SCIENCE

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*THE STRUCTURE OF PROTOPLASM.**

IT would be superfluous to dwell in this place on the deep and enduring interest that attaches to the microscopical study of protoplasm. Since the time when the studies of Cohn and Schultze led to the general recognition of protoplasm as the material substratum of vital activity—a conclusion so eloquently set forth by Huxley in his celebrated essay on the physical basis of life—this interest has continually increased, as we have come to see even more clearly that all biological phenomena are directly or indirectly traceable to the effects of protoplasmic activity, for we have thus been impelled to seek for an understanding of that activity in the morphological structure of protoplasm, as revealed by the microscope. It is small wonder that to this quest some of the ablest of modern biologists have devoted their best energies. And yet, if we take account of the actual

* This lecture is printed by permission of Professor C. O. Whitman, Director of the Biological Laboratory at Wood's Holl, and Messrs. Ginn & Co., the publishers of 'Biological Lectures delivered at the Marine Biological Laboratory, 1889–99,' in which it will appear. A more adequately illustrated special paper on the subject, containing more specific references to the literature, is now in press. It should be borne in mind that such delicate textures as those seen in the protoplasm of living cells cannot be properly illustrated by black and white figures. The accompanying text figures, though copied as accurately as possible from the original drawings, are of necessity relatively rude and schematic.

knowledge gained, we cannot repress a certain sense of disappointment, partly that microscopical research should have fallen so far short of giving the insight for which we had hoped, but still more because of the failure of the best observers to reach any unanimity in the interpretation of what is actually visible under the microscope. In any consideration of the general subject, therefore, it is well to keep clearly in view the fact that such disagreement exists, and that we are not yet in a position to justify any very certain or far-reaching conclusions.

I would like, at the outset, to express the opinion that, if we except certain highly specialized structures, the hope of finding in visible protoplasmic structure any approach to an understanding of its physiological activity is growing more, instead of less, remote, and is giving way to a conviction that the way of progress lies rather in an appeal to the ultra-microscopical protoplasmic organization and to the chemical processes through which this is expressed. Nevertheless, it is of very great importance to arrive at definite conclusions regarding the visible morphology of protoplasm, not only because of its intimate connection with all the problems of cell-morphology, but also in order to find the right framework, as it were, for our physiological conceptions, and thus to gain suggestions for further physiological and chemical inquiry. And this must be my excuse for reviewing a subject which is still so largely obscured by doubt, and of which the outcome gives, after all, so little satisfaction.

It is especially important in this field of biological inquiry to distinguish clearly between theory and observed fact, for theories of protoplasmic structure have always far outrun the actual achievements of observation. From the time of Brücke (one of the first to insist that protoplasm must possess a far more complicated organization than that visible under the microscope) speculation has gone steadily forward, to reach, perhaps, its most elaborate expression in Weismann's interesting, but unconvincing, work on the germ-plasm—an elaborate speculative system built out of hypotheses which, for the most part, float in the air without visible means of support. We need not consider this side of the subject *in extenso*, but I will ask attention, for a moment, to what is the most characteristic and, to the morphologist, the most interesting point in these speculations, namely, the doctrine of genetic continuity as applied to the corpuscular, or micellar, theory of protoplasm. We are all familiar with the successive steps by which that doctrine gradually developed. Harvey's celebrated formula, *ex ovo omnia*—or, as usually quoted, *omne vivum ex ovo*— took with Redi the far more philosophical form, *omne vivum e vivo*, thus expressing a truth which forms the very foundation of all biological teaching at the present day. The development of the cell-theory, long afterwards, enabled Virchow to pronounce the more specific aphorism, *omnis cellula e cellula* (1855), a statement involving the highly interesting conclusion that protoplasm is never formed *de novo*, but always arises from or through the activity of preëxisting protoplasm differentiated into the form of a cell. Still later a like conclusion was reached with respect to at least one of the structural components of the cell, namely, the nucleus, and the work especially of Flemming and Strasburger justified the saying, *omnis nucleus e nucleo*. Not long afterwards, the researches of Schmitz, Schimper and others showed that in plant cells some, if not all, forms of plastids (for example, the chlorophyll-bodies) likewise arise by the division of preëxisting bodies of the same kind. Thus the law of genetic continuity was gradually extended downwards from the grosser and more obvious characters of the organism

into the finer details of its structural elements. Genetic continuity, the origin of like from like, may now safely be regarded as a demonstrated fact in the case of all existing organisms and of all cells; it hardly falls short of the same degree of certainty as applied to the nucleus; it is probable in the case of various forms of plastids in plant cells; while the centrosome is now being weighed in the balance with the evidence for the moment apparently accumulating on the negative side.

Up to this point we have been dealing with matters of observed fact. The next and final step was, however, taken in the region of pure speculation, which had in the meantime been at work building upwards from hypotheses regarding the basic composition of protoplasm. Brücke's suggestion, that the cell might be a congeries of bodies more elementary than itself, found a much fuller expression in Herbert Spencer's theory of physiological units; but it was Darwin's theory of pangenesis that laid the real basis for what followed in the works of De Vries, Wiesner, Weismann and Hertwig. The common feature in all these later views is the conception of protoplasm, not as a homogeneous substance or mixture of substances, but as made up of a host of elementary ultra-microscopical corpuscles ('pangens,' 'biophores,' etc.), specifically different, capable of assimilation, growth and multiplication, and arising by division of preëxisting bodies of like kind. Developed as a purely theoretical hypothesis, and within somewhat narrower limits by Darwin, this conception was expanded and brought into more direct relation with observed fact, especially by De Vries and Wiesner, who showed how the assumption of such elementary self-propagating corpuscles at the basis of living matter enabled us to bring all the observed phenomena of genetic continuity under a common point of view. The fundamental hypothesis itself —*i. e.*, the genetic continuity of the ultimate morphological units—has, however, always remained, and still remains, a pure assumption, incapable of direct proof or disproof; for, with the exception of Altmann and a few of his followers, all are agreed that such elementary corpuscles, if they exist, must lie beyond the limits of microscopical vision. Altmann, however, has sought to identify the elementary units, or 'bioblasts,' with the visible protoplasmic granules; and, in his writings, the series of Latin aphorisms initiated by Redi culminates in the saying, *omne granulum e granulo* (!), but this conclusion has not been taken very seriously by most other investigators.

I have given this very brief sketch of the theoretical side of the question merely as an introduction, and shall dwell no farther on it at this point, since my main purpose is to ask attention to the visible, as opposed to the hypothetical invisible, structure of protoplasm. A subject so vast, displaying so great a conflict of opinion, must be very briefly treated within the limits of a single lecture; and I shall, therefore, confine the discussion in the main to the protoplasm of the echinoderm-egg, which is accessible to every one, has been made a classical object through the studies of such leaders of research as Flemming, Bütschli and Hertwig, and illustrates as clearly, perhaps, as any other the various interpretations of protoplasmic structure that have been given.

In thin sections of well-preserved material the protoplasm of a star-fish or sea-urchin egg gives the appearance, under a high power, of a fine meshwork or framework composed of innumerable minute granules, or *microsomes*, suspended in a clearer, less deeply staining, continuous substance (Figs. 1, *a*, and 4). The spaces of the meshwork, which measure from one to nearly two microns, are occupied by a third substance, clear, homogeneous, and

of only slight staining capacity, which has often been called the *ground-substance*. During cell-division the meshwork in the neighborhood of the dividing nucleus assumes a radiating appearance, giving rise to the so-called asters, or astral systems which are typically double, forming the *amphiaster* (Fig. 3, *b*). We may define the problems suggested by these appearances by a series of questions as follows:

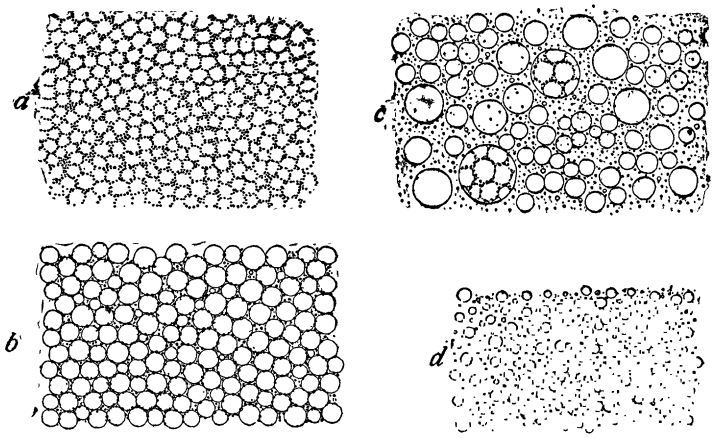

FIG. 1. (*a*) Protoplasm of the egg of the sea-urchin (*Toxopneustes*) in section; (*b*) protoplasm from a living star-fish egg (*Asterias*); (*c*) the same in a dying condition after crushing the egg; (*d*) protoplasm from a young ovarian egg of the same. (All the figures magnified 1,200 diameters.)

1. What is the actual structure that gives the appearance of a meshwork?

2. How faithfully does the preserved structure, as seen in sections, reproduce that existing in life?

3. What is the relation of the astral systems to it?

4. What is the finer structure and origin of the meshwork?

5. Can this structure be taken as typical of all protoplasm; and if not, what is its relation to other forms of protoplasmic structure?

After seeking for answers to these queries, we may finally inquire how they bear on the theoretical views briefly reviewed above. Incidentally, still another interesting question arises, namely: Is it possible to identify any one of the three elements in question—granules, continuous substance, ground-substance—as the *living* substance or *protoplasm* proper, as distinguished from a lifeless *metaplasm*, and, if so, what are its structural relations?

Could we positively answer all these questions we should have taken a long step forwards in the study of the cell. Far from this, however, in point of fact, hardly any two observers have given exactly the same answers to them. Leaving aside the earlier views, we find in the recent literature of the subject two principal general views with a number of modifications of each.

The first of these agrees with the early view of Klein and Van Beneden, that the protoplasm forms a net-work, *reticulum*, or thread-work, composed of branching fibers embedded in a homogeneous ground-substance which fills the interstices of the network, and with granules or microsomes lying along the course of the threads or at the nodes of the network. Many of those who adopt this interpretation further agree with their predecessors that the astral systems formed during cell-division arise directly through a rearrangement of the pre-existing network, about active centers of attractive or other forces, somewhat as iron-filings arrange themselves along the radiating lines of force in a magnetic field—an arrangement which bears a remarkably close though only superficial resemblance to the protoplasmic amphiaster. Boveri and some others, however, regard the astral system as having no direct relation to the preëxisting network, believing that the rays either arise from a specific substance ('ar-

choplasm'), distinct both from the general network and from the ground-substance, or are wholly new formations which, as it were, crystallize afresh out of the protoplasmic substance.

The second view is that of Bütschli, who believes it to be applicable to all forms of protoplasm, and who has been followed by a considerable number of recent investigators. Bütschli's interpretation differs entirely from the foregoing, the meshwork being regarded not as a network, but as an appearance resulting from the optical section of 'alveolar' or emulsion-structure. The spaces of the meshwork are drops of liquid occupying spherical spaces, or 'alveoli'; the 'fibers' are optical sections of the thin layers, or lamellæ, by which the drops, or alveoli, are surrounded. Even the astral systems receive the same interpretation, the astral 'rays' and 'spindle-fibers' being an optical illusion resulting from the radial arrangement of the alveoli, and hence of the inter-alveolar septa by which they are separated.

The greater number of observers of protoplasm have given their adherence to one or the other of the two widely dissimilar views just outlined, though there are others to which we shall return later. Some investigators have taken a position intermediate between these two extremes. Thus Reinke has maintained that the cytoplasm of the echinoderm-egg is alveolar, as described by Bütschli (though, as will appear beyond, he ascribes to this structure a different physiological interpretation), while the astral systems are fibrillar, as held by Van Beneden, and arise as new formations at the cost of the alveolar walls. More recently, Strasburger has developed the related, but still different, view that the cytoplasm of the cell at large consists of two distinct substances, namely, the *trophoplasm*, or general nutritive plasma, which is alveolar, and the *kinoplasm*, or the substance active in division, which is fibrillar and gives rise to astral systems consisting of true rays and fibers.

It is remarkable that the best observers, working in many cases at the same object, should have reached conclusions so diverse. It is obvious, further, that in the face of such contradictions it is impossible to give any discussion of the subject that is not more or less strongly tinged with the personal views of the writer. Such views, by whomsoever expressed, can at present have no more than a provisional value; and this is the last subject on which dogmatism should be allowed. It is with full recognition of these difficulties that I venture to state some of my own conclusions, partly because they may serve to explain, in some measure, to those who have not specialized in this field, how the existing diversity of opinion has arisen, partly because they have perhaps some bearing on the more general questions that were referred to at the outset. I shall take up in order the questions raised above.

The Nature of the Meshwork.—Although in earlier papers I was inclined to regard the meshwork of the echinoderm-egg as a reticulum, further studies have left no doubt whatever, in my opinion, that in the resting cell it is in reality an alveolar structure—or, as I do not hesitate to call it, an *emulsion*—such as Bütschli has described. I was first led to this conclusion through the study of sections of the eggs of sea-urchins (*Toxopneustes*) and star-fish (*Asterias*); but whatever doubt may have remained was completely dissipated by the study of the living eggs of *Asterias* (Fig. 1, *b*), *Echinarachnius*, *Arbacia*, *Ophiura* (Fig. 2, *a*), under high powers. All of these eggs give in life essentially the same appearance, though no two are exactly alike. In all, the protoplasm consists of innumerable closely crowded minute spheres suspended in a clear basis. The spheres may be called the alveolar spheres, or, more

briefly, the *alveoli*, though, strictly speaking, the latter term should designate the cavities which the spheres fill. The clear basis in which they lie, and which forms the interalveolar walls, may, with Mrs. Andrews, be called the *continuous substance*. Scattered about in the walls are numerous granules, or *microsomes*, far smaller than the alveoli, which often give the appearance of an irregular network. If now we compare these appearances of the living protoplasm with those seen in the sections mounted in balsam we find at first sight very considerable differences. More critical study shows, however, that the differences are almost wholly due to the effect of differential staining and to the difference of refractive index in the mounting media in the two cases. The alveoli of the living protoplasm form the spaces of the meshwork. The latter consists of the continuous substance with the granules suspended in it. In the section what especially strikes the eye is the meshwork; for the alveolar spheres do not stain, and their contours become indistinct in the highly refracting balsam, while the continuous substance stains slightly, and the granules intensely, thus giving the appearance of a conspicuous granular meshwork. We thus arrive at a definite answer to two of the questions propounded above, namely: (1) the meshwork shown in sections is not a network, but the expression of an alveolar or emulsion-structure, and (2) proper fixation does not produce a mass of coagulation-artefacts, but preserves the visible structure very nearly as it exists in life.

The above conclusions are based mainly on the study of star-fish eggs, but are confirmed by the facts observed in other forms. In *Arbacia* the emulsion is considerably finer, the alveoli measuring on an average no more than 1.0 micron, while the finer granules are relatively less numerous. The pigment-granules characteristic of this form appear to be nothing other than modified alveolar spheres. In *Toxopneustes* the alveoli measure approximately from 1.0 to 1.3 microns, while the granules are more numerous than in *Asterias*. In *Echinarachnius* the alveoli are less uniform in size than in *Asterias*, the largest measuring up to about 1.7 microns, while the granules are less numerous. The egg of *Ophiura*, finally, has an extremely coarse structure, the alveolar spheres measuring on an average 3.0 to 4.0 microns, while the granules, or microsomes, are also very large and, in the superficial layers of the protoplasm, even more numerous than in *Toxopneustes*. The protoplasm of *Ophiura* (Fig. 2) is highly favorable for study, not only on account of the great size of its elements, but also by reason of the remarkable fact that these elements are colored in life, the alveolar spheres being in most individuals distinctly of an olivaceous or pinkish-brown color, while

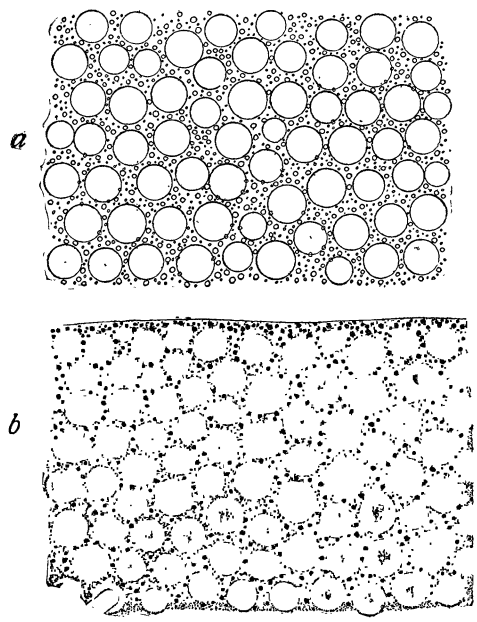

Fig. 2. (*a*) Protoplasm from a living ophiuran egg (*Ophiura*), slightly compressed, so as to spread the yolk-spheres somewhat apart; *b* the same as seen in a section (sublimate-acetic, iron-hæmatoxylin; 1,200 diameters).

the larger granules, or microsomes, are lemon yellow. This circumstance makes possible an observation of great importance, namely, that *all the elements of the protoplasm are liquid or viscid.* If the eggs of *Ophiura* be crushed by pressure on the cover-glass the protoplasm flows out, most of the alveolar spheres going in advance, while the granules and continuous substance lag behind. Meanwhile, the alveolar spheres often run together to form larger drops of all sizes, the origin of which is placed beyond question by their color. The same is true of the yellow microsomes, though this takes place less readily, and only under somewhat rough treatment. This demonstrates the liquid, or at least viscid, nature of both the spheres and the microsomes, and no less certainly that of the continuous substance in which both lie. As far as the alveolar spheres are concerned, the same observation may readily be made in the colorless protoplasm of *Asterias* (Fig. 1, *c*), *Echinarachnius*, or *Arbacia*, but I could never satisfy myself of the liquid nature of the microsomes in these forms. The case of *Ophiura* renders it highly probable, however, that the granules are liquid in these forms also—a conclusion which I confess was a surprising result to me; for we are so accustomed from our studies on sections to regard the granules as solid bodies that we are apt to forget that sections show us only coagulated material.

To sum up, a critical study of the living protoplasm of echinoderm-eggs shows that it is a liquid, or rather a mixture of liquids, in the form of a fine emulsion consisting of a continuous substance in which are suspended drops of two general orders of magnitude and of different chemical nature, as indicated by their staining reactions. The larger drops, forming the alveolar spheres, stain only slightly in hæmatoxylin, and constitute the so-called 'ground-substance' in the spaces of the meshwork; these have an average size, ranging in the various forms studied from 1.0 micron or less (*Arbacia*) up to 4.0 microns (*Ophiura*). The smaller drops, forming the granules or microsomes, are very much more minute, and stain intensely with iron-hæmatoxylin. The presence of the larger drops determines the primary alveolar structure as described by Bütschli. The smaller drops ('granules') lying between these give rise to the 'secondary,' or finer alveolar, structure as described by Reinke, and subsequently by Mrs. Andrews, as I understand these authors.

Relations of the Astral Rays to the Meshwork.—We may now make a brief digression to consider the third question propounded above, namely: What is the relation of the astral rays and spindle-fibers to the alveolar substance? It is easy to see, both in sections and in living material, that in a well-developed aster the alveoli are arranged in radiating lines between the astral rays (Fig. 4), precisely as Bütschli and so many others have described. The rays themselves are, however, something more than the radially arranged inter-alveolar septa, for, in the first place, they are often much thicker than these septa, and, in the second place, they stain more intensely than the continuous substance. A careful study of the rays in the echinoderms, and in many other forms (especially in *Nereis*, *Thalassema*, *Lamellidoris* and *Ascaris*), leaves, I think, no room for doubt that, in sections at least, the rays are actual branching fibrillæ, as described by so many observers since the time of Van Beneden, that thread their way through the continuous substance between the alveoli, often in a zigzag course. The strongest evidence that they are fibrillæ is given by the appearance of the cut ends of the rays as they appear in somewhat excentric or rather thick sections of the asters. In such sections, particularly in the case of large and coarse asters like those of *Nereis* (Fig. 3, *b*), the rays may be

seen in the clearest manner to terminate as they pass upwards towards the eye in well-defined cut ends, and I think no one who studies these preparations can doubt that in them the asters are true fibrillar structures.

We may now inquire in what manner the rays arise and grow, and what is the origin of their substance. In the growing aster

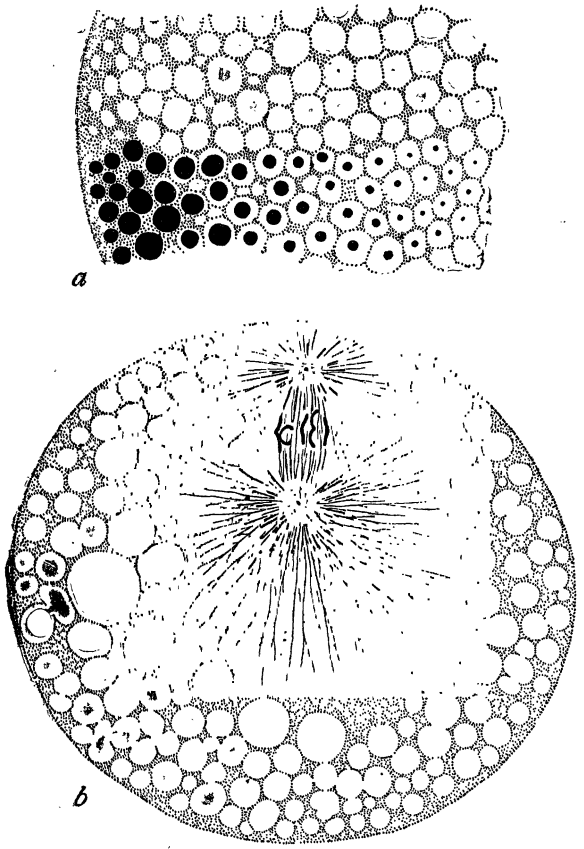

FIG. 3.—(*a*) Protoplasm and yolk-spheres from the egg of *Thalassema* in section. The upper part of the section shows the result of prolonged extraction of the dye (iron-hæmatoxylin); the lower half represents varying degrees of extraction (1,200 diameters); (*b*) egg of *Nereis* in section showing yolk-spheres and the first polar amphiaster above (600 diameters).

the rays progressively extend themselves from the center outwards, gradually losing themselves in the general meshwork. It has been maintained by some writers that the rays grow outwards from their bases like the roots of a plant, and in a certain sense this is undoubtedly true. But it is difficult to believe that all of the material of the rays comes from the base, *i. e.*, from the nucleus or the centrosome, for they often extend themselves throughout the entire cytoplasm, even in cases where, as in the sperm-aster of echinoderms, the center of the aster remains very small, and the nucleus still consists of a compact mass of chromatin (Fig. 4). It is more probable that they grow at the tip, continually extending themselves at the cost of the material lying in the meshwork. When the rays are followed out peripherally they may often be seen to run out into rows of granules like beads on a string. Van Beneden, who has been followed by many later writers, was inclined to regard the rays as essentially rows of microsomes strung together by a homogeneous, clear substance, *i. e.*, by the continuous substance, and I was led to the same conclusion in the case of sea-urchin eggs. A study of the asters in *Ophiura* throws doubt upon this conclusion, for it is here certain that the larger and deeply staining microsomes do not build up the ray, but are quite irregularly scattered along its course. The rays here mainly arise, I believe, in, and at the expense of, the continuous substance, and the linear arrangement of the microsomes is incidental to the differentiation of this substance along a definite tract which more or less involves the microsomes as it progresses. This conclusion probably also applies to other forms. The material active in the ray-formation appears to be the continuous substance, and, while the microsomes may, and probably in many cases do, contribute to the ray, they probably play the part of reserve material rather than of active elements.*

*As already pointed out, we cannot assume that the ray is *merely* an accumulation of the continuous substance on account of its different staining capacity.

To sum up, the general result indicates that the opinions regarding the aster-formation referred to above can in a measure be reconciled. In the case of echinoderm-

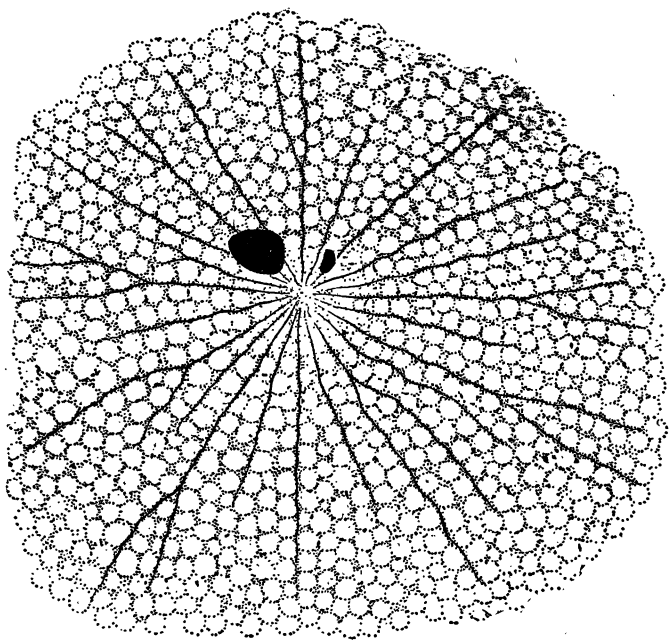

FIG. 4.—Section of sea-urchin egg (*Toxopneustes*), 1½ minutes after entrance of the spermatozoön, showing sperm-nucleus, middle piece and aster (about 2,000 diameters).

eggs Bütschli and Erlanger correctly describe the aster as involving a radial arrangement of the alveoli, but they have failed to recognize the fibrillæ that lie between them, and Boveri is, therefore, thoroughly justified in the contention that the astral systems cannot be regarded as merely a radial configuration of the preëxisting meshwork. I, nevertheless, think that Hertwig, Reinke and myself were right in the contention, which has been made also by many others, that the rays grow by progressive differentiation out of the general cytoplasmic meshwork, and that there is no ground, in the echinoderm-egg at least, for the recognition of a specific 'archoplasm' or 'kynoplasm' from which they arise.

Finer Structure and Origin of the Meshwork.—We may now consider what is, I think, the most suggestive of the questions propounded, namely, that relating to the finer structure and origin of the mesh work. We have thus far distinguished sharply between alveolar spheres, granules, or microsomes, and continuous substance. Morphologically considered, however, there is good reason for the view that all these are but different gradations of one structure. In the first place a nearly or quite complete series of size gradations exists between the largest alveoli and the microsomes (Fig. 1, *b*, *c*). Although most of the alveoli vary but slightly in size from the mean, a little search shows the presence of many smaller ones, and here and there they seem almost, if not quite, as small as the larger microsomes. In the second place, careful study of the 'continuous' substance in life, especially in the crushed protoplasm, shows that the larger microsomes in turn graduate down to granules so small as to lie near or at the limit of microscopical vision. The 'continuous' substance is, in other words, filled with granules, *i. e.*, drops of all sizes, ranging from the smallest visible ones up to the largest alveoli. It is this fact which Mrs. Andrews, as I understand her statements, has in view in maintaining that the coarser alveolar structure "is not, indeed, the final structure of the living substance, but is part only of an infinitely graded series of vesiculations of the protoplasmic form" and with this statement I entirely agree. But we cannot stop here. Irresistibly the further question suggests itself: Why should we place the end of this series at the end of microscopical vision

under a 1.5 mm. immersion objective—which is, of course, a perfectly arbitrary and artificial limit? It is impossible to doubt that powers still higher than any at our command would reveal the existence of granules still smaller, and that what appears as 'continuous' or 'homogeneous' substance is itself an emulsion beyond the range of vision.

We may now inquire whether the coarser visible alveolar structure is characteristic of all protoplasm. This question has in a measure already been answered, for in these very eggs we have seen the alveolar structure giving rise to a fibrillar one in the aster-formation—in other words, the protoplasm of the same cell may in different phases pass back and forth from one state into another. This fact appears in its clearest form when we study the growth of the ovarian ova, which gives us many additional suggestions of high interest. *The entire coarser alveolar structure, as described above—i. e., the foam structure of Bütschli—is in these eggs of secondary origin.* The very young living ovarian eggs consist of 'homogeneous' protoplasm, such as has been described by many botanists in the embryonic tissue-cells, through which are irregularly scattered a few small spheres and many excessively small granules. As growth proceeds both the spheres and the granules increase in size, the latter enlarging to form new spheres, while new granules continually emerge from the protoplasmic background into the limits of vision. In the middle stages of growth the protoplasm is thus converted into an emulsion, being filled with spheres of all sizes, ranging downwards from 1.0 micron to the smallest granules, but still showing no regular arrangement (Fig. 1, *d*). As the egg approaches maturity the spheres become differentiated into two groups, the larger ones becoming approximately of the same size, to form the alveolar spheres and crowding together, while the smaller ones remain as the microsomes and finer granules embedded in the remains of the continuous substance which forms the basis of the meshwork. In one sense, therefore, the alveolar spheres and the microsomes are only different stages in the same morphological series—though it should be remembered that they differ chemically as well as in size, and I do not mean to imply that the one may develop into the other—and both the alveolar and the fibrillar or reticular structures in these eggs are of secondary origin. If this be the case neither of these types of structure can be of fundamental importance; and I fully agree with the opinion of Kölliker, which has been adopted by an increasing number of later observers, that *no universal or even general formula for protoplasmic structure can be given.* The evidence indicates that alveolar, granular, fibrillar and reticular structures are all of secondary origin and importance, and that *the ultimate background of protoplasmic activity is the sensibly homogeneous matrix or continuous substance* in which those structures appear.

I do not mean to say that this is the only 'living' element in the cell. The distinction between 'living' and 'lifeless,' between 'protoplasmic' and 'metaplasmic,' substances is exceedingly difficult to define—largely on account of our vague and inconsistent use of terms, for in practice we continually use the word 'living' to denote various degrees of the vital activity. Protoplasm deprived of nuclear matter has lost, wholly or in part, one of the most characteristic vital properties, namely, the power of synthetic metabolism; yet we still speak of it as 'living,' because it may for a long time perform some of the other functions, manifesting irritability and contractility, and showing also definite coördinations of movements (as in the enucleated protozoan); and, in like manner, various

structural elements of the cell may be termed living in a still more restricted sense. In its fullest meaning, however, the word 'living' implies the existence of a group of cooperating factors more complex than those manifested by any one substance or structural element in the cell, and I am, therefore, thoroughly in accord with those who have insisted that life in its full sense is the property of the cell-system as a whole rather than of any one of its separate elements. Nevertheless, we are perhaps justi- in maintaining that the continuous substance is the most constant and active element, and that which forms the fundamental basis of the system, transforming itself into granules, drops, fibrillæ or networks in accordance with varying physiological needs.*

Whether any or all of these elements are 'living' or 'lifeless' depends largely on the sense in which these words are used; and it is well, therefore, to follow the example of Sachs, in substituting for these words, as applied to special structural elements of the cell, the terms 'active' and 'passive,' which properly admit of degrees of comparison. The distinction between 'protoplasmic' (active) and 'metaplasmic' or 'paraplasmic' (passive) elements, though a real and necessary one, thus becomes, after all, one of degree only.

We are thus brought to consider another point of some interest suggested by the comparative study of the facts described above. Bütschli states that in the true or finer alveolar structure, characteristic of protoplasm in general, the alveoli do not measure more than 2.0 microns, and as a rule are considerably smaller. This, he insists, is not to be confounded with a 'coarser vacuolization,' characterized by larger drops or spheres, which may secondarily arise in the finer structure. Again, Reinke and Waldeyer, in a somewhat similar manner, characterize as 'pseudo-alveolar' a structure arising secondarily through the deposit of passive metaplasmic products of metabolism, such as yolk-spheres, fat-drops and the like, in the living protoplasmic basis. Both distinctions break down, I think, in the light of the foregoing facts. In most of the forms considered—*Arbacia*, *Toxopneustes*, *Echinarachnius*, *Asterias*—the alveolar spheres are considerably less than 2.0 microns (1.0 to 1.7), and the structure is, therefore, a true alveolar one in Bütschli's sense; indeed, Bütschli himself describes and figures the protoplasm of the *Sphærechinus* egg as an example of that structure. In *Ophiura*, however, the spheres measure up to 3.0 to 4.0 microns, and are undoubtedly 'yoke-spheres' in the usual sense. It is, however, quite certain, from the ovarian development of these eggs, that they differ from the others only in degree, and that Bütschli's criterion of size gives no satisfactory ground for any real distinction. The alternative is to regard all the forms as pseudo-alveolar, irrespective of the size of the alveolar spheres, which are in all cases to be regarded as metaplasmic bodies; and this is the view which Reinke specifically applies to *Sphærechinus*. But if this view be adopted we seek in vain for any ground of distinction between such a fine 'pseudo-alveolar' structure as that of *Arbacia* and the 'true' alveolar structure of tissue cells, and are forced to the conclusion that in the latter case also the alveolar substance consists of passive or metaplasmic material —a view which has, in fact, been adopted by some writers. For my part, I am convinced that the entire distinction is without adequate basis, and that no definite boundary-line can be drawn between even the

* It is hardly necessary to state that this view is not original, except in so far as it has been directly suggested by the observations described above; for it has been more or less definitely maintained by many others, and I am only expressing what seems to be a growing opinion among workers in this field.

largest deutoplasm-spheres, vacuoles or other metaplasmic deposits, the alveolar spheres of *Arbacia* or *Toxopneustes* and those occurring in tissue-cells; and probably all are, in the sense indicated above, to be classed among the relatively passive or metaplasmic material.

How generally the alveolar, reticular or fibrillar formations may occur is a matter still to be determined by observation. It is probable that the alveolar structure will be found to be of more general occurrence than has been supposed; and, judging by the appearance observed in echinoderm and other eggs, and in coagulated albumen and other structureless proteids, I suspect that some cases of so-called 'reticular' formations will be found to arise through the more or less imperfect fixation of the alveolar, leading to the coagulation, contraction and breaking down of the alveolar walls,* though I do not for a moment mean to imply that such is the case with all reticula.

What light, if any, do the foregoing general conclusions throw on the theoretical views outlined at the beginning of this lecture? The answer must be: None that is clear and satisfactory, for the background of all the phenomena appears to lie in the invisible organization of a substance which seems to the eye homogeneous. Yet there is, I think, much in these conclusions to suggest, and nothing to contradict, the hypothesis that the 'homogeneous' or 'continuous' substance may be composed of ultramicroscopical bodies, by the growth and differentiation of which the visible elements arise, and which differ among themselves chemically and otherwise, as is the case with the larger masses to which they give rise. I will not enter upon a discussion of the question whether these bodies are merely molecules, more or less complex, or groups of molecules forming protoplasmic units or micellæ, but will only make three suggestions: First, if such units exist, they cannot be identified with the visible granules or 'bioblasts' of Altmann, but are bodies far smaller. Second, if there be any truth in what has been said above regarding the localization of 'living' matter in the cell, such protoplasmic units, if they exist, cannot properly be called 'biophores,' since life is a manifestation of the system which they form, and not of the individual units. The corpuscular, or micellar theory of protoplasm, as an hypothesis of morphological organization, should not be confounded with the physiological theory that biophores or pangens are 'elementary living units.' Third, by ascribing to these hypothetical units the power of growth and division, in accordance with the pangen theory, we are enabled to get a certain amount of light upon some of the most puzzling questions of cytology, such, for example, as the ultimate nature and origin of dividing cell-organs like the nucleus or the plastids, and especially such a contradiction as that presented by the centrosome, which may apparently arise either *de novo* or by division of a preëxisting body of the same kind. As De Vries and Wiesner have so suggestively urged, the power of division on which the law of genetic continuity rests and which is manifested by morphological aggregates of so many different degrees, may have its root in a like power of the primary units at the bottom of the series, out of which all the higher members are built. But while giving due weight to this suggestive hypothesis, we may question whether its acceptance does not introduce as many new special difficulties as those which it sets aside; while we must admit that it leaves untouched the fundamental problem of division. The solution of this problem may perhaps have to be sought in

* It may be well to point out that Rhumbler has produced true fibrillar and reticular formations in coagulated artificial gelatine-emulsions.

a quite different direction from the pangen hypothesis. Whether we shall succeed in finding it is another question.

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PICTURES IN THREE DIMENSIONS.

A CHICAGO publishing firm has put on the market a series of pictures in which a stereoscopic effect is produced by a device which seems not to have been used before in this country, but which is well known in Germany. Two photographs of an object are taken at distances apart equal to the distance between the eyes, and with objectives whose focal lengths are equal to the distance of distinct vision—that is, in the ordinary manner of making stereoscopic pictures. These two pictures are printed in two different colors, say red and green, so as to nearly but not quite overlap each other, and they are then looked at through spectacles composed of red and green glass. If the red picture is to the right and the green picture to the left, then the right eye looks through a green glass and sees in strong *black* the picture which is printed in red, but overlooks the faint green picture by the side of it; at the same time the left eye looks through a red glass and sees in sharp black outlines the picture which is printed in green, but not the faint red shadow at the side of it. In this way are produced the two halves of a stereoscopic impression, and a very good illusion of relief is obtained.

That the explanation above given is the correct one is proved by the fact that the images of near objects are plainly farther apart than those of distant ones; that if one looks attentively, with the glasses on, one can see the shadowy secondary pictures at the right and left of the principal one; that by putting on the spectacles wrong side up an inversion of the relief is obtained—near objects look far and far objects look near, so far as this is not interfered with by other elements of solid vision, as perspective, shadows, overlapping, etc., and that, by inverting the picture as well as the spectacles, the correct relief is again obtained; and, finally, by the fact that when one sees single an object in the foreground, one is evidently not fixating upon the plain of the paper, because the title of the picture, in plain black lettering below, is then perceived to be doubled.

The pictures of this issue are roughly made, and while the illusion is very strong it is not at all perfect; the distance between a child in the foreground and a building in the background will be, for instance, very distinct, but the child will be itself rather flat. With better workmanship, this method for securing vision in the third dimension ought to have an important future. The stereoscope has, for some reason, never lent itself to the purposes of art; this process, which has much less paraphernalia, and hence has its mechanicalness much less in evidence, may conceivably fill a more important rôle in this respect. However that may be, its usefulness for scientific purposes ought to be very great. There are countless intricate things which one desires extremely to represent in their solidity, and which it is unnecessarily hard for the reader to catch the bearing of when they can only be seen in the flat. Think for a moment how great would be the difficulties of the student of geometry if he had no more lifelike representations of his plane triangles than he has of his polyhedra and his parallelopipedons, and then imagine the pleasures that are in store for him if he has only to pick up his red and green spectacles to see the figures of solid geometry in all the reality which has hitherto existed for him only in the plane! And what rapid progress will be made in the imaginings of the stereo-chemist when he is given this ma-