SOME RECENT WORK ON THE STRUCTURE OF THE PLANT CELL WALL.*

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The original researches of Nägeli (26, 27) upon the structure of plant cell walls have stimulated discussion and debate, for more than sixty years. Today the Nägeli theory is still under scrutiny and the issue is by no means settled. The problems of plant cell wall structure are no longer exclusively those of the botanist, but in recent years have aroused the interest of physicists, chemists and even of the mineralogists. Direct microscopic observations have been supplemented with extensive studies under polarized light and with the X-ray. It has been only during the past ten or fifteen years that our knowledge of the physical structure of cell walls has advanced materially, beyond the stage at which Nägeli left it, almost three-quarters of a century ago.

It is the purpose of this paper to summarize briefly some of the recent and important work in this field, and to present a picture of plant cell wall structure as recent research has revealed it. No attempt will be made to review the vast amount of literature on the subject prior to the twentieth century, or even that of the early part of this century. Comprehensive and excellent surveys of this literature can be found in the monograph of Wisselingh (34).

The chemical and physical structure of plant cell walls varies widely in the different plant groups and in the same individual. The walls of the bacterial cells, of the algæ and of the mosses are very different from those of the higher plants. In any individual angiosperm there is an almost equally wide range of variation. The walls of root hairs, of epidermal cells, of woody fibers, of bast cells and of other tissues have but few

characteristics in common. There are, however, two characteristics possessed by most, if not all plant cell walls:

1. Plant cell walls are not chemically homogeneous, but are composed of two or more chemically distinct substances.
2. Plant cell walls are not physically homogeneous, but show stratification, striation and other indications of structural variation.

These facts have long been known and have been the subject of a great deal of study, yet research in the field of cell wall structure has never been more active or promising than at the present time.

One of the most interesting contributions to cell wall research is the work of Hansteen-Cranner (17). This investigator became interested in the toxic effects of Mg, K, and Na ions toward root growth. When a solution containing only one of these cations surrounded the root, all growth ceased. Signs of injury appeared in the region of elongation, i. e., where cell wall growth was most rapid. Further investigation revealed that the toxic effect was the result of changes in the cell wall itself and not the result of injury to the protoplast or nucleus. In solutions of the injurious cations the cell walls became swollen and in some cases burst, revealing the naked protoplast. Mg was most effective, solutions having a concentration of 0.0047% were sufficient to prevent root growth in some cases. Ca, on the other hand, even in solutions of 0.328% produced absolutely no sign of injury. The addition of Ca to Mg solutions not only prevented injury, but permitted normal growth.

It was further found that in dilute solutions of Mg, the roots excreted a cloudy white precipitate. This precipitate was produced by all roots tested and appeared the same in all cases. It contained no trace of protein, but consisted largely of phospholipoids.

In order to determine the origin of this material, the cell walls were freed from the cell contents, with the greatest thoroughness and care. The tissue was macerated and repeatedly washed until microscopic examination showed only cell wall fragments, and microchemical tests for proteins were completely negative. These cell wall fragments freed from every trace of protein material, gave the same precipitate,

indicating that it originates from the cell wall and not from the protoplasm. Hansteen-Cranner therefore concluded that the cell walls in question contained lipoid substances.

Since this original paper, Hansteen-Cranner has greatly extended and amplified his experiments (18, 19, 20), and has conclusively established the fact that the walls of all living plant cells contain relatively large amounts of phosphatides. He has shown that the plasma membranes are also largely, if not entirely, composed of these phosphatides, and that they are in direct and intimate connection with the phosphatides in the cell wall. The plasma membrane is not sharply delimited from the cell wall, but is continuous with the phosphatides that saturate the cell wall. During plasmolysis the plasma membrane does not separate cleanly from the wall, but retains fine thread-like connections with it. This fact, although largely ignored by workers in plasmolytic phenomena, has been previously reported by other investigators (19).

The Ca ion brings about a precipitation of these phosphatides, forming new membranes. The earth alkalies and the mineral acids act in a similar manner. The alkalies and the hydroxides in dilute concentrations act in the opposite way, producing a swelling and a gelatinization of the material. Whenever these ions come into contact with the phosphatides of the cell wall and of the plasma membrane, new membranes are formed—membranes having a widely different character from those normally present.

Hansteen-Cranner has thus demonstrated that the solid cell wall skeleton of cellulose or hemicellulose is permeated with phospholipoids. These phosphatides are not stable compounds, but are easily and extensively modified by changing conditions. Temperature changes, increases or decreases in acidity, the presence or absence of certain ions, and other factors bring about modifications, often extensive modifications, of these phospholipoids in the cell wall and plasma membranes. The formation, for example, of firm insoluble membranes with Ca ions throws much light upon the unfavorable influence that Ca ions exert upon water absorption, and possibly upon the difficulties some plants have in living upon soils rich in Ca. On the other hand, the formation of loose, gelatinous membranes in the presence of K ions may explain the favorable influence of this ion upon water absorption. The fact that phospholipoids bear sugar and probably are the path of sugar

movements from cell to cell, suggests a possible explanation of some of the problems of cell wall growth, or even may explain the idea that the outer layer of the protoplasm (phospholipoid) is itself transformed into cell wall material (1).

Grafe and his co-workers, in a series of papers (13, 14, 15), have confirmed Hansteen-Cranner's work and have carried out extensive investigations upon the chemistry of these phosphatides. From this work it becomes clear that these phosphatides have an important role in cell activities. Not only do the phosphatides determine and control in the large measure the permeability of the cell membranes, but there is also evidence that they and not protein, may form the chromatin of the nucleus and so be related to the whole heredity mechanism.

In a paper published after his death, Hansteen-Cranner (19) went so far as to consider the cell wall alive. Since the wall contains large amounts of phosphatides which are always in intimate union with the outer protoplasmic layers, he thinks that it should be considered a living and physiologically active structure.

This is a view to which few physiologists would subscribe, none-the-less it is an idea that challenges interest. Most botanists have long been accustomed to considering the cell wall as a passive, non-living framework surrounding and supporting the living protoplast. It now appears that no sharp line can be drawn between cell wall and protoplast, but that portions of the latter penetrate more or less completely, the intermicellar spaces of the former. Before the Hansteen-Cranner conception can find general acceptance however, much more must be known about the nature of these phospholipoids, and about their physiological relations with the protoplasm and with the cellulose crystals that form the cell wall skeleton.

Suggestive as this work is, it is the solid skeleton of the cell wall that has attracted the most attention. The physical structure of this framework may be studied in a number of ways:

1. Direct microscopical observation.
2. Microchemically.
3. With polarized light, and with the ultra-violet light.
4. X-ray analysis.

Direct microscopical observation was of course the first method to be used. It revealed the stratification of thick walls and the striation visible on many cell walls. The stratification is more or less distinct in cross section and its visibility varies with the water content of the wall, a fact which has led to the theory that differences in water content *cause* the stratification. The surface markings are of various types: spiral and other striations, cross bands, folds, etc.

The recent work of Aldaba (1) on cell wall structure shows that direct microscopic observation alone, under proper conditions, can give much more information about the structure and development of cell walls than was formerly possible. Aldaba has developed a method of isolating the developing cell intact. This permits a study of the entire cell directly, without resorting to sectioning. Using this method he has shown that some bast fibers are built up of a large number of lamellæ, which seem to arise as a transformation of the outer protoplasmic layer into cell wall material. This observation is of particular interest in connection with the work of Hansteen-Cranner, just discussed.

Microchemical studies have shown the kind, the amount and the location of the different membrane substances in the cell wall. They have shown the chemical changes that occur during the development of the wall, and have furnished a basis for theories of cell wall formation and growth. Wisselingh (34), and more recently Kisser (24), have through the use of microchemical methods shown that cutinized membranes are composed of three distinct lamellæ, an outer layer of pure cutin, an inner layer of pure cellulose, and a middle layer of cutinized cellulose. Wisselingh (34) has also demonstrated that the cork cell wall is likewise composed of three separate lamellæ, an outer layer of strongly lignified cellulose, a thin inner layer of cellulose usually more or less lignified, and between these, a thicker layer of suberin. Anderson (3), also using microchemical methods, has shown that it is possible to separate from one another, the lamellæ composing bast fibers of flax, and to study their structure when so isolated. The same author (4) has applied microchemical methods to a study of collenchyma cell walls and has shown that in such walls there is an alternation of pectic and cellulose lamellæ. The cellulose lamellæ can be separated from the pectic lamellæ and studied separately, for the finer details of their structure. Howe (23),

working on root hairs microchemically, finds a layer of pectic material and a layer of callose forming the wall. Wisselingh (33), Tiffany (32), and Wurdack (35), have shown that the cell walls of various green algæ are also composed of distinct lamellæ, containing one or more different chemical substances. Klein (25) has investigated the cell walls of some blue-green algæ and found them composed of lamellæ, in which the different cell wall constituents were more or less intermingled with one another. Bunning (7) and Shaw (30), found that this type of cell wall structure is present in the Sphagnaceæ and in the fruit coats of *Nelumbo lutea* respectively.

The papers here cited are sufficient to make clear the contribution that microchemistry is making toward solving the problems of cell wall structure. Microchemical studies of the plant cell wall have revealed it as a complex structure composed of distinct lamellæ, the lamellæ in turn being composed of one or more different chemical substances.

The units of cell wall structure, however, are submicroscopic and consequently must be studied in some other way. Most of our information about the fundamental units of cell wall structure has been derived from studies with polarized light and the X-ray.

Cellulose is doubly refractive and this double refraction supplies information regarding the finer details of its structure. As a result of his studies with polarized light, Nägeli considered the cellulose wall as being composed of submicroscopic crystalline micellæ that were definitely arranged in lamellæ. He believed each micellar unit to be surrounded normally with a film of water, and so separated from one another. The stratification visible in cross-section was explained by assuming that the micellæ were of different size and so adsorbed different amounts of water. As the water content of the wall decreased, the micellæ would approach one another, and the stratification would be less apparent. In completely dry cell walls the micellæ would be in direct contact and no stratification would be seen. Microscopical observations showed that the stratification actually does disappear as the wall is dried.

To account for the unequal swelling of cell wall in different directions (i. e., along the longitudinal, tangential and radial axes), Nägeli assumed that the micellæ were elongated. Cubical micellæ would adsorb water equally on all sides and so produce uniform swelling. Cellulose cell walls, however, do not swell

uniformly, but much more in the radial and tangential directions than in the longitudinal. If the units were elongated and arranged parallel to one another in the wall, the amounts of water adsorbed will not be equal on all sides, and therefore the resulting swelling must also be unequal, (Fig. 1).

This theory of water films apparently received support from the results of X-ray investigations which showed that when swelling took place the micellar units themselves did not increase in size, but merely altered their distance relations with one another (31).

Forsaith (9) has suggested an interesting modification of the Nägeli theory to account for the observed behavior of different woods. The checks and fiber ruptures in wood indicate a spiral structure in the cell wall, while the fracture
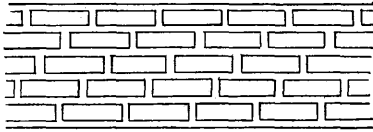

Fig. 1.   Diagram of micellar orientation according to Nägli.
(After Frey.)

surface of green wood broken along the grain is longitudinal. The thin-walled vessels split cleanly along their longitudinal axis and the edges of the break are smooth. Forsaith explains this by assuming the break to have occurred in the water films between parallel, longitudinally oriented micellæ. The spiral structure he explains by supposing the micellæ to be of a rhombohedral shape and so arranged that the water films on the ends of the micellæ form spiral lines of weakness (Fig. 2). This structure explains equally well the unequal swelling of wood blocks and the spiral and longitudinal cleaveage planes that occur in wood cells.

Fischer (8) however, has recently pointed out that evidence from both purely physical as well as physiological sides is strongly against the existence of such water films. If two smooth glass plates are pressed together and water is allowed to rise by capillarity between them, they are not pushed apart, but drawn tightly together. Even more conclusive is the fact that alcohol, ether and chloroform which enter the cellulose wall more rapidly than water, produce absolutely no trace of

swelling.   Were swelling the result of liquid films around the
micellæ, these liquids should produce it.   These facts have
made necessary a modification of the original Nägeli theory.
It is highly probable that the spaces between the micellæ are
not empty, as Nägeli believed, but are filled with a highly
hydrophilic colloid.   The general presence in cell walls of the
hydrophilic colloidal phosphotides discovered by Hansteen-
Cranner (loc. cit.) is of undoubted importance in this respect.
Other workers have suggested other colloidal substances.   In
young membranes this colloidal intermicellar substance may
be of pectic nature.   In young Closterium walls one can see the
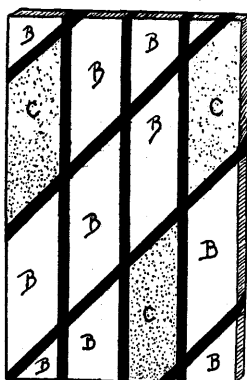

Fig. 2.   Forsaith's modification of the Nageli diagram of micellar orientation.
Solid black bands represent water films.
B, Cellulose units; C, Lignincomplex.   (After Forsaith).

double refraction of the cellulose gradually appear and increase
in the isotropic membrane (10).   In cellulose walls an amorphous
cellulose may form the colloidal matrix (21).   In cutinized and
suberized membranes, it may be the cutin and suberin (10) and
in lignified walls, the lignin.   That lignin is *between* the cellulose
micellæ and not *in* them is proven by the fact that lignified
walls give the X-ray pictures of pure cellulose (10).

The existence of double refraction alone is not sufficient to
prove the crystalline nature of cellulose units.   Double refrac-
tion can also be produced by non-crystalline, isotropic units
under certain conditions (2).   Ambronn (2) by studying the
behavior of cellulose under polarized light, has been able to
prove both the existence of micellæ in the cellulose walls and
the crystalline character of these micellæ.

If isotropic rods, (glass, for example), whose diameter and distance from one another are small relative to the wave length of light, possess a refractive index of N_1 and are imbedded in a liquid whose refractive index is N_2, the body will appear doubly refractive. If N_2 is varied, the double refraction varies accordingly. When $N_1 = N_2$, there is no double refraction, but when $N_1 \gtrless N_2$ a value arises. The curve of these variations is parabolic in form. By saturating the plant membrane with liquids of increasing refractive index (water, alcohol, glycerine, anilin, etc), Ambronn found his curve agreed with the theoretical curve, thus proving the existence of such submicroscopic rods in the membrane. Since he was never able
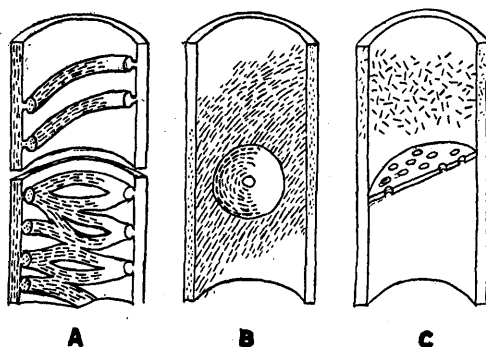

Fig. 3. The orientation of the crystalline micellæ in different cell walls.
A, Tracheæ with spiral and reticulate thickenings; B, Tracheid with bordered pit; C, Sieve tube. (After Frey).

to find a value of 0, i. e., his curve did not fall to the 0 point, he concluded that the rods (cellulose micellæ) were themselves doubly refractive (12).

Frey (10, 11, 12) has extended this work in brilliant fashion. He has developed a method of determining the orientation of the micellæ in the cell wall by using a polarizing microscope. Since the morphological long axis of the submicroscopic crystalline micellæ corresponds to the direction of the greatest refractive index, it is not difficult to determine the orientation of the micellæ in the wall. It resolves itself into a matter of determining the direction of the greatest refractive index.

The long axis of these micellæ often parallels the striations visible on the wall surface. In strong cell walls (bast fibers, etc.), the micellæ are united to form long fibrillæ, which are

usually spirally wound around the cell at steep angles. Groups of these fibrillæ can be seen by swelling the cell wall. They have recently been studied by a number of investigators, particularly in the commercial fibers. (Anderson (3), Ball (6), Nodder (28), Reimers (29) and others).

Frey (12) has determined the orientation of the micellæ in a number of different cell walls. The micellæ exhibit a wide variety of patterns and show no constant or definite arrangement common to all cell walls. In bast fibers they are arranged nearly parallel to the long axis of the cell; in sieve tubes and lactic ducts the arrangement is irregular, with no definite orientation; in tracheæ the micellæ parallel more or less the long axis, but in the spiral and reticulate thickenings are nearly perpendicular to the long axis of the cell; in tracheids they are arranged in a steep spiral except at the bordered pits, where they are concentrically arranged around the pore opening. (Fig. 3).

Cutinized membranes such as are usually present in epidermal cells consist of three layers: an outer layer of cutin, an inner layer of cellulose, and between, a layer of cutinized cellulose. This structure has been worked out microchemically (34). Studies with polarized light both confirm and extend this conception. Frey (11) has demonstrated that with polarized light it is possible to determine accurately the location and the degree of cutinization of such membranes. Cutin is optically negative, while cellulose is optically positive. With the insertion of a Gypsum plate Red 1 in the polarizing microscope, these two membrane substances give the contrasting addition and subtraction colors. The cutinized portions of the wall appear a brilliant yellow, while the adjacent cellulose appears bright blue. With the rotation of the stage through 90 degrees the colors are, of course, reversed.

Examination of the walls of heavily cutinized cells (epidermal cell walls of Clivia nobilis and Acuba japonica) under polarized light brings out distinctly the three layers. The outer layer of cutin is isotropic, probably because of the physical arrangement of the micellæ. The two inner layers of cutinized cellulose and cellulose, respectively, are both anisotropic, but the former is optically negative, while the latter is optically positive. The layer of cutinized cellulose shows a region of maximum anisotropism at its center, the degree of double refraction decreasing from the center toward the layer of pure

cutin on the outside and toward the layer of cellulose on the inner side. The cellulose layer, likewise, shows a higher degree of double refraction at its center.

The polarizer further reveals that in some cases (Acuba japonica) the layer of cutinized cellulose is not continuous, but that each epidermal cell has a separate, distinct, plate-like layer of its own. Frey has also shown that the boundaries between these three layers are sharp and distinct, there being no gradual transition from one to the other.

Ultraviolet light passes through cellulose but not through cutin, so photographs taken with ultraviolet light will show whether any cutin is present in the cellulose layer. This is not the case; the cellulose layer shows no sign of cutin even at the extreme outer edge of the layer. The boundary is sharp and definite. No study of the boundary between the cutinized cellulose layer and the outer layer of pure cutin can be made with ultraviolet light, since both appear black. This can be done, however, with polarized light, for the cutin layer is here completely isotropic, because of its physical structure, and the cutinized cellulose layer is anisotropic. Here again, the boundary between the two is sharp and definite, (10).

In this way studies of the membrane with polarized light have extended the results of microchemical investigations, as well as completely confirmed them. The use of polarized light in specific cases offers a much simpler and more precise method of learning the relations between the various cell wall lamellæ, than microchemical methods.

Pectic compounds are isotropic and can be detected in cell walls when relatively unmixed with cellulose, by the use of polarized light, (11). When pectic compounds occur associated with cellulose, the double refraction of the latter obscures the isotropic character of the former, (if the cellulose is present in appreciable amounts), and the presence of the pectic material cannot be clearly detected (4).

Hemicelluloses are at least in part doubly refractive, an indication that like pure cellulose, they are probably composed of crystalline micellæ (11).

Polarized light also gives evidence as to the relations of the lignin complex to cellulose. Lignified tissue is doubly refractive, but if the cellulose is removed, becomes completely isotropic (11). This indicates that the lignin complex is amorphous and that the anisotropic character of lignified walls is due to the

cellulose present. The removal of the lignin complex from lignified tissue does not affect in any way the degree of double refraction. The amorphous character of the lignin is also confirmed by X-ray analyses as has been mentioned previously.

In brief, polarized light offers not only a method of detecting and accurately localizing certain membrane constituents, but makes possible a determination of the orientation of the crystalline micellæ in the cellulose cell wall. It has been responsible for a great increase in our knowledge of the details, particularly the submicroscopic details, of cell wall structure. In speaking of the importance of polarized light, in relation to the evidence for the Nägeli micellar theory, Frey (10) says,

"Die hier summarisch aufgefuhrten Grunde, die für die Existenz der Micelle sprechen, und die Tatsachen die uber das Auftreten und die Eigenschaften der Intermicellarräume Auskunft geben, zeigen deutlich dass die Micellartheorie nicht mehr hypothetisch, sondern weitgehend bewiesen ist."

X-ray analyses have made possible a still further advance in solving the problems of cell wall structure. X-ray pictures of cellulose fibers give the interference patterns of crystal structure. The character of these interference diagrams indicates the arrangement of the crystalline units in the wall. Plant fibers have generally shown a crystalline fibrillar structure in which the crystals lie with their morphological long axis in approximately the fiber axis. The orientation of these fibrillæ varies in different fibers. In bast fibers of flax the fibrillæ run in a steep spiral, but the direction of the spiral alternates in successive lamellæ of the wall. In bast fibers of ramie and hemp, the fibrillæ also have a steep spiral arrangement, but the angle of the spiral varies in successive lamellæ. Cotton fibers show the same spiral structure, but here the spiral reverses its direction at points in the same lamella. The interpretations of X-ray photographs of the fibers agrees with these direct microscopical observations. Cotton, for example, gives an interference pattern that indicates a structure of spirally wound fibrillæ, while the diagram of flax fiber indicates a reversal of the fibrillar direction, (21).

Beyond confirming the presence of definite crystalline units in the cellulose wall, and indicating the arrangement of these crystals, the X-ray analyses have shown that an amorphous material is also present. To quote Herzog, (22),

"Aus den Röntgen-Bildern der Fasern ergibt sich die Anwesenheit nicht unerheblicher Mengen amorpher Stoffe— vielleicht auch amorpher Cellulose—neben den Krystallen. Man wird sie als Einbettungs—substance ansehen."

That cellulose is not a single chemical compound has also been suggested by Arrhenius (5) from studies of its reaction energy. Haller (16) came to the same conclusion from investigations on the behavior of the hydro- and oxycelluloses, derived from cotton fibers, when treated with NaOH.

This amorphous substance surrounding the crystalline units acts as an insulating material by preventing the crystalline micellæ from coming into direct contact with each other. Were no such substance present, the continuous stresses produced in the cell wall by such external forces as winds, would bring about a recrystallization, comparable to that occurring in steel under continuous hammering. Such a recrystallization would greatly reduce the resistance of the cell wall to such stresses. The presence of this amorphous, intermicellar, insulatory, colloid prevents this from taking place (21).

Herzog (21) suggests an interesting theory to account for the orientation of the crystalline micellæ in plant fibers. The first wall formed by the cell is amorphous (pectic material). In this amorphous substance the cellulose mother substance is assumed to be present as small droplets. These droplets rapidly crystallize. Since, however, they are under stresses brought about by the growth of the cell wall, they crystallize in definite directions. The long axis of the crystal conforms to the direction of the stresses, i. e., they are arranged more or less parallel to the long axis of the cell. The degree of tension determines the degree of crystallization. Such crystallization occurs in the manufacture of artificial fibers from cellulose solutions, and it is entirely possible that a similar crystallization takes place in the formation of the cell walls of fiber cells.

This cannot be the only factor involved, however, for the direction of these crystalline fibrillæ is not constant in all fibers, (flax, hemp, ramie, etc.). Such a theory could hardly account for the reversal of the direction of the spiral in bast fibers of flax, for example. It is possible that cellulose crystals in this case are isomeric, and that the alternate left and right hand spirals is the result of an alternation of isomeric celluloses (3).

The theory of Herzog also runs into difficulties when the case of sieve tubes and lactic ducts is considered. In these cell

walls, as Frey (12) has shown, the micellæ are irregularly distributed with no definite arrangement. These walls must also have been subject to the stresses of cell wall growth, yet here these forces have apparently produced no definite micellar orientation.

X-ray studies of cellulose walls confirm both the results of microchemical work, and the results of polarized light investigations. These three methods of study have established the crystalline micellar theory of cell wall structure upon an impregnable basis.

SUMMARY.

In the light of modern research, all cellulose cell walls, as well as those containing cellulose in considerable amounts, possess a submicroscopic structure of crystalline micellæ. These micellæ are imbedded in an amorphous matrix, the chemical nature of which varies in different walls and probably at different stages in the development of the same wall. The orientation of the crystalline micellæ is not constant in all walls, but varies widely.

From the standpoint of microscopic structure, the wall is a complex of several chemically different lamellæ. The lamellæ may consist of but one chemical substance, and alternate with lamellæ of other cell wall constituents, or the various constituents may be present in the same lamella.

This complex structure is saturated with colloidal phosphatides, that are in intimate union with the outer protoplasmic layers. These colloidal phosphatides are unstable and are readily modified by varying conditions. The physiological significance of their presence in the wall is not at the present time completely understood.

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