THE STRUCTURE OF PROTOPLASM AND OF INORGANIC GELS: AN ANALOGY.*

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SCHALEK and Szegvary,[16] and Svedberg,[20] have recently described remarkable instances of sudden liquefaction of inorganic colloidal gels which have a striking analogy in the collapse of the gel structure of the protoplasm of a dividing echinoderm egg when the latter is subjected to mechanical pressure. It is the purpose of this paper to call attention to this analogy.

Regional Changes in Protoplasmic Consistency during Mitosis.—The fertilised echinoderm egg undergoes marked localised changes in its viscosity during mitosis.† The viscosity of the inner protoplasm, constituting the core and the greater proportion of the total volume of the mature unfertilised echinoderm egg, is roughly comparable to that of concentrated glycerine (sp. gr. 1.25). Such a consistency permits smooth though slow flowing of the protoplasm out of a ruptured egg. The consistency of the peripheral protoplasm of the egg, forming a cortical layer which encloses the core, is that of a soft jelly.

The difference in consistency of the inner and the peripheral protoplasm of the unfertilised echinoderm egg was first pointed out by Chambers[6] whose results were based on microdissection. These results have been confirmed by the writer[18] by an electro-magnetic method of determining viscosity (and elasticity) values of sols, gels, and protoplasm. The method was developed by Freundlich and Seifriz.[10] As applied to

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† The viscosity values given here are based primarily on observations made by the writer on the eggs of the sea-urchin, *Tripneustes*, in Jamaica, B.W.I. These data support, in the main, the earlier ones of Chambers[3] on the *Echinarachnius* egg. More detailed observations on the regional changes in viscosity of the protoplasm of the dividing echinoderm egg, is to be found in recent publications by Chambers.[4, 5]

protoplasm, the method consists, briefly, in placing within the egg a minute (18 μ) particle of a magnetic metal (nickel), and attracting this particle with an electro-magnet. Such a particle in the centre of an unfertilised echinoderm egg (*Echinarachnius parma*) will, when attracted by a magnet of sufficient strength, rush through the inner protoplasm until it comes in contact with the more viscous cortical layer when its forward movement is arrested. Attraction of the particle when in the peripheral protoplasmic layer results merely in stretching of the protoplasm. (The elasticity of living protoplasm is in this manner accurately measureable.) It is thus evident that the inner protoplasm of the unfertilised echinoderm egg is of lower consistency than the peripheral protoplasm, the former being of the consistency of a highly viscous liquid,* while the cortical layer is of a soft gel consistency.

After fertilisation the viscosity of the egg protoplasm as a whole increases, until at mid-mitosis the peripheral cytoplasm surrounding each amphiaster is of high viscosity, possessing the consistency of a moderately firm jelly, *i.e.*, the consistency of a gelatin solution which has just set into a still plastic jelly.† Another, albeit crude, comparison can be made between the highly viscous peripheral protoplasm of the egg during the metaphase, and bread-dough.‡

There is no commonplace substance which helps one to visualise better the physical state of highly viscous protoplasm

* The comparison of the viscosity of the inner protoplasm of an echinoderm egg to that of concentrated glycerin made as a result of microdissection observations[17] was nicely corroborated by comparison of the rate of travel of an 18 μ nickel particle, attracted by a magnet, through the central protoplasm of an egg and through glycerin, the rate in both cases being approximately the same.

† Chambers[4] has been able to distinguish viscosity differences within the cortical layer during the metaphase of division. He finds the outer region of the peripheral jelly to be of lower consistency than the protoplasmic wedges which form the inter-ray substance of the amphiasters.

‡ The writer has previously attempted[17] to give some idea of the actual viscosity values of protoplasm by establishing an arbitrary scale of viscosity values, and by comparisons to gelatin solutions and other common substances. It should be remembered that these comparisons are relatively crude, but they give at least an approximate idea of the *actual* value of the consistency of protoplasm under various physiological conditions. Vague expressions, such as "slightly viscous," "more viscous," "liquid" (which may mean any consistency from that of ether to that of soft tar), "non-viscous" (an impossible expression), and number of turns of a centrifuge handle, all suffice, perhaps, for purely *relative* values of consistency, but give no idea of the actual viscosity of the protoplasm.

than bread-dough. Not only the high viscosity of dough but also its elasticity closely approaches in value that of protoplasm when in the condition of a moderately stiff jelly, a state in which it is often found. Elasticity, a property generally ascribed only to gels, is very characteristic of protoplasm, and is practically always present even when the living substance is relatively dilute. Freundlich and Seifriz[10] have found this to be true also of dilute colloidal "sols."

At the completion of mitosis the viscosity of the peripheral protoplasm decreases until there exists in the two blastomeres of the first cleavage a relatively uniform and moderate degree of consistency throughout the daughter cells, preparatory to the second division.

It has long been known that the dilute ground substance of the astral rays is in a state of flow, the currents being centripetal. It is possible that the hyaline matrix of the rays and polar spheres is an extravasation from the surrounding highly viscous cortical jelly; and also, that the return of the peripheral protoplasm to a lower consistency at the completion of mitosis is due to, or at least is accompanied by, a reabsorbing of the inner dilute matrix.*

* These observations on viscosity changes in the dividing echinoderm egg have been determined by the microdissection method. The method consists in the mechanical manipulation of exceedingly fine glass needles under very precise control. The needles are held in a microdissection instrument of which there are three well-recognised types; the original Barber pipette holder,[1] the Chambers microdissection instrument[8]; and the Péterfi (Zeiss) micromanipulator.[15]

The criteria used in determining viscosity values of protoplasm by the microdissection method are, the distance from a moving needle at which particles (microsomes) are disturbed, and the rate at which the protoplasm flows in behind a moving needle. Certain other methods of determining viscosity values of protoplasm, such as the centrifuge method of Heilbrunn[19] and of Weber,[23] and the electro-magnetic method of Heilbronn,[11] and of Freundlich and Seifriz,[10, 18] offer means of obtaining statistically precise values of the viscosity of protoplasm *provided* the type of protoplasm worked upon is such as to permit the use of the various methods.

The microdissection method of making viscosity determinations of protoplasm has certain decided advantages which make it peculiarly suited for ascertaining the consistency of the protoplasm of a dividing egg. One must fully realise that the dividing egg is not a homogeneous mass of protoplasm of which a single viscosity value can be given, but an intricate structure with marked localised differences in consistency. To determine these viscosity values—for example, of living chromosomes[9]—could not possibly be done by any method other than that of microdissection. Failure on the part of some workers to appreciate the presence of even the grosser regional differences in viscosity of the dividing egg, has led to some confusion and misinterpretation of experimental facts.

The Collapse of the Mitotic Figure.—If an echinoderm egg in the metaphase of mitosis is dragged, by a microdissection needle, to the periphery of the film of water (hanging drop) in which the egg is suspended for dissection, and is thus subjected to the pressure of the surface tension of the thin water film, this pressure will sometimes cause a sudden and complete collapse of the mitotic figure. The intricate karyokinetic structure of the dividing egg, consisting of a highly viscous jelly cortex, enclosing the polar spheres, astral rays, and spindle, disappears, leaving an apparently homogeneous mass of protoplasm, with not a vestige of spheres, rays, spindle, or other structural features of the previously existing mitotic figure. The collapse is so sudden and so complete that it gives every impression of being a purely mechanical structural breakdown.

The recent publication of Schalek and Szegvary,[16] and a similar note by Svedberg,[20] give instances of the collapse of inorganic gels which are closely analogous to that just described as occurring in the dividing echinoderm egg.

Gradual Gelation and Momentary Solation in Inorganic Colloidal Solutions.—The liquefaction phenomenon described by Schalek and Szegvary[16] is, briefly, as follows: A 6 to 10 per cent. concentration of an iron oxide sol may be made into a soft poorly elastic jelly by the addition of an electrolyte. The amount of electrolyte should be insufficient to cause flocculation; 100 millimoles of sodium chloride, or 22 millimoles of sodium sulphate (the concentration of electrolyte in the diluted sol) will cause the iron oxide sol to set into a gel which has the consistency of dough or paste, yet is no more opaque than the original sol. This gel has the remarkable property of becoming fully liquid again when shaken. The sol thus obtained from the gel by shaking is in every respect identical with the original sol. This newly obtained sol again gelates in time; and the second gel is of the same appearance and consistency as was the first. The gel gotten for a second time may again be transformed into a sol by shaking. The process can be repeated apparently without limit and with no noticeable change in the properties of either the gel or the sol. Samples of ferric oxide which are

three months old exhibit the phenomenon in precisely the same form.

The similar behaviour of a colloidal solution described by Svedberg[20] is as follows. The experiments were carried out by Börjeson, and have to do with a non-aqueous gel of metallic cadmium. By means of electric pulverisation a sol of metallic cadmium in alcohol (0.2 to 0.5 per cent. concentration) may be obtained with particles only 5 mμ * in radius. If such a solution is allowed to stand for some time the particles are oxidised to a certain degree and the solution sets to a jelly. The jelly formed is sufficiently solid to permit turning the receptacle over without spilling of the jelly; but if one introduces a glass rod into the jelly and makes a few movements with it, the system at once becomes liquid again and the viscosity is scarcely greater than that of pure alcohol.

The Analogy.—The similarity in the behaviour of the iron oxide gel described by Schalek and Szegvary, or the cadmium gel described by Svedberg, and the protoplasm of a dividing echinoderm egg at mid-mitosis when subjected to pressure, is apparent. In each case—the non-living inorganic colloid on the one hand, and the living substance on the other—the system when in the gel state, suddenly and completely collapses when subjected to mechanical disturbance. The two types of systems are markedly different in several fundamental respects—the one inorganic and non-living, the other organic and living—yet it is quite possible that this striking similarity in their behaviour in respect to a single physical change may rest on similarities in structure.

Theories of Gel Structure.—Theories of gel structure are so numerous, with so little general agreement among chemists upon any one of them that we shall do no more here than to briefly describe the best known of them, and indicate which the behaviour of the protoplasmic jelly and the behaviour of the inorganic gels tend to support. The structure of the gel state of lyophilic colloids has been postulated as that of a simple fine emulsion of globules dispersed in a liquid medium

* The symbol "μμ" commonly used to designate 10^{-9} meter, is misleading. A μ (micron) is a millionth part of a meter; a μμ, therefore, is a millionth part of a millionth part of a meter, *i.e.* 10^{-12} meter. The correct symbol for 10^{-9} meter (à μμ às commonly used) is "mμ," *i.e.* a thousandth of a millionth of a meter.

(Ostwald); as an agglomeration in flaky groups of freely movable ultramicrons (Zsigmondy, McBain—this is essentially the micellar hypothesis of Nägeli); as a mass of intersecting fibrils which may be of microscopic dimensions (Barratt); as interlacing and possibly anastomosing tenuous and flexible crystals of molecular dimensions (Procter); and as an equal distribution of molecules (Loeb). These phrase-characterisations of the prevailing theories of gel structure give no more than a superficial idea of the complete theories held by the authors. The theory of Loeb is fundamentally molecular. The theory of Procter is molecular in that while the interlacing tenuous crystals postulated may be of more than one molecule in diameter as well as in length, the forces involved are of the order of molecular ones. The remaining theories are colloidal in that the authors are avowedly dealing with particles of colloidal size.

The molecular theory of Loeb precludes any connected network structure with a structural unit greater than the molecule. The molecular hypothesis of Procter admits of this possibility.

The colloidal theory of Zsigmondy apparently opposes a firm union of the micellæ into a framework. There is no reason, however, why the micellar hypothesis should not include a fixed bridgework structure of jellies. This seems to be the opinion of Svedberg[21] who states that in the process of aggregation in a colloidal sol we may have two possibilities; first, where no bridges are formed between the aggregates, in which case the colloid is precipitated; and second, where bridges are formed and the particles arrange themselves into a three-dimensional network, in which case the colloid gelatinises. We have the choice of one of these several theories of gel structure, or of granting, what seems likely, that there are many kinds of structure in gels, just as there are many types of structure in crystals.

The Possible Structure of the Protoplasmic Jelly.—The behaviour of the two inorganic jellies described by Schalek and Szegvary, and by Svedberg, and of the protoplasm of a dividing echinoderm egg when subjected to pressure, as here described, is more readily interpreted on the basis of a network

hypothesis of gel structure. The remarkably sudden breakdown of the gel and protoplasmic structures when subjected to mechanical disturbance is so evidently like the collapse of a structural framework, that one is forced to the conclusion that the structure of the gels and of the protoplasm is a framework formed by the bridging of colloidal aggregates. Another fact which tends to support the likelihood of a bridgework structure in gels, is the extraordinarily low concentration of disperse phase at which gel formation is possible. A 0.2 per cent. concentration of cadmium sol is sufficient to exhibit the gelatinisation-solation phenomenon described by Svedberg.

Other Instances of Rapid Viscosity Changes in Protoplasm.—Chambers[7] describes the liquefaction of the protoplasm of marine ova and of Amoeba as a result of mechanical disturbance. If the protoplasm of an echinoderm egg is agitated by micro-needles during the solidifying process just prior to division, the protoplasm reverts to its original liquid state. "If the egg so treated is subsequently left undisturbed the solidifying process starts up again, with the result that the egg undergoes normal cleavage." A resting Amoeba is relatively solid. Upon mechanical agitation the Amoeba becomes more liquid. If the agitation is continued, all of the Amoeba liquefies. An Amœba experimentally brought into this state does not return to its previous firm condition, and ultimately the animal dies.

An instance of a very rapid change in protoplasmic consistency from the liquid to the firm condition, is to be observed in the protoplasm of the hyphæ of *Rhizopus*. The streaming protoplasm in the mycelium of *Rhizopus* is of rather low consistency. By pressure with a microdissection needle, sufficient to completely close a hypha, this streaming protoplasm of low viscosity may be caused to instantly assume the consistency of a rigid gel. Streaming, of course, is stopped. Later, without further disturbance by the microdissection needles, there is a reversal of the phenomenon and the protoplasm becomes liquid again. If a hypha is torn open when the protoplasm is in the liquid condition, the contents immediately and readily flow out of the hyphal thread. If a hypha is torn open when the protoplasm is of high

consistency, the gelled protoplasmic mass can be forced out of the hyphal thread by pressure with a needle, just as one would squeeze oil paint from an artist's tube. The exposed rod of protoplasmic jelly, free from its supporting wall, retains its cylindrical shape in the surrounding aqueous medium for some time.

It is probable that this marked and rapid change in viscosity which takes place in the protoplasm of *Rhizopus* is of the same general nature, but in the opposite direction, as that which takes place in the collapse of the highly viscous jelly of a dividing echinoderm egg, and in the gels of ferric oxide and cadmium. In the egg protoplasm and in the inorganic gels, there is a sudden collapse of the bridgework of the gel structure, while in *Rhizopus* the micellæ are rapidly bridged to form the highly viscous jelly.

Hydration as a Possible Factor.—It was suggested in the preceding discussion on the localised viscosity changes which the protoplasm of the dividing egg undergoes, that possibly the high consistency of the cortical region of the egg arises as a result of extravasation of the dilute ray and polar substance from the peripheral protoplasmic jelly; and that, at the completion of mitosis, when there is a return to a less viscous condition of the protoplasm as a whole, the hyaline matrix of the polar region is reimbibed by the surrounding jelly; that is, the entire process of reversible gelation is apparently one of dehydration and hydration. This suggestion is based on the fact that there is actually a separation of the original protoplasmic mass into two substances, one of very high and one of low consistency. It has elsewhere been suggested[17] that the pronounced changes in consistency which the protoplasm of *Rhizopus* undergoes are possibly the result of hydration and dehydration. That hydration and dehydration are, however, quite unnecessary for an ever so rapid and pronounced change from one viscous state to another, is evident from the behaviour of the ferric oxide and the metallic cadmium solutions. There is here no extravasation of dispersion medium when the sols gelate, or hydration on the sudden change of the gels into sols. It is clearly a case of collapse of structure, whatever that structure may be. It would seem, therefore,

that hydration does not necessarily play a part in the pronounced viscosity changes which take place in protoplasm as has often been thought to be true. *Viscosity changes in protoplasm, as in non-living inorganic jellies, are probably purely a matter of structural changes, of a reorientation of structural units whether micellæ or molecules, and are not due to, though they may be accompanied by, hydration or dehydration.*

The Sol State.—Schalek and Szegvary, and Svedberg refer to the liquid state of their colloids as "sols." There is apparently no reason to question this terminology, since, in the case of Svedberg's experiment, the viscosity of the liquid state of the colloid "is scarcely greater than that of pure alcohol." It is doubtful, however, whether the term "sol" is applicable to the liquid state of protoplasm. The consistency of the protoplasm of an echinoderm egg before fertilisation is that of a substance which flows slowly; a relatively high viscosity for a liquid, as the confirmed comparison to concentrated glycerine indicates. Whether the term "sol" is applicable or not depends entirely on our criterion of the sol state.

McBain[14] has shown that in sodium oleate the sol and gel states are identical in all respects (osmotic pressure, conductivity, refractive index, etc.), except in their purely mechanical properties rigidity and elasticity. Freundlich and Seifriz[10] have shown that even in elasticity there is only a difference in degree between the sol and gel states. Thus, they found that a vanadium pentoxide "sol" possesses a slight though readily measurable elasticity; that a solution of commercial gelatin of 0.7 per cent. concentration, which pours freely and smoothly, with no superficial indication of a gel state, possesses a pronounced elastic value; and that so dilute a solution of sodium stearate as 0.1 per cent. which appears as thin as water, and has an actual viscosity value not quite twice that of water, is also sufficiently elastic to permit an actual determination of the elastic value with the technique developed by the investigators. If these dilute solutions of colloidal substances possess a measurable elasticity, it is quite evident that still less concentrated solutions will be elastic, so that only with infinite dilution is the elastic property of the

sol so far reduced that it can be completely neglected. It is evident how impossible it is to draw a line between the sol and gel state when dealing with dilute colloidal "sols." Protoplasm never reaches as low a viscosity as that of a 0.1 per cent. sodium stearate solution. The determination of a large number of viscosity values of numerous kinds of protoplasm in different physiological conditions[17] has established an average protoplasmic consistency approaching that of glycerine, and seldom falling below that of machine oil. Further, protoplasm, no matter what its viscosity, nearly always exhibits a readily noticeable degree of elasticity. If elasticity alone is our criterion of the sol or gel state, then protoplasm is to be regarded as practically always a gel.

It would seem advisable to use the term "sol" with caution when referring to even dilute protoplasm, and to speak rather of a less viscous state.*

In the case of the collapse of the cadmium gel there is probably a complete breakdown of the bridgework of the jelly, since the sol is very thin, while in protoplasm the breakdown is probably only partial, *i.e.* there still remain groups of connected micellæ, which give to the liquid state of protoplasm its gel (elastic) characteristics.

The Rôle of Viscosity Changes.—Changes in protoplasmic consistency have, of late, received considerable attention from a number of investigators. Weber[22, 23] has made an extensive study of the effects of narcotics, gravity, Roentgen rays, etc., on the viscosity of protoplasm. Heilbrunn[13] has studied the effects of monovalent and bivalent cations on protoplasmic consistency. Heilbronn[11] has ascertained the viscosity of myxomycete plasmodia. Chambers[8] has made numerous observations on protoplasmic consistency, and Seifriz[17] has determined viscosity values of a variety of protoplasm.

* The term "coagulation" is also misleading when used to designate increased consistency in protoplasm. If *living* protoplasm ever coagulates it is certainly limited to such extreme cases as the change which protoplasm undergoes in a protozoan when it encysts, or in a seed when preparing for the winter's rest. It is possible that such protoplasm is a coagulum, an "irreversible" gel, which reverses into the physiologically active protoplasmic jelly through enzymatic activity at germination. There is no reason to believe that living protoplasm coagulates when in its physiologically active state. With the possible exception of the above cited examples, coagulation is ordinarily a death process.

Viscosity values play an important part in the ingenious suggestion of Cannon[9] on the nature of the centrosomal force.

Professor Péterfi has called my attention to a most remarkable change in consistency occurring in Amœba. When the organism is grown in an aqueous medium, the viscosity is relatively low. A furrow made by a microdissection needle in an Amoeba taken from a water culture is quickly closed. When, however, Amoebae are grown on an agar plate (with Knop's solution), the consistency becomes extremely high. After several days on such a culture medium, the viscosity of the organism is so high that a furrow made in it remains visible for a full half hour afterwards. Such Amœbæ are very sluggish in their movements.

One cannot carry on a study of viscosity changes in protoplasm without being impressed with the great range in values and the frequency with which changes take place. That changes in protoplasmic consistency play an important part in the physiological activities of the cell, is undoubtedly true. It does not seem justifiable, however, to allow our imagination to carry us so far as to see in viscosity changes the *cause* of certain physiological processes which the changes in consistency accompany. One hesitates to believe that such complex and little understood vital phenomena as anæsthesia and antagonism are nothing more than the manifestation of a single simple physical change in protoplasm, namely, a change in viscosity.

Mitosis is accompanied by pronounced regional changes in protoplasmic consistency. These changes play an important rôle in cell division. The amphiasters and the mitotic figure as a whole, could not be maintained were it not for the high gel consistency of the cortical protoplasm. Necessary as changes in viscosity appear to be for mitosis, they cannot be regarded in any sense as the *cause* of cell division.*

Summary.

When a dividing echinoderm egg, in the metaphase of mitosis, is subjected to the pressure of the surface tension existing between a cover slip and a thin film of water, the

* See in this connection the interesting discussion on the colloid chemistry of cell division by Spek.[19]

entire mitotic figure, consisting of a highly viscous jelly cortex which encloses the dilute polar regions and the spindle, suddenly collapses, leaving not a vestige of the structural features of the preceding karyokinetic figure. This collapse is analogous to the sudden breakdown of certain inorganic gels, namely, of iron oxide, as described by Schalek and Szegvary, and of metallic cadmium, as described by Svedberg. In all three cases the sudden liquefaction is brought on by mechanical disturbance, in protoplasm by pressure, and in the two inorganic gels by stirring or shaking. These analogous phenomena tend to support the micellar hypothesis of the structure of gels, a structure in which the colloidal units are connected one to the other to form a three-dimensional network.

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