The Structure of the Cells of Vegetable Fibers

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When wood or any vegetable material is decomposed, the fibrous substance is more or less destroyed. The fibrous structure disintegrates into its individual cell elements among which may be found, depending upon the raw material, woody and bast cells, tracheids, perenchymatous cells, tracheæ, cells from the epidermis, and others. Thus, the cell substance is morphologically not uniform. But even the isolated cells of a kind exhibit large differences in anatomical structure as well as substance.

A. The Anatomical Structural Elements of Fibers

1. Transverse Elements

In his "Raw Materials of the Vegetable Kingdom" J. Wiesner[1] describes that peculiar swelling resembling a string of beads, which cotton exhibits in a solution of cuprammonium (see Figure 1)[1a]. It was assumed that the phenomenon was caused by the tearing of cuticle which cannot withstand the expansion of the layers of cellulose underneath it, and by the rolling up of the torn cuticle at the annular bands. Subsequently the same swelling has been observed on numerous wood and bast fibers as well as vegetable hairs[2] whereby the primary layer of wood and bast fibers corresponds anatomically to the cuticle but is composed of a different substance.

A check-up on Wiesner's data with fibers of bamboo stalks showed that they, when suitably treated, swell very regularly in distances of about 10 to 30μ and that the annular knots are closer together at the end of the fiber than at the middle. By carefully treating the fiber with the diluted reagent under the microscope a swelling could be noticed without a simultaneous bursting of the primary layer and, where it did tear, no rolling together of the loose ends was observed, at the most, yellow colored fragments could be seen floating about in the solution. The globular expansion of the fiber dissolved at first, the annular knots withstanding much longer and showing strong double refraction between crossed Nicol prisms. When sections of fibers underneath the covering glass are treated with ammoniacal copper oxide (Schweitzer's reagent, cuprammonium) in such a manner that the reagent can attack at the cut ends in the direction of the axle of the fiber, it can be observed under the microscope that the fiber rapidly dissolves until the reagent comes to the next annular band whose substance resists for some time but which also finally dissolves, provided the reagent is strong enough, then, solution rapidly progresses to the next annular band when it is again retarded, etc. It is possible, occasionally, to dissolve the substance on both sides of an annular band to isolate the latter, and to separate it by moving the covering glass. It resembles a perforated disc or a ring through

Figure 1
Bamboo Fiber X200 Magnification
Formation resembling string of beads takes place in every layer on account of tangential inner skins and transverse elements.

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[1] J. Wiesner, Die Rohstoffe des Pflanzenreichs, 2nd ed., vol. 2, page 247, Leipzig, 1903; Maegeli had already in 1866 pictured a similar swelling of flax in iodine—sulphuric acid (Bot. Mitt., vol. 2, table 5).

[1a] For this photograph the micro-photographical equipment of the Kaiser Wilhelm Institute for Chemistry was at my disposal.

[2] For instance: F.v. Hoehnel, *Die Microskopie der technisch verwendeten Faserstoffe.* 2nd edition, Vienna 1905; H. Aisslinger, diss. Zuerich 1907; etc.

which the lumen respectively the remains of its protoplasm protrude.

These observations indicate that the phenomenon yields to an interpretation different from Wiesner's: the fiber at the annular bands contains crosswise structural elements which have firmly grown together with the primary layer respectively the cuticle and which thus are the cause of the peculiar globular bead-like swellings.

The crosswise structural element can not be composed of cellulose, xylan (wood gum) or mannan since its behavior in Schweitzer's reagent is different. It appears that there must be imbedded in the fiber an unknown substance which is the same or at least similar to the cuticle. This assumption is confirmed by the action of diluted acids which destroy both more easily than cellulose. The characteristic swelling in ammoniacal copper oxide is, then, not evident.

It has been known for a long time that vegetable fibers become brittle under the influence of acids and disintegrate into small pieces the length of which corresponds to the distance between two annular rings in the ammoniacal copper oxide solution. Upon this property a method for removing vegetable matter from woolen fabrics has been based, namely, carbonizing. The process consists of a destruction of the cuticle or primary lamella and of the substance of crosswise structural elements. The fibers then break at the annular bands.

The swelling in Schweitzer's reagent[3] is not equally pronounced for all vegetable fibers. Wood fibers, as a rule, show a well defined swelling, vegetable hairs somewhat less, while the bast fibers from textile fiber plants often yield only irregular and not so well defined swellings due to differences in the development of cuticle or primary layer and crosswise structural elements. The reaction disappears after treatment with alkalies and bleaching agents as well as after the mechanical destruction of the fibrous structure (for instance, in the beater).

The shape of the crosswise structural elements can not yet be given with any degree of accuracy. In some cases, as, for instance, with cotton, it seems as if a string had been wound around the fiber, in other words a ring which forms a part of the cuticle. The annular band of the bamboo fiber appears like a disc with an actual subdivision of certain parts of the membrane.

In order to obtain further data about the shape and purpose of these structural elements, the history of the evolution of the fiber was scrutinized. The old botanical literature contains reports to the effect that the fiber cell has developed by fusion of parenchym cells. Hence the crosswise structural elements might be considered as rudiments of the cuticles of the parenchym cells. This assumption, however, was soon rejected by H. v. Mohl and C. v. Naegeli, and modern botanical research also could not adopt it again[4].

There is the further possibility that the crosswise structural elements have subsequently been built into the already developed fiber, perhaps to reinforce it. They can already be observed in the fibers of beech sprouts about two weeks old and of green bamboo stalks which indicates that they develop comparatively early in the fibrous structure. They were more distinctly noticeable in woody fibers than in bast fibers. But the examination of the dead object is not sufficient to lead to a definite conclusion as to the purpose of the formation, and the botanical literature offers no solution to the question.

2. The Layer-like Structure and its Cause

On the isolated fiber ordinarily three layers or lamellæ can be distinguished which surround the lumen or central canal. The tertiary layer next to the lumen, the secondary layer, and the primary layer which covers the fibers. While the individual fibers still form a part of a fibrous structure, they are cemented together by another lamella which adjoins the

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[3] Other swelling agents like sulphuric acid along or in conjunction with other agents (glycerin), alkali alone or with subsequent treatment with carbon bisulphide, concentrated solutions of common salt yield essentially the same swelling reaction although it is mostly not as well developed. The swelling in concentrated solutions of hydrochloric acid meanwhile has been given by P. P. von Weimarn (Koll. Zeitschrift 44, 163, 1928).

[4] See also the remarks and bibliography in my work: *Zur Kenntnis der pflanzlichen Zellmembran* III. A. 466, 27, 1928.

primary layer. The secondary lamella is often expanded and in that case itself made up of layers[5].

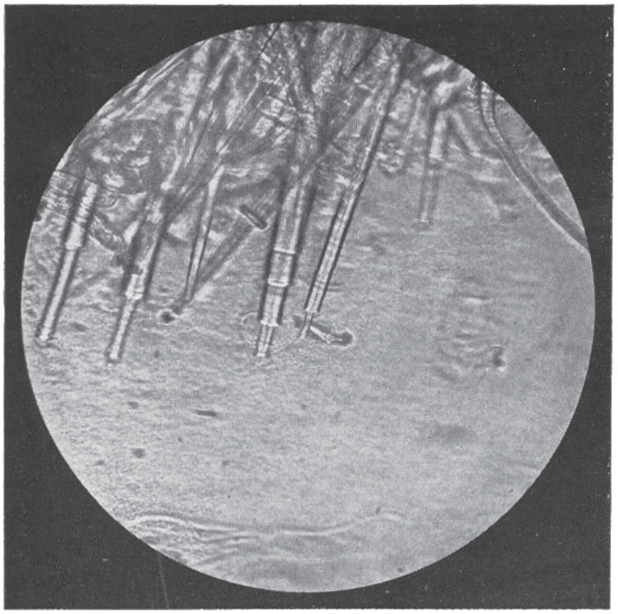

Figure 2
Bamboo Fiber X200 Magnification
Setback formation caused by presence of transverse elements.

Figure 2 shows the different layers of a bamboo fiber (see also the sketch). The upper ones have been taken off by ammoniacal copper oxide. At the end four layers are missing, then three, two, one, and finally there is only a loosening of the structure. The setback formation is caused by the presence of the transverse elements whose substance offers a greater resistance to the reagent than cellulose or carbohydrates of analogous structure. C. v. Naegeli explains the layer formation by assuming the presence of alternately more or less water in the layers[6]. E. Strassburger saw in the lines between the layers the boundary of independent layers. His view is known as the *Kontaktflächen* theory (theory of contact surfaces)[7].

As is shown in figures 1 and 3, after removal of individual layers the same swelling can be produced in the layer underneath as on the fiber when the primary layer or cuticle is present. Since, after removing the latter, the fiber simply dissolves without giving the bead-like swelling (cellulose itself, therefore, is not capable of producing the characteristic swelling) it follows that every individual layer is covered with a thin membrane whose substance is like or at least very similar to that of the primary lamella. Figure 3 shows the swelling of the second layer while the first layer is still attached and intact.

These two observations dispose of both explanations of the layer-like structure proposed by Naegeli and Strassburger. If the method of separating each layer with a membrane is carried through, there ought to be such a membrane between the last inner layer of carbohydrates and the protoplasm. It may then be the same as the tertiary lamella, the presence

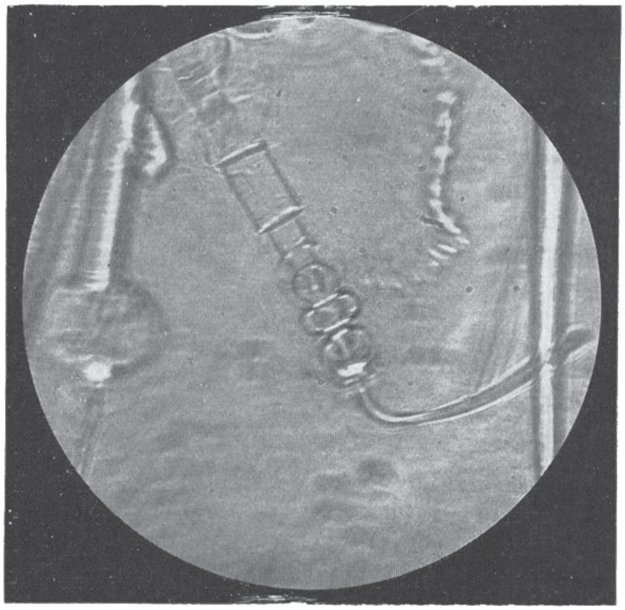

Figure 3
Bamboo Fiber X300 Magnification
Transverse elements of individual layers are in different places.

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[5] A historical review has been given, for instance by H. Reimers, *Mitt. d. deutsch. Forschungsinst. f. Textilstoffe.* Karlsruhe 1922. See also my remarks Vol. 61, 466, 1928. It will hardly be possible to arrive at a rational nomenclature before more is known about the chemical constitution of the different structural elements. Until then, it might be advisable to distinguish three lamellæ and to speak about their layers of tissue rather than vice versa as Strassburger does.

[6] C. v. Naegeli, see *Sitzungsber. d. Kgl. Bayer. Akad. d. Wissenschaften,* Muenchen, 1, 282, 1864; 2, 114, 1864; *Pflanzenphysiol. Untersuchungen.* Vol. II, München, 1866; C. v. Naelegi and S. Schwendener, *Das Mikroskop.* 2. Edit. Leipzig 1877, p. 433 a. 533. C. Correns, *Jahrb. wissensch. Botanik,* 23, 254, 1891; *Ber. d. Bot. Ges.* 11, 410, 1893.

[7] E. Strassburger, *Über den Bau und das Wachstum der Zellhäute.* Jean 1882; *Histologische Beiträge,* No. 2, 1889; *Jahrb. f. wissensch. Botanik.* 31, 511, 1898; G. Krabbe, *Jahrb. wissensch. Botanik,* 18, 346, 1887.

of which so far could not always be established with certainty.

That not only the thickened bamboo fiber exhibits the presence of sub-dividing membranes but that also other fibers, probably all with an expanded secondary lamella are likewise constructed is confirmed by Figure 4 which illustrates a fiber of bleached straw. Besides the structure of most fibers, apart from unessential differentiation, is alike which would also tend to confirm the above assumption. When repeating such experiments, it should be kept in mind that the pulp be prepared with as mild an agent as possible. I usually used the chlor-dioxide sodiumsulphite method[8]. Boiling under pressure yields only occasionally a suitable product. Chemical and mechanical after-treatment, such as bleaching, mercerizing or scutching have a detrimental effect upon the clearness of the swelling reaction.

3. Spiral Lamellæ

The spiral lamellæ are a fine subdivision which runs in a radial direction through the layers (see sketch). It is not readily visible on all fibers, and as a rule better noticeable in the outer layers than in the inner layers near the lumen which may be due to pressure exerted by the outer layers upon the inner layers. When a swelling agent is allowed to act upon the cross section of a fiber, the layers will swell to a different extent. The innermost layer swells most, and each following layer somewhat less, so that setbacks are formed[9].

The spiral lamellæ are independent in each layer and are inclined towards the axle of the fiber. The systems of spiral lamellæ in adjoining layers are always at an angle to one another and often run in different directions.[10]

This phenomenon was interpreted like the layers. Von Naegeli held that it was caused by a difference in content of water, and Strassburger believed two adjacent lamellæ to cause the effect. Following their way of reasoning by analogy which is very plausible, it can be inferred that the radial subdivision, like the subdivision in layers is effected by membranes. The substance of the latter probably is the same as that of the membranes between the layers since it has little resistance to acids. For instance, the layers of carbonized fibers can be lifted off with a needle and split lengthwise by pressure.

The purpose of the arrangement in spiral lamellæ and layers has to the author's knowledge not yet been discussed. If the fine membranes are considered to be a substance which cements layers and spiral lamellæ together, then the cell wall may be likened to a wooden plate made up of veneers glued together crosswise which has considerably more strength than a plain plate of equal thickness. The crosswise arrangement in the cell wall is effected by the spiral lamellæ of adjacent layers being at an angle instead of running parallel. Only recently has it been found that the strength of veneers can still be increased by using thin slats of wood glued together as the middle layer. That corresponds exactly with the system of spiral lamellæ. If such veneered plates were bent into tubes several of them inserted into one another and again glued together, an extraordinary strength would result. And that is the case with the crosswise arrangement of spiral lamellæ. S. Schwendener determined tensile strengths of several fibers which corresponded to that of iron, and in a few cases were even approaching the tensile strength of steel[11]. Thus, one can hardly be far off the truth when the purpose of the layers and spiral lamellæ is interpreted as a means to provide strength. The existence of membranes between layers and lamellæ would also furnish an explanation for the formation of the units of cell wall recently found by K. Hess and G. Schulze[12]. By treating bast fibers with acid and benzol, it was possible to separate from them certain macroscopial crystal-like bodies. They represent units of fibrils which are surrounded by membranes. Since the latter are more rapidly destroyed by acids than cellulose, the units of fibrils could be isolated as apparently homogenous complexes.

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[8] E. Schmidt u. E. Graumann, B. 54, 1860, 1921.

[9] See the picture in M. Lüdtke, *Zur Kenntnis der pflanzlichen Zellmembrane* III, A. 466, 27, 1928: as well as the other microphotograph.

[10] See H. Reimers, *Mitt. d. deutsch. Forschungsinst. f. Textilstoffe,* Karlsruhe 1922.

[11] S. Schwendener, *Das Mechanische Prinzip im Anatomischen Bau der Monocotylen,* Leipzig 1874.

[12] A. 456, 55, 1927; see especially Figs. 5-8.

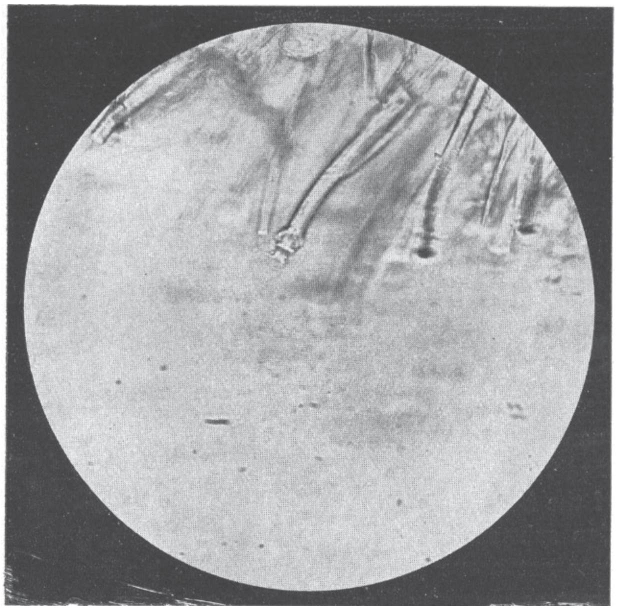


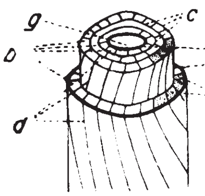
Figure 4
Fibers of Bleached Straw X200 Magnification
Layers and swelling less visible than in Figs. 1-3 on account of bleaching.

4. The Fibrils

But the spiral lamellæ are not yet the last microscopically visible structural element of the fiber. They can after previously treating them with acids or other reagents be split lengthwise. In this manner the so-called fibrils or bundles of fibrils are obtained (see sketch). Meyen, Agardh, and Crueger[13] isolated the fibrils quite some time ago but they were subsequently overlooked because v. Mohl and v. Naegeli[14] denied their existence. Only recently have a few investigations[15] again appreciated the part which the fibrils play in the microscopical structure of the fiber.

The width of the fibrils has recently been given as 0.2 to. 0.3μ by R. O. Herzog[16]. In such cases where the fiber has been subdivided by transverse structural elements the length of the fibrils will not be equal to the length of the fiber but to the distance between two annular ligatures. It can be determined by immersing a fiber in ammoniacal copper oxide and quick measuring under the microscope.

The fibrils can be made visible not only with chemical agents and by digesting[17] but also by simply treating mechanically, as for instance by grinding pulp whereby, of course, fibrils are not produced exclusively. They are also responsible for the appearance of dislocations or joints. These are bent places, especially in bast fibers, which have been caused by pressure. They can be imitated in principle by pressing partially digested pieces of wood between the fingers in the direction of the center of the fiber. Robinson[18], by applying higher pressure, pressed pieces of wood together and obtained similar results. In both cases, because of the loosening of the fibrils, respectively the fibers, small fissures are formed into which, during dyeing, the dye liquid penetrates easily and acts more intensively, and during maceration a quicker destruction is effected at these spots[19]. Joints occur almost exclusively on fibers of plants which due to their height and little lignification are strongly subjected to the action of the wind which expresses itself as pressure upon the fibers. The explanation recently offered by Herman Ambronn that dislocation takes place along inclined surface[19a] (this would require structural elements which so far have not been observed and could hardly be present), therefore can not be accepted. It is a case, rather, of a giving way of the inner membranes due to the pressure and then the fibrils give sideways. How the dislocation affects the individual fibrils remains to be investigated.



Sketch

a, Primary lamella
b, Layers of secondary lamella
c. Tangential inner skins between layers
d, Spirals
e, Fibrils or primitive fibers
f, Tertiary lamella
g, Lumen

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[13] J. Meyen, *Wiegmanns Archiv f. Naturgeschichte*, 4, 297, 1838, J.g. Agardh, *De Cellula Vegetabili* Lund 1852, *Bot. Ztg.* 11, 9, 1853; H. Crueger, *Bot. Ztg.* 12, 57 u. 833, 1854.

[14] H. v. Mohl. *Bot. Ztg.* 11, 753, 1853; C. v. Naegeli, *Bot. Mitt.* Bd. 2, 1866.

[15] F. Brand, *Ber. Deutsch. Bot. Ges.* 24, 64, 1906; Herm. Otto, *Beitr. z. allgem. Bot.* 1, 190, 1918; G. Haberlandt, ibidem 1, 501, 1918; R. O. Herzog, B. 58, 1254, 1925; *Zeitschr. angw. Chem.* 39, 297, 1926.

[16] R. O. Herzog, *Nat.* 16, 420, 1928.

[17] H. Otto, G. Haberlandt, Footnote [15].

[18] W. Robinson, *Transact. Roy. Soc.* (B) 210, 49, 1920.

[19] C. Correns, *Jahrb. wiss. Bot.* 23, 254, 1891.

[19a] *Koll. Zeitschr*, Zsygmondy, 36, 119, 1925.

The assumption that the fibrils like the spiral lamellæ, are glued together by extremely delicate membranes would explain the splitting by chemical agents and fermentation as well as the mechanical dislocations and would also make it understandable that artificial fibers do not show any dislocations at all.

5. About the Binding Material

C. von Naegeli put forward the theory[20] that the cell membrane as well as all organic structures are made of micelles which are arranged in submicroscopical rows, not to be confused with the fibrils. While micelles generally are surrounded by a film of water, other substances may also serve as imbedding material. R. O. Herzog and H. W. Gonell[21] because of the opening of certain spots in the X-ray picture, also thought that a foreign substance is present. But more recent investigations indicate that this appearance is caused by Beta-rays[22]. A deposition of a non-cellulose material between the micelles thus has become doubtful again, and can hardly be determined in this manner due to the slight amount present. Another point of view[23] held is that amorphous cellulose is the binding agent[24].

As has been shown, there exists a foreign substance, apart from the primary and tertiary layer, as transverse elements and as membranes in the isolated fiber cell, and it must also be assumed for reasons of analogy to be present between the spiral lamellæ and the fibrils. Its purpose is to act like glue, and to increase the strength combined with the special arrangement of the other structural elements. As its quantity amounts to but a few per cent, it is hardly to be expected that the X-ray analysis of the fiber will detect it. But even if a foreign substance is found by X-ray analysis, it does not prove that it represents the binding agent assumed by Naegeli. The substance of the membranes discussed here as well as mannans and xylans (wood gums), which also may be present in the cell wall and the presence of which has partly already been indicated[25], are also to be considered. (*To be continued*)

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[20] C. v. Naegeli u. S. Schwendener, *Das Mikroskop*, 2. Edit. Leipzig 1877, p. 424ff.; C. v. Naegeli, *Theorie d. Gaerung*. 1879, S. 137.

[21] H. W. Gonell, *Zeitschr. f. Physik*, 25, 118, 1924; R. O. Herzog, *Nat.* 12, 955, 1924; B. 58, 1256, 1925; *Zeitschr. angew. Chem.* 39, 297, 1926.

[22] R. O. Herzog u. W. Jancke, *Zeitschr. f. Physik*, 49, 27, 1928; see also K. Hess, C. Trogus, B. 61, 1982, 1928.

[23] P. Klason, *Verein d. Zellstoff u. Papier Chemiker u. Ingenieure*. 22, 373, 1924.

[24] See also F. Micheal, and W. Reich, A. 450, 59, 1926 and 466, 73, 1928. The authors isolated nitrogen containing substance from cotton. Compare also J. Wiesner, *Die Elementarstruktur*, Vienna 1892 in which plasm is said to be imbedded in the cell wall.

[25] M. Lüdtke, *A*. 456, 201, 1927; *A*. 466, 27, 1928.