. Plants die particularly soon when kept in air devoid of oxygen, in the dark; for example, a *Cactus*—a plant generally so obstinately retentive of vitality—died in five days (Saussure, *l. c.* 87). Plants bear being placed in such an atmosphere better when they are exposed to the alternations of day and night, since they exhale a small quantity of oxygen from their own substance by day, and from this form carbonic acid at night, which is again consumed by day. Plants are capable of holding out in this way a long time, although certainly in a very miserable way and without manifesting growth; but if the small quantity of oxygen which they form is removed by sulphur and iron filings, or the carbonic acid by lime water, they are unable to form these gases a second time, and die.

It is clear, from the preceding facts, that the respiration of green coloured parts during the action of light is related to the nutrient processes of the plant, since these become abnormal when the function is interrupted, but yet the plant can maintain its existence a long time under these conditions. But that which occurs in common to all parts, and which consists of absorption of oxygen and exhalation of carbonic acid, stands in immediate relation to the life of the plant. If the chemical process, which goes on unceasingly in all the organs of plants, through the action of oxygen gas upon vegetable substance, be interrupted, the plant, just like an animal, becomes asphyxiated, and death follows quickly. If we wish to speak of a respiration in plants, this oxygen-consuming breathing deserves the name far more than the exhalation of oxygen by the green organs, connected with the nutrient processes. In this immediate relation to life the respiration of plants corresponds completely with the respiration of animals; oxygen gas is a true vital air to plants. But the behaviour of the plant towards the atmosphere becomes the more complicated, that it does not merely absorb oxygen from without, like the animal, but also a part of that prepared in its own green organs.

Observ. Liebig must shut his eyes to facts lying open before him, when he persists ("*Agricultural Chemistry,*" 6th ed.) that the respiration consuming oxygen does not exist, that the absorption of oxygen has nothing to do with the life of plants, but is a process of oxidation, which occurs in dead wood as in the living plant, and that the exhalation of carbonic acid stands in no connexion with the absorption of oxygen, but that the carbonic acid simply rises in the stem with the water taken up by the roots, as in a cotton wick, and so passes out into the air.

Although the great diffusion of water and carbonic acid almost everywhere give full opportunity to plants, of appropriating the three principal elements of their substance (carbon, hydrogen, and oxygen), they have not always the opportunity of absorbing the quantity of nitrogen requisite for a vigorous development, whence the important part which nitrogenous substances play in manuring. The nitrogen of the air is a perfectly indifferent body towards plants. Even Saussure indicated that plants can only take up nitrogen in the form of solutions of organic substances or of ammonia; the latter has been especially maintained by Liebig, and his was the merit of demonstrating by experiment that ammoniacal vapours exist in atmospheric air, and that ammonia occurs in all rain and snow water; and on the other hand, of directing attention to the presence of abundance of ammoniacal salts in the ascending sap of the Maple, Birch, &c. Whether, however, as Liebig assumes, the ammonia contained in atmospheric air suffices to furnish the nitrogen contained in wild plants, and that an abundant supply of ammonia from the soil is necessary to cultivated plants, only because it is desired to stimulate them to the production of a great mass of the constituents of blood, is quite a different question. In the first place, no experiment has shewn that plants are capable of applying to their nutrition the ammoniacal vapours contained in the atmosphere; secondly, it is even doubtful whether this is the case with the ammoniacal salts which they take up by their roots, for, according to Bouchardat ("*Recherches sur la Végétation,*" 24), these salts, when absorbed by plants in watery solutions are poisonous to them in a state of 1000 or 1500 fold dilution. But it is proved by abundant experience that ammoniacal salts mixed with the soil, greatly further the growth of plants. These different results render it in the highest degree probable that the ammoniacal salts enter into combinations with the constituents of the soil, which exercise a different action upon the plants, from that of the pure salts. In this respect the investigations of Mulder upon the humous substances are of the highest value. According to these, carbonate of ammonia cannot exist for any time as such in humous, but is decomposed by the organic acids of the soil; since therefore compounds of ammonia with sulphuric and hydrochloric acids, &c., must be converted by the carbonate of lime in the soil into carbonate of ammonia, there exists the highest probability, that plants always receive ammonia in combination with the organic acids of the soil, which would explain the difference between the poisonous action of pure ammoniacal salts and their favourable influence when mingled with the soil. Moreover, it is not by any means proved that the air contains enough ammonia for us to regard it as anything like a sufficient source of nitrogen to plants, while Mulder's experiments point to a production of it in the soil; in any case the amount contained in the soil is very considerable, according to Kröcker (Berzelius, "*Jahresbericht,*" xxvi. 265) it amounts to 4045 pounds in a layer ten inches deep extending over a hectare in sandy soil, 20314 in argillaceous soil. From these circumstances as well as from the experiments of Boussingault and Mulder, it in any case follows, that the roots and not the leaves take up the substances which furnish plants with nitrogen, while, on the contrary, the leaves play the especially active part in the absorption of carbonic acid.

d. Elaboration of the Nutriment.

We know scarcely anything of the chemical processes in the interior of plants, on which depend the assimilation of the nutrient matter taken up, and the gradual conversion of this into the various compounds which the plant contains. In considering the nutritive processes of plants, two circumstances first strike us. 1, The uncommonly great agreement of all plants in respect to the production of a series of neutral hydrates of carbon, which furnish the material for the solid parts of plants, as also in respect to the formation of proteine-substances which play an active part in the process of development of the cell; 2, an infinite variety of chemical compounds, which are deposited in the different organs of particular groups of plants, in spite of the uniform structure and the agreement in the nutrient process, so far as relates to growth.

The chemists of our days, especially Mulder, have sought to make comprehensible the formation of such a surprising abundance of products by bodies so simply and uniformly organized as plants are. Since the plant is a complex of closed vesicles filled with fluid, the contents of which stand in reciprocal connexion by endosmose, this structure alone affords the possibility of the formation of the most varied chemical compounds. Even if we would suppose a plant to contain a fluid of the same composition in all its cells, this equilibrium could not last a moment; for on the one side the sap in the cells of one organ would acquire more consistence through evaporation, and thereby call into existence an opposition toward the other cells, while in the cells of another organ endosmose might cause the absorption of a thinner fluid, and thus give rise to a flowing of the sap from this organ to the former,—which would at once cause a multiformity of the composition spreading throughout all the organs. When we take into consideration, that on one side ammonia with organic compounds are taken up by the cells, while on the other side carbonic acid is decomposed, its carbon appropriated, and its oxygen given out, moreover that the cell-walls act *by contact* upon the contents of the cells, and that this action again differs according to the different chemical qualities of the cell-wall and contents,—it becomes explicable how the most manifold transformations of cell-contents and the formation of abundance of products come to pass in the Vegetable Kingdom, the only limitation that exists being the fact that the elementary substances do not combine together under all conditions.

This is all correct enough, but it does not advance us one step in the knowledge of the processes of vegetable nutrition. When we place the contents of all the vessels in a chemical laboratory in a condition of reciprocal connexion, we certainly expect that an innumerable series of chemical processes will result, but what they will be we know not, unless we know what the contents of each vessel consist of, and in what order and under what circumstances the contents of one come into operation upon the contents of another. It is of this that we are ignorant in plants, and so long as it remains uninvestigated, we can only set up more or less probable conjectures.

These circumstances will be my apology for treating this subject as briefly as possible.

One of the most general phenomena, since it occurs in all green-coloured plants, is, as we have seen, the absorption of carbonic acid, and the exhalation of oxygen gas. The experiments of Saussure demonstrate that this process stands in most intimate connexion with the formation of organic substances; nothing seemed easier than to explain this process. The neutral compounds of the plant (sugar, gum, starch, inuline and cellulose) are composed of carbon and the elements of water; it was only requisite to assume that the carbonic acid was decomposed in the leaves, its oxygen given out as gas, its carbon combined with water, which is never wanting in the plant, and the entire process was elucidated in the simplest way. This theory consequently met with universal acceptation, and in all books the decomposition of carbonic acid, taking place in the leaves, is spoken of as a settled fact, but we are without one proof that such is actually the state of the case. Liebig remarked, that it was far more probable that it was not the difficultly decomposable carbonic acid, but the readily decomposable water which was separated into its elements, and its oxygen given off, while its hydrogen entered into combination with the carbonic acid. The result was of course the same. There is no means of testing the correctness of either of these theories. But it is possible that they are equally false, that the carbonic acid does not enter into combination with the hydrogen of the water, but with another substance contained in the plant, and that oxygen becomes free by the decomposition of an organic substance previously formed. The latter is the opinion of Mulder, who assumes that the plant does not decompose carbonic acid because it is green, but while it is becoming green; new chlorophyll is constantly forming under the influence of light, with this originate the wax and starch associated with it, and an excretion of oxygen is necessarily connected with this; and this oxygen goes off partly in the form of gas, and in part oxidizes the colourless chlorophyll, and converts it into green. On the other hand, Draper, on account of the exhalation of nitrogen which he regards as necessary, assumes that chlorophyll acts the part of a ferment in the process of decomposition of carbonic acid, and in this itself suffers a decomposition, in consequence of which nitrogen is set free. Thus, at the very first step of the nutrition of vegetables, which was supposed to be the most thoroughly investigated, opinions become divergent; each has a certain probability, not one is proved. The only certainty is, that carbon and water remain within the plant, and are applied to the formation of its organized substance.

On the question of the combinations into which the absorbed nutriment first enters, the views of chemists stand in no better agreement. Saussure's experiments shewed that plants to which carbonic acid and water were afforded, acquired increase of weight equal to about twice the weight of carbon taken up. It may be considered probable, as Davy assumed, that the carbon absorbed enters at once into a neutral combination with the elements of water; in all probability this compound is soluble in water; since, therefore, dextrine is found in all green coloured organs, it is not unlikely that this, or in other cases, sugar is the form under which the said inorganic substances combine into organic substance.

But another probability is opposed to this notion, that the constituents of water and carbon enter at once into a neutral combination. All plants contain, besides the neutral substances, organic acids, in which the oxygen bears a greater proportion to the hydrogen than in water. Among these acids, oxalic is one of the most widely diffused,—scarcely a plant being without it. This acid stands very close to carbonic acid, since—supposing it anhydrous—it contains no hydrogen, and differs only from carbonic acid, by containing less oxygen. It may, with Liebig ("*Agricult. Chem.*," 6*th* ed.), be considered very probable, that the deoxidizing process connected with the respiration of the green organs, does not convert the carbonic acid and water at once into neutral compounds, but first only a partial separation of oxygen takes place, and the carbonic acid is changed into organic acids, first of all into oxalic, the hydrate of which, by separation of greater amounts of oxygen gas, can be transformed into malic, citric, and other acids. It may be assumed of all these acids that they are capable of conversion into sugar, starch, &c., by the addition of hydrogen. If this conception is adopted, the constant occurrence of vegetable acids appears a necessity for the nutritive processes of plants; and it will explain why plants will not flourish when they do not take up a certain quantity of basic substances, to combine into salts with these acids. On the conversion of an acid into a neutral substance, the base becomes free again, can unite with a new portion of acid, and so in the course of time, a comparatively small quantity of base may bring about the formation of a very great quantity of neutral compounds.

Observ. This notion of the importance of acids in the vegetable economy, has something very attractive about it, since it appears to solve a series of questions, but on closer examination a number of doubts present themselves. On the one side, the assumption that the acids are formed by a decomposition of carbonic acid, appears in any case too general, since in many plants with fleshy leaves, an acid is formed every night (thus at a time when no carbonic acid is decomposed), which acid is again decomposed by day. Here the acid is doubtless formed through oxidation of a neutral compound. On the other hand, that theory does not perfectly explain the case of the basic substances. If these had no other destination in the plant than the purpose of fixing free acids, it would be all one to plants whatever base was absorbed from without; any one could be substituted for any other. This is certainly, in some degree, the case with regard to bases which are very closely chemically allied, like potash and soda, or lime and magnesia, but this substitution is only compatible to a certain extent with the healthy growth of the plant. Particular plants require particular bases, lime, potash, &c., and die when they do not find them in the soil. Therefore, the specific properties of the bases stand in a definite relation to the nutritive processes of plants, albeit, the grounds of this relation are still unexplained. If, moreover, the acids form these transitional stages between carbonic acid and the neutral compounds, it is remarkable that so many plants produce an acid, and especially carbonic acid, in far greater quantity than is necessary for this purpose, depositing it, in combination with lime, in an insoluble condition, crystallized in the cells, and yet do not subsequently re-dissolve these crystals. It is true that nutritive substances (starch, fixed oils, &c.) are frequently produced in greater abundance than the requirements of the moment demand, and are deposited in the cells of particular organs, but these deposits are only temporary accumulations of food to be made use of subsequently; those deposits of insoluble salts appear much more likely to be intended to remove from the circuit of active juices, compounds which are superfluous to the plant.

Again, this theory does not explain the exchange of different bases at different periods of the age of the same organ. From the analyses of Saussure was derived the general rule, that young organs are especially rich in soluble alkaline salts, older plants in earthy salts and metals.

A second doctrine propounded by Liebig, is connected most closely with this opinion as to the office of the alkalies to neutralize the organic acids, namely, the notion that for every species of plant, the amount of oxygen of the carbonic acid contained in its ash, in the combustion of salts originating from vegetable acids, is constant, no matter what soil the plant may grow upon ("*Agricult. Chem.*" 6*th* ed.). For Liebig assumes that a plant forms no more of the acids which it produces, than is directly requisite for its vital operations, and that these therefore take just so much alkali as will fix these determinate quantities of acid. But weighty objections may be opposed to this doctrine. I have already observed that many plants do not produce the organic acids in that quantity which they would require were these converted into neutral compounds, but in very considerable superabundance, as for example, all specimens of *Cactus* unceasingly deposit extraordinarily large masses of tartrate or oxalate of lime in their cells, as insoluble crystals; the oxalic acid of these crystals is wholly withdrawn from the nutrient operations, yet elementary analysis would make its lime appear to exist in the state of carbonate, while at the same time, no conclusion could be drawn from its quantity, as to the amount of acid necessary in the nutrient processes of these plants. Moreover, all the alkalies which appear in the ash as carbonic salts, are not combined with organic acid in the living plant, but in many plants crystals of carbonate of lime occur; carbonic salts are deposited in the substance of many cell-membranes, and all cell-membranes are combined with alkalies and earths; consequently, we cannot draw from the analysis of ashes, as Liebig assumed, a proof of that law, and this is the less possible since, moreover, the fixed alkalies may be replaced by ammonia.

Whatever may be the character of the chemical action to which neutral compounds owe their origin, it is at all events, beyond doubt that they are produced by a deoxidizing process taking place under the influence of light. The effect of the deoxidation extends still further, for there can scarcely be a plant which does not contain compounds in which the oxygen is not contained in smaller quantity, in proportion to hydrogen, than in water, even if it be not altogether wanting. To this class belong chlorophyll and the wax connected with it, the incrusting substances of the wood-cells, the fixed and essential oils, resin, caoutchouc, &c. With the exception of the fixed oils, which doubtless originate from starch, we are ignorant from what other compounds all these constituents are derived; yet there can be no question that their hydrogen is originally obtained from water, and that their origin is connected with a separation of oxygen. It is remarkable of many of them, especially in the formation of essential oils, how much their production is favoured by the action of strong sunlight.

The compounds containing nitrogen stand in opposition to those devoid of it. Though in quantity they may stand far behind the latter, their importance in the vital phenomena of plants is not less; nitrogenous substances, as we have seen, line the cell as the primordial utricle, and consequently the contents of the cells are ordered under their immediate influence; they originate the development of new cells, and set in action the decomposition of carbonic acid. Doubtless these constitute but a few fragments of the great part which these substances play in the living plant; for many chemical processes, such as fermentation, the formation of hydrocyanic acid and amygdalin, the conversion of starch through diastase, &c., indicate that the first impulse to the transformation of all vegetable compounds, is principally given by the proteine substances. The great importance which these substances have in the vital economy of plants, is also denoted by their anatomical conditions, since they are contained in great abundance in all organs destined to further development, and which are endowed with more important physiological activity; *e. g.*, in the points of roots, in leaf and flower-buds, pollen-grains, the embryo-sac of the ovule, and in seeds; while in old organs, principally employed in conveying the sap, they occur in far inferior quantity.

It is as good as certain, from what has been stated above, that ammonia in combination with organic substances furnishes the nitrogen requisite for the formation of the proteine substances. In what organs and under what conditions these compounds are formed we know not. Mulder (*"Phys. Chem."*) is of opinion that they are formed at once in the points of the roots, and are diffused from here over the rest of the plant. But a determined fact may be opposed to this view, namely, the occurrence of salts of ammonia in ascending crude sap, which rather indicates that the formation of nitrogenous compounds takes place chiefly, if not entirely, in the leaves.

Of the formation of the other nitrogenous compounds of plants, such as the vegetable alkalies, indigo, &c., and of their import to the plant, we know simply nothing; I therefore consider it superfluous to make any further observations on them here.

e. Secretions.

In the consideration of the nutrient process of plants, the question presses itself upon us, whether, in the series of true formations which the mutual action of the substances contained in the plant produce, merely products which have a definite purpose in the nutrition and growth of the plant are found, or other compounds arise at the same time, which are of no further importance in the functions of the living plant, and must be removed from the cells carrying on the vital functions of the plant. This question cannot be answered with certainty so long, on the one hand, as the nutritive process is so imperfectly known, that in regard to the chemical processes connected with it, we possess merely more or less hazardous hypotheses, but not any knowledge whatever explanatory of the details; and so long, on the other hand, as we are unacquainted from physiological causes with the import of a great number of chemical compounds, which occur more or less, but yet not universally diffused throughout the Vegetable Kingdom; *e. g.*, of the essential oils, resin, the milk-saps, the vegetable alkaloids, &c., which substances are usually denominated secretions. A large portion of these substances, in particular the essential oils, the alkaloids, the majority of the milky juices, are in the highest degree poisonous both to the plants which prepare them, and to others when they are caused to absorb them. These secretions are commonly separated from the other matters within the plant, being either, as is frequently the case with the essential oils, enclosed in special cells, or contained in canals which run between the cells, as is often the case with essential oils and resin, and universally with the milky juices. In the majority of plants containing milky juices, these canals are lined with a special membrane, and are then called milk-vessels, but can scarcely be separated from mere canals destitute of proper membranes, running between the cells, since true milk-sap is found in the latter in many plants, as in *Rhus*.

Observ. Although the theory of the milk-sap is but distantly related to the subject of the present treatise, the cell, yet I cannot avoid touching here upon the views propounded by Schultz, since if they were confirmed, they would effect a complete metamorphosis of the theory of the nutrition of plants. Schultz has striven, for a long series of years, in many essays (especially in "*Die Natur der lebenden Pflanze*," 1823-28; "*Sur la Circulation et sur les vaisseaux laticifères dans les Plantes*," 1839; "*Die Cyclose des Lebenssaftes*," 1841), to demonstrate a complete analogy between the milk-sap and the blood of animals. According to him, the milk-sap is organized, and consists of a plasma becoming coagulated out of the plant, and of globules which correspond to the lymph and blood corpuscles. On the coagulation of the milk-sap, an elastic coagulum, like the fibrine of the blood, is said to separate, which is composed of caoutchouc, pure or mingled with wax and gum, enclosing the globules of fatty or waxy matter, the larger of which are clothed with a membrane. In addition to caoutchouc, the plasma contains sugar, albumen, gum, and salts, in solution.

In all this account of the analogous organization of the milk-sap and the blood, there is not a word of truth. The caoutchouc, as I have demonstrated by the simplest experiments ("*On the milk-sap and its motion.*"

—*Bot. Zeit.* 1843, 563) is not dissolved in the plasma, but forms the globules, which are destitute of enveloping membrane and of any organization whatsoever; the fluid part of the sap contains no caoutchouc, and does not coagulate, but dries in the air into a brittle crust, composed of gum, which may be re-dissolved in water, whereby the original character of the milk-sap is restored. Therefore the comparison of the milk-sap with the blood, in regard to its organization, is in every respect a mistaken one.

According to Schultz, the milk-sap exhibits a double motion, an internal one and a circulation. The internal motion, observed both in freshly effused milk-sap and in that still contained in the vessels, depends on the molecules of the sap (by which name the globules appear to be meant), sometimes joining together, and sometimes separating. The same process goes on upon the walls of the vessels, and it is most distinctly noticed that the said union and separation takes place, in the same way, between the molecules of the sap and those of the walls of the vessels, as between the molecules themselves, and in fact the attraction and repulsion of the portions of the sap take place in a definite direction, so as to communicate a progressive movement to the whole mass of sap.

It is impossible to make worse observations, and to interpret what is seen more incorrectly, than Schultz has done in regard to the internal movement of the milk-sap. If the globules are small, as is usual, they exhibit the molecular motion of Brown, and, indeed, after having been dried up and re-dissolved in water, just as well as when fresh; if larger, as in the milk-sap of *Sambucus Ebulus*, and *Musa*, there is no molecular motion. All the rest is pure fable.

The flowing movement is, according to Schultz's statements, completely independent of external influences, and goes on in the same way in perfectly uninjured plants as in detached organs and in separate layers cut off the plant, which would prove that it is not caused by mechanical effusion of part of the sap from the walls of the vessels. It is stated that it may often be observed in detached slices, that the sap flows onwards in a wounded vessel into the uninjured part of it, while it flows out from other wounds which lie in the direction of the current. Since therefore the sap flows in one portion of the vessels from the leaves to the root, and in another portion in the reverse direction, a kind of circulation is produced (called by Schultz *Cyclosis*), which, however, does not run through a definite and perfectly circular path, but parts into numerous circular courses, returning into themselves, in the manifold ramifications and anastomoses of the vessels.

That the sap must be in motion in an injured plant, is self-evident, for it is well known that it flows with force out of wounds in a lacerated milk-vessel: which is caused, not by contraction of the vessel, but by the pressure of the cells surrounding it, since the phenomenon presents itself in plants wherein the canals of the milk-sap do not possess any proper wall. To make out the behaviour of the milk-sap in the vessels, the experiments must necessarily be made on uninjured plants. From my own observations,—I, like Amici and Treviranus,—must deny its movement in the uninjured plant. A leaf of *Chelidonium* is sufficiently transparent when it is laid beneath the microscope with its lower surface upwards, and covered with a drop of oil and a glass plate, to allow of the appearances in the milk-vessels being seen. If we examine in this way a leaf of an uninjured plant growing in its pot, or even a detached leaf burnt at the cut surface of the petiole, to prevent effusion of the milk-sap, the sap, which at first is disturbed by the motion of the leaf and the pressure to which it is exposed in spreading it out upon the stage of the microscope, quickly comes into a state of rest; then, if the petiole is cut off with a pair of scissors, a most rapid current immediately commences, which goes on till the effused sap coagulates and prevents more from being poured out. If the same experiment is made on the leaves of *Tragopogon*, in which the milk-vessels run in tolerably parallel direction, a conviction may soon be obtained, by cutting off first the tip and on another the base of the leaf, that the sap always flows in the direction of the wound. When the sap is at rest in a leaf, the slighest pressure upon the leaf suffices to produce a most rapid flowing for a few seconds, and when the pressure is removed, it flows back in the opposite direction. Amici shewed that when, by an oblique position of the mirror of the microscope, the sunlight was thrown upon a part of the leaf on one side of the field of vision, the sap was set in motion, and the current was reversed when the light was thrown upon the opposite side. These experiments place it beyond doubt to me, that the *Cyclosis* has no existence, and that the movemant of the sap is produced by mechanical causes. The further proof of *Cyclosis* found by Schultz in the currents of the protoplasm contained in the cells, which he assumes to be the same milk-sap, contained in ramifications of the milk-vessels penetrating the cell walls, needs no word of refutation.

Schultz derives from the pretended organization and movement of the milk-sap, the conclusion that the latter plays the same part in plants as the blood does in animals. He therefore calls it *vital-sap* (*lebenssaft*) *latex.* I have shewn that the bases of his arguments are incorrect observations; but, independently of that, the milk-sap is wholly unfitted on other accounts to serve as an universal nutrient juice. In the first place, it only occurs in a comparatively small number of plants, and, in fact, without a definite relation to the rest of their organization and systematic position. Schultz, indeed, asserts the contrary, since he declares that he has found the milk-vessels in the majority of the families investigated by him; but his anatomical researches are altogether unworthy of trust, for he mingles together the most different things. In the second place, the composition of the milk-sap is quite unsuitable in the stated purpose. Schultz compares the caoutchouc coagulum with the fibrine of the blood. The comparison is, as shewn above, incorrect, because the caoutchouc is not dissolved in the fluid of the milk-sap; but leaving that out of the question, the composition and chemical properties of caoutchouc are such, that no constituent of plants could be named less fitted for the peculiar nutrient substance, for there does not exist an indication of a possibility that it is capable of metamorphosis within the plant. Thirdly, the composition of the milk-sap varies exceedingly in different plants, and frequently in closely-allied species, although most milk-saps agree in being poisonous. Side by side with the acrid milk-sap of *Euphorbia canariensis* stands the mild juice of *E. balsamifera;* beside the narcotic juice of *Papaver*, the acrid juice of *Chelidonium;* beside the narcotic of *Lactuca virosa*, &c., the innocuous juice of other species of *Lactuca;* beside the frightfully poisonous juice of *Antiaris toxicaria*, the harmless juice of

A. innocua. These objections are met, it is true, by Schultz with the assertion that the milk-saps of *Euphorbia*, &c., are not poisonous, but that the poisonous matter comes from reservoirs of secretion wounded at the same time as the milk-vessels; this, however, is a complete flight of imagination, for which not the shadow of a proof exists.

So the whole of Schultz's theory of the milk-sap is a tissue of the most unfounded hypotheses, offering the most glaring contradiction to positive facts.

Though the physiological import of the secreted fluids preserved in the interior of plants is uncertain, there is no doubt that the purpose of those secretions which occur upon the surface of plants might be more readily made out, if the fluids were excreted in sufficient quantity to be collected. Whether such excretions occur, is still unknown. Here, of course, we can merely have to do with those secretions which have a more general diffusion, since local exudations, which only occur in particular plants, like the acids in the glandular hairs of *Cicer arietinum*, the gummy secretions of *Primulæ*, *Sileneæ*, &c., can merely serve special purposes.

Such a secretion has been attributed by many to the root, especially by Brugmans ("*De mutata humorum in regno organico indole*," Ludg. Batav. 1789.—Up to the time of Schleiden, a number of authors have cited under this head a treatise by Brugmans, "*De Lolio ejusdemque varia specie*;" but this essay seems to have no existence), who thought he discovered that certain plants do not flourish in the vicinity of certain others, *e. g.*, *Avena* near *Carduus arvensis*, wheat near *Erigeron acre*, flax near *Euphorbia Peplus* and *Scabiosa arvensis*, &c. He ascribed this to the excretion of a watery fluid from the roots of the weeds, having the power of corroding the roots of the cultivated plants. These excretions were considered by others, for example by Plenk ("*Physiolog.*" 43), Humboldt ("*Aphorism. a. d. chemisch Physiol. d. Pflanzen.*" 116), Cotta ("*Naturbet. üb. Bewegung d. Safts,*" 49), as evacuation of excrements, and the utility of fallows was deduced from the hypothesis that the excrements must be allowed to decompose in the soil before other plants could flourish in it. But this excretion from the roots was denied by others, *e. g.*, Hedwig, and generally, speaking, no very great value was attached to it. The attention of physiologists was drawn again to the matter by Macaire Prinsep instituting, at De Candolle's suggestion ("*Mém de la Soc. de Phys. de Genève,*" v. 287), experiments which appeared to give positive results. Macaire found, namely, that plants which had their roots carefully dug up and placed in water, gave out into this, chiefly during the night, organic matters, which differed according to the kind of plant, being opium-like from the *Lactuceæ* and the Poppy, acrid from *Euphorbia*, mucilaginous from the *Leguminosæ*, &c. At the same time, he believed that he found acetate of lead taken up by the plant, again excreted in this way, further, that in water whereinto these secretions had passed, plants of the same species would not flourish, while other species could absorb it with impunity. From these experiments, De Candolle drew the conclusion that these excretions were to be compared with the urinary excretions of animals, and explained from the doctrine, that no organized being could use its own excrement for food, the fact of experience, that cultivated plants, the Cerealia for example, would not flourish for any long uninterrupted period upon the same soil.

The repetition of these experiments by others, left no doubt that Macaire had not gone to work with the requisite circumspection in making them. Braconnot (*"Ann. d. Chimie. et d. Phys."* tom. lxxii. p. 32) shewed that milk-sap was effused into water from the roots of plants of *Lactuca* which had been dug out of earth, partly in consequence of laceration, partly in consequence of irritation; but that earth wherein *Nerium, Euphorbia, Asclepias,* and *Papaver,* had grown, some of them for a series of years, was totally devoid of such excreted matters, and that merely traces of organic substances, neither bitter nor acrid, were met with in it, and these he attributed to the decomposition of the rootlets. The experiments of Walser (*"Unters. üb. d. Wurzelausscheidungen,"* Dissert. Tubingen, 1838) likewise gave a completely negative result, as did also Boussingault's (*"Ann. d. Chim. et d. Phys."* 1841, tom. i., 217). Moreover that the noxious salts absorbed are not excreted by uninjured roots, but only extracted by the water from injured roots, was shewn by the experiments of Unger (*"Ueb. d. Vegetat. v. Kitzbühel."* 149), and Meyen (*"Physiolog."* ii. 530), on *Lemna,* and Braconnot demonstrated that Macaire had made a clumsy mistake in his experiments, to prove the excretion of an absorbed salt of lead, since he overlooked that the close bundles of roots carried the solution of the lead salt over, into the vessel of water into which another portion of the roots of the same plant dipped, by capillary attraction.

Under these circumstances, we must regard the secretion of an excrementitious fluid by the roots as not proven. At the same time, it is certainly no evidence that the roots do not excrete at all. I lay no weight upon the reason mentioned by Schleiden, that the endosmose of the roots must be accompanied by an exosmose, for it is too hazardous to deduce the existence of a second phenomenon from one of which so little is known in regard to the forces active in it, as is the case of the absorption of the roots. A few other circumstances perhaps speak in favour of it. Many experiments shew that the roots of living plants exert a chemical influence upon organic substances placed in contact with their roots. Trinchinetti (*"sull. fac. absorb. d. radici."* 57) observed, that a decoction of humus underwent fœtid putrefaction when left to itself, but this did not take place when the roots of living plants were placed in it. In many cases it is observed that the roots exercise a solvent action upon solid organic substances; thus

Gazzeri saw this in Clover; Trinchinetti saw a root of *Nepeta Cataria* grow through the midst of a peach-stone, and the roots of *Viscum* penetrate into the periderm and bark of a tree. There can be no doubt, that these effects are produced by a substance excreted from the roots. Of what kind this is, we know not; yet Becquerel (Guillemin, "*Archiv. de Botanique,*" i. 398) has given an indication in this direction, since he found that roots excreted a free acid (probably acetic acid), or a substance which was converted into an acid in air. This circumstance reminds us that Lichens which live upon limestone dissolve the latter, and form their fruit in excavations of it, which can only be through secretion of a free acid. Whether the above-mentioned effects are to be ascribed to the free acid excreted by roots, or to the secretion of other compounds is not made out. According to Becquerel's researches, this excretion of a free acid occurs not only from the roots, but from the other parts of plants—the bulbs, tubers, buds, and leaves. Becquerel brings it into connection with the evaporation of acetic acid in human perspiration; if this analogy were recognized and the secretion thus interpreted as a true excretion, there would still be no inconsistency in imagining it to exercise a function, contributing towards the accomplishment of the purposes of the living plant, even in its excreted condition.

Observ. Moldenhawer ("*Beiträge z. Anatomie d. Pflanzen,*" 320) expressed the opinion that the organic substances used by plants for their nutrition, underwent a chemical decomposition by a fluid secreted from the roots, and were thus prepared for assimilation. This theory has been revived, in recent times, by Schultz ("*Die Entdeckung der wahren Pflanzennahrung*"). He believes that he found living plants (roots as well as leaves) decompose solutions of the most varied organic substances, with evolution of oxygen, before they absorbed them; thus humous-extract becomes acid, milk-sap decomposed, and cane-sugar converted into starch-gum. From this he concluded that plants act on the assimilated compounds in a manner analogous to that of the intestinal canal of animals upon their food. How much of truth or error there exists on this matter must be decided by future researches of chemists.

While some discover a removal of excrements in the secretion of a watery fluid by the roots, others ascribe the same purpose to an aqueous secretion through the leaves. Isolated observations had long ago indicated that water is excreted, during the night and morning, in the form of drops of liquid, if not from all, yet from a great many leaves, since the drops of water which are formed at the points and serrations of leaves; owe their origin to a secretion, and not to the dew. This subject was especially followed out by Trinchinetti ("*On a hitherto undescribed function of the Plant,*"—*Literat. blatt. zur Linnæa*, xi. 66); he found little glands (which he called *glandulæ periphyllæ*) at the spots where the excretion took place; the fluid secreted from these, though it appeared at first like pure water, contained organic substances, and passed into fœtid decomposition. Similar observations were made by Rainer Graf (" *Flora*," 1840, 433).

While this excretion of water occurs only in very small amount in most plants, many of the family of the Aroideæ, especially *Calla æthiopica* (Gärtner, " *Beiblätter zur Flora*," 1842, 1), *Arum Colocasia* (Schmidt, *in Linnæa*, vi. 65), evacuate water in larger quantity from the points of their leaves, so that it flows off in drops; this occurs in the most striking degree in a plant described as *Caladium destillatorum* (" *Ann. of Nat. Hist.*" *sec. ser.* i. 188), in which each leaf—it is true, of colossal size—gave off about half a pint every night. The water flows here (as in *Arum Colocasia*) from an orifice in the neighbourhood of the point of the leaf, upon the upper surface, in which terminates a canal running along the border of the leaf, while smaller canals, running along the principal nerves, open into this.

The water secreted, in all these cases, contains but an extremely small quantity of organic substance in solution.

It is probable that the secretion of water in the pitchers of *Nepenthes*, *Sarracenia*, and *Cephalotus*, should be reckoned with the above. According to Völcker's account (" *Ann. of Nat. Hist.*" *sec. ser.* iv. 128), the fluid secreted by *Nepenthes* contains only 0,27—0,92 per cent. of solid matter, consisting of citric and malic acids, chlorine, potash, soda, lime, and magnesia.

We have no data which would enable us to determine accurately how far this secretion of drops of fluid water is (as according to Trinchinetti) for the purpose of evacuating substances, which, if they remained in the plant, would exercise an injurious influence upon its health; yet this hypothesis hardly appears probable, when we take into account the extraordinarily small quantity of organic compounds removed in this way, together with the circumstance that they bear none of the characters of a substance beginning to suffer decomposition.

The same holds good, also, in regard to the water excreted from the leaves in the form of vapour. This likewise contains, as the observations of Senebier and Treviranus shewed, an extremely small quantity of organic matter, but is nevertheless capable of putrefaction. Experiments which were made by Bonnet, Duhamel, and Treviranus (" *Phys.*" i. 494), to hinder the evaporation, by smearing the leaves with oil and other substances, shewed that the leaves died. This result may, however, be just as well attributed to a positive injurious effect of the oil, in withholding air, as to a suppression of the evacuation of injurious matter. Manifold experience puts it beyond doubt that repression of the evaporation from the leaves by unfavourable conditions of weather, produces disease, often connected with the formation of Fungi, but this result may be caused quite as much by a disturbance of the normal nutrient processes of the plant connected with the evaporation of a large amount of aqueous vapour, as by the retention of an organic substance which should have been excreted by the leaves.

f. Evolution of heat.

With the nutritive processes of plants is connected their power of producing heat. That plants possess this power may be demonstrated by simple observations, but these require great accuracy and certain rules of precaution, to avoid arriving at false conclusions; for in determining the proper heat of plants, not only does the mostly very small amount of heat which is capable of raising the temperature of the plant a little above that of the air, render great caution necessary in making the experiments, but, under common circumstances, so much heat becomes latent, through the active excretion of aqueous vapours from the leaves, that the temperature of the plant, in spite of the latter producing heat, sinks below the temperature of the surrounding air. Therefore to arrive at accurate results, it is not merely necessary to use a very sensitive thermometric apparatus, but also to cut off the refrigeration by evaporation.

That seeds when germinating, as they lie heaped in large masses, evolve a considerable degree of heat, is a fact long known from the malting of grain, but the cause of it was incorrectly sought for in a process of fermentation. To Göppert *("Ueber Wärmeentwickelung in der lebenden Pflanze")* is due the merit of having demonstrated that such is not the case, but that the evolution of heat is connected with the process of germination. Seeds of very different chemical composition (of different grains, of Hemp, Clover, *Spergula*, *Brassica*, &c.) made to germinate in quantities of about a pound, became heated, at a temperature of the air of 48°—66°, to 59—120° Fahr.

It was likewise shewn by Göppert, that full-grown plants, also, such as Oats, Maize, *Cyperus esculentus*, *Hyoscyamus*, *Sedum acre*, &c., laid together in heaps, and covered with bad conductors of heat, cause a thermometer placed among them to rise about 2°—7° (*Spergula* as much as 22°) above the temperature of the air. Dutrochet succeeded, with the help of Becquerel's thermoelectric needle, in demonstrating an evolution of heat in plants standing alone ("*Ann. d. sc. nat.*" 1839, ii. 77); but here the cold of evaporation must be cut off by placing the plant in an atmosphere completely saturated with water. Under these circumstances, the temperature of all vegetating parts, the roots, the leaves, the young juicy shoots (but not those of hard wood), were elevated from about one 1-6th to 1-12th of a degree. The evolution of heat exhibited a daily maximum and minimum; the latter occurred about midnight, the former about noon, yet not at the same hour in different plants, for the time varied from 10 A.M. to 2 P.M.

Observ. The earlier experiments to determine the temperature of plants, by sinking thermometers in holes bored in the trunks of trees, were completely incapable of giving a decisive answer to the question whether plants evolve a proper heat, since a number of circumstances, the effect of which cannot be taken into account, are influential upon the temperature of the tree, namely, the direct warming action of the rays of the sun, the cooling influence of evaporation, the sometimes warming, sometimes cooling communication of the temperature of the soil, through the medium of the ascending sap, which exercises an influence according to the time of year, and the difference of depth to which the roots penetrate, not to be accurately determined in isolated cases. Under these circumstances, it is readily explicable that the experiments made by different observers do not agree. While Nau found that the mean temperature of the tree agreed with the mean temperature of the air, Schubler found the tree 1½° to 2¾° colder than the air in summer, and in spring, on the contrary (March, May), about 1½° to 3° warmer. While in the experiments of Schubler, made on pretty thick trees, the temperature of the latter never attained the extreme of the temperature of the atmosphere, Reaumur saw slender trees heated 18° to 29° above the temperature of the air, in the sun. Under these circumstances, the slight evolution of heat of single plants must vanish without leaving a trace, in the considerable, and, in some cases, discordant variations of temperature, dependent on external influences.

A very great evolution of heat occurs in the blossom of the Aroideæ. This is considerable even in our *Arum maculatum*, and, according to Dutrochet's researches ("*Comptes rendus*," 1839, 695), rises to 25°—27° above the temperature of the air. But this phenomenon is seen in far higher degree in *Colocasia odora*, in which plant it has been investigated by Brongniart ("*Nouv. Ann. d. Muséum*," iii.), Vrolik and Vriese ("*Ann. des Sc. Nat.*" *sec. ser.* v. 134), and Van Beek and Bersgma ("*Obs. thermo-elect. s. l'élév. de temperat. des fleurs d. Colocas. odor.*" 1838). These last observers found the maximum of heat 129°, when the temperature of the air was 79°. The seat of the strongest evolution of heat alters during the time of flowering; namely, after the spathe has opened, the anthers manifest the greatest heat; they begin to cool down with the emission of the pollen, after which the upper part of the spadix, covered with abortive stamens, grows warm.

Similar observations—not, however, made with the thermometer, and therefore not fitted to give an accurate determination of the heat given off by flowers—have been made on *Arum italicum*, *A. Dracunculus*, *Caladium viviparum*, *C. pinnatifidum*, and *Calla æthiopica*, by Saussure, Göppert, Schultz, Treviranus, Gärtner, and others.

The evolution of heat in the blossom of the Aroideæ exhibits a daily maximum and minimum, which, however, it is remarkable, that different observers found to occur at different times of the day; thus, in *A. maculatum*, the maximum occurred in the morning (Dutrochet), whilst Senebier found it occur after six o'clock in the evening; in *Colocasia odora*, Brongniart found the maximum at 5 A.M; Vrolik and Vriese, as well as Van Beek and Bergsma, about 3 P.M.; and Hasskarl, in Java, at 6 A.M. (" *Tidschr. v. naturl. Gesch.*" vii. *letterkund Berigt.* 26); as also Hubert found, probably in the same plant, the greatest heat after sunrise, in Madagascar.

In very few cases has evolution of heat been observed in the blossoms of other families. Saussure, by means of an air-thermometer, found the flowers of Gourds 1° to 3°, those of *Bignonia radicans* 1°, of *Polyanthes tuberosa* $\frac{1}{2}$°, and Mulder those of *Cactus grandiflorus* 1°—2° Fahr. warmer than the atmosphere.

There can be no doubt that the evolution of heat from flowers results from the respiratory process connected with the formation of a large quantity of carbonic acid. Saussure found that a blossom of *Arum maculatum* consumed in twenty-four hours, before its heating, or after it had ceased, five times its own volume of oxygen, while a warmer blossom consumed thirty times, its spathe five times, the bare portion of its spadix thirty times, and the part covered with flowers 132 times its volume of oxygen. Vrolik and Vriese (" *Ann. d. Sc. Nat. sec. sér.*" xi. 62) found the heat of a blossom of *Colocasia odora* increase about 9° to 10°, when brought into oxygen gas, while no evolution of heat took place at all in carbonic acid.

In like manner, there can be no doubt that in germinating seed, the respiration of which is equally connected with the consumption of oxygen and the exhalation of carbonic acid, the evolution of heat stands in connection with the formation of carbonic acid; but whether this source furnishes all the liberated heat, or a part of it depends upon the vegetative process of the germinating seed, cannot be determined in the present imperfect state of our knowledge of the chemical transformations of the substance of the seed connected with germination.

In vegetating organs the source of heat is evidently different. It is true, as we have seen, that oxygen is consumed and carbonic acid formed by all organs, but since on the whole a greater quantity of carbonic acid is decomposed in the green-coloured organs, than is formed in the remaining parts, more heat must be consumed than produced in the respirating process of vegetating organs. But evolution of heat must be connected with the nutrient process, for the plant forms its organic substance, if not wholly yet in great part, from gases and liquids. Since then the growth of the plant exhibits a daily exaltation, occurring about noon, it is quite in accordance that the evolution of heat also should occur in increased degree at the same time.

B.—THE CELL AS AN ORGAN OF PROPAGATION.

a. *The Multiplication of Plants by Division.*

Multiplication by division occurs under different forms according to the lower or higher stage of organization of the plants; for the lower it is, the more does the individual cell possess the power of independently producing a new vegetable, whether by simple division or by the formation of a bud; while the higher the organization of the entire plant stands, the more does the capability of maintaining an independent vitality leave the individual cells and become committed to smaller or larger assemblages of cells, which must become developed into an organ of complicated structure, before their separation from the parent plant, to ensure their growing up into independent plants

Multiplication of plants by division of every individual cell is a very common phenomenon in the lowest forms of Algæ. In the generality of cases, the dividing cell parts into two, more rarely into four cells, in which again the same process of multiplication may be repeated. This is of universal occurrence in the unicellular Algæ, *e. g.*, in the Diatomaceæ, Desmidiaceæ, &c.; after the division, the newly-formed cells either separate from each other or remain joined together in colonies arranged in rows or flat layers, more or less firmly connected by a mass of mucilaginous matter, thus forming a transition towards the plants composed of numbers of cells.

The same process is repeated in the many-celled Algæ, for example, in the Oscillatorieæ; in the first instance, growth of the single individual is the result of the process of division of the cells in these plants, but the extraordinary readiness with which they break up into separate pieces, or, as in *Nostoc*, the single cellular filaments separate from each other by solution of the connecting mucilage, together with the power of the single pieces to grow up again into new plants, give great facility to the multiplication of the individuals by division of their cells.

The capability of multiplying in this way by unceasing division of the cells, appears to be unlimited in many lower plants, such as the Diatomaceæ, Oscillatorieæ, &c.; at all events, any other mode of propagation has been either rarely or not at all discovered in them; in other cases, however, and especially in the Desmidiaceæ (*see* Ralfs' "*British Desmidieæ,*" 5) this division is confined within definite limits. After a series of divisions have taken place, this process ceases, and the formation of spores begins.

Among the plants possessing a thallus composed of numerous cells, the development of single cells or groups of cells into independent plants occurs chiefly in the Lichens, where very frequently the layer composed of globular cells breaks up, by the cells falling apart into the form of powder (*gonidia, lagerkeime*), either at particular points or all over the thallus, these cells falling upon foreign bodies and becoming developed into new plants, if they find a favourable station. But this phenomenon is to be regarded as more or less a result of disease, for the normal development of the thallus is interfered with by it, and if the formation of gonidia occurs to a great extent, is perfectly arrested; thus this mode of multiplication of Lichens becomes the more inconsiderable in proportion to that by spores, the more favourable the station to the normal development of the plant, and *vice versâ*. The same phenomenon is met with again in the leaves of the Jungermannieæ, which frequently break up more or less completely into pulverulent masses of isolated cells; but it has not yet been observed whether these are capable of further development into new plants. But the formation of the so-called *gemmæ* occurs normally in many frondescent Liverworts, especially in *Lunularia, Marchantia,* and *Blasia.* These structures are developed, in hollow receptacles of various form, from a stalked cell, which is converted by repeated subdivision into a cellular nodule, which becomes detached, readily strikes root, and grows up into a new plant. (*See* Mirbel, "*Recherch. s. l. Marchantia polymorpha.*")

Far more important, or perhaps merely better known, through the masterly researches of W. P. Schimper ("*Rech. Anatom. et Morph. s. l. Mousses*"), than in the Liverworts, is the part played by multiplication through independent growth of single cells in the Mosses, for almost every cell of the surface of these plants is capable of conversion by repeated division into a cellular nodule, which grows up into a leafy stem, whence is explained the extraordinary diffusion of these plants, even of such species as never bear fruit in particular localities. Schimper observed this process on the rootlets of the Mosses, partly directly, partly after they had become converted into a green structure composed of confervoid filaments, resembling the proembryo; he found the same proembryo-like structure grow out from the leaf-cells of many species, (*e. g., Orthotrichum Lyellii*), and confirmed what Kützing had already seen, that even the cells of torn leaves will produce similar growths under favourable circumstances. In particular cases also, compound organs (the leaves of *Mnium palustre, M. androgynum,* the antheridia of *Tetraphis pellucida,* &c.) are developed into tuberous structures, spontaneously separating.

From the fact that the cells of different parts of the Mosses are capable of becoming developed into a bud or a proembryonal confervoid structure producing a bud, it follows that in these plants, notwithstanding their already rather complex structure, the subordination of the individual cell to the purposes of the whole is still but small, and that the individual life even here readily acquires the preponderance. But whether in the higher plants the individual cell is still capable of coming forth independently in an analagous manner and giving rise to the formation of a bud by development of a cellular mass in its interior, or whether a complete group of cells must co-operate from the very beginning for the formation of the bud, we shall not be able to decide until we shall have traced back the normal development of buds to their first origin. If, however, it should be the case that the formation of a bud starts originally from a single cell, this is still incapable, in the higher plants, of forming a bud, when it is separated from the rest of the plant before it has produced a new individual and this has grown up to a certain point of development, at the expense of nutriment produced by other cells. Therefore in all the more highly organized plants only organs of considerable size, composed of numerous cells and containing a certain amount of assimilated nutriment, are capable of laying down the foundation of a new plant.

I have explained above, the doctrine that a branched plant is composed of as many individuals as it possesses ramifications. Taken strictly, this is not absolutely true, for a perfect plant possesses not only an ascending axis, clothed with leaves, but a descending axis, a root. In many plants (in all leafy Cryptogamia, and in the Monocotyledons), even the primary axis is imperfect, for merely the ascending portion of it exists, while a primary descending axis is wanting, and is replaced by secondary axes which shoot out from the lateral surfaces of the stem. The same incompleteness exists in every branch, it consists merely of an ascending axis, therefore corresponds simply to half a plant, as also each ramification of the root represents the corresponding half of a complete plant.

Since, however, the individual parts of a plant very generally possess the power of producing that part of a complete plant in which they are deficient, when either a sufficient supply of nutriment has been stored up in their interior to last, or the requisite sustenance is still conveyed to them by the parent plant, until the completion is attained and they can prepare their own food independently, there exists, as a rule, little difficulty in producing a new individual furnished with all necessary organs, from a single part of a plant. This is most readily effected with an ascending axis, since, on the whole, this is very prone to produce radical fibres from its lateral surfaces, and thus to become placed in a condition to sustain itself independently. It is more difficult to raise a new plant from a detached descending axis, since such a root is obliged to produce a leaf-bud, from which the future stem has to grow up; a reproduction which in general is much less readily effected than the formation of lateral roots from an ascending axis. Finally even a detached leaf may give origin to the formation of a new plant; in this case it must form both root and leaf-bud, to which, generally speaking, the leaves have but very slight tendency.

The readiness with which both descending and ascending axes are formed at places where they do not make their appearance in the natural course of vegetation, varies extremely in different plants, while at the same time we are unable to find a reason for this variation in the organization of the particular species of plants; in many species, for instance in the rooting of Cacteæ, Willows, &c., this development takes place so readily, that it can be counted on with the greatest certainty, while in others the development of the wanting organs, for example, of roots and still more of leaf-buds in *Pinus*, never or but very rarely occurs. In general the formation of the said organs takes place the more readily the richer the detached part is in parenchymatous cellular tissue, and the more assimilated nutriment there exists deposited in it, at the expense of which it may be sustained until the organ necessary to make it a complete plant is formed; but this rule is only valid for the extreme cases, and, mostly, we cannot say what is the reason, they are readily or not all inclined to such production.

In very many plants, the formation of buds, which grow up into distinct plants, is a regular operation, independent of external causes. These frequently separate spontaneously from the parent in a rather rudimentary condition, and grow into independent plants subsequently; in other cases, such separation occurs after the parent plant is dead and decayed, through particular ramifications of it remaining alive.

In the plants having a thallus, we meet with the formation of shoots which have not the form of the ordinary branches, but in which the formation of the parent plant is repeated. Thus, in the Algæ, new plants are not unfrequently produced, both from the frond and from the disk-like base of this, or out of stoloniferous prolongations of it. In the Liverworts and Mosses it is a very general condition for single branches, the so-called innovations, to repeat the form of the main stem, and when this decays, to appear as the stems of new plants. In the higher plants, ramifications very frequently occur, deviating in form from the ordinary leafy branches, and destined to serve for the multiplication of the plant. They present themselves either in abbreviated and thickened forms (as bulbs and tubers), in which case they do not generally produce roots of their own until detached from the parent, or, on the contrary, they exhibit a predominant longitudinal growth (as runners or stolons above or below the surface of the ground), in which case, roots are developed, and they sustain themselves independently before their separation from the parent. The branches destined to the multiplication sometimes spring from the normal place, from the axis of a leaf (*e.g.*, the bulbels of *Lilium tigrinum*); sometimes they originate from abnormal metamorphoses of flower-buds (the bulbels of the inflorescence of many species of *Allium*, the tubers of *Polygonum viviparum*); sometimes they break out, as the so-called adventitious buds, from spots which do not normally bear buds. The latter occurs on the roots of a large number of trees (*e. g.*, Poplars, Wild Cherries, Plums, &c.), as well as on the leaves of many plants (*e. g.*, *Aspidium bulbiferum, Malaxis paludosa,* and *Bryophyllum calicinum*).

The pollarding of a plant frequently causes the development of shoots. The formation of roots generally takes place readily when the descending sap is arrested anywhere in its downward course by cutting through the bark, especially when, at the same time, light is excluded from the wounded spot, and this kept moist. In this case, the roots break out in most plants from the thickening which is formed at the upper border of the wound. On the other hand, the plant is caused to form leaf-buds in unusual places when the whole of the leafy part is cut off; for then leaf-buds are formed beneath the bark, both on the lower part of the stem and on the roots, breaking through the bark, and growing up into stems. Most Dicotyledonous trees possess this power until they have attained too great an age, but most of the Coniferæ are devoid of it. This capability of forming leaf-buds is so great in many plants, that every fragment of the root may be used for raising new plants from it,—for example, in the horse-radish, *Maclura aurantiaca,* &c.

It is most difficult to induce the formation of buds on the leaves. Detached leaves have very great tendency to form roots, when they are placed in moist earth; they afford, under such circumstances, the peculiar example of a plant which fully exercises the functions of nutrition, but is altogether incapable of growth. Such rooted leaves sometimes attain an age far exceeding their usual period of existence; thus Knight, for example, saw the leaves of *Mentha piperita,* which he had caused to produce roots, maintain themselves fresh for more than a year, and assume almost the aspect of evergreen leaves (Knight, "*Selection from the Physiol. Papers,*" 270). Growth into a new plant is only possible in such a rooted leaf when it developes a leaf-bud; in general, this does not readily happen. There are plants, it is true, as already mentioned, on the leaves of which leaf-buds are regularly developed; and a considerable number of plants have been noticed, on which buds had formed accidentally, on particular leaves, still connected with the plant, *e. g., Drosera, Portulaca, Cardamine pratensis, Glechoma hederacea,* &c.; but, on the whole, these examples are rare. Buds are most readily formed on detached leaves when these have a fleshy consistence; their development has been observed in particular on the bulb scales of *Eucomis regia, Lilium candidum, Hyacinthus, Scilla maritima,* on the leaves of *Ornithogalum thyrsoides,* &c.; moreover, not unfrequently on the leaves of different species of *Crassula* and *Aloë.* Buds are formed much less readily than on such succulent leaves, on leathery leaves,—for example, of *Citrus, Aucuba, Hoya carnosa, Ficus elastica, Theophrasta,* &c., although these strike root freely (See "*On some unusual Cases of Bud-formation;*" Munter, "*Observations on special Peculiarities on the Mode of Multiplication of Plants by Buds,*"—*Bot. Zeit.* 1845, 537, *et seq*).

A detached portion of a plant is not, however, merely capable of producing the organs wanting to form a perfect plant, but it is also in a condition to become blended with another plant, and lead a common life with it, on which capability depend the numerous garden operations which are known under the not very apt name of "ennobling" (*veredeln*, grafting). The conjunction of young, succulent parts, still in course of development, is a necessary condition of this blending. This condition is very easily fulfilled in Dicotyledonous plants, because there exists between the bark and the wood a layer of elementary organs in course of development, the so-called *cambium*, and thus there is little difficulty in so uniting the two plants, that this layer, of both parts, meets at least at one point. But in the Monocotyledons, in which the vascular bundles lie scattered through the whole stem, and no definite cambium layer exists, the conditions are far more unfavourable. It is true, according to De Candolle's account ("*Physiol.*" ii. 787), the gardener Baumann, of Bollwiler, succeeded in grafting *Dracæna ferrea* on *Dr. terminalis;* but the graft died after one year. But the experiments of Caldrini ("*Ann. d. Sc. Nat.*" 3*me ser.* vi. 131) on the grafting of Grasses, had a more favourable result, for he succeeded in grafting even species of different genera, *e. g.*, Rice upon *Panicum crus galli* with success, a result which is explained by the fact that, in the Grasses the lower part of the internodes enclosed in the leaf-sheath remains for a long time soft and succulent. A second necessary condition of the blending of growth, is great similarity of the two plants; they must not only be nearly allied botanically, but have a great agreement in the composition of the sap.

Observ. 1. The possibility of grafting plants upon one another is determined, in general, by their systematic position, yet many anomalies occur. While it is usual that different species of one genus can be grafted upon one another, and in many cases it is even possible in species of nearly-allied genera, as, for instance, Pears on Quinces, on *Cratægus Oxyacantha*, or on *Amelanchier vulgaris*, while *Syringa vulgaris* at least grows to *Fraxinus excelsior*, to *Phillyrea latifolia*, *Olea europea* to *Fraxinus* (De Candolle's "*Physiol.*" ii. 791) and *Castanea vesca* to Oaks; yet, on the contrary, in many cases an union, or at least the maintenance for a long endurance of the graft, cannot be secured, in spite of far closer botanical affinity, *e. g.*, between Chesnuts and Beeches, or Apples and Pears.

Observ. 2. The propagation by division is in many cases of the highest practical value. Although the case occurs here and there, that a particular branch of a plant disagrees from the rest of the branches of the specimen in certain small peculiarities of growth, the colour of the leaves, the doubleness of the flowers, the character of the fruit, &c., possessing the properties of a special variety, yet this is an exception to the rule. Every part detached from a plant retains this agreement after its separation, and thus propagation by division affords the means of multiplying certain varieties which could not, or only with uncertainty, be propagated by seed. Cases certainly do occur in grafted trees where the composition of the sap of the stock exercises a certain influence upon the characters of the fruit of the graft, but on the whole, this is an exception. (Gärtner has given a comparative account of the observations on this subject, in his "*Experiments and Observ. on Hybridation*"—"*Versuchen und Beobacht. üb du Bastardbildung*," 606.)

b. Propagation by Spores and Seeds.

In all vegetables which attain their full normal development, the period of vegetation is succeeded by that of fructification, whether, as in the lower plants, the same cells which in youth executed the vegetative functions, in their subsequent period of life become organs of fructification, or, special organs of fructification become developed.

Observ. The universality of this proposition is truly only borne out by analogy with the majority of plants, for in the present condition of our knowledge we cannot determine whether all vegetables fructify. In many lower plants we are still unacquainted with any fructification, either because they are really deficient in them, as may be possible for instance in the Yeast-plant, or that we do not know all the stages of their development. The latter is the case in many lower plants; the difficulty of studying them is increased by the fact that a large number of forms have been described as peculiar species, especially among the Algæ, which are only earlier stages of development, and in many cases abnormal examples produced by unfavourable external conditions of plants frequently belonging to totally different families.

The organ destined for a germ may always be traced back to an origin from a single cell. When this cell, at the epoch of its separation from the parent plant, contains no rudiment of a new plant, but only an organizable fluid, or, in rarer cases, a few secondary cells firmly blended with its membrane, and this cell, after its separation from the parent plant, under the influence of external circumstances favourable to the excitement of vegetation, grows up directly into a new plant through expansion of its membrane and production of new cells in its interior, this is called a *spore* (*spora, keimkorn*). The formation of spores takes place without fertilization, and plants which are propagated by spores are termed *Cryptogamia* or *Exembryonatœ.*

When, on the other hand, the propagative cell (as *embryo-sac*) forms part of a compound organ, and through previous impregnation, produces in its interior the rudiments of a perfect plant, furnished with stem and root (the *embryo, keim*), and this becomes detached with the enveloping parts formed by the further development of the ovule, from the parent-plant, these envelopes together with the embryo, are collectively termed the seed, and the plants which bear seeds, *Phanerogamia* or *Embryonatæ.*

Observ. As will appear below, all the plants bearing spores are not unisexual, but the impregnation in them stands in a totally different relation to the production of the new plant, from what it does in the Phanerogamia. In the latter, the formation of the embryo is the immediate result of the impregnation; when this does not take place, the seed cannot germinate. In the Cryptogamia, on the contrary, which have an impregnative process, neither the cell which forms the spore, nor the spore itself become impregnated, but this is formed and becomes capable of germination without a previous impregnation, and impregnating organs are found, sooner or later, upon a germ-plant, or *pro-embryo,* growing from the spore, upon the action of which organs depends the development of the yet imperfect plant into a complete vegetable.

a. PROPAGATION BY SPORES.

a. Propagation of Thallophytes.

There is considerable variation in the modes of development of the spores in the different groups of Cryptogamous plants. It will not be without interest to take a brief glance at the principal modifications.

In the Fungi we are above all struck by the production of an enormous number of spores, so that in proportion to the great mass formed by the spores, and in the higher Fungi in proportion to the large sporangium, the vegetative part of those plants, the thallus, composed of loosely-connected filaments, and in most cases devoid of any definite outline, exhibits an inconsiderable development.

In the lowest forms of Fungi, the *Coniomycetes* and *Hyphomycetes,* the formation of the spores, notwithstanding the innumerable shapes under which these plants present themselves, is extremely simple, their production depending on a breaking-up of the fructifying part of the Fungus into its constituent cells, or into granules composed of several cells closely connected together; whence Léveillé says, correctly, that the Fungus consists, in its simplest form, of a simple or cellular filament terminating in a spore. When we come to the *Mucorineæ,* we already find an advance, for here, as in *Ascophora,* the extremity of the filament expands into a vesicular cell, in the cavity of which a mass of spores are formed by free cell-formation. A similar origin of the spores is met with also in the higher forms of Fungi, in which, however, the single cell producing the spores no longer constitutes the entire organ of fructification, but large sporangia appear under the most varied forms, wherein the parent-cells of the spores are collected together in a definite layer, which sometimes lines the cavity of the sporangium, as in the *Gasteromycetes,* sometimes forms a globular nucleus imbedded in the substance of the sporangium, as in the *Pyrenomycetes*, and sometimes appears as a membrane lying free upon the outer surface of the sporangium, as in *Discomycetes* and *Hymenomycetes*. In the higher Fungi, the number of spores formed in a parent-cell is definite, and we meet at once here that fixed numerical relation, which remains the same in the formation of the spores of the Cryptogamia and of the pollen-grains of the Phanerogamia throughout the whole Vegetable Kingdom, according to which, usually four, more rarely eight or sixteen, spores or pollen-grains are formed in a parent-cell, while the number may also sink on the other side to two or one. Among the Fungi, four spores are formed in the majority of cases (in the *Hymenomycetes*), sometimes only two or one in a cell; in a few groups, as in the *Tuberaceæ* and *Discomycetes*, the number rises to eight (Léveillé, "*Rech. s. l'hymen, d. Champign.*"—*Ann. d. sc. nat. sec. ser.* viii. 321; Corda "*Icones Fungorum*").

In regard to the form of the parent-cells, two modifications occur. In the *Pyrenomycetes*, *Discomycetes*, and *Tuberaceæ*, they appear as longish utricles *(asci)*, in the cavity of which the spores are developed by free cell-formation, after a previous production of a nucleus, and then frequently *(e. g., Peziza)* each spore again divides by a septum into two, sometimes even into more, cells. In the *Lycoperdaceæ* and *Hymenomycetes*, on the contrary, four (in rare cases only two, or one) protrusions of the wall of the parent-cell are formed, each of which becomes the seat of the production of a spore. These parent-cells are called *basidia*.

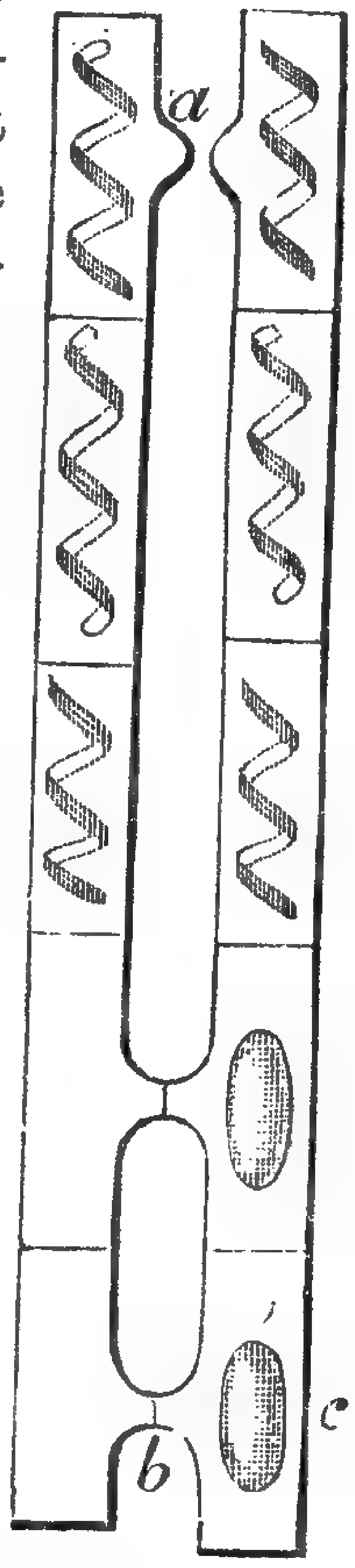
From the small size of the spores of most Fungi, it is not decided whether the cell-membrane of the spore secretes a special layer upon its outer surface in all cases (a kind of cuticle). In a great number this may be easily perceived; like the outer coat of pollen-grains, it is frequently covered with reticularly connected ridges, little spines, &c. In germination, the coat of the spore extends itself into a filament, which in the minute mildew-like Fungi is capable of growing on into a perfect plant. Whether this production of a new Fungus from a single spore occurs also in the higher Fungi, or whether the filaments which grow forth from a number of spores germinating side by side, must become combined into a common tissue, has yet to be decided by observation. The latter is at all events a common process. (*See* Ehrenberg's "*De mycetogenesi, Nov. Act. Nat. Cur.*" x. p. 1, 161.)

In the Lichens the fructification of many Fungi (*Pezizeæ* and *Sphæriaceæ*) is repeated most exactly. In the interior of the thallus is formed a gelatinous nucleus of elongated cells, converging towards the central point, and embedded in an abundance of intercellular substance. A portion of these cells become tubular (*asci* or *thecæ*) and produce the spores. In the naked-fruited Lichens the thallus opens above the nucleus, and the latter spreads out into a more or less flat disk (the thecal layer); in the covered-fruited, it remains enclosed in the thallus. In each of the parent-cells eight spores are formed by free cell formation, and in very many cases these form two, four or a greater number of secondary cells in their interior. Very few observations have been made on the germination of these spores. According to Holle (" *Zur Entwickelungsg. von Borrera ciliaris.*"—On the development of *B. ciliaris*, Diss. 1848, Göttingen), the secondary cells break through the primary spore cell as filaments, and are converted into cells outside the spore. According to Meyer's account (" *Nebenstunden mein. Beschaftigung.*" 175), the outer membrane of the spore is not torn, and when a number of spores germinate side by side, the filaments into which they grow out become blended together, and contribute jointly to the formation of a new plant.

According to the observations of Tulasne (" *l'Institut,*" No 849), the inner spore-coat, both of simple and compound spores, grows out into one or more filaments, which soon ramify and acquire septa, and whose short interlacing branches form little cushions, upon which little colourless cells accumulate, and in which the green cells forming the rudiments of the cortical layer of the new plant, make their appearance.

We meet with a far greater complication of phenomena when we look towards the spores of the Algæ, even though here no co-operation of two sexes occurs. This latter may indeed seem doubtful in a number of Algæ, in which a so-called *copulation* occurs, but a more minute examination of this process shews that it bears no analogy to sexual reproduction. This conjugation presents itself most distinctly in the so-called *Conjugatæ* (the genera—*Zygnema*, fig. 49, —*Tyndaridea*, *Mougeotia*, *Staurocarpus*, &c.), in which it was observed first by Vaucher. The filaments of these Confervæ lie parallel, side by side, or bent in a ziz-zag manner towards each other, and send out from their cell-walls towards the the nearest cell of the neighbouring filament, a blunt branch (*a*), which grows together with a similar and corresponding branch of the other cell coming to meet it, upon which the partition in the cross-branch (*b*) becomes absorbed, and the solid matter of the contents of both cells becomes balled together into a mass in the cavity of one of them, or in the connecting branch, this mass acquiring a cellulose membrane, and in this way being converted into a spore (*c*). The following circumstances tell against this process being considered as an act of impregnation. The contents

Fig. 49.



Two cells of *Zygnema* just in the act of conjugating.—*a*, commencement of the formation of the connecting branch; *b*, connecting branch; *c*, spore.

of the two cells are exactly similar; sometimes all the cells of one filament take away the contents of the cells of the other; sometimes this happens only to a part of the cells, while the rest empty themselves into the cells of the second filament; and sometimes spores are formed in cells which have not copulated, all this taking place without any definite rule.

Copulation has recently been discovered in many uni-cellular Algæ, in particular by Morren in *Closterium* (*"Ann. d. Sc. nat. sec. sér."* v. 257), by Ralfs, in the Desmidiaceæ, and by Thwaites (*"Ann. of Nat. Hist."* xx. 9, 343) in the Diatomaceæ. Remarkable as the whole process of copulation is, its product is, in many respects, enigmatical in no less degree. In the copulation of uni-cellular Algæ, two new individuals are generally formed; thus there is no increase connected with this mode of propagation, but frequently only one new individual is formed, and thus is presented the strange phenomenon of a propagation resulting in a diminution of the number of individuals, since the copulating individuals die. In the Diatomaceæ, moreover, the individuals produced by copulation are much larger than their parents. In the majority of copulating Algæ, particularly in the Desmidiaceæ and *Zygnemeœ*,* the spore produced from the union of the contents of the two cells has not yet been seen to germinate, and it is not improbable that it ought to be regarded, not as a spore, but as a sporangium, that is to say, as a cell, the contents of which become developed into numbers of germs (*See* Agardh, *"Ann., d. Sc. nat. sec. Sér"* vi. 197; Hassall, *"Brit. Fresh-water Algœ,"* 24; Ralfs, *"Desmidieœ,"* 10).

In by far the greater number of the Algæ, the spores are not formed by copulation, but in single cells, either, as in the lower forms, in the vegetative cells towards the close of their existence, or in special fructification cells.

The spores of a very large number of Algæ, either before their exit from the parent-cell, but principally in the period just succeeding the emission, exhibit a movement, which is often very rapid. These movements have not unfrequently been taken for animal, voluntary motions, and have given origin to the most fabulous conceptions concerning the transformation of animals into plants. We owe the first extensive and accurate observations on these moving spores to the younger Agardh (*"Ann. d. Sc. nat. sec. Sér."* vi. 193), who called them *Zoospores.* According to his researches, they occur in the *Nostochineœ, Oscillatoriœ, Conferveœ, Conjugatœ, Ectocarpeœ, Ulvaceœ*, and *Siphoneœ.* The following is his account of their development. During the later periods of the growth of the cells, the chlorophyll, which in the young cells of these plants forms a homogeneous mass, becomes transformed into globules, which towards the close of the cell's life assume a spherical shape, become detached from the wall of the cells and balled together in

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* Erroneous in regard to Zynemeæ, *see* Vaucher, Meyer, and, more recently, Pringsheim. *Flora*, Aug. 1852.—A. H.

a globular lump in the middle. A "swarming" now begins to be evident in this mass, the granules become isolated, and swim about the cavity of the cell. A papilliform protuberance is afterwards produced from the cell-wall, which tears at its apex, and the spores making their way out by this orifice swim about in the surrounding water. By degrees they begin to withdraw towards the darkest part of the water, become attached to any solid body, and begin to germinate, by an expansion of their membrane. Agardh observed a transparent process (beak, *Schnabel*) at that end of these spores which always went first in the movements. But the true organ, on which this movement depends, is not this beak, which itself is motionless, but, as Thuret first shewed ("*Ann. d. Sc. nat. sec. Sér.*" xix. 266), there exist at the brighter coloured end of the spore, ciliæ of various lengths moving rapidly, and by their vibrations causing the motion of the whole spore. The number of these ciliæ differs in different genera. Thuret found in *Conferva glomerata* (*see* tab. 1, 23, 24,) and *rivularis*, two ciliæ on each spore, in *Chœtophora elegans* four, on the spores of *Prolifera* a circle of very numerous ciliæ, (*see* tab. 1, 19—22, which represent the spore (19) and its first stages of development, after Thuret); subsequently ("*Ann. d. Sc. nat. 3me. Sér.*" iii. 274) he made known that the spores of *Ectocarpus* have two, those of *Ulva* and *Enteromorpha* four ciliæ. These observations obtained full confirmation by others, especially by Fresenius ("*Zur Controv. üb. die Verwandl. von Infus. in Algen*), and by Alex. Braun (repeated by Siebold, "*Ann. d. Sc. nat. 3me. Sér.* xii. 151). The opinion that these spores possess animal life during the period of their movement, and become plants at the moment of germination, does not, however, depend merely on a confusion of their movements with the voluntary motion of animals, but derives an apparent confirmation from the fact that in very many cases each of these spores contains a red spot (according to Nägeli a red oil-drop), which was taken for an eye by Ehrenberg and others. Even before Thuret had made known his observations upon the organs of motion of the zoospores, Unger ("*Die Pflanze im Momente der Thier-werdung*") had published very minute observations upon the formation and motion of the very large spores of *Vaucheria*. In *Vaucheria*, the single granules of chlorophyll are not developed into minute spores furnished with a few ciliæ, but the entire mass of chlorophyll of the terminal joint of a filament, or of globular protuberances seated upon lateral branches, after being separated from the contents of the rest of the fibre by a septum, becomes balled together into one common spore, which makes its way out by a slit in the cell-membrane and exhibits rapid advancing and twisting movement. It is covered all over with countless very short ciliæ. The whole of the formation of the spore occurs early in the morning, its exit from the parent-cell usually takes place about 8 A.M., and after its motion has endured for half-an-hour, or at most two hours, it comes to rest, the outer coat covered with ciliæ, disappears very rapidly (by decomposition ?) and germination commences by the coat of the spore growing out into a filament.

Observ.—These observations first demonstrated the existence of ciliæ in the Vegetable Kingdom. It may be distinctly seen in *Vaucheria* that they do not belong to the cell-membrane (spore coat), but to a membrane clothing this. What the corresponding condition is in the zoospores, is as yet unexplained, since a membrane enveloping the whole spore has not yet been observed in these. Perhaps this may arise solely from the small size of the spores and the tenuity of their coating membrane, perhaps, however, the coat only exists locally around the beak and the points of insertion of the ciliæ. Mettenius, indeed ("*Beiträge zur. Botanik,*" i. 34), assures us that the ciliæ are in connexion with the contents of the spores, but he has not offered sufficient evidence of this. When we compare these motions with the ciliary phenomena of animal cells ,and with the motions of the seminal filaments of the higher Cryptogamia, no doubt can remain that the movements of the ciliæ are the cause and not the effect of the movement of the spore, as Nägeli ("*Unicellular Algæ,*" 22) believed; an opinion against which V. Siebold has already declared. The action of poisonous substances, such as alcohol, opium, and iodine, immediately arrests the motion.

It appears possible for the formation of zoospores to originate from one single granule of chlorophyll, while in other cases, where only one or few spores are developed in a cell, (*e. g. Draparnaldia, Chætophora*), perhaps larger sections of the mass of chlorophyll, or even the primordial utricle, by becoming constricted into separate segments, are the parts concerned in the formation of the spores. The actual conversion into a spore is not accurately known in its intimate processes, but must consist essentially in the formation of a cellulose membrane around the chlorophyll granules. It has already been remarked that in *Vaucheria* the whole mass of chlorophyll of a cell becomes coated with a membrane. Intermediate forms between these two extremes are met with, thus Saulier ("*Ann. d. Sc. nat. 3me. Sér.*" vii. 157) found in the genus *Derbesia*, very closely allied to *Vaucheria*, that neither the entire mass of chlorophyll collected into one spore, nor did its grains remain isolated, but separate groups, each composed of hundreds of grains of chlorophyll, became gathered up into globular masses, acquired a membranous coat and formed a short beak and a circle of ciliæ upon the surface.* Unger ("*Linnæa.*" 1843, 129) observed a perfectly analogous formation of the spores of *Achlya prolifera*, which, according to Thuret ("*Ann.*

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* See further on this subject, Thuret, "*Ann. des. Sc. nat.* 3 *Ser.*" tom. xiv. and xvi.; Cohn on *Hæmatococcus,* Nova. Acta. vol. xxii., and on *Stephanosphæra*, "*Annals of Nat. Hist.*" Oct. and Nov. 1852.—A. Braun. "*Ueb. die Verjungung,*" Leipzig 1851. The active zoospores have no cellulose membrane when first set free.—A. H.

d. Sc. nat. 3me Sér." iii. 274), likewise possess a circle of very numerous ciliæ.

Whether, as Agardh assumed, the power of motion in the spores of the lower, and the want of it in those of the higher Algæ (the *Ceramieæ*, *Florideæ*, and *Fucaceæ*) warrants a rigid division of these plants into two sections, appears very doubtful, for according to Decaisne and Thuret ("*Ann. d. Sc. nat. 3me Sér.*" iii. 10) not only do the spores of the Fucaceæ present the same coat covered with short ciliæ as those of *Vaucheria*, which, however, either from the size or some other cause are motionless, but there also occur in the Fucaceæ small moving spores bearing two ciliæ, enclosed in special cells, sometimes on the same plants that produce the spores, sometimes on distinct specimens. The said observers, indeed, have not recognized them as spores, but interpreted them as seminal filaments, but they have not the least resemblance to these, while they agree with the zoospores in form and in the presence of a red point, the so-called eye. It is truly a remarkable circumstance that one plant should bear two kinds of spores, differently formed, but the same occurs again as an universal rule in the *Ceramieæ* and *Florideæ*, for these plants bear not only the generally recognized spores, and gemmæ testifying their nature as such by generation, which originate, like pollen-grains, in a parent-cell dividing into four chambers (the so-called *tetraspores*), but other spores also, which are not produced in fours in a parent-cell, and are contained in variable numbers in fructifications of the most diverse shapes (*capsula*, *glomeruli*, *favella*, &c.). The spores of this second kind germinate, as Agardh has shewn, like the tetraspores, their membrane extending itself on one side into a root-like prolongation, on the other into a filament which divides into cells, and grows up into a plant.

Decaisne and Thuret observed a most peculiar circumstance in the spores of many Fucoideæ; namely, the spores had not completed their development at the time of their maturation and detachment from the parent plant, for, after this, commenced a division into the proper germinating spores (in *Fucus serratus* and *vesiculosus* into eight, in *F. nodosus* into four, in *F. canaliculatus* into two secondary spores).

Martins thought he had found, in the spores of *Fucus*, that the separate spores did not grow up into new plants, but as in the Fungi, a number of germinating spores became conjoined to form one common plant. This has been sufficiently refuted by Agardh, Decaisne, and Thuret. The spores of the Fucoideæ germinate like those of all other Algæ, by expansion of their internal coat on one side, into a root-like fibre, on the other into a filament which becomes subdivided into cells.

** *Propagation of the Cryptogams having Stem and Leaves.*

While in the three families of Cryptogamia possessing a thallus (with the exception of the Charas, to be mentioned presently) all attempts to discover male organs has proved the more vain the further the investigation of these plants has advanced, in the more highly organised families of Cryptogamia, on the contrary, in which there exists separation of the organs of vegetation into stem and leaf, the last few years have seen the discovery of convincing proofs of the existence of two sexes.

In the last century, when Hedwig in particular devoted himself to the investigation of the Cryptogamia, the idea that two sexes must exist in all Cryptogamous plants, was quite predominant; and thus, often enough without a trace of consideration, the most diverse parts were, from mere opinion, separated as male organs. This brought the whole effort to discover impregnating organs into discredit, and the opinion that all the Cryptogamia were devoid of male organs, and developed their spores without previous impregnation, became more and more diffused. It is true that organs had been discovered in certain Cryptogamous families, especially the Charas and Mosses, which from the time of their appearance, from their position, &c., stood in evident relation to the fruit; but since no positive influence could be proved to be exerted by them upon the young sporangia, their function as anthers was denied; although it was at the same time admitted they had a certain analogy with them, whence they were, indeed, called *antheridia*. In more recent times, two circumstances seemed chiefly to strengthen the earlier doubt which had been entertained as to the function of the antheridia. My own researches, namely, shewed that the spores of the higher Cryptogamia do not, as had been previously supposed, exhibit a resemblance in respect to their development and structure, to the seeds of the Phanerogamia, but that the most perfect agreement exists between them and the pollen-grains of the Phanerogamia. From this it necessarily, yet strangely, appeared that organs of perfectly like structure fulfilled the function of germs in one part of the Vegetable Kingdom and in the other part constituted the male, impregnating organs; but, little as the formation of a pollen-grain depends upon an impregnation, no one circumstance shewed itself in the development of the spore, at all more resulting from the co-operation of an impregnating organ. Still more doubtful did the theory of the impregnation of the Cryptogamia necessarily become, when Nägeli made the discovery, in the Ferns, of antheridia in many respects resembling those of the Mosses, which were not formed upon the full-grown plant at the same time as the rudiments of the sporangia, but occurred upon the germ-plant (*pro-embryo*), while the perfect plant was devoid of them.

Under these circumstances, Schleiden seemed to be warranted in characterizing the effort to discover impregnating organs in the Cryptogamia, as a mania. But by good luck, certain men who had this mania did not allow it to lead them astray in their researches, and as often happens, nature this time proved so rich that, not indeed was what had been sought found, but instead of this a series of conditions, the existence of which was previously altogether unsuspected. The researches relating to this point are, it is true, still far from their completion, since at the present moment nothing more than a preliminary notice of isolated conclusions already arrived at can be given; but these, although isolated, cause us to expect with certainty in this field a series of the most striking discoveries.

The Mosses have served for a very long period as the main props of the view that two sexes and an impregnation occur in in the higher Cryptogamia. Not only was attention naturally called in these to the constant occurrence of the antheridia, and their great development, but trustworthy experience, formerly of Bruch, more recently of Schimper ("*Rech. s. l. Mousses.*" 55) demonstrated that Mosses which have antheridia and the rudiments of sporangia upon the same stem always bear fruit, while diœcious Mosses never set fruit in localities where only female specimens grow. No one has succeeded in making out the mode in which the antheridia act upon the rudimentary fruit; but the physiological fact just mentioned does not lose its force on that account.

A second family indicating the necessity of an impregnation, were the Rhizocarpeæ, since numerous observations had shewn that the large and small spores of these plants could not be separated without preventing the former growing into new plants. Schleiden, indeed, had extended his theory of the development of the embryo from the pollen-tube to this family, and arranged them with Phanerogamia. But nothing was gained by this, for, on the one hand, Schleiden's whole theory of impregnation proved a false beacon; on the other, Schleiden's statements as to the Rhizocarpeæ were not confirmed, and this more particularly in the most essential point, the mode of origin of the embryo.

Then unexpectedly appeared Count Leszcyc-Suminski's essay on the development of Ferns ("*Zur Entwicklungsgesch. der Farrenkräuter,*" 1848), the contents of which at first seemed fabulous, so contradictory were they to all that was known of the organization and development of plants. But a more minute study of this treatise —a comparison of the author's results with nature—soon shewed that although he had been deceived in a few particulars, his account was far from being a creation of the fancy, and that his researches had broken open a path to a long series of discoveries.

In all families of the leafy Cryptogamia (with the exception of the Lycopodiaceæ*) antheridia have been discovered, exhibiting it is true considerable variations of external form and structure in the different families, but collectively agreeing in the circumstance of developing in their interior very delicately-walled cells, at first containing an amorphous substance coloured yellow by iodine, in place of which, at the epoch of maturation of the antheridia, a deli-

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* Now found in these also, *see* note further on.—A. H.

cate filament presents itself, displaying several spiral convolutions, thickened at one end and running off to a very fine point at the other. The filaments manifest lively motions, exhibiting differences according to the manner in which they are rolled up, in some cases while still enclosed in the cells where they are developed, but more particularly after they have emerged into the water from antheridium, which opens when ripe. Thus, when the filament is rolled up like a watch-spring, the motion is more or less rotatory, but if it is coiled over in the form of a cork-screw, the movement is at the same time an advancing one. In these movements the thin end of the fibre almost always goes first. Minute observation, which in many cases is very difficult, both from the rapidity of the motion (which, however, is readily arrested by poisons), and the great delicacy of the whole structure, shews that the movements arise from extremely delicate and comparatively long ciliæ, of which two are usually found at the thin end of the filament, and which only seem to occur in larger numbers in the Ferns. The filament itself exhibits no independent motion, as indeed, altogether, the kind of motion does not indicate any will. The term seminal filaments has been not inaptly applied to these filaments.

Observ. The first observation on the motion of the contents of the antheridia was made by Schmidel ("*Icones plantarum,*" 1762, 85) in *Jungermannia pusilla.* The imperfection of the microscopes of that period, however, seems to have prevented his seeing the seminal filaments, and he probably only observed the cells in which the filaments were enclosed. The same seems to have been the case with the observations made by Fr. Nees von Esenbeck ("*Flora,*" 1822, 1, 34) in the antheridia of *Sphagnum.* He considered the moving bodies which he saw to be globular monads, and did not doubt their animal nature. The spiral filaments themselves were discovered by Unger in the Mosses and Liverworts ("*Ann. d. Sc. nat.* 2, *Ser.*" xi. 257); in accordance with the then prevalent notions on spermatozoa, he regarded them as animals, and applied to them the name of *Spirillum bryozoon.* Recent years have scarcely added to his observations on the seminal filaments, more than the fact that two ciliæ exist at the thin end of the filaments, which Unger had overlooked (Decaisne and Thuret, "*Ann. d. Sc. nat.* 3, *Ser.*" iii 14). Plate 1, figs. 26—28. Seminal filaments of *Sphagnum;* fig. 26, represents two anther-cells with the seminal filaments enclosed; fig. 27, one of the latter seen from the side (from Unger). To me the filaments appear to have the form which I have represented in fig. 28.

The structure of the Moss-anthers is very simple. It consists of a simple sac, with a wall composed of a single layer of cells, which, according to Unger, are applied upon the outside of a large cell, while according to Schimper they are enveloped on their outer sides by a continuous membrane composed of intercellular substance. When mature, this coat is torn at the apex, and the contents, now dissolved into a mucilaginous fluid, issue from it.

The anthers of the Liverworts possess a structure completely analogous to that in the Mosses (Gottsche, "*Act. Acad. Nat. Cur.*" xx. 1, 293), only the wall of the sac, at all events in many species, is composed of two layers of cells.

The anthers of *Chara,* of which Fritzsche ("*Ueber den Pollen,*" 6) has given the most accurate description, possess a highly complicated structure. Into the globular cavity enclosed by the eight cells containing red-coloured granules, projects a flask-shaped cell, almost as far as the middle; from its apex run out a mass of fine confervoid filaments, which are divided up very closely into joints, and in each of the cells is developed a seminal filament. The existence of an infusorial motion of these filaments was observed by Bischoff ("*Cryptog Geir.*" 1, 13); their exact form (plate 1, fig. 25, from Thuret), and the two ciliæ, by which they approximate closely to seminal filaments of the Mosses, were first made out by Amici (whose essay on this subject has not been printed) and Thuret ("*Ann. d. Sc. nat.* 2 *Ser.*" xiv., 66).

In the Ferns the most different parts had long ago been interpreted, without any judgment, as male organs, even the stomates of their leaves, the *annulus* of their capsules, &c., when Nägeli ("*Zeitschr f. Wiss. Bot.*" 1, 168) made the unexpected discovery that antheridia containing moving seminal filaments, occur upon their pro-embryo. This was contrary to all theory, yet as the observations of Thuret ("*Ann. d. Sc. nat.* 3 *Ser.*" xi. 5) and Leszcyc-Suminski shewed, nevertheless proved well founded. The structure of the antheridia of these plants bears a considerable resemblance to that in the Mosses; they are composed of a pedicellated cell, in the cavity of which is formed a second cell, filled with the small cellules containing the spiral filaments. The entire organ bursts at its summit, and extrudes its mucilaginous contents enclosing the seminal filaments. The latter are ribbon-like and flattened down, possessing, according to Suminski (plate 1, fig. 29) about six, according to Thuret numerous ciliæ. Schacht ("*Linnæa,*" 1849, 758, &c.) agrees with the last statement, and states that the ciliæ are attached upon the narrow curves, and not on the thick end at the widest curve of the filaments.

Thuret found the same organ on the pro-embyro of the Equisetaceæ.

The last Cryptogamia on which the spiral filaments have been found are the Rhizocarpeæ.* Nägeli ("*Zeitschr f. Wiss. Botanik.*" iii. 199) succeeded in finding them in *Pilularia.* The pollen-grains (small spores) undergo a change after they have been discharged from the anthers, by the inner coat bursting the outer, and afterwards tearing, itself, to emit minute cellules which are filled with mucilage and starch. In these minute cells a vacant space is subsequently formed at one end, in which appears a spiral filament, turning round and round, and leaving the cell the thin end foremost. The same phenomena have been observed by Mettenius in *Isoëtes* ("*Beitr. z. Bot.*" 1, 17).

Thus have antheridia and seminal filaments been found in all the leafy Cryptogamia, with the exception of the Lycopodiaceæ.† Whether seminal filaments occur in any other of the Thallophytes besides the Charas, remains to be seen. It is true that Nägeli ("*Die neuer Algensysteme,*" 186; "*Zeitsch. f. Wiss. Bot.*." iii. 224; "*Bot. Zeit.*" 1849, 572) has stated that antheridia occur in the Florideæ, the essential parts of which consist of

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* † Hofmeister ("*Fruchtbildung, Keimung, &c., der Cryptogamen,*" *Leipz.*, 1851) has since shewn that the small spores of *Selaginella* produce seminal filaments, exactly in the same way as those of Isoëtes.—A. H.

cells 1-900th of line in diameter, with a scarcely visible spiral filament within ; but it may be permitted, considering the difficulty which such minute size of the organ opposes to observation, to doubt, with Mettenius, whether there are really seminal filaments.*

The uniformity of the seminal filaments contained in the antheridia of the leafy Cryptogamia, leaves no doubt, in spite of the difference of structure as above described, that these organs are of the same physiological nature. The circumstance, however, that these organs present themselves at such different stages of development of the plants, must appear in the highest degree surprising and indicative of altogether unlooked-for differences in the propagation of these vegetables. From the study of the Phanerogamia, we are accustomed to regard the organs of fructification as the last stage of vegetable development, since their formation puts a period to any growth of the vegetative axis, and the maturation of the seed frequently involves the death of the parent organism. We meet with the same condition in the Mosses, in which the antheridia and the rudiments of the sporangia are developed at the same time, the full development of the fruit succeeding the ripening of the anthers. In the Ferns, on the contrary, the condition is diametrically reversed. The development of the sporangia follows the usual law, but the formation of the antheridia takes place upon the pro-embryo after the spores have germinated, never to be repeated in the plant growing up from the pro-embryo. In the Rhizocarpeæ, finally, the cells which enclose the seminal filaments are first developed after the pollen-grains (small spores) have been shed; they are as it were diœcious plants, in which only the female plant arrives at perfect development, the male being arrested at the stage of a germinating pollen-grain, which only produces seminal cells, and then dies.

Before I pass to the consideration of the female organs of fructification of these plants, it will be necessary to speak of the spores and their development.

I have already indicated that the spores of the higher Cryptogamia agree completely with the pollen-grains of the Phanerogamia in regard to their development and structure. Not only in a portion of the Cryptogamic families, namely in the Equisetaceæ, Ferns, and Lycopodiaceæ, does the sporangium fully agree with the theca of an anther in morphological respects (" *Morph. Betracht. des Sporang. d. m. Gefäss. verseh Kryptog.,"*—Mohl " *Verm Schrift,"* 94), but the development of the four spores in a parènt-cell, and their structure, as has been more minutely pointed out above, are completely in agreement with the development and

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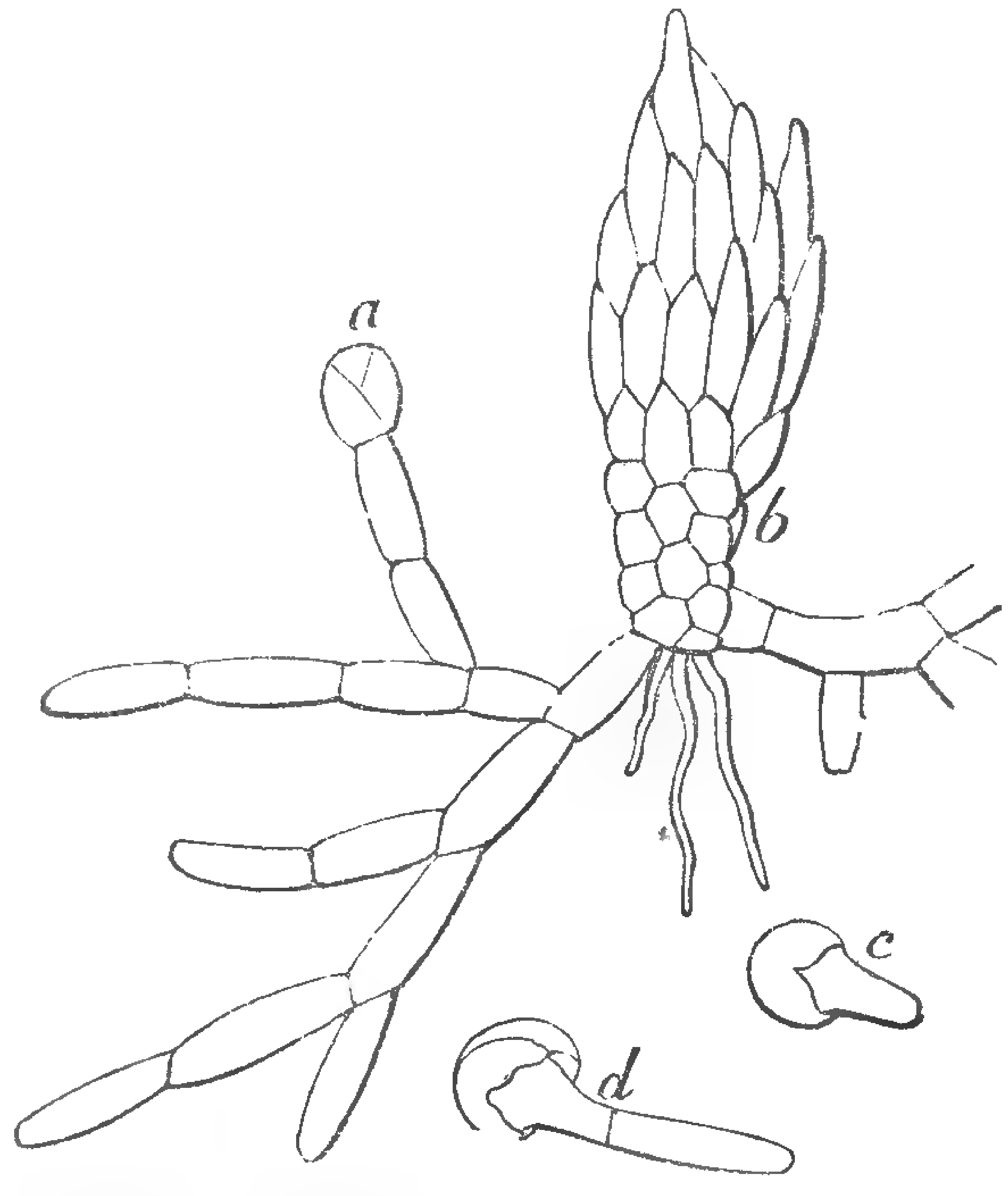
* The recent observations seem to indicate the existence of sexes in the Lichens, (" *Itsigsohn"—Bot. Zeit.* 1850, 51), and the Fungi (" *Tulasne, Comptes rendus,"* 1851, Berkeley and Broome, " *Brit. Association,"* 1851.) —A. H.

structure of the pollen-grains. Just as the latter are developed in the anther without the co-operation of another organ, does this occur also in the spores. In certain Cryptogamia (the Rhizocarpeæ and Lycopodiaceæ) we find the peculiar condition, that spores of two kinds are developed simultaneously, in a wholly analogous manner in parent-cells, in capsular receptacles of two kinds, the spores larger and smaller, possessing exactly the same structure, except that one kind are larger and have a tougher outer coat. But in the Rhizocarpeæ, only the larger exercise the function of spores, the smaller, as above stated, developing the cells which contain seminal filaments; in the Lycopodiaceæ, on the contrary, both kinds of spores produce plants.*

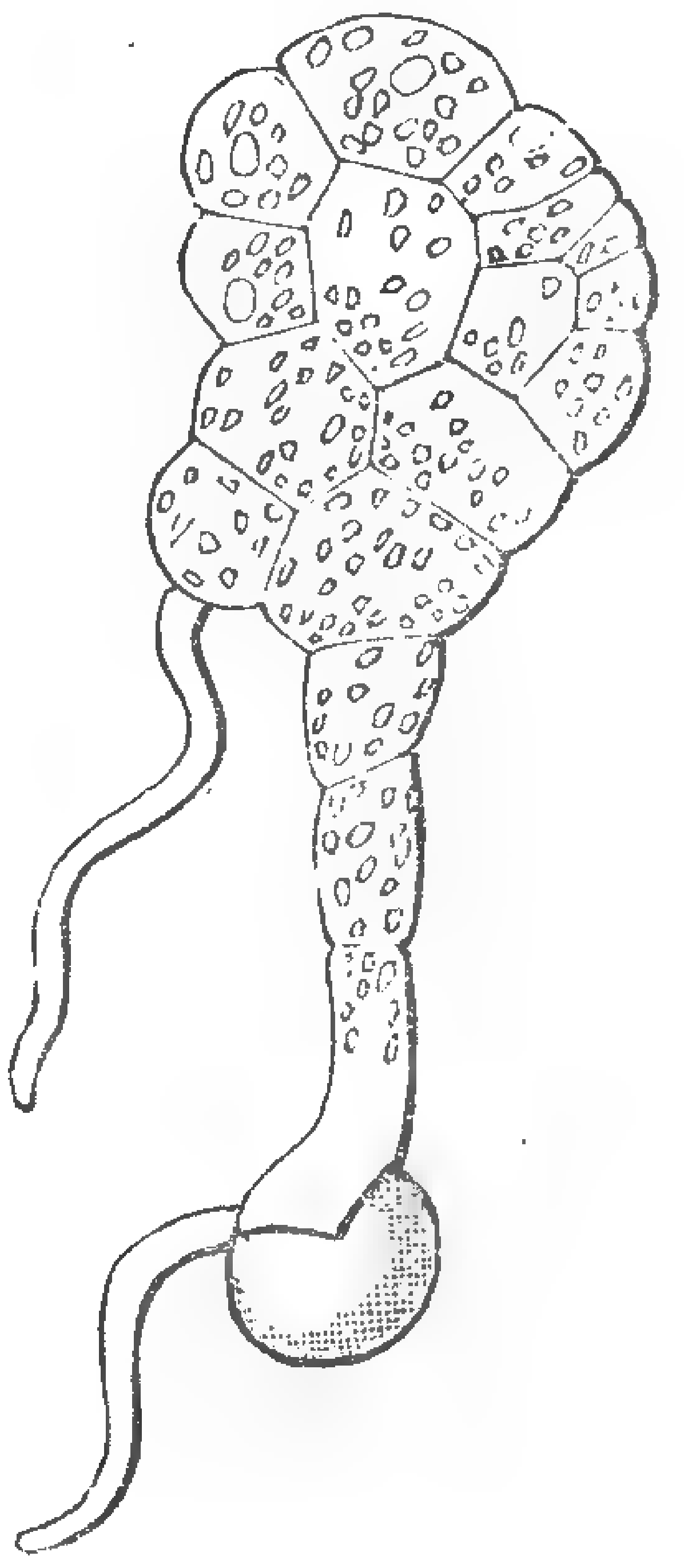
The germination of the spores is as little dependent as their origin upon a previous impregnation derived from the antheridia, unless perhaps this be the case with the Charas, in which the relation of the antheridia to germination is altogether unknown. In germination (except in *Chara*) the spore does not grow at once into a plant like the parent, but is first developed into a thallus-like, cellular structure, totally devoid of vascular bundles, the so-called pro-embryo, which appears under very different forms in different plants of these tribes. In the Mosses (fig. 50) it possesses the form of a branched Conferva, in the Ferns (fig. 51) the shape of a cordate leaflet not unlike a frondose Liverwort, in the

Fig. 50.



Pro-embryo of *Funaria hygrometrica* (according to Schimper) *a*, rudiment of a bud; *b*, a young stem; *c*, first development of the pro-embryo from the spore; *d*, development further advanced.

Fig. 51.



Young pro-embryo of *Pteris serrulata* according to Leszcyc-Suminski.

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* An error. *See* page 121, note; also Report on the Reproduction of the higher Cryptogamia, by A. Henfrey. "*Trans. Brit. Assoc.*" 1851. —A. H.

Equisetaceæ of an irregular mass of cells divided into many lobes. The development of the pro-embryo is extremely simple in these plants. The spore-coat (fig. 50 *c. d.*) becomes expanded in germination, bursts through the outer membrane of the spore, sends out hair-like prolongations serving as rootlets on one side, and becomes prolonged on the other into the form of a cylindrical cell, which becoming divided by septa into a number of cells, and so on by continued growth and cell-multiplication, is gradually developed into the perfect pro-embryo. In these plants no part of the spore seems to be pre-determined for the production of the said parts, but every point of it to be capable of the development described according to the position in which it may be placed.

But the germination of the large spores of *Lycopodium, Marsilea, Pilularia, Salvinia,* and *Isoëtes*, is more complicated ; in them not only is that part of the spore, which by the contiguity of the four cells in each parent-cell, has acquired a more or less evidently three-sided pyramidal form, the only germinal point of it, but the pro-embryo is developed up to a certain stage in the interior of the spores, and issues from the rent in the outer spore-coat, as an already parenchymatous structure, of different form in different genera.

The pro-embryo of the Mosses is capable of transforming one or more of the cells seated upon its various ramifications, immediately into buds, which grow up into leafy stems, so that here we have the peculiar condition of one spore giving rise to the development of a number of plants.

The pro-embryos of Ferns, Rhizospermeæ, Equisetaceæ, and Lycopodiaceæ, on the contrary, are incapable of the immediate production of leaf-buds, and produce upon the uppermost layer of cells, one, or mostly a number of peculiarly-formed organs, which, following the example of Leszcyc-Suminski, are called ovules, from which organs, but not until after an impregnation by the antheridia, which discharge their contents at the same time, the future plant grows out under the form of a bud ; when this impregnation fails, the pro-embryo remains infertile.

In the Ferns and Equisetaceæ the pro-embryo produces the antheridia with the ovules, at the same epoch ; in the Rhizocarpeæ, on the contrary, the parent plant which furnishes the large spores, forms at the same time smaller, for the purpose of producing antheridia, and these small spores, as already mentioned, in like manner exhibit a kind of germination, the product of which consists not of an embryo, but of antheridial cells. In the Lycopodiaceæ the conditions are still obscure. (*See* note p. 121.)

The ovule consists of a large cell belonging to the tissue of the pro-embryo, with four cells or rows of cells overlapping it on the outer surface of the pro-embryo, and leaving an intercellular passage between them leading down from the open air to that cell.

Count Leszcyc-Suminski, the discoverer of these ovules in the

Ferns, observed the penetration of the spiral filaments into the canal just referred to. His idea that he saw the lower part of a spiral filament become transformed into the embryo, is doubtless the result of a mistake, readily to be pardoned in such difficult investigations, which does not damage the discovery we owe to him. There can be no doubt that in the rest of the plants under consideration, the spiral filaments are the bearers of the impregnating substance, since in the Rhizocarpeæ, the spores which are allowed to germinate separately from the small spores producing the spiral filaments, are capable indeed of forming a pro-embryo, but not of producing a plant from the ovules of this.

The plant, which is developed in the lower cell of the ovule, is organically connected with the pro-embryo; it is a bud growing up from it, so that the leafy stem thence produced has no primary descending axis. (An error; *see* p. 137.—A. H.)

According to Hofmeister's researches, the relation of the antheridia of the Mosses to the rest of the plant is again different. It has long been known, as already mentioned, that the rudiment of the fruit of these plants remains undeveloped when no antheridia are produced. This is explained by Hofmeister's investigations; according to these, the rudiment of the fruit of the Moss (the so-called *archegonium*) greatly resembles the ovules of the Ferns, since underneath the so-called style, lies a large cell, which by subdivision is converted into a cellular body, growing downwards and becoming blended with the stem at the one end, and becoming prolonged upwards, and developed into the sporangium at the other. So that while in the Ferns, &c., the spore only forms the pro-embryo without impregnation, and the impregnation is necessary for the development of a leaf-bud, which grows up into the leafy stem forming the sporangia, the spore of the Mosses forms the pro-embryo and the leafy stem without impregnation, and this operation only causes the development of the spore-producing part of the plant (*see* W. Hofmeister, "*üb d. Fruchtbild. und Keimung d. höh. Kryptog.*"—*Bot. Zeit.* 1849, 793; Mettenius, "*Beitr. z. Bot.*" 1. (Also Hofmeister, "*Fruchtbildung, Keimung, &c., der Cryptogamen,*" 4to, Leipzig, 1851; and Henfrey's *Report* in the *Transactions of the British Association*, 1851; and Memoir on the "*Reproduction of the Higher Cryptogamia,*" &c.—"*Ann. of Nat. History,*" sec. 2. vol. ix., 1852—A. H.)

b. PROPAGATION BY SEEDS.

Proceeding to the theory of the impregnation and the formation of the embryo in the Phanerogamia, we arrive upon ground which has been levelled by the researches of the last ten years. In no part of our science has careful investigation, penetrating with untiring patience into ultimate details, yielded more brilliant results, yet in no other part have the hardly-earned facts been so violently opposed, the conclusions, safely established, being even still continually called in question on the strength of superficial investigations.

Observ. As the minute exposition of the historical development of the theory of the sexes of plants would occupy far too large a space, an indication of the main points must suffice. Although the cultivation of many monœcious and diœcious plants might have led, even in ancient times, to the idea that plants were furnished with sexual organs of two kinds, this truth was not recognized until towards the end of the 17th century. First announced in England by Grew, Ray, and others, this theory obtained its first scientific establishment from R. J. Camerarius of Tübingen ("*De sexu plantarum epistola,*" 1694); but it was Linnæus more especially who securely established this new theory by his researches, and gave it universal diffusion by the preponderating influence he exercised in Botany, and by the displacement of all earlier systems by his Sexual System. When, finally, Kölreuter, succeeded by a longer series of experiments in demonstrating the possibility of producing Hybrids in the Vegetable Kingdom ("*Vorlauf. Nachricht einig. d. Geschlecht d. Pflanzen betreff. Versuche.*" 1761—1766), the theory of the sexuality of plants was as firmly established as it could be without a knowledge of the changes which the pollen-grains undergo upon the stigma and the processes occurring in the ovule. The last century did not essentially advance further in reference to this point. The excellent researches of Malpighi, if not forgotten or misunderstood, were at all events not completed; as to the structure and characters of the pollen and as to its relations to the stigma, numerous incorrect observations were published. With this imperfect knowledge of the processes occurring in the interior of the ovule, it might easily be thought possible that fertile seeds should be perfected, at all events, in particular cases, without the co-operation of the pollen, and a number of observations were made known, partly in favour of such exceptional cases, and partly with the object of refuting the entire theory of the sexes of plants; thus Spallanzani and others asserted that female specimens of Hemp, Spinage, &c., had borne fertile seeds; Henschel believed that road-dust, powdered charcoal, sulphur, &c., might be substituted for the pollen; Schultz stated, as the result of his observations, that the pollen need not necessarily come in contact with the stigma, but might impregnate from a distance by an *aura seminalis;* and Lecoq thought he had found that fertile seed might be developed without application of pollen to the stigma in monocarpic, but not in polycarpic, plants. The doubts thus excited were set at rest for ever by the brilliant discovery of Amici, that the pollen-grains germinate upon the stigma and that their internal coat grows down in the form of a tube through the style into the ovary, and comes into connection with the ovule (1823—1830); a discovery to which Gleichen had already come very near, but had not properly followed out. The universality of this process has indeed been denied, but day by day the opposition becomes more completely silenced. Parallel with the researches on the structure of the pollen and its relation to the stigma, went the investigations on the ovule and the origin of the embryo, which had been taken up again from the last-mentioned period by Treviranus, and subsequently carried out further by Rob. Brown, Brongniart, Mirbel, Schleiden, Hofmeister and others. In the midst of this new development of the theory of impregnation, not the sexuality, but the respective import of the sexual organs, was unexpectedly called in question, by Schleiden stating that he had discovered that the embryo was not the product of the ovule, but originated in the tube growing into the ovule from the pollen-grain, whence the pollen-grain was to be considered as the true ovule, the plants hitherto regarded as male as the female, and *vice versâ*. Here again it was Amici, who by decisive observation solved the doubts arising out of this theory, and demonstrated the new doctrine to be false, a result which soon obtained full confirmation from other investigations, especially from the extensive observations of Hofmeister and Tulasne.

* *The Pollen.*

As the development and structure of the pollen-grains have already been spoken of in the account of the development of cells, I shall confine myself here to a few remarks upon this organ.

The perfect pollen-grain consists of a cell, usually roundish or elliptical (elongated into a filament in *Zostera*), which, excepting in certain water-plants, is coated on the outside by a membranous layer, which owes its origin to a secretion, and, in particular cases, is separable into two or three superincumbent layers. The outermost membrane, corresponding to a cuticle, is mostly rather tough, uniform, or covered with granules, spinules, projecting linear and often reticulated ridges, mostly coloured, and the seat of a more or less abundant secretion of a viscid oil. The internal coat is a colourless, uniform, soft, and extensible cellulose membrane. Its cavity is filled with a viscid fluid, rich in protoplasm, sometimes transparent, sometimes rendered opake by granules swimming in it (*fovilla*). In the pollen of very many plants the outer coat forms one or more regularly arranged folds inwards, in which it very frequently exhibits pore-like, thinner places at one or more points; in like manner, very many pollen-grains without the folds, have similar pore-like places, varying from one to a very considerable number, which when large are closed by a piece of the outer coat serving as a cover.

When a pollen-grain comes in contact with water, it powerfully absorbs this, through the endosmose excited by its dense fluid contents, swells up and tears in many places, in consequence of the strong expansion its membranes undergo through the absorption of water. If the pollen-grain opposes the pressure of the absorbed water through the toughness of its membrane, the inner membrane is driven out, in such pollen-grain as have pore-like places in their outer coat, in the form of a papilla, which often extends into a rather long, cylindrical tube (*e. g.*, in Dipsaceæ, Geraniaceæ, Cucubitaceæ). As this phenomenon occurs in pollen-grains which have been long dried, and in fact very suddenly, it can be attributed only to mechanical expansion dependent on the peculiar structure of the parts referred to, and not to an actual growth.

But when fresh, living pollen comes in contact with water which contains organic substance in solution, *e. g.*, with the stigmatic secretion of the fluid of the nectaries of flowers, its inner coat grows out, in one or more places, in the form of a tube, the length of which, by true growth depending on nutrition, often comes to exceed the diameter of the pollen-grain a hundred times.

Observ. The granules of the fovilla have given rise to many false assertions; Ad. Brongniart, in particular, thought he had discovered that they agreed in form and size in each species of plant, and had an independent motion, whence he compared them with the spermatozoa of animals ("*Ann. d. Sc. nat.*" xii. 40., xv. 381). Rob. Brown also ("*A Brief Account of Microscopic Observ. on the Particles contained in the Pollen of Plants,*" 1828), although he discovered at the very time the molecular motion of the fovilla-granules, was of opinion that a change of form might be perceived in the larger granules (which he called particles). Against these statements I was compelled to declare most positively ("*Ueber d. pollen,*" 30), I neither found a definite form and size of the granules in the pollen of any given plant, nor could detect in them movement of any other character than that of the molecular movement; to similar results came Fritzsche ("*Ueb. d. pollen,*" 24), who shewed that these very grains which had been asserted by Brongniart and Brown to change their form, were nothing but starch grains, while other seeming granules were drops of oils; the majority of the smaller granules may, however, as in all protoplasm, consist of proteine compounds. These granules are invisible in many fresh pollens, since the fluid in which they swim has the same refractive power as the granules, whence such pollen-grains are as transparent as glass lenses; when their fovilla is mixed with water the granules at once become visible.

The fovilla seems always to be at rest in the pollen-grain when it comes from the anther, unless *Zostera (Fritzsche l. c. 56)* forms an exception. But when the pollen-grain has germinated upon the stigma, the fovilla exhibits a circulation similar to that of the protoplasm of *Vallisneria* and *Chara,* flowing downwards in a broad stream into the pollen-tube, and back upwards on the opposite side.

Observ. This phenomenon was first seen by Amici in *Portulaca* ("*Ann. d. Sc. nat.*" ii. 68), subsequently in other plants, especially in Gourds and in *Hibiscus syriacus* ("*Ann. d. Sc. nat.*" xxi. 329). Since it appears that no other observer (except Schleiden, who saw the circulation in pollen-tubes which had been developed in nectar) has been able to see this phenomenon, it may be permitted me to mention how the observation is to be made. In *Portulaca* it is not difficult, if a freshly-impregnated stigma is exposed to bright sunshine for a few minutes, the style then removed from the flower with forceps, and the stigma upon which the pollen tubes are very quickly formed, is observed dry, with a power of at least 200 diameters. In the Gourd (for as Amici told me himself, his observations were made on this plant, which in Italian is *Zucca,* and not on *Yucca* as it is stated in all books) a layer must be sliced from a stigma powdered with pollen an hour previously, and this slice pressed moderately between two glass plates, to heighten its transparency.

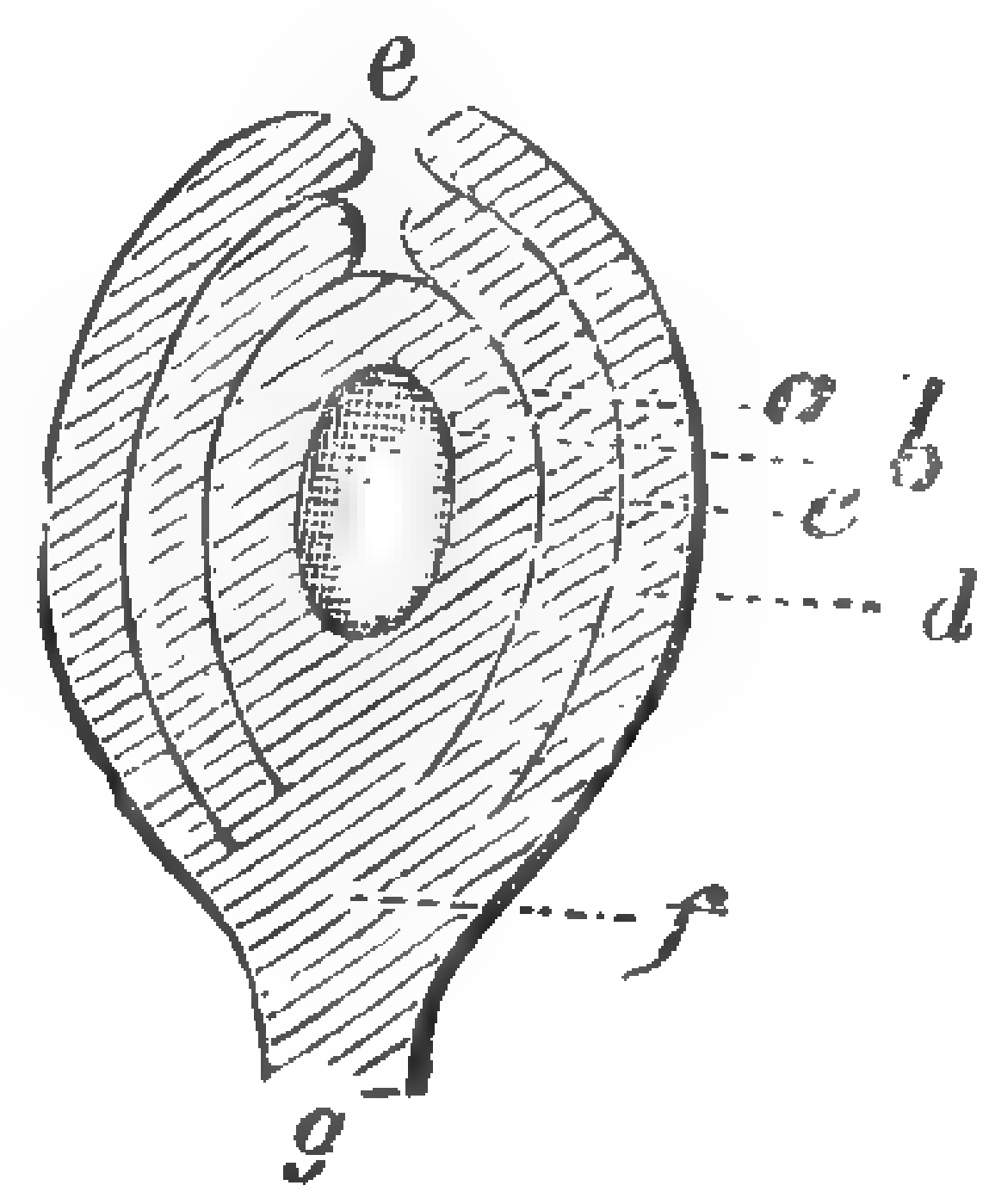
In the development of a filament from the internal coat of the pollen, we meet with a new analogy between the pollen-grain and the spores of Cryptogamous plants, since we have evidently before us a process of germination resembling that we observe in the spore. But the pollen-grain does not seem to be capable of a further development, under favourable external circumstances, into a plant like the parent, yet Reisseck and Karsten observed that under certain circumstances, *e. g.*, when pollen-grains were enclosed in hollow stems like that of the Dahlia, their inner coat was capable of an abnormal development, and of conversion into lower forms of Fungi.

** *The Ovule.*

The Ovule (*ovulum*, *Eichen*),—of late years called by the adherents of Schleiden's theory of impregnation the seed-bud (*samenknospe*) or gemmule, consists essentially of a parenchymatous papilliform growth from the ovary, of the so-called *nucleus* (*ei-kerne*, *nucleus ovuli* fig. 52, *a*), the *tercine* of Mirbel, in which towards the epoch of impregnation one cell becomes more enlarged, displacing a greater or smaller portion of the parenchyma of the nucleus and forming the *embryo-sac* (the *quintine* of Mirbel).

In far the greater number of cases the ovule does not stand still at this first stage, in which it consists merely of a naked nucleus, but undergoes, before impregnation, a more or less extensive series of changes, which relate partly to the formation of enveloping, membranes, enclosing the nucleus, and partly to alterations of form dependent upon curvatures of the different parts of the ovule.

Fig. 52.



Transverse Section of an ovule—*a*, Nucleus; *b*, Embryo-sac; *c*, Inner coat of the Ovule (*primine*); *d*, Outer Coat (*secundine*); *e*, Micropyle; *f*, Chalaza; *g*, Funiculus.

The coats of the ovule originate in this way: at a variable distance from the summit of the nucleus, an annular collar of cells makes its appearance, growing into a thicker or thinner coat which gradually rises up round the nucleus and contracts over its apex leaving only a little orifice, the *micropyle* (*ei-munde*, fig. 52, *e*). In the majority of ovules, a second coat (fig. 52, *d*) is formed in the same way, lower down than the first (fig. 52, *e*) which it encloses. That part of the ovule where the simple or double coat is connected with the base of the nucleus (fig. 52, *f*), is named the *chalaza*, and when beneath this there exists a cylindrical portion, it is called the *funiculus* (*nabelstrang*, fig. 52, *g*).

Observ. Since the changes of form, which the ovules of most plants undergo in the course of their development, exercise no influence upon their impregnation, I shall be content to indicate briefly their principal modifications. When the axis of the ovule remains straight, as it is always at first, so that the micropyle is situated at the summit of the ovule, and the chalaza coincides with the hilum, both lying at the extremity of the ovule opposite the micropyle, the ovule is called *orthotropous* or *atropous* (*geradläufig*). When the ovule curves over on the end of the funiculus, so that the upper part of the latter comes to lie parallel with one side of the ovule and grows together with it, the ovule is named *anatropous* (*gegenläufig*). In an ovule of this kind the chalaza lies at the geometrical summit of the whole, the funiculus coherent with the ovule forms a ridge running along one side (the *raphe*), the *hilum* (the point of insertion of the funiculus) lies beside the micropyle, at the lower end of the ovule, and the axis of the nucleus is straight. But when the nucleus itself is curved to one side by an unequl growth of its two sides; so that the micropyle comes to lie beside the *chalaza* at the base of the ovule, and the highest point of the ovule is formed by the curved side-wall, the ovule is called *campylotropous* (*krummläufig*).

Although not difficult of investigation, the knowledge of the structure of the ovule advanced very slowly. An excellent foundation was laid by Malpighi; but it was Robert Brown, who first opened the path to further progress, by his description of the ovule of *Kingia.* The researches of Brongniart and Mirbel, which latter clearly unfolded the mode of origin of the different forms of the ovule from the orthotropous, but gave a very incorrect account of the coats of the ovule, were followed by the observations of Fritzsche, who cleared up the latter point, and the extensive investigations of Schleiden, who, through a large quantity of detailed research, earned very great credit by making known the different modifications of the structure,—the varying number of the coats,—the universal occurrence of the embryo-sac,—the origin of this from a cell, &c. Hofmeister ("*D. Entsteh. d. Embryo der Phanerog.*") traced back the earliest stages of development of the ovule further than any previous observer, and found (in the Orchideæ) that it takes its origin from a single cell of the epidermis of the placenta, this cell dividing by a cross section into two cells, one lying above the other, the upper of which, is converted by further subdivision into the cortical layer of the nucleus, and the lower, into the central cellular cord, the uppermost cell of which becomes the embryo-sac.

According to the ordinary view, the ovule is to be considered as a bud, the axis of which is metamorphosed into the funiculus and nucleus, the leaves into the coats of the ovule. The order in which the coats are developed, might certainly be fairly urged against this opinion; but I cannot question its correctness, since it is not unfrequent in malformed ovaries, for the ovules to grow out into leafy shoots.

With regard to the physiological import of impregnation, it is perfectly a matter of indifference whether the ovule is regarded as a product of the carpellary leaves, according to the theory advocated by Robert Brown and De Candolle, or it is assumed, with Schleiden, Endlicher, and Unger, and others, that the placenta is always an axial structure. It would lead me too far to relate the reasons for and against these two theories; each of which is true of a portion of the Vegetable Kingdom, but neither of which, and especially the latter, can be exclusively applied to all plants, without coming into contradiction to the clearest facts.

Detailed researches on the structure of the ovule are to be met with, especially in the works of Mirbel ("*Rech. sur la structure et developpement de l'ovule végétale,*" *Ann. des Sc. nat.* xvii), Schleiden ("*Ueb. die. Bildung des Eichens*" *Act. nat. cur.* xix. p. 1. "*Grundz der wiss. Botanik*"), Hofmeister ("*Die Entstehung des Embryo der Phanerog.*" and Tulasne ("*Ann. des Sc. nat 3me Sér.*" xii.).

⁂ *The Origin of the Embryo.*

The impregnation of the ovule by the pollen is an indispensable condition to the origin of an embryo in it. It is true that the ovary may grow up into a fruit, and the ovule into a seed normally formed on the exterior, without this, but the latter is incapable of germination, because it contains no embryo. In the naked-seeded Phanerogamia (the Cycadeæ and Coniferæ), the pollen falls upon the freely-exposed ovule, and impregnates it immediately; in the rest of the Phanerogamia, in which the ovules are enclosed in an ovary, the impregnation is effected through the medium of the pistil, with the stigma of which the pollen must come in contact.

In the majority of plants, the ovary is not perfectly closed above, its cavity being prolonged upward into a very narrow canal, which runs through the substance of the style; or if the borders of the carpellary leaf where this forms the style, are not blended together, it has the form of a groove running on the inside of the style. The cellular tissue which forms the wall of this canal, is distinguished from the rest of the tissue of the style by softness and transparency, and frequently also by the absence of colour. At the epoch of the perfect development of the pistil, there exudes among its cells (which are usually much elongated, but may also be roundish) a mucilaginous fluid, which so loosens the connection of the cells, that they may be readily separated, and through the expansion caused by the excreted fluid, they frequently quite close up the canal of the style. This cellular tissue, which, after Ad. Brongniart, is called the *conducting tissue*, appears at the upper orifice of the canal, where it is frequently enlarged into a large globular or lobulated body, free to the external air, and this constitutes the *stigma*. The cells forming the stigma are ordinarily less elongated than those lying in the interior of the style, and are often more firmly blended together. The outermost layer of them does not form a continuous, smooth epidermis, but its cells are usually in the form of papillæ of variable length; and papillæ of this kind present themselves along the whole of the canal of the style, upon the surface of the conducting tissue. At the opposite extremity of the canal, the conducting tissue stretches into the cavity of the ovary, and here, in general, runs on its wall to the points of insertion of the ovules, where it appears in very different forms, varying according to the structure of the ovary, the number and position of the ovules, &c.; sometimes covering the many-ovuled placenta as a broad layer; sometimes running, in the form of a narrow strip, to a single ovule; sometimes projecting, in a conical shape, into the cavity of the ovary, and coming into direct contact with the micropyle of an ovule, &c. The conducting tissue is by no means to be regarded as a special organ, but consists of a modification of the tissue of the carpellary leaf, occurring at particular parts,—usually of its upper surface, where this forms the canal of the style. In other cases, however, this modification of the tissue may go out through the substance of the carpellary leaf to its posterior surface, as in the Asclepiadeæ, in which this forms but a very small part of the colossal style, or in *Lomatogonium*, where the coherent borders of the carpellary leaves consist of stigmatic substance along the whole of the ovary.

The pistil is incapable of fertilization, until after the secretion of the above-mentioned viscid fluid upon the stigma, for though the pollen-grains indeed adhere to the stigma from being more or less glutinous, they cannot be any further affected. But as soon as this secretion has appeared, the germination of the pollen-grains commences, often in a few minutes, in any case in a few hours. The inner coat breaks through the outer in the form of a cylindrical tube, which applies itself to the stigmatic papillæ (sometimes, as in *Matthiola annua*, penetrates into them), grows downwards among them, and penetrates between the cells of the conducting tissue. Ordinarily only one tube is emitted from each grain, but in those grains which possess several pore-like points on their outer coat, and in which the portion of the inner coat situated beneath those places always becomes developed into a tube, one grain not unfrequently produces several tubes, the number having been seen by Amici to amount to 20—30. The pollen-tubes make their way, by continuous growth at their ends, through the conducting tissue of the style into the ovary, attaining, in long-styled plants, like *Cactus grandiflorus*, for instance, a length which may exceed the diameter of the pollen-grain several thousand times. This considerable length alone, but still more the circumstance that the wall of the pollen-tube is often exceedingly thin in proportion to its cavity, shews that its formation does not depend upon mechanical extension of the pollen-membrane, but on a growth, the requisite nutriment for which is drawn from the viscidfluid poured out among the cells of the conducting tissue.

The rate at which the growth takes place varies very much in different plants, and is not subject to any universal rule. The first result of it is an attachment of the pollen-grain to the stigma, so that it can no longer be readily wiped off the latter. According to Gärtner, this often takes place in even half a minute, while, in other cases, many hours may elapse (in *Mirabilis* and the *Malvaceæ*, as many as 24—36). The growth of the pollen-tube down the style likewise occupies very varied periods in different plants. In many plants, several weeks pass before the pollen-tubes have passed through a style only a few lines long, while in others, even when the style is very long, a few hours suffice (*e. g.*, in *Cactus grandiflorus* and *Colchicum*). After the pollen-tubes have penetrated the stigma, the secretion of the latter ceases, and its tissue begins to die away, while the lower part of the pollen-tube is still in a growing condition. The fovilla passes downwards in proportion as the tubes are elongated, so that the pollen-grains collapse on the stigma soon after their application upon it. The pollen-tubes being so long, the fovilla must certainly become more and more considerably diluted by the absorbed fluid, yet it seems always to become more or less granular and opake. The pollen-tubes are distinguishable from the cells of the conducting tissue, partly by their opake contents, and partly by their smaller diameter (which is often very small, *e. g.*, in *Orchis Morio* about 1–180th of a millim, in *Digitalis purpurea* 1–166th, in *Cheiranthus Cheiri* 1–280th, in *Capsella Bursa-pastoris* 1–332).

Arrived in the ovary, the pollen-tubes, when not immediately led to the mouths of the ovules by special arrangements of the conducting tissue, creep in a mostly very serpentine course along the placenta, among the ovules, and finally penetrate singly, or several together, into the micropyle canals of the ovules.

Observ. A considerable time elapsed from Amici's first observation on the emission of the pollen-tubes upon the stigma of *Portulaca* (1823), before their further path to the ovule was detected; for though Brongniart (1826) demonstrated, by numerous observations, that the pollen-tubes penetrated the conducting tissue, he thought he found that their lower ends burst, and that their fovilla was conveyed to the ovules by the conducting tissue. Amici (1830, "*Ann. d. Sc. nat.*" xxi. 329) discovered the perfect course to the ovule, but even in 1832, Robert Brown was still in doubt whether the tubes penetrating the ovules of the Orchideæ were pollen-tubes, or, more probably, tubes formed in the style, and to which he applied the name of *mucous tubes,* a doubt which was completely settled by Amici's researches, as was also the opinion advanced by many later observers, that this phenomenon does not occur in all the Phanerogamia:—shewn to be totally mistaken, by the extensive researches of Schleiden, Hofmeister, &c.

It is one of the most puzzling phenomena existing, that the ends of the pollen-tubes reach the micropyles of the ovules, the admission to which is not always very simple; since this rencontre seems to be left to pure accident, it might be conjectured that for this purpose a very large number of pollen-tubes were necessary. Yet such is not the case. It is true that in the majority of plants, the number of pollen-tubes which are developed upon the stigma is very considerable, and we not unfrequently see whole bundles of them penetrate the ovary, which is readily accounted for by the vast number of pollen-grains found in the flowers, a tolerable proportion of which generally reach the stigma. Thus Kölreuter found 4863 pollen-grains in the flower *Hibiscus Trionum,* and according to Amici's estimate the pollen-grains of an anther of *Orchis Morio* can furnish 120,000 pollen-tubes. But the number of pollen-grains necessary for impregnation is by no means large. For example, in Kölreuter's experiments on *Hibiscus Trionum,* 50—60 pollen-grains sufficed to impregnate all the ovules in the ovary (over 30); when fewer pollen-grains were placed upon the stigma the ovules were not all impregnated, for instance, by 25 pollen-grains only 10—16 ovules. In *Mirabilis Jalapa* and *longiflora* one, or at most three, sufficed to impregnate the ovule.

It is not necessary to the success of an impregnation that the pollen should pass immediately from the anther to the stigma, for it seems to remain capable of fertilizing for some days in all plants, while in some it retains its power even for a year. Thus Kölreuter found that the pollen of *Hibiscus Trionum* kept fresh three days, that of *Cheiranthus Cheiri,* fourteen days; the pollen of *Phœnix dactylifera* is said to be capable of being preserved for a year in the East; and the same time has been asserted for *Cannabis*, *Zea*, and *Camellia.* (*See* Gärtner "*Befruchtung der Gewachse*," 1, 146.)

In order to explain the course of the processes which go on in the interior of the ovule, it will be necessary for me to return to its structure. Towards the epoch of impregnation, the embryo-sac has mostly become greatly enlarged in proportion to the other parts. In many plants it is still enclosed in the interior of the nucleus, so that its upper end, directed towards the micropyle, is still covered by one or more layers of parenchymatous cells belonging to the nucleus. In other plants (for example in the Orchideæ and Syngenesia), the embryo-sac (pl. 1, fig. 12, *s*; 13, *s*) has by this time wholly displaced the entire nucleus, or at least the upper part of it (in the Leguminosæ also the inner coat of the ovule), and in certain cases, in particular in *Santalum*, has become so much elongated that it projects freely out of the micropyle. The pollen-tube which has penetrated into the micropyle (pl. 1, fig. 14, *p*: 15, *p*.) in its further elongation, thus comes either immediately in contact with the apex of the embryo-sac, or with the layer of cells covering it; in the latter case it penetrates between these cells, and in this way likewise reaches the embryo-sac.

In the latter there is always a more or less abundant quantity of protoplasm. In the later period, just before the pollen-tube reaches the embryo-sac, a portion of the protoplasm becomes attracted into the upper end, next the micropyle. In this protoplasm nuclei appear, usually to the number of three (pl. 1, fig. 12), and give rise to the formation of as many cells (pl. 1, fig. 13, *b*; 14), which more or less completely fill up the upper part of the cavity of the embryo-sac, and are termed the *germinal vesicles* (*embryobläschen*). The triple number, although usual, is not universal, for in many plants (*e. g.*, *Agrostemma Githago*, according to Hofmeister) only one germinal vesicle is formed, while in other cases, as in *Funckia cœrulea*, a larger number present themselves. One of them also, as Hofmeister observed in *Canna*, may displace the rest before impregnation through its predominating enlargement. With these cells necessary for the origin of the embryo, a variable number of other cells are also formed in other parts of the embryo-sac (pl. 1, fig. 4, *f*), chiefly in the end turned away from the micropyle, more rarely in the central region. But this cell-formation is neither an universal phenomenon, nor does it stand in relation to the impregnation.

When the pollen-tube has reached the upper part of the embryo-sac, its growth is either immediately arrested, or it becomes elongated a very little more, so that its obtuse, somewhat inflated end usually penetrates laterally between the embryo-sac and the surrounding cellular layer (pl. 1, fig. 14, 15), or, in rare cases (*Narcissus poeticus*, according to Hofmeister; *Digitalis purpurea*, and *Campanula Medium*, according to Tulasne), introverts the membrane of the embryo-sac for a short space. In extremely rare cases (in *Canna*, according to Hofmeister), the pollen-tube breaks through the membrane of the embryo-sac, and thus comes immediately in contact with the germinal vesicles. In the great majority of cases, however, as already observed, the pollen-tube is separated from the germinal vesicles by the membrane of the embryo-sac, and frequently even, the point at which the end of the pollen-tube is in contact with the embryo-sac, does not correspond exactly to the point at which a germinal vesicle lies in the inside of the embryo-sac (pl. 1, fig. 15). Therefore the only way in which a material effect can be produced by the pollen-tube upon the germinal vesicle, is by the fluid part of the fovilla transuding through the membranes of the pollen-tube, the embryo-sac, and the germinal vesicle. It cannot be demonstrated that such a transudation does take place, but it is in the highest degree probable, since it is incomprehensible how the impregnation of the germinal vesicle could take place without it.

The pollen-tube begins to decay more or less rapidly after it has reached the embryo-sac. Its growth is arrested, as before noticed, and the fovilla contained in it undergoes a visible change in its characters, acquiring a granular, half coagulated aspect; the pollen-tube itself is by this time evidently dead, and disappears sooner or later (sometimes, however, not until the seed is ripe), apparently through absorption.

Shortly after the meeting of the pollen-tube with the embryo-sac, but only when this has occurred, the further development of the germinal vesicle begins, this exhibiting a rapid growth, and usually displacing the two other germinal vesicles which ordinarily accompany it (pl. 1, fig. 15); it is only in rare cases that two or more of these vesicles simultaneously undergo enlargement. The form which the growing germinal vesicle assumes is very unlike in different plants; in many it grows but moderately in the longitudinal direction, and thus becomes ovate; in others, particularly in the Scrophularineæ and Cruciferæ, it grows into a long cylinder, which frequently does not much exceed the pollen-tube in diameter, and exhibits a clavate expansion at its lower extremity. During this enlargement, the protoplasm, which originally filled up the germinal vesicle pretty uniformly, becomes principally collected at the lower end, after which cell-formation by division commences (pl. 1, fig. 15, 16). In this conversion of the germinal vesicle into a cellular body, to which Hofmeister applies the name of *pro-embryo* (*vorkeim*), abundance of modifications present themselves in different plants. In all cases the vesicle first divides by a transverse wall into two cells, one above the other (pl. 1, fig. 16, *a*, *b*.); the lower of these may at once become converted into a parenchymatous body (the *embryo*) by successive subdivisions, as occurs in *Monotropa*, or, as is ordinarily the case, the formation of the embryo does not commence until the pro-embryo has been changed into a compound cellular body by successive subdivisions. In this process there may be formation merely of cross-walls, so as to change the pro-embryo into a confervoid, jointed (pl. 1, fig. 17, *a*; 18, *a*) frequently elongated row of cells lying one above another (for example, in the Scrophularineæ and Cruciferæ), or the filamentous pro-embryo may pretty early pass into a mass of cellular tissue by longitudinal division of its cells (for instance, in *Statice, Tropæolum, Zea, Fritillaria*, &c.). Whichever takes place, the terminal cell of the whole structure is sooner or later metamorphosed, by preponderating growth and cell-division in different directions, into a cellular structure, at first of globular form (pl. 1, fig. 17, *b*; 18, *b*), which, the more fully it becomes developed, the more marked contrast does it present to the other part of the pro-embryo turned towards the micropyle end (called the *suspensor, Träger*, or *Aufhängefaden*). The ulterior development shews that this mass of cells formed at the end of the pro-embryo is in the rudiment of the embryo. It may persist, in plants with the so-called "homogeneous embryo" (*e. g.*, in the Orchideæ and in *Monotropa*), in the form of a globular or elliptical body, composed of a variable number of cells (pl. 1, fig. 18); but usually the cotyledons shoot out at the end turned away from the suspensor, a little below the actual extremity (in the Monocotyledons in the form of a sheathing leaf, in the Dicotyledons in the form of two opposite leaves,) and after this the apex is developed into the terminal bud (*plumule, federchen*).

In this way the embryo is always suspended in an inverted direction, with the point of its stem downwards, in the embryo-sac. Its radical extremity, as is evident from the mode of origin of the embryo, is not free, but blended with the cells of the pro-embryo; frequently it does not at once become clearly distinguishable from the cells of the pro-embryo, but the line of demarcation becomes continually more definite with the advancing development, since the cells of the embryo are always densely filled with organic matters, while the cells of the suspensor usually contain only a little opake sap, and are thus far more transparent than those of the embryo, from which they are also frequently distinguishable by much greater size. The further the development of the embryo progresses, the more, in most cases, does vegetation cease in the cells of the suspensor, so that, if even, as in the Orchideæ, it still exibits a considerable growth during the development of the embryo, and exists when the seed is ripe, it at all events forms but a dead, readily detachable appendage of the radicle, upon the embryo of the ripe seed.

The origin of the embryo, which is formed out of a cell of the pro-embryo, and not free in the cavity of the embryo-sac, bears great resemblance to the formation of a bud, and especially to the formation of the stem-producing buds developed on the pro-embryo of the Cryptogamia; yet there exists an important distinction from the formation of buds, in the fact that the lower end, connected with the suspensor, becomes detached from this, and is capable of further development, in consequence of which the primary axis of the embryo can become elongated downwards, in germination, as a tap-root, which is not the case in any buds, or in the young stems of the Cryptogamia,* the axis of which is only capable of prolongation upwards.

Observ. 1. Schleiden's theory of the origin of the embryo ("*Einige Blicke auf die Entwickelungsgeschichte des veget. Organismus*," Wiegmann's "*Archiv.*" 1837, 1, 289—"*Ueber die Bildung des Eichens und Entstehung des Embryo*" *Act. acad. nat. Cur.* v. xix., p. 1.) is completely opposed to the foregoing description of this process, since, according to him, the embryo is not formed in the cavity of the embryo-sac, but in the lower end of the pollen-tube, which introverts the wall of the embryo-sac, and penetrates more or less deeply into the depression thus formed. If this theory were true, the germinal vesicle would not be an independent product of the ovule, but of the clavate, expanded extremity of the pollen-tube, and the suspensor would be the remainder of the latter, running into the introverted portion of the embryo-sac. In the whole province of Vegetable Physiology, seldom has a theory excited so much curiosity as this theory of impregnation. No conviction was more firmly established than that the pollen was the impregnating organ, hence the wonder that it should be exactly the reverse. The confusion was great, for the theory emanated from a man who shewed by his numerous and excellent researches on the ovule, published at the same time, that he possessed an acquaintance with his subject, such as few others had, and who in every word expressed the conviction that the matter did occur as he asserted, and that a mistake was out of the question. And others were not wanting to make known confirmatory observations (Wydler, "*Biblioth. Univers.*" 1838, Oct.; Géléznoff, "*Bot. Zeitung,*" 1843, 841), or to support the new doctrine on theoretical grounds, and teach it as a settled truth (Endlicher and Unger, "*Grundz. der Botanik*"). It is true that the old notion had its defenders, but these maintained the fight a long time with little success. Some who did not know how to use the microscope, thought, nevertheless, that an opinion might be arrived at here, in which the thing depended wholly and solely upon a fact to be determined by the microscope, from other grounds, but such was utterly without value by itself; others, Meyen in particular ("*Physiologie,*" iii), certainly had recourse to the microscope, but were content with superficial observations, and thus were not very fortunate in their intended refutation of the new theory, for observations, in some of which not even the penetration of the pollen-tube into the ovule, or the embryo-sac were seen, were not calculated to drive an opponent like Schleiden out of the field, and the latter could justly interpret some among such discordant observations as Meyen's in his own favour. It was Amici again who now for the second time came forward with an observation marking an epoch in the theory of impregna-

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* An error; the axis of the Ferns, &c., originates from a free embryonal vesicle, and has an abortive descending axis, like the Monocotyledons.—A. H.

tion, and, by his researches on the impregnation of the Orchideæ ("*Sulla fecundazione delle Orchidee*,"—*Giorn. Bot. Italian. Anno* 2), made an end of the new theory at one blow. Amici's treatise was soon followed by a confirmation of what he had seen by myself ("*Bot. Zeitung*," 1847, 465), and others; and these were quickly succeeded by the extensive researches of Hofmeister ("*Die Entstehung d. Embryo d. Phanerogamen*") and of Tulasne ("*Ann. d. Sc. nat.* 3 *Ser.* xii), which contained a full confirmation of the results obtained in the Orchideæ, and demonstrated that the impregnative process is the same in its essential circumstances throughout a long series of Phanerogamia, so that this subject may be considered as quite settled in its principal features.

Obs. 2. The so-called naked-seeded Dicotyledons (the Cycadeæ and Coniferæ) present some very important differences from all other Phanegamia, in reference to the production of their embryo; the circumstances are unfortunately not all cleared up by the foregoing researches. The differences depend, not so much upon the fact, that the pollen-grains fall immediately upon the naked ovules in these plants, for nothing is essentially altered by this, since the pollen-grains here germinate on the point of the nucleus in the same way as in other plants, and are thus spared the circuitous route which the pollen-tubes have to make through the conducting tissue of the pistil. The distinctions lie in a great complication of the structure of the ovule, and in the manifold deviations in the structure of the embryo.

In the Coniferæ, the nucleus is in great part displaced by the enlargement of the embryo-sac; the latter becomes filled with cellular tissue, out of which from three to six cells, arranged in a circle near the upper end, become more considerably enlarged than the rest, and these constitute what are called, by Robert Brown, the *corpuscula*,—by Mirbel and Spach, the *secondary embryo-sacs*,—and also become filled up with cellular tissue. The pollen-grains germinate on the point of the nucleus, and send down their tubes through the upper part of it; and the slowness with which this process takes place in many species is remarkable, for in *Larix europœa*, according to Géléznoff, the pollen-tubes do not emerge from the granules till after thirty-five days; and in *Pinus sylvestris*, Pineau states that full a year passes before they grow down through the nucleus to the embryo-sac, whereby evidently the impregnation is also postponed for this long period. When the pollen-tubes have arrived at the embryo-sac, they break through it, and through the cellular tissue lying between its membranes and the secondary embryo-sacs. The observations on their subsequent course are discordant. Pineau believed he had discovered that the ends burst, and poured out the fovilla into the secondary embryo-sacs. According to Géléznoff, the pollen-tubes would break through an inner membrane immediately enclosing the fovilla, and grow into the secondary embryo-sac. In like manner, there is an obscurity as to the origin of the embryo. Apparently there originates in the secondary embryo-sacs, from the cells already contained in them, a pro-embryo of most peculiar form: in *Pinus*, the upper part of it is composed of a rosette of four to five cells, to which an equal number are applied below, these extend themselves into a long filament, which again bears four cells at its extremity constituting the rudiment of the embryo. As the intermediate cells grow down in the filamentous form, they break through the lower end of the secondary embryo-sacs, grow onward in the cellular tissue lying in a cavity of the primary embryo-sac, and push the embryo out of the secondary embryo-sac. In this way are formed as many embryos as there are secondary embryo-sacs; but the four or five cells forming the thread-like suspensor may separate from each other, and every one form a special embryo. The embryo itself, moreover, exhibits a peculiar growth, for while its cotyledonary end is composed of a connected, well-defined mass of cells, its radical extremity is formed of a loose mass of cellular tissue, which grows back on the suspensor, its cells only becoming more compactly conjoined at a later period. Finally, in *Thuja*, a whole mass of such suspensors are formed, which terminate in an embryo below, side by side, in one embryo-sac. The numerous embryos originating in one ovule seem all to be equally capable of living, and are developed up to a certain point, but then, from some unknown cause, all die away except one. (Robert Brown, "*On the Plurality and Development of Embryos in the Seeds of the Coniferæ*,"—*Ann. Nat. Hist.*, 1. *Sér.* xiii. 368; Mirbel and Spach, "*Notes sur l'Embryogenie du Pinus Laricio*," &c., "*Ann. des Sc. nat.*," 2 Sér. xx. 257; Pineau, "*Sur la Formation de l'Embryon chez les Conifères*,"—*Ann. des Sc. nat.* 3 *Sér.* xi. 83; Géléznoff, "*Sur l'Embryogenie du Meleze, Bulletin, de la Societe de Natural. de Moscou*," xxii., "*Ann. des Sc. nat.*" 3 *Sér.* xiv.)*

Observ. 3. If Schleiden's theory of impregnation had proved true, it would have furnished incontestible proof that no embryo can originate in the ovule without application of pollen to the stigma. With the confirmation of the earlier view of the import of the pollen-grain, the doubt again arises whether the geminal vesicle is not in isolated cases capable of development into an embryo without impregnation. Improbable as such an exception seems, when we look at the thousands of experiments which declare the necessity of impregnation, the absolute impossibility of it can the less be proved that undoubted cases of the possibility have been shewn in the Animal Kingdom. The greater the accuracy in the observations, indeed, the more clear it became that the cases in which it was supposed that the development of fertile seeds without impregnation had been observed, in the hemp, spinach, &c., arose from mistakes, but certain cases still remain in which the problem has not yet been solved. In reference to this, mention must particularly be made of the Euphorbiaceous plant, *Cœlobogyne ilicifolia*, described by John Smith ("*Linn. Trans.*" xviii. 510), in which not a trace of anthers could be found, either by Smith, or by Francis Bauer, Lindley, and others, and yet it bore perfect seeds. Gasparrini likewise asserts ("*Ann. d. Sc. nat.*," 3 *Sér.* v. 206) that the figs developed in summer never contain male flowers, and yet produce seeds which contain an embryo.

c. THE CELL AS AN ORGAN OF MOTION.

Although plants in general appear completely fixed and motionless, a close examination leads to the detection of movements of

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* Hofmeister has recently shewn that great analogy exists between the *Corpuscula* and the *Archegonia* of the Cryptogamia. *See* Hofmeister, "*Keimung, Entfaltung, &c., der hoher. Cryptogamen*," &c., Leipzig, 1851; also reported in Henfrey "*On the Reprod. of the Cryptogamia*," &c.—"*Ann. of Nat. History*," *Ser.* 2 ix. 1852."

the most diverse of their organs, which are sometimes dependent on the influence of certain universally-diffused agents, such as gravity and light, sometimes are excited by stimuli accidentally affecting them, and sometimes occur independently without the existence of any demonstrable external cause. Great as the similarity to animal motion is in many of these movements, they are always devoid of the character of volition, so that altogether no more definite and profound distinction between plants and animals can be found, than the total want of voluntary motion in the former and the presence of this same in the latter.

Observ.—Unfortunately it is extremely difficult to make out, in many cases, whether a motion is voluntary or not, yet repeated unprejudiced observations will very rarely leave a doubt about it. In no other investigation does the observer need calm reflection in so high a degree as here, for hundreds of examples shew how readily the imagination steps in and leads to erroneous conclusions in the observation of the enigmatical movements of plants. Warning examples are furnished by observations on the "swarming" spores of Algæ, on the Diatomaceæ, Oscillatorieæ, &c., in abundance; shewing how soon, when once the kind of motion has been mistaken and these plants conceived to be animals, their entire structure has become misunderstood, and imaginary eyes, intestines, feet, and other animal organs have been discovered, which more temperate observers have recognized as things differing as widely as the poles.

In examining the movements of plants we must first of all exclude those cases in which motion of an organ is caused by the more or less complete drying up of different layers of it, producing unequal contraction and thereby curling of the parts. The rapidity of the motion produced in this way depends on the mechanical conditions of structure; it may be slow or very rapid. The former is the case when no external hinderance opposes the movement of the drying organ, the latter when the curving part is blended with other parts, so as to be hindered from following its contraction, whereby a gradually increasing tension arises in it, the final result of which is a rupture and a sudden relief of the stretched part, like the recoil of a metal spring. In general, the layers of an organ which contract most strongly in drying are those which are composed of larger, thinner-walled, and more globular cells, while a layer composed of thick-walled, small, and elongated cells suffers less contraction, and therefore forms the convex side of the curved organ.

Observ. Examples of these hygroscopic movements are of every-day occurrence, and it will suffice to indicate a few of them. Among these are,—the contraction into a globe, which the ramified stems of many plants, such as *Anastatica hierochontica*, *Lycopodium lepidophyllum*, undergo in drying; the dehiscence of anthers, the bursting of most dry fruit, the rupture of the outer seed-coat of *Oxalis*, the twisting of the awns of many grasses. In particular cases even isolated pieces of cell-wall exhibit movements of this kind, when their various layers differ from one another in hygroscopical respects, *e. g.*, in the elaters of *Equisetum*, the peristome of the Mosses, &c. The cause of these motions is usually so conspicuous, and the proof that they result from desiccation so readily shewn, since wetting the dried organ brings it back into its old form, that the cause has but rarely been misconceived, and such motions ascribed to a vital force, irritability, &c., in the way Purkinje so strangely did, in regard to the opening of the anthers, in a special work ("*De cellulis antherarum fibrosis,*" 1830).

Passing to the movements of living plants, we meet first, as one of the most mysterious phenomena, the locomotion of many lower aquatic Algæ, the Diatomaceæ, Desmidiaceæ, and Oscillatorieæ, which, on account of this, have been so frequently regarded as animals. In the Diatomaceæ and Desmidiaceæ, the motion consists of a slow waving backwards and forwards in the direction of their longitudinal diameter, during which no change of form, such as curvature or the like (which indeed would be impossible in the Diatomaceæ, on account of their siliceous lorica), can be observed in the cell constituting the plant. Neither can special organs of motion (such as ciliæ) be discovered, and Ehrenberg's idea that he detected a moveable foot, similar to that of the Mollusca, must be attributed decidedly to erroneous observation.

The organic process upon which this motion depends is altogether uninvestigated. Nägeli ("*Gattungen der einzelliger Algen,*" 20) explains the motion by supposing, that in the absorption and excretion of fluid matters connected with the nutrient processes of these plants, the attraction and repulsion of the fluids are irregularly distributed over the portions of the surface, and that these currents are so active as to overcome the resistance of the water; but this explanation is devoid of any positive basis. The external circumstances in which the plants are placed have influence over the motion so far, that when the little plants lie hidden in mud, they rise up to its surface if the sun shines upon it, and they bury themselves in the mud when its surface becomes dried up (Ralfs's, "*British Desmideæ,*" 20).

The motion which presents itself in the *Oscillatoriæ* is more complicated, since not only does the entire plant move backwards and forwards like a little rod, but a pendulous swinging of the filaments to and fro occurs, together with a curvature in a spiral direction (*See* Kützing, "*Phycol. Generalis,*" 181; Fresenius, "*Ueber Bau and Leben der Oscillarien,*" *in the Museum Senkenbergianum*, iii. 284). This curvature deserves our attention in a higher degree, that these plants are composed of a simple row of flattened cells enclosed in a membranous sheath. Under these circumstances, a curvature of the filament cannot depend (as in the higher plants) upon a different relative contraction or expansion of different cells lying side by side, but must arise from a different behaviour of the different lateral surfaces of the two side walls of the individual cells, either the side becoming concave in the motion undergoing abbreviation, or the opposite side expanding. The locomotion of the entire filament is influenced in the same way as that of the Diatomaceæ and Desmidiaceæ by illumination or drying up of the mud, and the movement from a dark towards an illuminated place, is, in particular, very distinct (Dutrochet, "*Mémoires,*" i. 112).

Observ. This is, of course, not the place to enter into the much contested question whether these beings are actually plants, and not rather animals. The former is, as I at least believe, incontestibly proved by Kützing ("*Die Kieselschaaligen Bacillarien*"), Ralfs ("*British Desmidieæ,*") and others. But it deserves mention that the contraction into a spiral form occurs not unfrequently in still higher degree than in the *Oscillatorieæ,* in most undoubted plants, namely, the *Zygnemeæ* (*See* Meyen, "*Physiologie,*" iii. 566).

Rapid advancing and retreating movements, like those the lower Algæ exhibit, are unknown in those organs of higher plants, consisting of a single cell or row of cells, which might, in reference to their structure, be compared with the plants above referred to, yet we find in such simply constructed organs, phenomena of curvation which are indeed most closely connected with their growth, but may possibly be brought into connection, in many respects, with the phenomena of motion. I include among these the phenomenon, that many filiform cellular processes grow in a definite direction, and attach themselves upon foreign bodies.

The pollen-tubes are, above all, to be recalled to mind here, curving, as they do, after their exit from the pollen-grain, to come in contact with the hairs of the stigma, applying themselves upon these, and penetrating into the conducting tissue of the style. This phenomenon has often been compared with germination, and correctly, for in that curvature, in the penetration of the pollen-tube into the conducting tissue, we meet with the same phenomena, only in a more simply organized part, as in the radicle of a germinating plant. Still greater is the analogy with the radicles of many Cryptogamia, whether these are protrusions of single cells, as in many *Confervæ* and in the Liverworts, or simple rows of cells, as in the Mosses. In these capillary roots we find the same tendency to grow downwards, and the same adherence to foreign bodies. One might be inclined to seek the cause of this curvature of the cells, and their adherence to foreign bodies, in a retardation of the growth of those parts of the cell-membrane which come in contact with the foreign bodies, behind that of the free parts of the membrane. But it is possible that the conditions are far more complicated. For if we compare these phenomena with the processes which are presented to us in the compound organs of the higher plants, we find in the movements of these capillary organs, corresponding processes to those which, in the higher plants, are produced by not less than three causes (the influence of gravity, light, and contact of solid bodies). Since, however, the external influences upon which these movements depend, are as yet altogether unexamined, and thus nothing but empty guesses can be expressed regarding them, I feel that I ought to be content with the indication, that even in the simple cell, phenomena of motion occur which are comparable with those of the compound organs.

With regard to the motions of the parts of higher plants, so far as they are connected with their growth, we are first struck by the determinate directions of the root, the stem, and the leaves. To no phenomenon have we been rendered—by having it daily before our eyes—more indifferent, than to the definite direction in which every part of a plant lies in reference to a perpendicular line; and yet in the circumstance that the stem grows upwards, the root downwards, and the leaf with its upper surface turned towards the sky, we behold a series of the most wonderful phenomena, the causal relations of which are unfortunately but too little understood. These positions of the various organs seem to us so natural, that it is only by the exceptions which occur in many plants, and by the effort of a dis-arranged part to regain its normal position, that our attention becomes attracted to the fact that this position is the result of a series of mysterious processes, which, though unnoticed, are ever active in the plant.

Experiments of the simplest kind, in particular such as were made by Duhamel, have long since shewn that the earlier endeavours to explain the growth of the root downwards and of the stem upwards, from the influence of the darkness and moisture of the soil upon the root, and the brightness and dryness of the air upon the stem, were mistaken, for under all circumstances, be the position and the surrounding media of a germinating seed what they may, whether this germinate in the earth, in air or in water, in darkness or under the influence of light, the radicle and the plumule will curve until they have acquired their normal direction. The acuteness of Knight (*"Phil. Trans."* 1806; *"A Selection from the Physiolog. Papers,"* 124) obtained the first success in demonstrating sure evidence of the connexion of this phenomenon with the effect of a determinate force, of gravity, in fact, by making seeds germinate on wheels rotating rapidly, under which circumstances the radicles turned towards the periphery, and the plumules towards the centre of the wheels. This experiment was afterwards extended by Dutrochet to the leaves, whereby he shewed that the leaves are also subject to the effect of gravity, for these turned their lower faces towards the periphery of the wheel (Dutrochet *"Mémoires,"* ii. 54).

Observ. It is difficult to conceive how any naturalists could question the value of the evidence furnished by this experiment, in which the effect of gravity was replaced by that of centrifugal force. But on the other hand, the explanation given by Knight of the mode of action of gravity in determining the direction of plants must be regarded as unsuccessful. In this explanation Knight started from the different manner in which the stem and roots grow longitudinally. The root, as is well known, grows only at its extreme points. Knight believed that the half-solidified substance of these points immediately followed the attraction of gravitation, and curved downwards. With regard to the stem, on the contrary, in which a series of internodes are undergoing elongation simultaneously, Knight thought that gravity could not act upon its already formed, solid, organic substance, but affected only its contained nutrient juices, that in a stem out of the perpendicular direction those juices would be drawn to the lower side, which would consequently be more actively nourished, thence would grow more vigorously in the longitudinal direction than the upper side, and so cause a curvature of the stem upwards. If this explanation were correct in regard to the roots, it would follow from it that the point of a root could not penetrate into a fluid of greater specific gravity than its own substance; but the experiments of Pinot, Mulder, and Durand ("*Ann. des. Sc. nat.* 3 *Sér*," iii. 210—*Botanical Gazette*, i.) shew, that the radicles of germinating seeds penetrate into mercury, whence it is clear that the points of the roots are not directly attracted downwards by gravity, but that the latter causes alterations in the root, through which an active curvature downwards is brought about. We find indicated here an explanation which bears a certain resemblance to Knight's explanation of the growth of the stem. With reference to the latter, it is at once clear that Knight regarded as a self-evident fact, the circumstance that the curvature of the stem is a consequence of its growth. But this seems in the highest degree improbable, if we note on the one hand, that in many organs, even when they exhibit no further growth (as in leaves, tendrils, &c.), curving movements occur which depend upon a frequently very transitory expansion of their cellular tissue wholly independent of their growth; and remember, on the other hand, that nothing is more common in stems and branches, than the manifestation of a much more vigorous growth on one side, giving to them a very eccentric position, without any curvature being produced by this one-sided growth. Still less tenable must this explanation appear when we consider that the direction upwards does not occur in the stem of all plants, but that many follow a horizontal course, and that the shoots of many plants, for instance, of the Weeping Ash, have a very strongly marked tendency to grow downwards, without any observable occurrence of a diffence in the mode of growth from that of the stems growing upwards. This indicates that there must exist in the different stems differences of organization unconnected with their longitudinal growth, on which it depends that the same external conditions cause in one a curvature downwards, and in the other a curve upwards. That these modifications of the internal organization are based upon conditions not very readily detected, may be concluded from the fact, that the shoots of different varieties of the same plant, as of the Ash or Beech, may behave quite differently in this respect; that in almost all our trees, for instance in the Firs, a difference of direction exists between the primary and secondary axes, and that frequently, on a sudden, without perceptible external cause, the points of one or more secondary axes turn upward and grow in the vertical direction in the manner of the trunk, of which large specimens of *Pinus Cembra* in particular exhibit the most beautiful and striking examples.

To Dutrochet belongs the merit of having called attention to the difference between the organization of the stem and the root, which must incontestibly be taken into consideration before all else, in discussing the movements now referred to, and gives hope that their further investigation will solve much that is still doubtful in respect to the movements of plants. Dutrochet ("*Mémoires*," ii. 1) endeavoured to trace the curvature of the stem upward and that of the root downward from the endosmose exercised in the parenchymatous cells of these organs. He found that a plate cut longitudinally, in the direction of a radius, from an herbaceous stem, curved in water so as to render the epidermis concave; while a plate cut out of a young root exhibited the opposite curvature. The cause of these different curvatures he found, in the decreasing size of the pith-cells from within outwards in the stem (these alone coming into consideration on account of the preponderating size of the pith and the proportionately small thickness of the bark), and in the decreasing size from without inwards of the cortical cells of the root, these alone being of importance in regard to the root where the rind is so much more developed. This tendency to curve exists, although in less degree, when the different parts are not placed in water, in consequence of the cells being full of sap, as in the natural condition of plants. The different sides of the root and stem possess the tendency to this curvature in an equal degree so long as these organs are in a perpendicular position, and thus the force of one side is kept in equilibrium by that of the opposite side. But when a stem or root is placed in an inclined position, according to Dutrochet's view, the effect of gravity causing a flow of the concentrated sap toward the lower side of the organ, limits the endosmose exercised by the cells of this side, while the cells of the upper side which come in contact with a less concentrated sap are unrestrained in their endosmose, and in their expansion consequent thereupon. Thus the tendency to curvature arising from the endosmose in these acquires the preponderance, and causes an upward curvature of the stem and a downward of the root. Notwithstanding that many errors occur in the statements of Dutrochet's treatise, and that the manifold modifications which present themselves in the directions of stems and shoots in different plants, a few only of which have been indicated above, cannot as yet be explained from their structure, yet this author has the credit of having demonstrated the elementary truths: 1, That the curvature of the root and the stem is independent of their growth; 2, That the moving organ must be looked for in the soft parenchymatous cells; and 3, That the curvature effected by the cells is not produced by a contraction of that side which becomes concave, thus drawing over the other part of the organ, but, on the contrary, the curvature arises from a swelling of that side of the organ which becomes convex.

Both stem and root are only capable of retaining the perpendicular direction which they assume through the influence of gravity, when they are wholly removed from light, or light is freely admitted to all sides of them; when the light shines only on one side of a plant, the latter becomes more or less diverted out of its normal direction.

It is an every-day's experience that this is the case in a high degree with young and still soft stems, since in plants which receive light on one side only, the stems curve strongly towards the side whence the light comes. In plants which are very sensitive to light, like germinating Cruciferæ, I found that the influence of light might wholly overcome the effect of gravity, for when I suspended some of these in a horizontal direction, in a blackened box, closed on all sides and at the top, and lighted through the open lower end by a mirror, the plants were compelled to turn their stems vertically downwards.

This curvature is produced in unequal degrees by the differently coloured rays of the spectrum, and this independently of their illuminating power, being caused most of all by the blue rays; and, according to Payer ("*Comptes rendus*," xvii), in general only by that part of the spectrum lying between F and H, a statement, which, however, would undergo some modification through the experiments of Dutrochet (which, it is true, were not made with the aid of a heliostat, but with red glass, and consequently were imperfect), for according to these experiments, even the red rays produced curvature, although in slight degree ("*Ann. des. Sc. nat.* 2 *Sér,*" xx. 329).

It is proved that this curvature is produced by the illuminated side, and that the convex side only mechanically follows its curvature, by the fact that when the concave side is removed from the convex side by a longitudinal incision, it curves more strongly than before, and the convex side springs back into the upright position (Dutrochet, "*Mémoires,*" ii. 74).

Observ. The fact last stated completely refutes De Candolle's explanation, which appears, at first sight, to give a very simple cause for the curvature of the stem towards light falling on it. De Candolle thought ("*Mém. d. l. Société d'Arcueil,*" 1809, ii. 104) that in accordance with the common experience of plants which receive but little light growing very much longitudinally; plants which received light only on one side would grow much longer on the dark side than on the lighted side, and thus would curve towards the source of light.

We find a similar contrast in the dependence of stem and root upon light, to that of the movements produced in these parts by gravity, for the root turns away from the light; a phenomenon which was first discovered by Dutrochet in germinating plants of *Viscum album*, was subsequently demonstrated more extensively by Payer ("*Comptes rendus,*" xvii), Durand, and Dutrochet ("*Ann. des. Sc. nat.* 3 *Sér,*" v. 65), by experiments, chiefly on the roots of Cruciferæ and Compositæ: and of which proof may frequently be obtained in hot-houses, from the aerial roots of *Cactus grandiflorus* and other plants. The only cases in which this retreat from light has been shewn with certainty in upward growing parts of plants, are the tendrils of *Vitis* and *Ampelopsis quinquefolia*, as was first observed by Knight ("*Phil. Trans.*" 1812, 314; "*Physiol. Papers,*" 164); while other tendrils which I tested in this respect either gave no decided result, or turned towards the light ("*Ueb. das Winden der Ranken u. Schlingpflanzen,*" 77).

Observ. Dutrochet asserts that the stems of all twining plants have the property of turning away from light. From very numerous observations on plants with climbing or twining stems, I must declare this to be altogether incorrect, for, like other plants, they turn towards the light. But I have no definite experience to enable me to decide whether the hook-like curvature of the end of the stem of *Vitis*, *Corylus*, &c., and further, the downward direction of the shoots of *Fraxinus pendula*, are (as Dutrochet asserts) to be attributed to the influence of light.

We are quite deficient of anything like a sufficient explanation of the curvature of plants caused by light. It is not even made out whether this curvature is a result of an irritability of the cellular tissue, or of the alteration of endosmotic condition of the cells through the increased evaporation caused by light. The latter hypothesis seems to be opposed by the circumstance, that these movements occur just as well when the plant is under water as when in air; at any rate we have at present no evidence that light causes an excretion of water from the submerged parts of plants which it shines on, as in plants which are exposed to air. The curvature does not appear to be any way connected with the presence or absence of the green colour, since the light-avoiding tendrils of the Vine are coloured quite as green as the stems of most plants, and since the roots of certain plants (of *Allium Cepa* and *Allium sativum*, according to Durand and Dutrochet) turn towards the light.

An explanation must, of course, give an account as well of why particular parts avoid light, as of why others curve towards it; I may, therefore, pass over the earlier explanations, which only refer to the latter point, and many of which are vague in the highest degree, as for example "light attracts the plants," &c.; but the explanation given by Dutrochet ("*Mém.*" ii. 60; "*Ann. des. Sc. nat. 3 Sér,*" iv. 72) must be touched upon. Dutrochet derived the curvature of the stem and root from the supposition, that the cortical cells of the illuminated side lose a portion of their sap in consequence of the known effect of light, to increase the evaporation from plants, and the cells therefore contract. It depends then on the structure of the cortical layer whether, in consequence of such contraction it curves so as to become concave or convex on the outer surface; in the former case, the illuminated organ will curve towards the source of light; in the latter case, in the contrary direction. Now, Dutrochet asserts it is a general rule that the larger cells lie externally in rind of all those stems which curve towards the light, on which account when a strip of such rind is laid in water it curves inwards; a rind possessing such a structure, in consequence of this, curves outward and draws the stem with it, when it loses part of its sap through the influence of light. On the other hand, all stems and roots avoiding light possess a rind of opposite structure. In criticising this theory we will leave out of the question the doubt above referred to, the complete uncertainty whether light can cause greater amount of discharge of aqueous juices from the cells of the illuminated side of the rind of plants lying under water; but we must therefore the more distinctly advance that the statements of the anatomical facts given by Dutrochet are altogether erroneous, he himself having contradicted these statements by anatomical facts mentioned in other parts of his writings. With regard to the rind of the stem of plants striving towards light, the statement that these curve inwards in water is most decidedly incorrect, of which I have convinced myself in a great number of plants, and in particular in the *Phytolacca decandra*, especially cited as an example by Dutrochet, for the rind of all the plants which I investigated in reference to this question curved outwards in water. It is equally untrue that the rind of roots curves outwards, for in most roots just the opposite occurs. But when Dutrochet, in explaining the avoidance of light by roots, ascribed the said structure to their rind, he forgot that he had stated directly the reverse of this structure of the rind, in explaining the direction of the root downward. In this way he mixed the anatomical facts together, like a conjuror does his cards, just as they were requisite at the moment to explain any movement. Dutrochet had still another subsidiary hypothesis for the explanation of the movement of the stem, according to which the fibrous parts of the stem, *i.e.*, the young wood, were caused to curve outward by absorption of oxygen. He states that as light sets free oxygen in the green cells of the rind, a portion of this is conveyed to the young wood, the latter then, by curving, assists the curvature commenced by the rind. Disregarding the fact that the entire theory of the curvature of the wood through the absorption of oxygen rests upon very uncertain experiments, two circumstances are opposed to it; in the first place, the curvature of plants is almost exclusively produced by blue light, while this is completely incapable of causing evolution of oxygen from green parts; in the second place, according to Payer's experiments ("*Comptes rendus*," 1842, 26th December), the curvature takes place also in nitrogen and hydrogen. Since the pretended curvature of the young wood would be in the way of the movement from the light in the tendrils of *Vitis*, in the shoots of the Weeping Ash, &c., they are eliminated by the statement that in these plants the young woody layer is so thin and weak that its effects are imperceptible. It is clear the author knew how to get out of a difficulty.

While the stem and the root only exhibit movement when they seek to regain the natural position out of which they have been removed, it is different in the leaves, for these have not only the power, in a high degree, of returning to their natural position, when artificially disarranged, but (with the exception of the stout leathery or fleshy leaves) almost all thin leaves, and particularly compound leaves, present different arrangements by day and by night, a phenomenon to which the terms *sleeping and waking* have been applied. As in the stem the normal position is the perpendicular, with the point of the stem turned upwards, so in the leaf is the horizontal, in which its upper, darker-coloured surface is turned towards the sky; into this position it is brought back by the influence of gravity, when it is disarranged, and it is diverted from it by the influence of light falling obliquely on it, or artificially thrown upon it from below, the leaf constantly striving to turn its upper face to the light.

The movements which the leaves make under these circumstances frequently take place so quickly, that the leaves of many plants follow the daily course of the sun; at the same time they are often far more extensive than those movements we observe in the stem. Not only is the leaf in general far more capable of curvature of its flat and extended substance, in consequence of the greater pliancy of this than the axial organs, but the movement of the whole leaf is favoured by the circumstance that in a great number of leaves, there lie, both at the base of the petiole, and in compound leaves, also at the base of each leaflet, little enlargements (articulations) composed of soft, succulent parenchyma, which, on account of the abundance of their cellular tissue, and because, at the same time, the vascular bundles passing down through the middle of the articulation can oppose but slight resistance to the curvature, are capable of a far stronger degree of curvature than the other stem-like parts of the plant.

That the various positions to which the terms waking and sleeping are applied, are produced by the alternating influence and absence of light, and that the diminishing temperature and increasing moisture of the air coming on with night, do not play any essential part in this, is shewn especially by the experiments of De Candolle, who succeeded in reversing the periods of the sleeping and waking of plants, by illuminating them at night and keeping them in the dark by day. In very sensitive plants, also, artificial withdrawal of the light, even for a short time, as the dim light which exists during a great eclipse of the sun, suffices to make the leaves go to sleep; while, on the other hand, many plants, especially the different species of *Oxalis*, require bright sunshine to make them expand their leaves fully.

The movements made by leaves in going to sleep differ in the highest degree in different plants: sometimes they consist of a sinking, sometimes of an elevation, of the leaf, in compound leaves at once of sinking, elevation or twisting, sometimes of folding together of the leaflets; in general the leaves present a smaller expansion during sleep than by day, not, however, so that we can say with E. Meyer, they always seek to return to that position which they possessed in the bud; since not unfrequently, for example in *Oxalis*, the position of the sleeping leaf differs essentially from its position in the bud. Neither must the term sleep lead to the assumption that the movements by which leaves pass into their nocturnal position depend upon a relaxation, since, on the contrary, the parts from which the motion issues, that is the joints, are in a state of considerable tension during the sleep of leaves.

The flowers of a large quantity of plants exhibit changes of position by night analogous to those of leaves, the corollas folding up; in the Compositæ the capitules shutting up, &c. Here also the times of sleeping and waking have been reversed by artificial illumination (Meyen, "*Physiologie*," iii, 495).

Undoubted as it is that the movements of sleeping and waking, both in leaves and in flowers, are dependant upon the influence of light, yet they do not always occur in such a way that the waking takes place in the morning when the daylight has reached a certain definite degree, and the sleep begins in the evening when the twilight has brought the light down to the same degree, but the waking frequently precedes the dawn of day by several hours (*e. g.*, in the leaves of *Mimosa pudica*), while the sleep commences when there is still tolerably strong light. This condition presents itself in a still more striking degree in many flowers, than in leaves. As a general rule, the openness of the flowers is indeed regulated by the light, so that the majority open in the morning from six to seven, and close in the evening at from six to seven, but in many flowers the opening takes place at the very commencement of dawn, while they go to sleep even before noon, or at least early in the afternoon; on the other hand, some plants require a longer illumination by the sun to cause their opening, so that the flowers of various plants open gradually at the different hours of the morning until noon, on which peculiarities Linnæus founded his "flower-clock." These variations may be partly independent of light, and may be caused by the circumstance that every species of plant requires a certain degree of temperature to open its flowers. (*See* Fritzsche, "*Sitz. bericht der Acad. zu Wien*," Jan. 10, 1850.) In the flowers of many plants we meet with the remarkable deviation that they open first in the evening, reach their full expansion at midnight, and close again in the morning, a phenomenon which, so far as we know, has no parallel in the leaves; perhaps this phenomenon is analogous to the circumstance that the tendrils of *Vitis* turn away from the light.

Observ. Since the far simpler movements which the influence of light produces in stems and roots have not yet been adequately explained, we can much less expect that the experiments to elucidate the movements of leaves should have been more happy. The full development of the cellular tissue in the articulations of the leaves renders it much easier to demonstrate in them, than in the axial organs of plants, that the motions of plants are caused by curvature of the parenchymatous tissue, and not by contraction of the spiral vessels or elongated cells (as was assumed by Malpighi and all physiologists up to Link's time, evidently misled by an erroneous idea of analogy between the movements of plants and those of animals depending upon contraction of the muscular fibres). To demonstrate this is merely required the easily performed experiment of cutting away the cellular tissue, without injuring the vascular bundle, in the articulation of any leaf possessing a distinct thickening there; this operation lames the leaf. Our whole knowledge is essentially confined to this fact. For, much as has been written concerning the sleep of plants, nothing whatever is yet made out of the manner in which light acts upon the cellular tissue, whether, as Treviranus assumes ("*Physiologie.*" ii. 750), the activity of the latter is excited by light in consequence of an irritability of the cellular tissue; or, as Dutrochet thought ("*Mémoires,*" i. 525), the excretion of oxygen occurring under the influence of light brings about an increased ascent of sap, and a consequent turgescence of the cellular tissue, or, on the contrary, according to Dassen's hypothesis, superabundance of crude sap produces the nightly sleep; or whether, as Macaire supposed, the absorption of carbon, combined with excretion of oxygen, occurring under the influence of light, is to be regarded as the cause of the movement. In particular the variations in the movements of leaves, some of which sink down while others rise up in sleep, have not yet been traced back by anatomical research to any definite difference of organization. It is true Dutrochet ("*Mémoires,*" i. 469) took much pains in endeavouring to make out the cause of motion through anatomical investigation of stems and leaves, whereby he arrived at results similar to those in his above-mentioned investigation of the axial organs, since he thought he found, besides the curvable cellular tissue, a curvature of the young fibrous tissue produced by absorption of oxygen; but a minute exposition of his views appears to me to be superfluous. The complaint has been made, in other quarters, of the work of Dutrochet, that it is incomprehensible. I would not complain of this so much, as that the illogical conclusions of the author, and the arbitrary style in which he introduces unfounded statements of facts (with which I have already found fault above), have increased in proportion with the complication of the phenomena which were to be explained. A wide but difficult field still lies open here to the experimental physiologist.

Besides the movements already described independent of external material influences, peculiar motions of particular organs are met with in a number of plants, ensuing only through the action of stimuli accidentally effecting them, whence a *sensitiveness* or *irritability* has been ascribed, to these plants.

Observ. We meet with such phenomena of irritability in the leaves of a not very large number of plants of the families of Leguminosæ, Oxalideæ and Droseraceæ. Among the Leguminosæ, it is principally in plants of the genus *Mimosa*, of which *M. pudica*, above all, has been the subject of minute investigation; besides these, there are the various species of *Robinia*, and some species of *Æschynomene*, *Smithia* and *Desmanthus*; in the family of the Oxalideæ probably all the plants possess more or less distinct traces of irritability, but only the pinnate-leaved *Biophytum sensitivum* in a high degree; among the Droseraceæ, the leaves of *Dionœa muscipula* have a most remarkable irritability, while our indigenous species of *Drosera* only exhibit traces of it.

In my opinion, a dull irritability exists in the stems of twining plants, and tendrils.

The same property is exhibited also by the stamens of species of *Berberis* and *Mahonia*, by *Sparmannia africana*, of many species of *Cactus*, *Cistus*, of many plants of the section *Cynarocephalæ;* moreover by the stigmas of *Martynia* and *Mimulus*, the style of *Goldfussia anisophylla*, and the column of the style of *Stylidium*.

Among the plants possessing irritable organs, *Mimosa pudica* especially has been the subject of repeated investigations. The common petiole of this plant is connected with the stem by a much enlarged articulation, and similar articulations are met with at the bases of the secondary petioles and of the individual leaflets. When strongly irritated, as for example by shaking, the entire leaf sinks by a bending of the articulation situated at the base of the inner petiole, the secondary petioles approach together, and the leaflets, curving forwards and upwards, apply themselves together, like tiles on a roof, upon the secondary petioles, so that the whole leaf assumes the position of a sleeping leaf, which gave rise to the idea formerly entertained generally, that this motion is the same as that which occurs when the leaf goes to sleep, an opinion incorrect in many respects.

The motion of the articulation of the petiole may be produced by direct irritation of it, but the stimulus must act upon the under side of the joint, that becoming concave in the motion; even a slight touch upon the joint in this part will cause a sinking of the leaf, while strong stimulus, even wounding, of the upper side of the joint has no effect. But at the same time stimulus affecting other parts of the plant is propagated to the joint and causes it to move, provided the irritation be strong enough.

The articulation is composed of an accumulation of parenchymatous cells containing chlorophyll, each also exhibiting in its interior a larger or smaller globular mass of a substance strongly refracting light (oil ?). The latter substance, however, does not appear to be essential since it is absent from the cells of other irritable organs. Through the middle of the joint run the vascular bundles entering the petiole, united into a comparatively slender cord. There is nothing at all peculiar in these anatomical conditions, they perfectly resemble what we find in many other plants, not irritable. The only circumstance to be regarded as essential is, that the parenchymatous tissue existing in comparatively large quantity, exhibits a considerable distention, so that it strives to occupy a larger space than is allowed by the mechanical conditions in which it is placed. If we cut a plate longitudinally out of the middle of the joint, which of course will consist of the woody bundle in the middle, and of a layer of parenchymatous cellular tissue at each side, and then cut this plate lengthways into thin strips, the middle of which is composed of the vascular bundle, and the two sides of cellular tissue, the latter pieces immediately expand about 1-5th longitudinally, whence it is evident that the vascular bundle is too short in proportion to the turgescent mass of cellular tissue of the articulation, and that the latter is compressed in the direction of the longitudinal axis in the uninjured joint.

Observ. According to the description of Dutrochet ("*Rech. sur la struct. intime des anim. et veget.*" 1824; "*Nouvell. rech. sur l'endosmose,*" 1828), and Brücke ("*Müller's Archiv.*" 1848, 434), the cellular tissue both of the upper and under side of the articulation has a tendency to curve inwards strongly. I do not find this confirmed. Of course, if a strip of the vascular bundle is left connected with the inner side of the plate of parenchyma above-mentioned, only the outer side of the cellular tissue can expand, while expansion is prevented on the inside by the rigid vascular bundle; under these circumstances a curvature of the whole plate must naturally take place.

In uninjured articulations, the expansion of the cellular tissue of the upper side maintains equilibrium with the cellular tissue forming the under side, which prevents curvature of the whole. But if the cellular tissue is cut away down to the central vascular bundle on the upper side of the articulation of a leaf still attached to the plant, the cellular tissue of the under side having now lost its antagonist can pursue its expansion, and the leaf thus becomes at once pressed upwards at a sharp angle; the reverse occurs when the cellular tissue of the under side is removed.

Observ. This fundamental experiment which first threw light upon the anatomical system by which the movements of plants were caused, was made as early as 1790 by Lindsay, but was again forgotten, so that the discovery he established was made a second time by Dutrochet ("*Sur la struct. intime,*" *&c.* 1824).

According to the common statement, which rests upon the experiments of Dutrochet, a leaf robbed in the above described way of one side of its thickened joint, loses its power of motion entirely, and after the removal of the lower portion of the cellular tissue of its articulation can rise up no more, and can sink down no more after the loss of its upper portion. But, as Brücke ("*l. c.*" 452) correctly observed, this is not altogether true, since such a leaf still performs the movements of sleeping and waking, although in a much less marked degree (especially when the cellular tissue of the under side is removed); and moreover, as will be mentioned farther on, has not altogether lost its irritability.

It is clear that the movements of a leaf upwards and downwards, dependant upon one-side expansion of the cellular tissue of the articulation, may take place in a variety of ways. In the first place, if the cellular tissue of the upper side swells up and thus acquires a preponderance over that of the under side, a curvature downwards must take place, and, *vice versâ*, swelling of the under side of the tissue must raise the leaf; on the other hand, the same result must occur when the cellular tissue of one side becomes lax, and thus gives that of the opposite side the opportunity of following its natural tendency to expand. It is possible also that both these conditions may exist at the same time.

From the erroneously assumed immobility of a leaf, in which the cellular tissue has been cut away from one side of the articulation, Dutrochet (*"Nouv. rech. sur l'endosmose,"* 47), drew the conclusion, that the movement of the leaf always occurred through the cellular tissue of that side of the articulation which becomes convex in the curvature, expanding actively, while the tissue of the side which becomes concave remained perfectly passive. As already observed, the fact upon which this conclusion rested, is not perfectly correct. A leaf which has had the upper side of its articulation cut away, of course immediately rises up nearly perpendicular, but it does not remain in this position; in a few days it recommences the performance, more weakly though it be, of the sleep-movements (sinking and rising). It is, therefore, clear that the expansion of the under side of the articulation, produced by removal of its antagonist, as a general rule, raises the leaf higher than in the natural condition, yet at the same time that this expansion is not constant, but undergoes a daily increase and decrease. The same circumstance (only in less degree) presents itself after the under side of the joint is removed. We must conclude from this that the expansion of one side of the articulation plays the principal part in the elevation and depression of the leaf, but that in this motion the opposite side likewise undergoes a change, and, indeed, a relaxation.

If the said view of Dutrochet was not wholly correct in regard to the sleep-movements, still less was it in reference to the irritable movements. It is clear that if the depression of a leaf resulting from irritation is caused by the active expansion of the upper side, overcoming the resistance of the under side, the tension must increase in the whole articulation, and the latter must become rigid. Now, Brucke (*"l. c."* 440) shewed that the articulation of an irritated leaf becomes in no slight degree relaxed when this is depressed; we must, therefore, assume that the motion arising from irritation depends not upon an increased expansion of the upper side of the joint, but principally upon a relaxation of its under side. This is also borne out by the circumstance, that a leaf of which the upper side of the articulation has been cut away, sinks (although not to the same extent as an uninjured leaf) when irritated, which would be impossible if the movement had its source solely on the upper side.

This relaxation, as Brucke also shewed, either does not occur at all in a sleeping leaf, or at least in a far weaker degree than in an irritated leaf. Hence it is clear, as I formerly remarked on other grounds (*"Ueb. die Reizbarkeit der Blätter von Robinia."*—Mohl, *"Verm. Schrift."*), that the movement of irritability is not identical with the sleep movement. Evidence of this is also offered by the circumstance, that a sleeping *Mimosa* leaf is at least quite as sensitive to irritation as a waking one, and performs the movements of irritability very rapidly and to quite as great an extent.

Concerning the internal occurrences, on which the relaxation of the lower half of the articulation, resulting from irritation, depends—whether, as Brucke assumes, but as appears to be highly improbable, a portion of the cell-sap issues out into the intercellular passages, or a relaxation of the cell-walls takes place—we know simply nothing.

Observ. Dutrochet subsequently ("*Mémoires*," i., 537) retracted the theory above-mentioned, concerning the depression of an irritated *Mimosa* leaf, and set up the opinion that this movement downwards does not depend upon the expansion of the cellular tissue of the upper side of the articulation, but upon curvature of the younger layers of wood, which, in consequence of the irritation, absorb oxygen from their vicinity in a way not further explicable, and are thereby caused to curve downwards. After a short time, and from an equally unknown cause, this oxidation of the fibrous tissue ceases, the power of curving belonging to the cellular tissue again acts, and causes the elevation of the leaf. Leaving the arbitrary character of the whole of this explanation out of the question, there is evidence against Dutrochet's theory in the experiments of Brucke, which indicate that the depression of the leaf is connected with relaxation of the articulation, for if the articulation were bent by the curvature of the woody bundle, the cellular tissue of the under side would be strongly compressed, which must rather increase than diminish the tension of the joint.

The leaf of *Mimosa* is sensitive to stimuli of every kind; shaking, wounding, burning, contact of irritating fluids, electric shocks, &c., all act in the same manner. Quick repetition of an irritation exhausts the sensitiveness towards it tolerably soon. The more vigorous the vegetation of the plant is, the higher the temperature in which it is placed, the more sensitive it is found to be.

It has already been observed that the direct irritation of the articulation of the leaf is not necessarily required to produce the movement of irritability, but that the effect of a stimulus acting on a distant part is conducted to the articulation, under which circumstances, it depends on the irritability of the whole plant and the strength of the stimulus, how far the manifestation of irritability becomes diffused from the irritated point. In reference to this conduction of the stimulus, the researches of Dutrochet and Meyen led to the conclusion that it was conveyed by the vascular bundles, and not by the parenchymatous cellular tissue; for on the one side the conduction of the stimulus was interrupted by cutting away the vascular bundles, and on the other side wounds on the rind, when the incision did not penetrate the wood, were not followed by movements of the leaves. This conduction is comparatively slow; according to Dutrochet's measurements, it amounted to 8—14 millimeters in a second in the petiole, to only 2—3 millimeters in the stem.

Investigation of the other irritable plants, the leaves of *Dionœa*, *Oxalis* and *Robinia*, the stamens of *Berberis*, *Cactus*, &c., furnished no result which admits of any essential addition to what has been stated of *Mimosa.* The moving organ was always found to consist of abundance of parenchymatous cellular tissue, which, however, did not differ from ordinary cellular tissue in its visible properties, and the contents of which, in like manner, presented nothing characteristic, since they consisted of the usual substances, starch, chlorophyll, &c., so that the conjecture is, indeed, not over bold, that irritability may be a property belonging to cellular tissue generally, which, however, can only display itself outwardly, when developed in a higher degree, and where especially favourable conditions exist in the structure of an organ. The circumstance which is so distinctly marked in *Mimosa*, that the side of the sensitive organ, which becomes concave in the movement, is alone capable of receiving the stimulus, while the opposite side is perfectly insensible, appears to be universal; at all events this condition exists in like manner in the leaves of *Dionœa*, the stamens of *Berberis*, and in tendrils.

In the majority of cases, the movement of an irritable plant is very transitory, when the plant is not organically injured by the stimulus applied. Few experiments have been made on the effects of long-continued irritation. An experiment of Desfontaines affords evidence that a plant may become accustomed to a weak stimulus; that author carried a *Mimosa* with him in a coach, and in a short time the plant became accustomed to the jolting motion, and its leaves, which at first had closed up, reopened. It is otherwise with tendrils and twining plants, which, when they come in contact with a foreign body, curl over the point of contact, and in this way partially embrace the support. A return to the former position is impossible, since through this curvature a portion of the tendril or twining stem lying above the point first irritated is brought in contact with the support, and in like manner stimulated to the curving movement; in this way the movement of curvature advances up the plant until the whole length has become wound round the support.

Observ. The view propounded by me ("*Ueber den Bau und das Winden der Ranken und Schlingpflanzen*") that the curling round the support results from an irritability excited by contact, has not had to boast of any particular approval, yet I do not find that anything better has been put in its place. When Treviranus ("*Physiol.*" ii. 746) says that this phenomenon is caused by a slowly and inertly acting elasticity, which is chiefly called into activity by contact with foreign bodies, I must confess that the meaning of these words is quite incomprehensible to me; and when Schleiden ("*Grundzüge*," 2. *ed.* xi. 543) states it is a phenomenon of growth, which determines the direction, that is, the peculiar form of the tendril, and the growth of the twining plant, he appears simply to be ignorant of the fact which comes under consideration, since every accurate examination of tendrils and twining plants shews that the curling round the support is a phenomenon totally independent of the growth.

The external action of ponderable or imponderable agents is necessary to the production of all the movements hitherto mentioned; but besides these, there occur in isolated cases motions which, so far as existing experience reaches, are wholly independent of external influences.

It is held as an enigmatical phenomenon that a twining plant which stands at a distance of one or more feet from its support, reaches this in order to grow up it; the cause of it is sought sometimes in a mysterious power in these plants of seeking out the supports, sometimes in their asserted property of turning away from light, &c., but the matter is explained in the simplest manner by a peculiar motion with which the stems of these plants are endowed. The younger internodes of twining stems are quite straight and their vascular bundles run, like those of other stems, parallel with the axis of the stem; but when an internode has attained a certain age it begins to curl (according to the species of plant, to the right or left) around its own axis, in consequence of which the vascular bundles acquire a spiral course. This curling occurs only in a short length of the stem in each single period of time, but it advances gradually from below upwards, proceeding from one part of the stem to another, without ever becoming recurrent The upper part of these stems, always slender and pliable, hangs over in a curve; and since it must follow the curling of the lower part, it is continually carried round in a circle like the hand of a clock; then if a solid body stands within the circle described by the point of the stem, the latter becomes pressed upon the solid body, the irritability peculiar to it becomes excited, and thus the twining round the support is produced. (For the more minute details of this process, *see* my essay above referred to.) We do not at present possess an explanation of these movements and of the circumstance that they occur constantly, either to the right or to the left, in each species of plant; but it cannot be doubted that the movement here also has its origin in the parenchymatous cellular tissue, since the perfectly visible distinction between the stems of twining plants and those of other vegetables, depends on the relative abundance of succulent cellular tissue in the former, and since in many plants, *e.g.*, in *Cynanche Vincetoxicum*, the stem becomes more inclined to twine, the more its succulence is favoured by the shade and moisture of the locality in which it grows.

Observ. The circular movement of the stem just described has nothing to do with the twining round the support; in fact, that part of the stem which has undergone the torsion is incapable of twining round a support, and the movement of curvature, which causes the twining, occurs only in the younger part of the stem, the fibres of which still retain their straight course. This may be caused not only by the younger parts of the stem being the softer, more juicy, and, in consequence of this, more moveable, but also, and principally, by the circumstance that in old curled parts of the stem the cellular tissue of the rind has already attained a considerable longitudinal extension, compared with the parts situated nearer the axis.

Whether the movements which Dutrochet observed ("*Ann. d. Sc. nat.* 2 *Sér.*" xx. 306) in the stems of *Pisum sativum*, are identical with the above-described circular movements of twining plants, with which, as I shewed in the "*Botanische Zeitung*," 1845, 118, Dutrochet was but very imperfectly acquainted; or whether, as appears to follow from his description, they depend upon a rotation of the stem unconnected with torsion, I cannot decide, since I have not yet repeated these observations.

Motion is also produced without external influence in tendrils, which, in like manner, is capable, although in less degree than the circular motion of twining plants, of bringing them in contact with foreign bodies. For, when a tendril has attained its full length, up to which time it is straight, it curls up together spirally from its point to its base, in such a way that its upper side forms the outer side of the spiral. When the tendril is brought in contact with a foreign body by this movement, its irritability is excited at the point of contact, and the above-described convolution round the support commences, which progresses from below upwards along the tendril.

These movements of tendrils and twining plants have not attracted the attention of naturalists in so high a degree as the movements of the leaves of *Hedysarum gyrans*. This plant possesses ternate leaves; the middle leaflet exhibits the ordinary sleep-movements, sinking by night and rising by day, but the very small side-leaflets present, day and night, a jerking motion, by which they are alternately raised and depressed. Similar movements are presented by the lateral leaflets of *Hedysarum gyroides*, according to Mirbel, also of *H. vespertilionis*, and according to the statements of Nuttall ("*Genera of N. American Plants*," ii. 110), those of *H. cuspidatum*, and probably of *H. lævigatum*. Few plants have been so much observed on account of a physiological peculiarity, as *Hedysarum gyrans*, but unfortunately all attempts to give a tenable explanation of its movements have been fruitless.

A similar motion, occurring without external cause, was discovered by Lindley in the labellum of an Orchideous plant, *Megaclinium falcatum*, and more minutely observed by Morren ("*Ann. des Sc. nat.* 2 *Sér.* xix. 91). This movement consists of a slow depression and elevation of the labellum, repeated in periods of a few minutes. From Morren's anatomical investigation, it appears that this motion must be caused by an alternating expansion, first of the upper, and then of the under, part of the cellular tissue, which forms the claw of the labellum; but the cause of these expansions remains just as obscure as that of the movements of the leaves of *Hedysarum gyrans*.

WORKS ON BOTANY

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