INVESTIGATIONS
ON MICROSCOPIC FOAMS
AND
ON PROTOPLASM

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EXPERIMENTS & OBSERVATIONS DIRECTED TOWARDS A SOLUTION OF THE QUESTION OF THE PHYSICAL CONDITIONS OF THE PHENOMENA OF LIFE

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TRANSLATOR'S PREFACE

In bringing an English translation of this work before the public, I feel that a word or two of explanation is due to my readers. Many people regard the translation of French or German scientific works as unnecessary, holding that every student of science should have a knowledge of these languages. Without wishing to controvert this opinion generally, I may state the reasons which originally prompted me to undertake this translation. In the first place, the investigations here described are of so fundamental a nature as to be of interest not only to workers in all the various branches of Biology, and to physicists, but perhaps even to those who are not professed students of science at all. In the second place, this work, lying as it does for the most part on the border-line between two sciences so distinct as Physics and Biology, is full of the technicalities of both these sciences, and is therefore by no means easy reading in the original for a modern scientific specialist, however great his knowledge of the German language. For these reasons it seemed to me that a translation of Professor Bütschli's valuable investigations might form an acceptable addition to English scientific literature.

In preparing this translation certain German words and phrases were found especially difficult to render into English. Above all, this was the case with the two words

"Entmischung" and "Ausbreitung," applied to the peculiar physical phenomena described fully on p. 15 and p. 62 *et seq.* respectively. Not being able to find English equivalents for these words I applied to Lord Rayleigh, Sec. R. S., for advice, and with his kind help I have coined the word *desolution* for "Entmischung," while "Ausbreitung" I have rendered at his suggestion by the word *extension* or *superficial extension.* There is no need for me to explain these terms here, as that is done in the text at the places indicated.

Protoplasm is conceived of in this work as having the structure of a froth or foam in which minute droplets of a watery liquid take the place of air in the bubbles of an ordinary foam. Such a structure is termed by the author "Wabenstructur," *i.e.* honeycomb structure; the separate vesicles, bubbles, or droplets of the foam are termed "Waben," *i.e.* cells of a honeycomb. The latter word has been rendered throughout by the term *alveolus,* and the structure is generally termed *alveolar.* The most superficial layer of radially directed alveoli, which gives the appearance of a striated border, has been termed by the author the "alveolar layer" ("Alveolarschicht") *par excellence.* In order to avoid confusion this has been rendered in many places *marginal alveolar layer,* in other places simply *alveolar layer.*

The plan has been followed of printing the book in two types, in order that the student may be able to obtain first of all a general idea of its contents, without entering into details, by reading the portions printed in the larger type consecutively.

Finally, it is my pleasant duty to express my thanks for the assistance I have received in preparing this translation. Without Professor Ray Lankester's kind help the work would never have been undertaken. To the Author

and to my friend Mr. Hatchett Jackson I am greatly indebted for the trouble they have taken in looking over the proofs, and for making many valuable suggestions and corrections. My obligations to Lord Rayleigh have already been stated.

E. A. M.

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INTRODUCTION

In the preface to the studies published by me in 1876, upon the primary developmental processes of the ovum, cell division, etc., I pointed out that the morphological method of consideration, which had led to such brilliant results for the comprehension of multicellular organisms, fails to be of service to us when we attempt to penetrate deeper into the essential nature of the elementary organism—the cell. I expressed the view "that the phenomena exhibited by and in the elementary organism could not assume an intelligible form except through a knowledge of the physical and chemical conditions of their origin and cessation." I also attempted in this work, and, as I believe, for the first time, to bring into requisition a property of fluid bodies,—namely, surface tension, in order to explain the phenomena of the division of the protoplasmic cell body, of which I had made a careful study.

In the following investigations I believe I am able to bring forward a contribution towards a more accurate physical explanation of certain peculiarities of living matter or protoplasm. Since it is far from my intention to enter at present into detailed historical disquisitions upon the question of the structure and nature of protoplasm, I will only put forward here a few historical remarks upon my own position with regard to this question, in order to indicate the train of reasoning which led to the investigations.

In 1878 I found an opportunity for the first time of expressing my opinion upon the alleged reticular structure of protoplasm, which had come more to the fore at

this time through the works of Frommann, Kupffer, Heitzmann, and others. I remarked at that time that the facts which had become known concerning this point "do not, however, seem to me by any means so noteworthy and so unconnected with former observations as was usually represented. From the protoplasm of many Protozoa in which appear single scattered vacuoles there is a gradual transition to be found to completely alveolar or, what is the same thing, reticular protoplasm, where the alveoli are so densely crowded that their real protoplasmic walls take on a honeycombed arrangement, which in optical section appears reticular." I further remarked that in the hyaline cortical layer and the pseudopodia of Rhizopods, we had before us structureless homogeneous protoplasm. Thus, as far back as 1878, I represented the view that the reticular structure of protoplasm described by various investigators was a honeycombed or alveolar structure.

My extensive dealings with Protozoa of very various groups, to which I had to devote myself during the following years, gave me the opportunity for many an observation upon protoplasmic structures, which more and more confirmed me in the view I had already expressed in 1878. In the years 1884 and 1885 I was first able to study more thoroughly relations of this kind—in 1884 *Noctiluca;* in 1885, a series of marine Rhizopods, *Actinosphærium,* and certain Ciliata. More definitely than before I expressed my conviction that the so-called reticular structures should be interpreted as honeycombed, and founded this conception upon the proof of the indubitable honeycomb structure of the so-called "alveolar layer." I also brought forward proofs of the reality of the protoplasmic structures, the resemblance of which to the products of the coagulation and precipitation of various substances might awaken a perfectly justifiable suspicion as to whether they did not also belong to the same category of phenomena. I soon found occasion for engaging still more thoroughly in studies of this kind, when in the years 1886-88 I undertook to do the Ciliata for Bronn's *Klassen und Ordnungen.* In my own studies upon this group I was able to avail myself of the

assistance of two talented pupils, Dr. Schuberg and Dr. Schewiakoff. In their works upon Ciliata (1886 and 1889), which were carried on in continued collaboration with me, they have brought forward in support of my conception, essential contributions from within the limits of this group of Protozoa. On the ground of their investigations, as well as of others of my own, I was able in my description of the Infusoria to give a somewhat broader and more detailed exposition of my view (pp. 1317, 1392). The experience gained up to this point had called forth the conviction that a phenomenon of fundamental importance was before us; a conviction which I expressed at that time (1888) in the following words:—"We are here confronted with a phenomenon of the same widespread occurrence and significance as the building up of higher organisms from cells, without possessing at the outset a guiding and explanatory idea, just as was the case with the observers of cellular tissue before the cell theory had been founded." Although convinced that the structure of protoplasm was in general alveolar, I yet thought it necessary at that time (p. 1392) to make a concession to the theory of its spongy structure, inasmuch as I admitted "that at times adjacent alveoli may break through into one another, and thus a spongy structure would come to be formed in places." This remark was particularly inconsistent in the case of the endoplasm, since I at the same time represented its nature as fluid, and such an assumption excludes any idea of the kind.

As a proof, to a certain extent, of the significance which the theory of the honeycomb structure of protoplasm might possess for the conception of protoplasm as a whole, I also described in 1888 the consequences which result from it for the growth of protoplasm, by trying to show that the difficulty in conceiving of growth by intussusception could be got over upon the basis of my theory.

As is obvious from this proposition and from the view quoted above from my work on Protozoa, I cherished the idea, ever since the universal occurrence of such structures in protoplasm became clear to me, that in this fact an essential reason was to be sought for many of the

peculiar properties and activities of this substance. According to my conception the structure of protoplasm corresponded to that of the minutest microscopic foams, with the difference that the alveoli of ordinary foams contain air, while protoplasmic foams contain a watery fluid. If such microscopic foams were successfully manufactured, ought they not to show certain peculiarities of protoplasm, and could not an accurate study of them furnish an essential contribution towards confirming or correcting my view? This question forced itself upon me more and more strongly. Whether the results obtained in this direction might or might not be favourable to my view, it was to be hoped in any case that they would contribute to the clearing up of the protoplasm question.

PART I

OBSERVATIONS

A. Investigations upon Oil-Foams

1. *Preparation and Structure of the Foams*

THE reflections and considerations set forth in the preceding pages impelled me to try if it were possible to produce artificial foams of the fineness that I believed to exist in the instance of protoplasm. Although it was scarcely to be expected that such attempts would produce results at all considerable, I thought nevertheless that something or other of importance might possibly be attained by such a course. Hence I sought to follow it up, as soon as time and opportunity offered, on the completion of my work upon Protozoa. Experiments of this kind could at first be little better than a blind groping about, as it were, in the hope of finding a possible starting-point from which advance might be made in a more methodical and confident manner. I began this attempt with a feeling of vague uncertainty, such as the alchemists must have felt in their hopeless experiments. This uncertainty was, as may be easily conceived, heightened by the fact that I was setting foot in a region in which I was very little at home, and the difficulties of which were hence far beyond my ken. Still this ignorance proved perhaps, if anything, serviceable; with a sufficient appreciation of the difficult problems of molecular

physics in which I set myself to dabble, the experiments would perhaps have never been undertaken.

Various fruitless attempts were made first with different kinds of emulsions, which led to no satisfactory results, since they were not to be deprived of the character of an emulsion, *i.e.* of minute drops suspended in a relatively abundant fluid matrix. A foam of fine structure was, however, for the first time successfully produced by the mixing of two fluids. Without describing here the previous experiments that gave no result, I will proceed to make a few remarks on the attempts that were first successful. If a very thick solution of commercial soft soap (potash soap) be shaken up thoroughly with benzin or xylol, a fine emulsion is formed, since the benzin distributes itself in the soap solution in drops varying in size from those of moderate fineness to the very minutest. If this emulsion be then left to stand, the lighter benzin droplets rise to the surface, and become arranged, through the thinning out of the layers of soap solution between them, into a fine froth, just as bubbles of air rising to the top of a soap solution collect gradually on its surface into an ordinary lather. The description and explanation given by Plateau for the latter case is without doubt also suitable for the froth here described. The whitish foam, in which benzin plays the part of air in an ordinary soap lather, attains to a considerable degree of fineness, but is not to be compared in this respect with the froths which I obtained later in another way. I have not taken any measurement of the average size of its meshes, since such benzin foams are difficult to investigate, but they stand somewhere on the boundary between the macroscopic and the microscopic, since at least their larger meshes are visible with the naked eye or with a weak lens. Nevertheless the durability of froths of this kind is striking. I have kept such a froth for two years now in a tightly-stoppered bottle without its having essentially altered. Perhaps in the course of time its meshes have become somewhat coarser, but its original character has been completely retained.

Experiments of various kinds, especially electrical, which I performed upon such benzin froths did not lead to definite

results. Drops of such a froth placed under benzin, on quicksilver with which is connected one pole of an induction apparatus, while the other touches the drops, show a distinct spasm at each closing or breaking of the current. I do not, however, believe that this phenomenon is connected with their frothy structure, but that it is to be regarded in just the same way as the alteration in form of a drop of water under similar conditions.

I was urged to further experiments in manufacturing fine froths by Quincke's communications (1888) on the diffusion of watery fluids through fatty oils. As is well known, the above-named physicist was able to determine by various experiments that such a diffusion may take place. My experiments also, to be communicated in the sequel, are in favour of this happening, or at least are not easily explicable without such a supposition.

Since Quincke made use of the experience he had obtained with regard to the phenomena of movement, or, more properly streaming, produced by relations of surface tension in fluids, and particularly in oil-drops, in order to construct a hypothesis concerning the phenomena of streaming in protoplasm, and took the opportunity of occupying himself more specially with protoplasm in general, it is permissible for me to state more exactly the relations of Quincke's investigations to mine. As I have already remarked, I took from Quincke's work the idea of using fatty oils for the production of finely-structured foams, since I considered possible, as will be presently described, the conversion of the oil into froth by the diffusion demonstrated by Quincke. Moreover, I recognise willingly that Quincke's investigations and hypotheses stimulated me to undertake experiments based upon my own view of the structure of protoplasm, in order to subject the correctness of my conception to a thorough test. On the other hand, my experiments and ideas were, from the very beginning, on an altogether independent footing, the outcome of my experience with regard to the finer structure of protoplasm. The idea of the alveolar structure of protoplasm guided me from the commencement, and, as has been said, prompted the experiments.

I have frequently in conversation communicated my views upon the probable structure of protoplasm to my colleague, Prof. Quincke, and emphasised the fact that certain properties of protoplasm might well be connected directly with this structure,

before he published his hypothesis of protoplasmic movement. In his communication of 1888, Quincke still treats protoplasm as a simple fluid, and nowhere speaks of its froth-like structure. When he lays stress (1889), after the publication of my first report (1889), on the frothy structure, I can only recognise in this fact the influence of my experience, although he nowhere mentions this in his publication, which deals with protoplasm and the phenomena of movement exhibited by it.

The train of reasoning which led to the experiments with fatty oils was as follows. If a mixture of oil and very finely ground down particles of a substance easily soluble in water, be brought into water, the latter will enter by diffusion into the oil. The fine particles of soluble substance will attract the water and become converted into minute drops of a watery solution. The closely-compressed drops are able to convert the oil in which they are suspended into a fine froth in this manner. Although this reasoning did not prove perfectly correct, yet the experiments prompted by it led to gratifying results.

Olive oil that had stood for a long time in a bottle in the laboratory was first employed for the experiments. As soluble substances, common salt, cane sugar, and potassium nitrate were tried. The method pursued was as follows. A very small quantity of the soluble substance, taken on the tip of a knife, was pulverised as finely as possible in a small mortar, and then rubbed up into a thick paste with a drop of olive oil. Small or minute drops of this mixture were placed on a cover-slip provided with wax feet at the corners, and the cover-slip was then inverted over a drop of water of sufficient size upon a slide. As a rule, the ordinary Heidelberg tap-water was used, which contains relatively little dissolved matter, but sometimes distilled water was also tried. But since the experiments gave similar results in both cases, the ordinary town water was used in consequence exclusively. The wax feet on the cover-slip were, as a rule, high enough for the drops of the oil mixture to be in contact with the surface of the slide without, however, being compressed.

In the manner described, it was possible to convert the

above-mentioned olive oil by means of either cane sugar or common salt into a very fine froth, while the attempts with potassium nitrate did not yield favourable results, and hence were not further continued. The behaviour of the oil-drops when brought into water is, as far as it was followed out, somewhat as follows. Microscopic observation shows, in the first place, that the pulverisation of the substance mixed in with the oil is, in spite of all care, comparatively coarse, and that, besides particles of the finest size, a considerable number of coarse fragments are present in addition. A watery fluid can soon be observed round these fragments in the oil. Finer and coarser droplets appear, and not infrequently fragments of the enclosed substance are extruded from the surface of the drop and dissolve in the surrounding water; or at times even the watery fluid that has made its appearance in the oil pours out eruptively into the surrounding water. The fact that a lively and fairly regular exchange takes place by diffusion between the oil mixture and the water is shown by the active streaming movements of the latter, which can be well followed if Indian ink is mixed with it. I have followed these movements to some extent in some drops of oil mixture prepared with common salt, and can report on them as follows. After transferring the drop of mixture to the slide it is soon observed that in the higher regions the water streams from all sides towards the drop, and, on the contrary, in the lower regions, *i.e.* on the slide itself, the water streams away from the drop radially. These currents gradually become slower, but can be followed for about twenty minutes, when they either die down or continue very feebly. It was often observed that the upper current, at first purely radial in direction, gradually changed in such a way that at one region of the drop an out-streaming current was formed even at the higher level, while at other places the in-streaming currents continued, but had slightly altered their directions in consequence.

The above-mentioned streaming movements admit of an easy explanation. The water immediately surrounding the drop takes up salt solution, either by diffusion or by the direct emergence of single particles, becomes specifically heavier thereby, sinks down

on to the slide, and spreading out upon it, streams in all directions away from the drop, while in the higher regions it is replaced by pure, specifically lighter water, which therefore streams from all sides towards the drop. The correctness of this explanation is confirmed by the fact that the same streamings are also obtained by allowing concentrated salt solution and pure water to approach one another under a cover-slip—a process which can be carried out with the retention of a fairly sharp boundary between them. The current in the water, which is directed towards the boundary, goes on in the upper region, while in the lower region the current flows away from it; on the other hand, in the salt solution the current towards the boundary is below, the current away from it uppermost, since the salt solution of the intermediate region, having become specifically lighter, continually ascends. The streaming movements are distinct but fairly slow. Corresponding streamings appear if glycerine is brought in contact with water.

After the drops of oil mixture, prepared in the manner stated, have stood about twenty-four hours in a damp chamber, they become completely opaque and milk-white. The particles of soluble substance have vanished, but here and there larger drops of fluid (vacuoles) are visible in the oil. The closer investigation of drops that have thus become opaque shows that they have become converted into a more or less finely-structured foam throughout their entire mass. On account of their opacity the drops must naturally be pressed out into a thin layer, if it is desired to determine their finer composition. Hence a more suitable method is to clear them up gradually by addition of glycerine to the water under the cover-slip, or rather by replacement of the water by glycerine. One can then follow plainly the way in which the clearing up gradually penetrates from the surface of the drop into the interior, and finally, after a short time, pervades the whole drop equally. The gradual clearance of such a drop of oil-foam by glycerine is a sure proof that the glycerine diffuses through the oil, so that its alveoli become filled after a time with watery glycerine. In consequence of this the froth-drop naturally becomes much more transparent, on account of the diminution in the difference of the refractive indices. I defer for the present the more detailed description of the structural relations of foam-drops produced

in this way, from olive oil and sugar or salt, and will forthwith proceed to discuss the further experiments which were performed in order to manufacture such foams, and to explain their formation.

The attempt to obtain similar drops of oil-froth with cod-liver oil and common salt gave bad results, since only a defective foam with large vesicles was formed. On the other hand, tolerably good results were obtained with boiled linseed oil and common salt. For certain reasons I experimented also on the behaviour of a thick mixture made up with paraffin oil and common salt. As was to be expected, no proper formation of foam took place in the paraffin oil; the salt, however, dissolved gradually with formation of droplets, but very slowly. Hence diffusion of water through the paraffin oil certainly takes place, although very slowly.

It has been already pointed out above, that the original train of reasoning which led to the experiments upon the formation of foam in oil was not, as a matter of fact, completely confirmed. I demonstrated that the particles of the substances mixed with the oil were relatively coarse in spite of the finest pulverisation; hence it seems impossible to ascribe the alveoli or foam vesicles of a successful oil-foam of this kind, as a rule of extreme fineness, to the drops of fluid produced by the solution of the enclosed particles. For this reason some other source of the formation of the finest droplets of watery fluid must be present in the oil. To clear up this point I instituted a series of experiments, to enumerate which is of no further interest, since they soon led to the result that even in pure olive oil, placed in similar drops in H_2O under the cover-slip, numerous very minute droplets of fluid very soon make their appearance, causing it, at least in places, to become finally quite opaque and of a minute foam-like structure. In a few hours after setting up such a preparation, numerous very fine droplets of fluid may be noticed in the oil; these drops increase continually in quantity, so that after one or two days the drop has become quite turbid. In particular, the lower edge of the drop, *i.e.* the edge of the surface by which the drop rests on the slide, has then become quite

black and opaque (in transmitted light), so that a dark somewhat irregular margin completely surrounds the drop like a girdle (see Fig. 1). The phenomenon does not perceptibly proceed with greater intensity or speed, if the olive oil is heated beforehand for some time on the water-bath over sugar or common salt; hence, any solution of these substances in the oil is without direct influence. On the other hand, the production of froth takes place quite strongly, if some few crystalline fragments of salt or sugar are enclosed in the oil-drops. Drops of fluid then form as a rule round the fragments of salt; but curiously enough, this does not occur at times round certain of the fragments, and moreover, not round those of sugar. The oil-drop becomes frothy in exactly the way described above, but this process appeared, however, as has been said, to go on more intensely than in the pure oil-drops (see Fig. 1). In the vicinity of the drops of fluid, which had formed round the salt crystals, there appeared to be in no way any special crowding of the froth droplets, which were concentrated, as depicted, more especially in the marginal zone. The explanation of the intense crowding of the droplets of froth in the lower marginal region of the oil-drop may be somewhat as follows. The formation of the droplets depends, without doubt, on water being taken up into the oil, which takes place in a way that will be treated more in detail later. As a consequence, the formation of droplets will occur principally in the marginal region of the oil, bordering on the water. But since the droplets consist of a watery solution, and hence are specifically heavier than the oil, they will sink gradually in the oil-drop, and, as a result, collect principally in the region of its lower margin. Since the droplets when sinking press against one another, they cause, if the conditions are suitable, the formation of a froth, in a similar manner

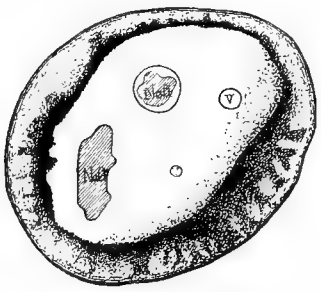

Fig. 1.

to the ascending air-bubbles in a soap solution, or the earlier described benzin droplets in a froth of soap and benzin.

Drops of almond oil and cod-liver oil, which were brought into water, behaved in just the same way as the olive oil already investigated. Cod-liver oil especially became turbid very quickly and intensely, and turned completely into a fine frothy structure in the lower region.

These experiments led me to suppose that the formation of foam in oil-drops in water might depend on the presence of small quantities of soap dissolved in the oil. The dissolved soap strongly attracts water which diffuses into the oil, and the watery solution of soap thus formed, not being soluble in oil any longer, separates out in minute particles, which by further absorption of H_2O become minute droplets. This hypothesis appeared also very probable, if not certain, from special experiments directed to the point. It was not found possible to deprive olive oil of its property of becoming gradually turbid and frothy in H_2O, by heating it with water and shaking it repeatedly; indeed it is improbable that oil can be thus completely deprived of such soap as it may contain. On the other hand, the influence of soap in the olive oil on the production of froth was shown very plainly, when the amount of contained soap was increased by warming the oil for some time with Venetian soap, even though the latter was not noticeably dissolved. A drop of such oil, brought into water in the usual manner, begins to turn frothy immediately; at the same time wave-like streaming movements (superficial extension-currents) appear on the surface, called forth by local extension-movements of the soap. In a few hours the drop became quite frothy. A similar result is obtained if a few particles of Venetian soap are enclosed in a drop of pure olive oil, which is then brought into H_2O under a cover-slip. Such drops also immediately show lively wave-like extension-currents, and minute droplets stream out on all sides from the particles of soap into the surrounding oil. After a few hours the oil-drop becomes finely frothy throughout, therefore white and opaque. I have not followed out this method of preparing such oil-lathers more accurately, so that I cannot

say if it is as good as that described below, or possesses any special advantages.

It is an interesting fact that white of egg exerts the same influence as soap on the conversion of olive oil into froth. The olive oil (*a*), used for the experiments hitherto described, was allowed to stand some days over dried pulverised white of egg, and then filtered off. Drops of this perfectly clear oil were brought into water under the cover-slip in the way described. Numerous extremely minute droplets of fluid appeared at once in the oil-drop, which in a short time became turbid. Simultaneously it took on the peculiar circulating streaming movements, described below for drops of oil-foam in glycerine. A superficial current, both from the upper and lower edges of the drop, streams out radially from all sides, and runs towards its equator, where the two streams coming from above and below meet, and pass into a horizontal internal current, travelling from the equator on all sides towards the centre of the drop. Here this internal current divides in all cases into an ascending and a descending stream, which feed the two streams first described. As shown later, this peculiar mode of circulation depends in every case upon phenomena of extension which come into play particularly at the upper and lower edges of the drop. Oil treated in this way with white of egg becomes even after a few hours totally turbid, and in places has a pronounced frothy structure. Whether this effect upon the oil is due to the white of egg itself, or whether it depends on a formation of soap by the alkali in the white of egg, I leave undecided, though the latter supposition seems to me the most probable. The experiments described make it, however, very probable that the conversion of the oil-drop into foam in the water depends on its containing soap. Hence the extremely fine oil-foams prepared as above described from drops of a thick mixture of oil and common salt or cane sugar must also be considered from this point of view. It is not the mere presence of small particles of common salt or sugar in the drops that brings about the formation of a foam, but the first origin of the fine droplets of froth are rather to be referred to the soap naturally contained in the oil. The fact that the formation of foam goes on much more energetically and completely under these conditions may be due partly to the sugar or salt in the oil producing a stronger permeation of the oil by the water, and partly to the resulting infiltration of the oil with numerous drops of salt or sugar solution favouring the formation of the fine droplets of froth.

On the other hand, it cannot be well assumed that salt or sugar furthers the formation of soap in the oil-drops.[1]

If my view as to the formation of froth in oil-drops is correct, this process belongs to the category of phenomena which Berthold, and after him Fr. Schwarz, have termed processes of *desolution*.[2] They understand by this the separation from one body of another dissolved in it under certain conditions which remove or diminish the solubility of the latter. Schwarz gives various methods of producing such processes of desolution artificially, whereby the originally-dissolved body, after being separated out from the so-called "homogeneous mixture," appears in the form of drops or vacuoles. Mastix or resin in weak alcohol, as well as the precipitation membrane produced from soluble glue (Traube's β-glue) by a solution of tannin, are said to show these vacuoles. For the resins mentioned, the phenomenon is explained by the fact that they formed a homogeneous mixture of two bodies, of which one is soluble in alcohol, the other not; the precipitation membrane produced from β-glue consists of a modification which is soluble, and another insoluble, in H_2O, and hence gradually exhibits a process of desolution under the influence of water. It is of interest that this process of desolution leads, in the glue membrane, to the formation of frothy honeycomb-like structures (so-called reticular structures), although here the ground substance of the membrane certainly does not possess a really fluid consistency. Finally Schwarz brings in the "separating out of the fluid droplets of soap, which arise if oil containing oleic acid is brought into a watery solution of potassium carbonate, or disodic phosphate, or in weak am-

[1] I cannot, however, refrain from referring to a circumstance which does not harmonise well with the explanation attempted, namely, the fact that even in drops of chemically pure oleic acid which were placed in water, minute droplets appear after a little while, although not so plentifully as in usual olive oil. If the oleic acid had stood twenty-four hours over pulverised white of egg, the formation of droplets in water was considerably more energetic and rapid, so that the deeper region of the drop became quite turbid.

[2] For this term see the Translator's Preface.

monia," as an example of similar desolution processes. My interpretation of the formation of droplets in oil, obtained quite independently, thus harmonises in essentials with Schwarz's ideas. I can also cite as a good example of such a process of desolution, connected with the formation of frothy structures, the behaviour of the mixture of collodion solution and clove oil usually employed for fixing sections on the slide. This mixture, when spread out into a thin layer on the slide, usually shows a beautiful finely frothy structure after hardening and removal of the clove oil by means of turpentine. By colouring the frothy collodion membrane with aniline stains the structure can generally be easily studied. Its great resemblance to the fine reticular structures of protoplasm makes this method of sticking on sections seem not without its dangers in investigations of protoplasmic structures. What is the exact course the process of desolution takes in this case I have not investigated more closely, but probably the warming of the mixture, as a result of which the solvent medium common to both the collodion and the clove oil is driven off, leads to the separating out of the latter in the form of minute droplets, until the stiffened layer of collodion finally obtains the frothy net-like structure.

After determination of the important influence of soap on the formation of froth in the oil, it naturally followed that the employment of a salt suitable for producing soap, such as K_2CO_3, would cause the process to go on much more energetically and better. Experiments also showed the correctness of this supposition. By such a method not only were the most regular and finely structured froths obtained, but also a series of important facts upon phenomena of movement and other matters were ascertained in drops of these froths.

With further experiments, however, it was soon found that the nature of the oil is of great and all-important influence upon the formation of good and finely-structured drops of oil-lather. A fortunate chance had originally brought into my hands an olive oil that had stood for a long time in a little bottle, and which happened to be just in the

suitable condition for the success of the experiments. When I made further experiments with freshly bought oil, I only obtained very defective results. A long course of experimentation then proved that the fresh yellow oil is, as has been said, unfit for the experiments, but that one can prepare good material from it, however, by long warming up to 50°-60° C. I heated small samples of unsuitable fresh oil in flat watch-glasses in thin layers in a warm chamber, such as we usually employ for embedding objects in paraffin, and which is kept at a constant temperature of 54° C. The yellow oil becomes by degrees quite colourless and of a thicker consistency with continued heating. Under these conditions the warming must always be continued eight to ten days or longer, till the oil has attained the proper consistency. Since commercial olive oil is in all cases very variable in its nature, which moreover changes with the age of the oil, the length of time that is necessary for warming it cannot be determined once and for all, and it can only be ascertained by repeated testings whether the oil that is being warmed has gradually attained the right consistency. Later I attempted to shorten the time of warming by the employment of higher temperatures—a method which also works well. Although I did not determine the point more exactly, the result of my experience was, that, as a rule, heating the oil up to about 80° C. for two or three days has the same effect as when it is done at 50° to 60° C. for eight or ten days.

As has been mentioned, the oil becomes considerably thicker and more viscid during this process. I am further of opinion that the right degree of consistency of the oil is of special importance for the success of the experiments. Oils that have become too thick give very good foams, but they are unsuitable for the experiments to be described hereafter, on the phenomena of streaming in the drops of oil-foam, since the too great viscidity of the oil is without doubt a hindrance to the streaming movements. Later on I shall make a few remarks upon the special relations of the froths prepared from oils that have been rendered viscid.

Oil that has become too viscid can in general be cor-

rected by mixture with some that is too fluid. I have usually improved to some extent my samples of oil in this fashion.

I will not report here in more detail upon the numerous experiments which preceded the discovery of the above described method. Since it seemed an obvious hypothesis that the free oleic acid mixed with the oil must be of influence upon the formation of soap and froth, I attempted to improve the unserviceable ordinary oil by addition of a few drops of pure oleic acid; but this addition, as well as that of a volatile oleic acid (valerianic acid), proved quite useless. The attempt to obtain a utilisable product by dissolving mutton-suet in the olive oil met with just as little success; nor was the olive oil rendered any more serviceable after separation of the more easily congealed glyceride by means of a freezing mixture.

As to other oils I experimented with almond oil, boiled linseed oil, cod-liver oil, and refined bone-oil (watchmakers' oil, so-called). All the oils mentioned are more or less serviceable when they possess the proper consistency; but since, however, they offered no special advantages, I usually returned again to olive oil. Furthermore, the manufacture of froth-drops with Na_2CO_3 and $NH_4NH_2CO_2$ was tried; but the experiments were, as a rule, more successful with K_2CO_3, on which account this salt alone was finally employed. At the commencement I used carbonate of potash finely pulverised, and freed as far as possible from water; later, however, I convinced myself that the experiments succeed better if the salt is slightly damp. Hence I proceed now to breathe several times on the small sample of salt, while pounding it in the mortar, till it is moderately damp, and then to rub it up well with the drop of oil into a thickish paste. This paste is immediately made further use of in the way described, since after standing long it loses its valuable properties. Little feet of paraffin serve for the support of the corners of the cover-slip in these experiments, since wax, or cobblers' wax, becomes friable under the action of the K_2CO_3 solution, which is gradually formed under the cover-slip.

The processes which go on while such a drop of paste placed in water, is converted into foam are, as far as they can be observed under the microscope, somewhat as follows. The drops of the paste when in the water pass into more or less violent undulatory movements, since here and there particles of K_2CO_3 pass from the paste into the surrounding water,

and quickly dissolve in it, and by their action on the oil call forth, sometimes in one place, sometimes in another, local extension-currents. At this period, and usually also at the moment when the cover-slip with the drop of paste is laid on the drop of water, a more or less considerable number of small and minute oil droplets separate off from the drop of paste, for which reason the latter generally becomes surrounded by a zone of such little droplets. If the oil is well suited to the production of foam, these little droplets become, so to speak, instantaneously converted into foam-drops, so that it can be thus determined with some certainty if the oil in question is in the smallest degree not quite suitable. In the drops of paste there gradually appears an increasing number of larger or smaller droplets of fluid, as a result of which it becomes more and more opaque. From time to time eruptions of such drops of fluid into the surrounding water take place on its free surface, which are naturally accompanied in their turn by superficial extension-currents. These extension-currents doubtless also promote the conversion of the drop into froth, since, as will be shown later, violent extension-currents frequently bring about absorption of the surrounding fluid in the form of minute drops. In a relatively short time the drop of paste becomes quite opaque and milky white in transmitted light. With the extinction of the currents from the interior and of the superficial extension-currents, the drop, which formerly had more or less irregular and variable contours, rounds itself off, for the most part, completely, and then finally remains perfectly quiescent. This rounding off of the drop usually takes place in a relatively short time—about one-half to one hour. After about twenty-four hours the process is entirely ended, and the drop is suitable for further investigation.

Naturally, with this conversion of the oil-drop into foam, its volume increases considerably, upon which I shall make more precise statements below in the proper place. As a rule, during the process more or fewer bubbles of gas, *i.e.* CO_2, appear in the drop, which are expelled from the K_2CO_3 by the free oleic acid; later they gradually vanish again. I do not, however, think that the forma-

tion of CO_2 is indispensable for the success of the experiments.

Successfully prepared drops are, as has been said, completely round, and, as follows from this, quite fluid. In transmitted light they appear of an even dark-yellowish brown, which was usually a sign to me that the process had taken a favourable course. They are permeated by coarse drops of fluid or vacuoles in more or less abundance, while their evenly frothy general substance is much too finely structured for its composition to be recognised under these conditions. On the surface of such drops there collect, as a rule, more or fewer fine granular structures, which are probably a hard, not easily dissolved soap. They are of no importance when they do not appear in too great quantity, since they can, for the most part, be washed away by a current of water. Were the oil too fluid, and hence unsuitable, foam is not evenly formed throughout the whole mass of the drop; sometimes it is only full throughout of larger drops of fluid, without being properly frothy, while at other times, between finely frothy portions, there are to be found more or less homogeneous portions of oil. Of course these relations can only be made out with sufficient distinctness when the drops are strongly compressed.

Were the oil too much thickened it lost its fluidity in the process, as follows from the fact that such drops did not round themselves off, but retained more or less irregular contours. Although I am not able to explain this phenomenon properly, I must nevertheless call attention to it. It seems to show that on thickening peculiar alterations in the oil take place which I am not in a position to follow up further, but which, however, are most important for the success of the experiment. If these alterations exceed a certain measure, they prove harmful in turn. As a proof, I may adduce the following. Very strongly thickened and quite viscid cod-liver oil, rendered more fluid with ordinary cod-liver oil, was made up into paste with K_2CO_3 in the usual manner, and placed in water. At the commencement the drop became quite finely frothy, but towards the evening the foam had almost entirely broken up, and the next morning had entirely vanished, all but a few very transparent drops and some finely granular cloudy masses and threads. Also, the froths manufactured from very viscid, thick olive oil, which had

stood two months in the sun, showed themselves quite abnormal in the fact that they were very transparent; for their investigation no clearing up with glycerine was requisite. By remaining longer in the weak solution of K_2CO_3 under the cover-slip, these froths were in like manner relatively quickly attacked and destroyed, while those obtained from moderately thickened oil could remain without harm in the solution for many days.

As I mentioned above, the extremely minute drops of oil that are split off become frothy immediately. This fact naturally leads one to suppose that the production of froth can also be brought about by placing an oil-drop in a solution of K_2CO_3. Experiments proved successful, but slowly, with more concentrated solutions of K_2CO_3, although with a moderately strong solution the drop was finally changed after some days into an even, fine froth. A much more energetic formation of froth goes on in solutions of from 1 to $2\frac{1}{2}$ per cent. The drops when brought into the solution become milk-white at once, and a circulatory streaming is set up, similar to that which was described earlier (see above, p. 14) for the oil-drops treated with white of egg or soap. The edge of the drop gradually becomes darker and more opaque, and sometimes retort-shaped processes project from the surface, in which the very peculiar relations of the currents are difficult to understand. By continued growth of the dark margin of the drop, the whole drop finally becomes opaque. After twenty-four to forty-eight hours the formation of the froth is completed; the froth is very fine and regular. Nevertheless, drops of oil-lather obtained in such a manner proved from various experiments unsuitable for the observation of the phenomena of streaming, for which reason I did not continue to employ this method of preparing foam. I should be inclined to think, however, that with more elaboration it might develop into a very simple and good method. It is interesting to note that the oil-drops which have stood a longer time in a more concentrated solution of K_2CO_3, without having formed good froths, after being transferred to water develop quickly into good froths, which harmonises well with the explanation of froth production given above.

Successfully prepared drops of oil-lather are, as remarked, completely milk-white in reflected light, and, if at all thick, quite opaque in transmitted light; smaller drops, on the other hand, or larger ones pressed out into a thin layer, appear brownish yellow in transmitted light. The frothy structure can be studied without further trouble in the smaller drops that split off, since they are sufficiently trans-

parent. The larger drops require, as was said, clearing up with glycerine. Although they then become very transparent, it is nevertheless indispensable for the study of their structure to compress them more or less strongly, in order to be able to observe them in a very thin layer. The thinner this is, the more clearly the structural relations are shown.

After clearing up with glycerine, the drops are seen to be diminished very considerably in volume, just as is a mass of protoplasm under the same conditions. This very circumstance is, in my opinion, decisive in determining the structural condition of such drops as foam-like, and not in any way as bodies of a net-like or spongy structure. Since the principal mass of the froths is oil, which is not itself capable of swelling, the diminution of volume can only depend on a process corresponding to the so-called plasmolysis of plant cells. It can only be explained by the fact that the mass of oil is honeycombed throughout by numerous minute spaces quite closed off from the exterior, and filled by a watery fluid, which, when subjected to diffusion with glycerine, naturally give off more H_2O to the surrounding glycerine than it takes up of the latter. The consequence will be, therefore, a plasmolytic decrease of size of the spaces filled with watery fluid, and hence, also, of the whole drop. For further details on this point see below.

As already mentioned, the microscopic investigation of such froth-drops shows at once that, as a rule, they are more or less abundantly filled throughout with larger drops of fluid (vacuoles, up to ·015 mm. in diameter). Very varying relations are naturally met with in this respect; occasionally one obtains drops completely, or nearly completely, devoid of the larger vacuoles, and which only consist of the finest foam, while other drops are very full of vacuoles, so that without closer investigation they appear to possess a coarsely vesicular structure. Such froths often proved themselves especially favourable for the phenomena of streaming. The principal mass, which encloses the larger vacuoles, gives the impression of an evenly and finely granular structure with low magnification; only when investigated with the best and

strongest systems (Zeiss Apochr. 2 mm., Ap. 1·30 and 1·40), and by employing strong oculars (comp. Oc. 12 and 18), is it seen for certain that we are dealing here with a very fine foam-like structure. Such a very fine microscopic froth does not, as a rule, appear any different from a macroscopic soap or beer-froth. There is this difference, however; the microscope only represents clearly an image that falls in one plane, and therefore only brings into view a plane section through a froth of this kind. Moreover, there are still a number of relations to be taken into consideration in connection with the peculiarities of microscopic vision; they will be further discussed below. As a result, the microscopic image of such a froth will appear as a meshwork or network, the meshes of which are formed of the most varied kinds of polygonal figures. Very numerous transitions from triangular meshes to those with many angles will be found.

As is well known, a number of laws obtain for the formation of microscopic froths which Plateau (1873 and earlier) developed with exactitude, and which are chiefly as follows. A froth represents a system of thin lamellæ of fluid, the arrangement of which is always such that three lamellæ meet at one edge, each making with its neighbour an angle of 120°. Since each lamella, in consequence of its surface tension, exerts a pull upon the common edge in which they meet, it is clear, *a priori*, that as long as the three lamellæ have equal tensions—and this is invariably the case in ordinary froths—equilibrium can only be established between the three lamellæ under the condition stated. The edges in which the lamellæ of froth touch one another are connected amongst themselves in such a way that three edges meet in a nodal point, so that the lamellæ form the most varied polyhedral figures, in which the rule obtains that the angle, which every two neighbouring edges form in the nodal point, amounts to 109° 28′ 16″ (see Plateau, T. I. p. 315). If one attempts to build up a system of lamellæ under the conditions stated, and assumes an equal length of edge in all lamellæ that meet, a system is obtained composed of nearly regular dodecahedra, a natural result, since the dodecahedron comes nearest to the conditions to

be fulfilled, with an inclination of 116° 33′ 54″ formed by the surfaces meeting at one edge, and an angle of 108° which the edges, that meet at one corner, form one with another. A soap lather formed of bubbles as equal in size as possible, visibly consists mainly of dodecahedric alveoli. They naturally can never, however, be regular dodecahedra, since the figure is one that does not quite satisfy the conditions to be fulfilled. Since, however, we are dealing with fluid lamellæ, this deficiency in the angles can easily be compensated, and the condition of equilibrium established, if the lamellæ equalise the difference in the angles of contact, by curving slightly towards the edges at which they meet one another. As a natural consequence, only the angles formed by the tangential planes of the curved surfaces at their edge of contact amount to 120°. That such curvings of the lamellæ frequently occur in macroscopic froths, so as to establish conditions of equilibrium, is shown at once by observation; similarly the edges are also frequently curved in the same manner, in order to comply with the condition that they should form at the nodal points angles of 109° 28′ 16″ with adjoining edges.

Considering what has been stated, it will readily be understood that the alveoli of froth may form polyhedra of the most various kinds, from tetrahedra to those enclosed by the highest possible number of sides, and therefore that the image of our microscopic froth will show polygons of very different kinds. Nevertheless one condition will always obtain, that in a nodal point or an edge only three lines meet one another, which may, however, enclose very variable angles. The latter point depends, in the first place, on the fact that in such fine microscopical froths as are under consideration here, in which the breadth of the meshes remains, as a rule, under ·001 mm., it is not possible to distinguish in the microscopic image whether the three lines radiating from a nodal point are the sections of three lamellæ meeting one another at one edge, or whether the union of three edges is before us. Further, the section of the plane of the image may pass through the edge at which the lamellæ meet one another in any sort of way, or rather

the edge by which they unite can be orientated in very different ways with regard to the plane of the image. In addition to this point there is the fact that in alveoli of such small diameter, it is, of course, no longer possible to ascertain whether the sections of the lamellæ or their edges have a slight curvature; as a rule, it is as much as one can expect if the meshwork can be at all plainly recognised.

This description shows, on the one hand, that, as has been said, there may occur a great variety of alveoli, a possibility which seemed at first doubtful, and on the other that one must by no means expect to find angles of 120° or 109° everywhere, so that objections as to the regular frothy nature of the drops described are not to be raised on this account. Should there exist a doubt, however, as to whether the fine meshwork is the image shown by a foam-like structure, it can easily be set aside by the fact that in such froths, which are in one part more coarsely, in another part more finely structured, a transition between the coarser portions of the foam and the finest can be clearly traced. Since, however, the former can be recognised with ease and certainty as froths, this is a proof that the finest portions also, in which only the network is distinguishable, must possess the same structure. Still more decisive in this respect are the results given by the investigation of defective foams, or such as have been again disorganised by long keeping, strong pressure, or the addition of unsuitable fluids. Such foams contain portions of homogeneous oil in which are scattered singly droplets varying in size from the coarsest to the very minutest. In these isolated droplets of froth, even in the finest of not quite 1 μ in thickness, it is possible to convince oneself that one is dealing with more feebly refractile and, since they are always spherical, fluid droplets. If the tube of the microscope be lowered a little from the median sharp focus, they increase in lightness, while by slightly raising the tube, on the other hand, they become dark. It is further easy to follow out how, by the gradually increased crowding together of such very minute droplets, the portions with a frothy structure originate, and in these in turn

it is possible, by lowering and raising the tube, to determine clearly the same state of things in the finest meshes (see Photogr. I. and II.) I lay special stress on this because, as we shall see later, pictures of a fine network can also be produced by the microscope as optical delusions when small, strongly refractile granules or spherules are in close apposition to one another. On this account I must at once lay emphasis on the fact that, as a rule, I failed to demonstrate the presence of strongly refracting granules or spherules of a solid nature in the froths, even with polarised light, by which they appear perfectly dark when the prisms are crossed.

The optical relations, just described, of the meshes or alveolar spaces of the froths, are also definite evidence against the assumption of a net-like or spongy structure, if such an assumption still required any refutation after all that has been stated. But since, however, it is a question of such extremely fine microscopical relations, that the determination is so difficult in many ways, attention may be drawn here to yet another circumstance. We shall see later, that the froths under the influence of induction shocks show distinct bursting of their alveoli; a similar effect can be also produced by the addition of certain fluids. It is possible to follow out the way in which neighbouring froth vesicles or alveoli suddenly burst into one another, exactly as they do in macroscopic froths. When superficially-placed froth vesicles suddenly burst to the exterior, the very small drops of froth take on jerky, springing movements, which is easily explained by the fact, that at the spot where such a vesicle bursts the surface tension is suddenly very much decreased. As a result of this the stronger pressure of the remaining surface impels the whole drop of froth for a short distance forwards in the direction of the radius passing through the spot on the surface at which the vesicle burst.

In the investigation of the fine froths the attention is at once arrested by the fact that the nodal points in which the edges[1] of three alveoli meet one another are always dis-

[1] I speak here and in the sequel of the edges of alveoli, being indifferent as to whether sections of lamellæ or actual edges are to be understood thereby,

tinctly thickened and appear darker. It is a consequence of this that the froth appears with a low power, or with cursory observation, to be composed of closely-packed fine granules. The reason of this phenomenon must be chiefly as follows. If one investigates in macroscopic froths the union of three lamellæ at one edge, or the union of six lamellæ at a nodal point, as the case may be, it is found that here the lamellæ do not simply meet one another, but that the limiting surfaces of the neighbouring lamellæ pass into one another with a concave curvature (see Fig. 2). A consequence of this must be, that the edges are somewhat thicker than the rest of the lamellæ; but since the corresponding relations in the fine microscopic froths are much too small for it to be possible to make out distinctly the true form of these nodal points, only a general appearance of a rounded thickening of the nodal points must arise. If the nodal points of macroscopic froths are studied more closely, it is further very often seen that they are occupied by minute air-bubbles, which often bulge them out more or less into a swelling. This is interesting at once for the reason that it shows that such small vesicles or bodies in the froths collect at the nodal points, and further, because it proves the possibility that in the microscopic foams the nodal points may in part be thickened by the inclusion of very small foam vesicles, no longer recognisable as such, which cause them to stand out more strongly. Finally, yet a third cause is to be mentioned, which produces the appearance of dark nodal points in the framework of the meshes, and to which I am now inclined to ascribe an essential share in this effect. It has been already pointed out that the optical appearance of the alveoli of the foam, *i.e.* bodies of feebler refracting power enclosed in a more strongly refractile medium, is of such a kind, that when focussed

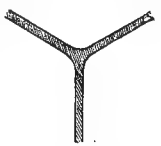

Fig. 2.

since, as has been set forth above, this distinction cannot be drawn in practice. In any case, the three lines that are actually to be observed, which meet together in the nodal points, are, as a rule, sections through three lamellæ, which meet at one edge.

accurately in the middle, they appear moderately light; with a slightly deeper focus, lighter; but with a higher focus, as darker round points. But since even in a strongly compressed froth a number of layers of alveoli lie one over the other, with even the sharpest focus, alveoli must come into vision at the three foci named. Now if there lies, as will often occur, an alveolus under a sharply-focussed nodal point—one, that is to say, seen with a high focus—it will produce the effect of making the nodal point appear as a rounded dark spot, which with the slightest lowering of the tube changes into a clear alveolus.

The appearance of the nodal points depends in part at least on this circumstance, yet without doubt another optical phenomenon must come into consideration. For if a layer of froth be studied, one so thin that it is formed only of a single layer of the minutest alveoli, the nodal points are distinctly noticeable, provided that the alveoli of the froth are not altogether too fine (see Photogr. I.) It follows from this that the nodal points are shown up even without a layer of other alveoli under them. If the middle of the alveoli be sharply focussed, the nodal points appear just as full as the edges of the alveoli, no darker than the latter, but distinctly thickened, corresponding to the explanation above of the way in which three fluid lamellæ meet one another. If now the tube be lowered in the slightest degree, the nodal points show up as very dark points, resembling granules (see the Photogr.), while the rims of the alveoli connecting them appear considerably lighter, and the contents of the alveoli much lighter still, of course. The appearance of dark granules deposited in the nodal points is so strong that only the complete absence of such granules in the finely drawn out and apparently quite homogeneous marginal portion of such a very thin layer of froth, or in other cases, the want of any such granules in the parts of the oil that are not frothy, puts an end to the idea of very minute granular depositions. That we are here dealing with a special optical phenomenon, and not with granular contents, or with a special structural relation of the froths, is plain at once from the fact that

this phenomenon, as has been said, is only to be observed by focussing somewhat below the middle line. An explanation of it may be found in the following considerations. If small, closely packed air-bubbles in a thick solution of gum be studied under the microscope with a low power, by focussing as sharply as possible on the equator of an air-bubble it is seen that in the dark marginal zone, where each bubble touches a neighbouring one, a clear spot of light makes its appearance, so that in two neighbouring bubbles these spots always stand exactly opposite. Nägeli and Schwendener have already (1865) made a theoretical investigation into this phenomenon, and have referred it to the reflection of light at the underside of the air-bubbles. If now the tube be lowered slightly from the middle focus, the clear spots decrease in brightness, but become, on the other hand, broader, so that they traverse the whole dark marginal zone as radial light bands; simultaneously the bands of neighbouring air-bubbles *vis-à-vis* to one another become confluent, so that one obtains a kind of clear net, which is stretched out at the point of contact between the air-bubbles. Now since in our froth lamella we have before us, in the same way, very closely crowded droplets of a less refractile fluid in one more strongly refractile, something similar must take place. The clear, radial bands produced by reflection of the light will be relatively very broad here, since the diameter of the vesicles is very small. These clear bands naturally fall on the middle portions of the edges of the alveoli and make them lighter, while the nodal points become no lighter, and hence appear relatively dark by the effect of contrast.

I take this opportunity to state that in successfully prepared good froths I could not demonstrate any granular structures whatsoever, which by their deposition had in any way added to the actual distinctness of the nodal points. It was rarely that I observed in some froths rounded bodies, more or less scattered, of about the size of a small alveolus, and hence having nothing to do with the nodal points.

Since the problem with regard to the true structure of

the oil-foams was not so easy to solve as it might have originally seemed, on account of the fineness of the microscopic structure, and since, in particular, it was difficult to decide, by simple observation, whether it was possible for granular deposits to make their appearance in considerable quantity in addition to froth vesicles, I took great trouble in various ways to find out a method of reducing the froths again to some extent. Since, as has been mentioned, strong induction shocks call forth continued bursting of the froth vesicles, I tried if it would be possible to obtain the desired effect by long-continued action of the intermittent current. The result was, however, a negative one.

Finally, chance led me, as is so frequent, the correct way. If drops of foam, well washed out with water, be left to stand undisturbed under the cover-slip without addition of glycerine, the water gradually evaporates, and the drop of froth thus coming into contact with the air gradually loses its frothy nature again completely. The water of the froth vesicles slowly evaporates (or rather the latter burst, partly from the contact of the air with the surface of the froth-drop), and the soap left behind dissolves in the oil. Thus, after some days the drops have again become as perfectly clear and transparent as the oil originally employed for their preparation. The smaller and the minutest drops then show no trace of any deposits, even when viewed with the strongest magnifications, while the large drops still contain isolated small froth vesicles. Granular elements, however, are either entirely wanting in the drops, or only isolated granules are to be found, of medium size and moderately strong refractile power. As has been said, when they are present, they occur in such small quantity as not to interfere in the least with the transparency of the drops. Once I also saw fairly large clear crystals, approaching in form to rhomboidal plates, together with needle-like crystals in very limited quantity in the drops, as well as some gritty bodies, which perhaps had arisen by strong compression of such crystals.

From these results it can hence be concluded with complete certainty that solid deposits do not occur to any

considerable extent in the foams, and that, therefore, their structure depends solely on their nature as foam.

This conclusion receives further confirmation from a very interesting circumstance with regard to the perfectly clear and transparent oil-drops that are obtained in the way described from froths. If water is allowed access afresh to drops of this kind, the smaller and the more minute ones become changed, as if by a magic touch, instantaneously into the most beautiful drops of foam again, with all the characteristic structural relations described earlier. The larger drops also become frothy at once down to a considerable depth, and in a relatively short time have again acquired a frothy consistency throughout. This astonishing behaviour may be explained by the fact, that with the drying up of the froth-drops the soap [1] contained in the froth vesicles is again taken up by the oil and dissolved, so that in this way a drop of oil is formed richly impregnated with dissolved soap, which, with addition of water, at once passes rapidly back into froth again. If, therefore, we may see in this process, on the one hand, a further confirmation of our views as to what goes on in the formation of the froths, it offers, on the other hand, also one of the finest examples of a so-called desolution process. From all that has been stated, it can be concluded with perfect certainty, that my view as to the structure of the froth-drops is well grounded, and agrees with all the results of observation.

In successfully prepared froths the breadth of the finest meshes varies between about ·005 mm. and ·001 mm. or less. When such drops of froth remain undisturbed for some weeks, the alveoli gradually become arranged in layers corresponding to their relative sizes. The finest froth collects in the uppermost layer, and further below it becomes coarser and coarser. If the drop was defective in froth, so that homogeneous oil was present in addition, the latter gradually assumes the highest position in the drop. This phenomenon naturally depends on the greater specific gravity of the contents of the alveoli in comparison to the oil, but offers, however, a further proof of the complete fluidity of the froths as well as of their frothy structure, since neither net-like nor granular structures could behave in this way. One can, moreover, easily convince oneself of the

[1] Or other unknown substances also, which assist in the formation of froth.

fluid nature of the froths, a fundamentally important fact, by pressing, inclining, or pushing them, by which it is proved that well prepared foams are perfectly fluid, and flow scarcely more slowly than the oil employed in their preparation.

A phenomenon of especial importance is exhibited by the surface of successfully-prepared foams of even composition. With moderate magnification they appear surrounded by a delicate, somewhat clearer border. To the exterior this border is limited by a sharp and rather dark line; to the interior, its limit in like manner appears fairly sharp, though less so than externally. Investigation with the highest magnification proves that this border is delicately and minutely striated vertically to the surface (see Fig. 4, Plate V., and the Photographs III. and IV.) The comparison with the system of alveoli of the neighbouring deeper portions of foam, which are immediately within the border, show in the clearest manner that we are only dealing with the outermost layer of the alveoli, directed radially to the surface, which gives rise to the border. From these results it is also easy to understand that this border can only come into prominence in a froth of composition as regular as possible, for if the meshes are very irregular in size an even border cannot well be formed.

The thickness of this border, which I have named the *alveolar layer*, naturally depends on the size of the alveoli of the foam; if they are of considerable size, the border also will be thicker. In the foams investigated by me the thickness of the alveolar layer varied between about ·0005 and ·005 mm.; alveolar borders so thick, however, were only observed here and there in foams prepared with NaCl; in the fine ones prepared with K_2CO_3 they were never thicker than between ·0005 and ·0007 mm. Recently, however, I have frequently observed coarser foams of the latter kind which possessed very fine alveolar layers (see Photogr. IV.) of greater thickness.

The origin of the border is easily explained, since it is only a consequence of the laws which the arrangement of the froth lamellæ obey. As has already been pointed out several times, the froth-drops are completely fluid, so that

they assume the shape of a spherical drop, if not acted upon by any special influence, whether from within or from without. Their surface will therefore be curved like that of a sphere. Nevertheless, it is of course impossible for the surface of such a froth to be a simple spherical surface; the tension of the lamellæ, which attach themselves to the surface, naturally tend to bring about a dipping in of the surface at these points of attachment, so that each alveolus or froth vesicle of the superficial layer projects slightly over and above the general surface of the sphere, even though with a very feeble curvature. As a matter of fact, I could never observe this projection of the alveoli of this layer with perfect distinctness in the finest froths, although it often wore the appearance; on the other hand, in the coarser ones it was very prominent (see Photogr. III.) At the point of insertion of a lamella reaching to the surface, the tensions *a* and *b* of the two external curved lamellæ (see Fig. 3), touching one another, come into effect, and maintain an equilibrium with the tension *c* of the lamella first mentioned. If this most external layer of froth is formed of alveoli of equal size, it is easy to see that the lamellæ of the external layer that reach to the surface must all be placed vertically to it, so that equilibrium may be established. Since, however, the three lamellæ meeting one another in one edge at the surface—or rather their tangential planes—must form angles of 120° each to each, at the edge in which they meet, if both the external lamellæ lie nearly in the general surface of the sphere, then the lamella reaching from the interior must be directed radially to the surface, in order to form equal angles with both of them.

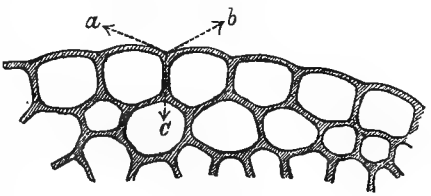

Fig. 3.

One question still requires consideration before we proceed to further investigations. It was noticed that the drops of oil-lather behave as an ordinary fluid, inasmuch as when other factors are excluded, they assume a spherical

form. But since one is accustomed to see macroscopic froths in very varied forms, this point will require still some explanation. The spherical form of drops of fluid can be interpreted as a consequence of the capillary pressure produced by surface tension, which, as is well known, is always directed towards the centre of the curvature of the surface, and is inversely proportional to the radius of the curvature. Hence, a freely suspended mass of fluid will only attain to a condition of equilibrium when the surface tension is equal at every point, a state of stability only realised in the spherical form. If we consider our froths of microscopic fineness, and very regular composition, their surface cannot be taken as the surface of a regular sphere, although this fact is not sharply recognisable; but we must certainly assume, as I have already shown, that each of the superficial alveoli projects with a feeble convexity. As a consequence, the capillary pressure must be the same over the whole surface if equilibrium is to be established. A curvature of the surface differing in strength or in direction must doubtless exert an influence on the capillary pressure, even though not directly, as at the surface of a homogeneous fluid, but by alteration of the curvatures of the single components, *i.e.* of the convex bulging surfaces of the superficial alveoli. A more accurate study shows that the more curved is the general surface, the stronger must be the convex curvature of each individual bulging surface, and *vice versa*. But since the total surface pressure represents the sum of the effects of the pressures of each single bulging surface, and their pressure becomes greater towards the interior in proportion as they are more convex, it follows that such a froth behaves in general as an ordinary fluid, the pressure of which increases and diminishes with the curvature of its surface. If this is the case, then such a froth must assume the spherical shape as the one form in which equilibrium obtains, and only show other shapes under the influence of special external and internal forces.[1]

[1] The above remarks can be represented more accurately in the following manner. If the surface of the froth is level, the radially-directed lamellæ of the most external layer of froth will be vertical to the outer surface, and

The fluidity of the described froths naturally demands that the so-called alveolar layer should also be fluid. Although the distinctness and sharpness with which it

hence parallel to one another. Under these circumstances the lines of section *ac* and *bc*, which the two tangential planes at the points of attachment (*a* and *b*) of the two neighbouring radial lamellæ produce with the plane of the

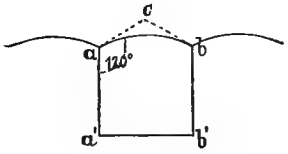

Fig. I.

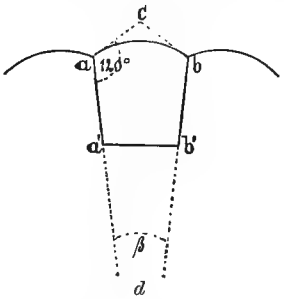

Fig. II.

paper, will form at their point of intersection an angle of 120°, as follows at once from the triangle *abc*. If, however, the surface is curved, the two neighbouring radial lamellæ will not be parallel, but will form an angle β with one another (see II.) Then it follows from the quadrilateral *acbd*, that the angle which the two tangential planes include at $c = 120° - \beta$. *Mutatis mutandis*, it follows in the same manner that with a concave curvature of the whole surface, the angle included by the tangential planes $= 120° + \beta$. But since the transverse measurement of the alveoli *ab* evidently always remains nearly the same (in any case it does not increase, but, if anything, becomes smaller), then as the angle *c* diminishes the radius of the segment of the circle described in it becomes smaller, and hence the curvature stronger, and *vice versa*. That with strong curvature of the surface the transverse measurement of the alveoli must, as has just been pointed out, become less, but in no case greater, follows from the following considerations. Since, as is well known, the sphere is that body which, with the same volume, possesses the smallest surface, a portion of froth imagined as limited by plane surfaces will continually diminish its surface during the transition into the spherical form, from which it follows that this change of form is not accompanied by any tendency to widen out the alveoli of the alveolar layer, but that they would rather tend, on the contrary, to become narrower. The same reasoning holds, however, also in the spherical rounding off of a portion of the froth, the surface of which presented various degrees of curvature.

With regard to the question discussed here, it is of special interest to note that Budde (*Zeitschr. f. physik. Chemie*, Bd. vii. 1891, p. 586) has recently shown that fine emulsions of chloroform droplets, which arise by the action of soda on a solution of chloral, show a distinct tension in relation to the remaining fluid, and hence form a constant marginal angle with the wall of the vessel.

stands out in successfully manufactured drops might well awaken the supposition that one is dealing with a skin-like hard covering, yet more accurate investigation shows its complete fluidity. It is quite astonishing to see how easily such drops, together with their border, flow along, and how the latter, in spite of its fluid nature, maintains itself throughout. This again just shows that it owes its origin to physical laws, which continue to act during the movement of flow.

It is at once readily understood that the same conditions which give rise to an alveolar layer at the surface of the froths must bring about the formation of a similar radiate layer round each of the more considerable vacuoles in their interior. This is also entirely confirmed by accurate investigation of the froths (see Photogr. I.-III. and V.) Everywhere one notices round the vacuoles the finely striated border, depending on the radiate arrangement of the lamellæ arranged closely round the wall of the vacuole. As a rule, I only found a distinction between the external alveolar layer and this border to the vacuoles to the extent that the latter was usually not so sharply and distinctly marked off from the neighbouring irregular alveolar substance as was generally the case with the external alveolar layer.

It was mentioned above that the alveolar layer is marked off from the external fluid by a sharp, dark border, which appears like a delicate darker skin or pellicle. Since ordinary drops of oil also appear, when sharply focussed, to be limited by a corresponding delicate dark border, I am convinced that this border limiting the alveolar layer is no special structural feature, but only an optical phenomenon.

In the account given of the alveolar layer, emphasis was laid on its formation out of very small alveoli quite regular in size. In general it is a striking fact in the investigation of the froth-drops that their peripheral, and therefore, of course, their entire superficial region, consists, as a rule, only of very minute or small alveoli. Larger ones, up finally to those so considerable in size that they merit the denomination of vacuoles, make their first appearance at some depth below the surface. This phenomenon shows up

most distinctly in the photographs of these foams which supplement this work (see Photogr. I.-III.) Although I am not able to give any plausible explanation for this state of things, it seems to me not without significance, especially with regard to similar phenomena in protoplasm. Even in the drops of foam photographed in I. and II., which were adhering to the underside of the cover glass, and hence were drawn out to the smallest possible thinness, this phenomenon shows up distinctly; in fact, a progressive diminution of size towards the edge can be observed in the alveoli. The most external and thinnest marginal region of this adhering drop at first gives the observer the impression of being made up of quite homogeneous oil, and not of alveoli; and it would of course be conceivable that with such a minimum thickness of the layer of oil, the foam vesicles would be pressed out of it, so that an outermost border of homogeneous oil would be formed. Very careful observation shows, however, that this apparently homogeneous border really exhibits very faint indications of frothy structure. In the photographs this can be plainly recognised in places. So far as the size of the alveoli in this apparently homogeneous external margin can be ascertained in the photograph, it is about the same as the size of those in the more sharply defined zone bordering on it.

On what does the fact depend of the alveoli of this external margin being so pale and indistinct that it appears all but homogeneous? Since the layer of oil becomes thinner and thinner towards the margin until it finally is reduced to a minimum, it may for one thing depend upon the fact that the delicate most external lamellæ between the vesicles of the foam become shallower and shallower, and naturally at the same time fainter (see Fig. 4). Moreover, the foam vesicles in the external zone, which runs out quite flat, must themselves be very strongly compressed from above downwards, and hence pressed strongly against one another laterally, which necessarily causes an attenuation of the oil-lamellæ between them to a minimum of thickness. Both these factors taken together may explain, as it seems

Fig. 4.

to me, why only traces of frothy structure are to be found in the external margin.

Yet a further point may be touched upon at this opportunity. In the manipulation of these drops of foam under the cover glass, one has occasion to observe, if the drops stick more or less to the glass, that fine lamellæ or threads of the frothy mass stretch across between drops squeezed apart. I was able to observe fine lamellæ of this kind, which consisted of only a single layer of alveoli, in optical section, when it could be seen most distinctly that, as was to be expected, the partitions between the alveoli stand vertically to the two surfaces of the lamella (see Fig. 4, Plate X.) In the finest threads, which stretch out between neighbouring drops and naturally break very soon and become retracted into the contiguous portions of froth, I could not observe any structure, and hence believed formerly that they were only formed of the ground substance of the froth, *i.e.* oil. But I have become somewhat doubtful on this point in consequence of my experiences with regard to the scarcely recognisable frothy structure of the greatly attenuated marginal portions of drops already described, and now prefer to assume that such finely drawn-out threads also retain a frothy structure, but that their structure can no longer be plainly observed from causes similar to those obtaining in the strongly attenuated marginal portions. In every case where such threads show even the slightest swelling, the latter is always distinctly frothy, even if occasionally only composed of quite a few alveoli.

2. *Some more exact Statements as to the Alterations in Volume of the Drops of Foam under the Influence of the surrounding Fluid*

Since it seemed to me of great importance for the correct explanation of the froths, to determine somewhat more accurately the alterations of volume already mentioned, I recently performed some experiments which were directed towards solving this question. For this purpose two narrow glass strips of 0·20 mm. in thickness were fastened with

paraffin on a slide parallel to one another. The layer of paraffin between these strips and the slide was of excessive thinness, as the strips were pressed firmly down on the melted paraffin. The cover-slip with the drop of oil mixture was then placed on the strips, and the water so far drawn off from under it that the cover glass was firmly pressed down upon the slips. Then the edges of the cover glass, which rested on the glass strips, were firmly cemented with melted paraffin from without. In this manner the distance between the cover glass and the slide was kept sufficiently constant, so that in the experiments to be described in the sequel, errors of any kind, through pressure of the cover glass on the drops, appear to be excluded.

Two preparations set up in this manner contained each three drops of the oil mixture, which may be denoted by the letters *a*, *b*, *c*, and *d*, *e*, *f*.

On the 28th May, at 11 A.M., immediately after setting up the preparation, the drops showed the following diameters. The sign (*m*) added to the numerical statement indicates that the drop in question was not quite circular, so that the statement represents the arithmetical mean of the greatest and least diameter.

I.—Diameter of $a = 0{\cdot}720$ (*m*)
„ $b = 0{\cdot}488$
„ $c = 0{\cdot}565$
„ $d = 0{\cdot}385$
„ $e = 0{\cdot}469$
„ $f = 0{\cdot}803$ (*m*)

At 6 P.M. on the same day the volume of the drops had already much increased, and on the 29th May, at 10 A.M., it had grown still more strongly, as shown in the following table:—

	28/5. 6 P.M.	29/5. 10 A.M.
II.—Diameter of *a*	1·336 (*m*)	1·605 (*m*)
„ *b*	0·951 (*m*)	1·084 (*m*)
„ *c*	1·092 (*m*)	1·503
„ *d*	0·707	0·784
„ *e*	0·925	0·997 (*m*)
„ *f*	1·388	1·481

After the last measurement on 29th May, at 10 A.M. (see Table II.), the preparations were thoroughly washed out with semi-dilute glycerine, and then left to stand in this fluid. After about an hour the drops had already become much smaller. Since the drops *e* and *f* flowed together after a short time, this preparation was not further taken into account. The decrease of volume was further maintained, so that the diameters of the three drops of preparation I., which had again become completely round, were, at 9.30 A.M. on the 30th, about as follows :—

III.—$a = 0{\cdot}899$
$b = 0{\cdot}572$
$c = 0{\cdot}668$

The glycerine was then washed out with water ; the increase in size of the drops was quite visible in an hour's time, and their diameters on the following day, 1st June, at 11.30 A.M., had attained the following dimensions :—

IV.—$a = 1{\cdot}747$ (m)
$b = 1{\cdot}285$ (m)
$c = 1{\cdot}567$ (m)

As results from a comparison with Table II., the dimensions of all three drops are now somewhat larger than at first, which no doubt depends on the fact that originally they were not formed in pure water, but in a weak K_2CO_3 solution, which, like glycerine, naturally exerts an osmotic effect.

Finally, on the 1st June, the water was once again replaced by half-diluted glycerine. The drops now adhered somewhat strongly to the glass, so that with the contraction that took place they became more or less sausage shaped. Their diminution in size was again speedily very striking, and by the following day, 2nd June, at 10.15 A.M., they shrank to the following dimensions :—

V.—$a = 0{\cdot}937$ (m) $[+ 0{\cdot}038]$
$b = 0{\cdot}609$ (m) $[+ 0{\cdot}037]$
$c = 0{\cdot}673$ (m) $[+ 0{\cdot}005]$

If one takes into regard the errors which necessarily result from the somewhat irregular shape of the drops, the agreement in the size of the drops with that which they previously possessed in glycerine (see Table III.) is quite striking. I have added to Table V. in square brackets the differences of measurement as compared with Table III. This reaches the maximum in one drop of 6 per cent. I do not doubt that the repetition of the experiment would have succeeded oftener still, but I had no occasion to continue it further.

If the demonstrable and indubitable fluidity of the froth-drops be taken into consideration, the observations here set forth upon the plasmolysis of the drops, as the process may aptly be termed, may serve to remove all doubts which could be raised, and which have already been raised by Frommann (see further below), as regards the frothy nature of the drops prepared by me.

Since to many people the notion of a diffusion of watery fluids through lamellæ of oil is somewhat unusual, though the experiments related here prove it occurs beyond a doubt, I have also performed some experiments on this point with aniline colours. If the drops are brought into a moderately concentrated solution of methyl green in water, they are coloured strongly greenish blue after about twenty-four hours, and after forty-eight hours the colouring had even gone completely through the larger drop (diam. about 1·5 mm.), though after twenty-four hours it still showed a white centre. By pressing the drops more strongly it could be plainly made out that the contents of the alveoli were coloured green, and hence the solution of methyl green had penetrated into the alveoli.

3. *Radiate Appearances in the Drops of Oil-Foam*

In good froths, which have stood quietly for some time, a more or less pronounced radial striation can be not infrequently observed, as well beneath the whole surface, as round the larger vacuoles of the interior. This radiate appearance can usually be increased, or even produced, if,

in a drop made transparent by half-diluted glycerine and strongly compressed, a diffusional exchange of fluid be set up, either by adding concentrated glycerine, or by the addition of water. Concentrated salt solution has also been occasionally employed with good results. As has been said, after some time one observes in places, or in successful preparations over the whole surface of the drop, fine radiate markings directed radially to the surface, which penetrate more or less deeply into the froth-drop, sometimes even to a considerable distance. The radial striation often appears especially well marked round the larger vacuoles of the interior, and it then attains not infrequently an extension equivalent to the diameter of the vacuole. A closer microscopic investigation of this radiate appearance shows, that it depends on the meshes or alveoli being disposed one behind the other in a more or less pronounced radial arrangement. I have convinced myself of this in the clearest manner, and the photograph (VI.) of such a radiate structure, which is in my supplement to this work, also shows this to some extent, although unfortunately it was taken from a very defective preparation, and has not itself come out particularly well.

The conditions under which these radiate markings are especially produced are of themselves a proof that diffusion currents play a part in giving rise to them. I am not able to give more precise information as to the manner in which the influence of the diffusion is expressed by them, but it appears to me certain, as has been said, that the diffusion between the contents of the alveoli and the surrounding medium, or the contents of larger vacuoles, is the *primum movens* in the process.

A peculiar observation which I frequently made on oil-drops appears to me to belong to this same category of phenomena, and perhaps it throws further light on the appearances already described in the foam-drops. In my experiments I often used oil evenly mixed with a lamp-black purified by extraction with alcohol, or by heating to the glowing point for some time. When drops of such an oil were brought into water, it could usually be very

plainly seen under the microscope that the particles of lamp-black at the superficial region of the oil-drop, down to a greater or less depth, arranged themselves after a short time in rows, all directed radially to the free surface of the drop. As a result the marginal zone presented a beautiful radiate appearance to a greater or less extent. As has been mentioned, this phenomenon appears in ordinary drops of olive oil, usually with great distinctness. I obtained it, however, still better and more distinctly when some particles of anhydrous calcium chloride were enclosed in the oil-drops. Crystals of nitre served in the same manner; on the other hand, the inclusion of drops of glycerine in the oil was not so good. With enclosures of the kind named a radiate striation could often be observed round the drops of solution of nitre or calcium chloride, which had become formed round the particles enclosed in the oil. The fact, therefore, that these radiate appearances are also strengthened by the diffusion processes, which are doubtless set up by the particles enclosed in the oil-drops, appears to support the view expressed above as to the cause of the striation in the drops of oil-lather. If it were possible to introduce into the foam-drops particles of some substance that attract water strongly, I think that radiate appearances would appear much more marked. Unfortunately no means for effecting this have as yet been in my power, since the drops break up on raising the cover glass.

The very same radial striation can, moreover, be easily observed in drops of paraffin oil mixed with fine lamp-black, and it therefore does not depend directly on the chemical quality of the oil. I have frequently repeated of late the experiments with paraffin oil which were performed at an earlier date, and have again observed radiate appearances very well and very distinctly. Indeed I have obtained the impression that they develop quicker and better in paraffin oil than in olive oil. Since radiate appearances can also appear under some circumstances as optical effects round air-bubbles, I may lay special emphasis on the fact that the radial striation in the oil or froth-drops makes its first appearance gradually, and frequently

reaches so far towards the centre as to set aside any doubt as to the reality of what has been described.

The radiate arrangement of the particles of lamp-black was first observed when I studied the action of the electric current on the drops. Under the influence of the constant current the radial striation as a rule appeared very soon; nevertheless I should not like to assume off-hand a closer connection between this phenomenon and electrical processes.

4. *Fibrous Structures in Drops of Oil-Foam*

In the ordinary drops of oil-foam, which showed well the phenomena of streaming that are to be described later, it was often observed that an appearance of fibres was noticeable at the so-called centre of extension-currents, *i.e.* at the spot where a current from the interior reaches the surface and thence flows away superficially on all sides. The fibres followed the paths of the currents in their course, and hence resembled to some extent a bundle of sheaves passing out from the interior to the surface, where they spread out. This appearance was naturally not immutable, but became modified in details more or less, since the spot in question was the seat of continuous streaming movements.

If the very much thickened and exceedingly viscid olive oil, already mentioned on p. 20, was worked up with K_2CO_3 into froth-drops in the way known to us, there were formed, as has been already described, finely structured foams of great viscidity and transparency, but quite good in other respects. Since, however, they take the shape of irregularly lobed masses between the cover-slip and slide, and no longer assume a spherical form like the ordinary well-prepared froths, it is clear that they are no longer fluid, but rather deserve to be termed of a solid nature, or at all events they are in an intermediate condition of consistency to which the term solid is more appropriate. This also follows from the fact that these froth-drops do not show the slightest tendency to streaming movements, and when squeezed or pressed do not begin to flow. If they are drawn out by pressure

into threads or bridges, which finally break through in the middle, the broken halves of these threads certainly contract to some extent, but they do not gradually flow back perfectly, as they ought to do in a fluid froth.

Any one who has followed out the gradual thickening of the oil used will allow that in this process a sharp limit between a firm and a fluid condition can be drawn just as little as in the drying up of a solution of gum, but rather that both conditions pass gradually one into the other. Hence, for the foams just spoken of the consistence cannot be stated with absolute definiteness.

If such foams, the microscopic character of which is on the whole just the same as in the case of the more fluid foams, be subjected to pressure or tension, *e.g.* by rapidly drawing off the fluid under the cover glass, they naturally become stretched and drawn out in certain places or regions. Here and there portions of the foam are forced apart; between the portions coarser or finer threads are stretched like bridges. The very variable appearances that may chance to be formed in this way scarcely require more detailed description. It can be seen in them, however, that wherever the action of such tensions makes itself felt, fibrous structures appear (see Plate VI. Fig. 2, *a*, *b*). In the stretched threads, which are spread out like bridges, it is naturally at once seen that the direction of the fibres coincides with the direction of the pull to which they are subjected. A more thorough microscopic investigation leads, as was to be expected, to the result that the fibrous appearance solely depends upon the extension and stretching of the meshes in certain directions. Thus, for example, one can often discern plainly in the fibrous bridges stretched between two portions of froth, how the drawn out fibrous framework of the bridge passes into the usual irregular framework of the portions that are not stretched. Not infrequently also, in the larger portions of froth pressed out in this way, one remarks quite irregular and tangled fibrous structures, which can easily be explained by the fact that at these spots simultaneous or successive strains took effect in different directions.

The distinctness of this fibrous modification of the alveolar structure in the froths described is naturally only a consequence of the great viscidity of the substance of their framework, which causes the meshes to persist for a longer time in a state of tension. When the framework is a more fluid substance, as in the ordinary oil-lathers, a fibrous structure will also appear as the effect of tension, but it will change again rapidly into the ordinary condition. If, however, the action of tension remains persistently in certain spots in the same direction, and the ground substance is fairly fluid, fibrous structures will still possibly come under observation. A case of this kind is that formerly described in streaming froths, and we shall frequently come across similar cases in the description of protoplasmic structures. It appears to me a point of a certain degree of importance, that the froths described as having a nearly firm framework show no marginal alveolar layer. This fact appears to me quite intelligible, since the laws which cause the formation of the marginal alveolar layer only attain their full power under the condition that the framework is a perfectly fluid substance.

5. *The Durability of the Oil-Foams*

The oil-foams can be kept for a relatively long time. When put up in glycerine they show no noticeable change for four to six weeks. Then, however, the froths gradually deteriorate, slowly becoming coarser in structure through the bursting of the alveoli. At last, also, homogeneous portions of oil, no longer of a foam-like structure, appear in them. I have not followed out more closely the process of degeneration in the froths.

We have, as yet, only studied the drops of foam under the cover glass. If the cover glass be taken off, the drops as such break up, since they are somewhat specifically lighter than the surrounding fluid (H_2O or glycerine), and hence ascend to its surface. Here they spread out into a thin layer, which, sending out numerous irregular processes, breaks up into small drops. In breaking up, however, the

foam-like nature of the drops remains unchanged, even when the preparation is left uncovered for a long time.

6. *The Phenomena of Streaming Movement exhibited by the Oil-Foams*

If successfully manufactured drops of oil-foam, obtained from oil correctly prepared according to the above prescription, be carefully washed out with water under the cover-slip—an operation effected in the well-known manner, by drawing water through with filter paper, and best done from the two sides alternately, in order to remove any solid particles adhering to the surface of the drop—then striking processes of movement are at once set up in the drops. As long as they remained in the weak solution of K_2CO_3 they were perfectly quiescent. The movements of the drops of foam, when free from pressure and hence quite opaque, take place in such a manner, that without any striking change of shape, they creep somewhat rapidly backwards and forwards, under the cover glass. At the same time, the direction of movement changes fairly often, though it also happens that a drop may retain for a long time, or permanently, the direction of movement it has once taken up.

As has been said, the movements of progression were frequently very energetic; thus, I once observed a drop which in one minute traversed 0·45 mm.; usually, however, the forward movement was less rapid. When it was remarked above that these movements go on without particular changes of form, the statement is so far correct, that the changes are not very striking; still, they are not wanting. Frequently the drops become somewhat elongated in the direction of the forward movement; bulgings out of the edge also appear here and there, which, for the most part, quickly vanish again. A change of shape is therefore not wanting —only, on the whole, it is slight. In spite of the great opacity of the drops, it can be observed that lively streaming phenomena take place in them. Every bulging out of the edge is accompanied by a stream which starts from the interior, and spreads out on the surface; the creeping pro-

gressive movements are without doubt in connection with such streamings, although no definite conclusion on this point can be obtained in the opaque drops.

To obviate any possible objection that pressing the cover glass or anything of the sort may cause the movements of the drops, I remark especially, that experiments were also carried out with perfectly firmly fixed cover glasses, which rested on strips of glass fastened with paraffin, and that just the same results were then obtained.

If the water be slowly replaced under the cover glass by semi-dilute glycerine, a system of very energetic circulating currents is gradually set up in most drops, such as has briefly been mentioned earlier for certain oil-drops (see Fig. 5). Thus, from the upper edge of the drop, which is in

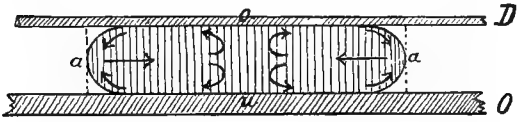

Fig. 5.

contact with the cover-slip (D), as well as from the lower edge, which lies on the slide (O), a superficial current, streaming out on every side, travels towards the equator (a), where the two streams unite and now pass inwards as a common stream towards the centre of the drop; from this spot the centripetal stream bends upwards and downwards into the two currents first mentioned. It may be observed, however, in drops displaying such a streaming motion, that frequently streams suddenly start here and there from the interior towards the free edge, and disturb the circulation described, though it usually soon regains the upper hand. Small drops, however, which rest on the floor of the slide, not infrequently show from the first another mode of streaming, viz. an axial stream passes out from their interior towards a point of the equator, spreads out here on every side, and rushes along in the superficial regions towards the hindmost point, where it gradually bends round again into the axial forward stream. The mode of streaming last

described is, as a rule, connected with a forward movement of the drop in the direction of the axial current. If such drops are watched for some time, a slowing down of the axial current, and the appearance of a new one, directed towards another point of the edge, can often be observed, upon which the drop naturally moves forward in the new direction.

If the larger drops, which show the above described circulatory streaming, are more or less pressed by the cover-slip, an object best effected by pushing a splinter of a moderately thick cover glass under the edge of the cover-slip, removing the paraffin feet, and then drawing off the glycerine as required, the phenomena of their streaming movement gradually take on the character that has just been described for the smaller ones. Although the currents rushing from above and below towards the equator usually continue for some time longer, there usually appear marginal centres, from which the currents spread out; a single such centre in the moderately large drops, or frequently several or many in the larger ones. The more or less energetic streamings from these centres finally suppress the original circulatory currents. The middle-sized drops, which develop one such centre of extension-currents, take on, as a rule, an elongate oval shape, for the most part with a slightly widened anterior end, in which the centre of the extension-currents is placed. At the same time, they move forward energetically in the direction of the current which passes along the axis to the edge where the streams spread out. I have observed such drops, which in one minute travelled about 0·12 mm. As I only took a few measurements, it is not to be supposed that the measurement here given has reference to a maximum of rapidity. We have to deal here not merely with a displacement forwards of the centre of extension, or with a stretching of the elongate oval drop, but rather with a movement of it forwards as a whole, like a simple amœba. This can easily be determined by simple observation, but may also be definitely proved by marking the position of the anterior and posterior end by means of a micrometer. I have already

briefly described the processes of streaming in a drop of this kind, which moves forward with a single extension centre, and the figures, which will be given in the sequel of corresponding streamings in oil-drops, furnish a sufficient explanation of it. One point, however, still requires brief mention. It is frequently seen that the hinder end of such a drop takes no further part in the streaming, and is also marked out from the rest of the drop by its somewhat different glassy appearance. Particles of dirt, or of lamp-black which has been mixed with the glycerine, collect at the hinder end, without in the main changing their position. From this it follows, that at the hinder end a condition of relative quiescence prevails, and that this region takes relatively little share in the streamings. Later on, when discussing the similar streaming movements, which can be called forth in ordinary oil-drops, we shall go more closely into the state of things observable at the hinder end of the drops.

Not infrequently a drop of the kind just described is observed to run towards one of the strips of cover glass employed as supports. Indeed, it would even seem as if any drops in the neighbourhood of such a strip of glass have a tendency to wander towards it. The drop then applies itself more or less closely to the strip of glass, by the spot at which the superficial streams spread out from a centre, and continues to stream quietly, with, as it seemed to me, even increased force. Such a drop, however, was never observed to come free again from the glass strip of its own accord.

It is even more curious when two drops run towards one another. Neighbouring drops seem inclined to do this, coming into contact with one another by the centres of their extension-currents. The streaming then becomes much stronger in both the drops; this increase of strength takes place, however, from reasons to be discussed later, even before they directly touch one another. While the surfaces of contact are visibly flattening out against one another, the streaming is much intensified in both drops. It is noteworthy how long a time passes before the drops flow together all of a sudden. Although I took no accurate

account of this interval, I think I am not in error in estimating it at some minutes. After complete union, an entirely new centre of extension-currents is usually formed, according to which the shape of the combined drop becomes directed.

If a drop in its forward movement comes towards one at rest, or approaches a relatively quiescent spot in the margin of a larger drop, the approach of its centre of stream lines calls forth a corresponding streaming in the second drop also. I shall go into the explanation of this phenomenon below.

Larger drops usually form several or numerous centres of extension-currents. In the accompanying Fig. 6 is

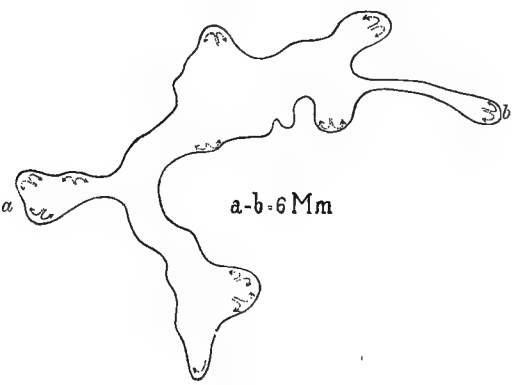

Fig. 6.

represented one of the finest examples of this kind which came under my notice. The strongly pressed drop in question had not less than eleven centres of streaming, some of which had developed into long pseudopodium-like processes. Such drops show, as was to be expected, no actual forward movement as a whole; on the other hand, the actively streaming centres of the extension-currents usually grow out like pseudopodia. Now since the streaming of one or other of the centres frequently becomes gradually slower and finally ceases, while, on the other hand, another is developed more strongly, or even entirely new centres arise, the result is that such drops show, as a rule, a striking amœboid change of form. In a relatively short time, after

half an hour or an hour, a drop of this kind has altered its shape very considerably. That drops of such large size when under strong pressure move but little forwards as a whole, may partly depend also on the fact that, having relatively large surfaces of contact with the cover glass and slide, they meet with a proportionately large resistance from friction. When a single one of their pseudopodial processes streams strongly forwards, as, for example, the one denoted by *b* on Fig. 6, it may happen that, as it continually grows farther out, without being followed by the principal mass of the drop, it finally breaks off from the latter, owing to the bridge connecting it with the main body becoming more and more attenuated, until it breaks. In this way the process mentioned, denoted by *b* in Fig. 6, separated off soon after the drawing was finished, and then moved on as an independent drop in the direction of its centre of extension-currents. Similar phenomena of division, if it be wished to so term this case, have often been observed by me in a similar manner.

It is frequently seen that a strongly streaming centre of extension-currents gradually suppresses a neighbouring weaker one. One of the lateral streams from the first centre gradually overcomes the opposing current of the latter, and thus finally brings by degrees the whole centre to extinction.

Continuance of the Streaming Movements

Successfully manufactured drops show the described phenomena of streaming for at least twenty-four hours, during which time the streams gradually become weaker and weaker, and finally cease. Frequently, however, I could follow them for from forty-eight hours to three days. Finally, in May 1889, after several attempts, an oil was successfully combined, which yielded drops of peculiarly good streaming powers. In one of the preparations the largest drop of froth, made from this oil on 28th May, still streamed distinctly, though feebly, on the 3rd of June, so that in six days it had not completely come to rest.

The fact that it was one of the largest drops which showed this long continued streaming is a confirmation of a phenomenon which was also plainly seen in studying the smaller drops. Very minute drops, consisting of only relatively few alveoli, as often occur (see p. 19) in the preparations, were never seen by me to pass into the condition of streaming. Larger drops of perhaps 0·05 to 0·1 mm. diameter usually showed very fair streaming movements, which did not, however, last long, becoming extinct after one or a few hours. Streamings of such long continuance as have been mentioned above can only be observed in relatively large drops. The continuance of the streaming stands therefore in direct relation to the size of the drop, which harmonises well with the explanation of the phenomena which we shall come to speak of below.

Influence of the Temperature, etc., on the Streamings

If streaming drops are warmed on a Max Schultze's hot stage up to 40° or 50° C.,[1] it is easy to observe that

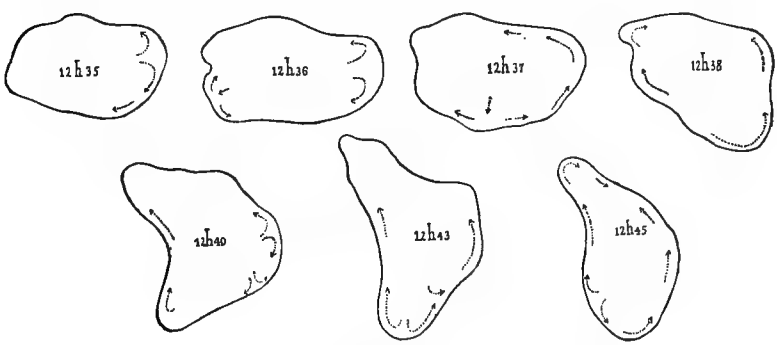

Fig. 7.

the streamings become much more quick and intense. The same is true of their forward movements. In the same way it may be observed how drops, which have already come

[1] The temperature is of course somewhat lower than is shown by the thermometer of the stage.

to rest, begin to stream anew with heating, or that such drops as were unwilling to stream well succeed in doing so with a higher temperature. When several centres of streaming are present, the drops show a rapid change of form, accompanied by the appearance of new centres and the disappearance of earlier ones. An astonishing case of this kind is figured by me in the accompanying Fig. 7; the period of time in which the amœboid change of form depicted took place was not more than about ten minutes.

I was unable to ascertain any influence exerted by gravity on the streaming movements. Preparations with streaming, and usually somewhat strongly compressed drops, were placed vertically by bending the microscope back, and observed for some time in this position. The streamings appeared, however, to be in no way distinctly influenced, and took place equally well both in the direction of gravity as well as against it, or in any other direction. Although these experiments are not free from objection, yet I wished to mention them briefly.

I also instituted some experiments to determine the possibility of any influence of light on the processes of movement. These experiments were performed with drops that were not pressed and which were in glycerine. The preparations were placed near the window on a piece of black paper, and in addition the half of the preparation turned away from the window was covered with black paper in such a way that at least one of the drops was just half covered by the paper. Over the preparation a glass vessel was then placed, of which the half turned away from the window was covered by a black cloth. The few experiments carried out up till now have shown no influence of light. The drops sometimes wander into the light, sometimes into the dark, most frequently the former. It was certainly striking that for the most part their movements were more or less in the direction of the light that reached them, *i.e.* either towards the window or away from it; but this result may also be only a matter of chance, on account of the number of experiments being too small to establish it.

Reaction of the Drops of Foam to Electricity

Since it seemed to me from the outset very important to investigate the influence of electric forces on the phenomena of streaming movement in the drops of foam, I have occupied

myself for a long time, and repeatedly, with this object. Unfortunately, however, I must confess that the results obtained are not very satisfactory. This may depend partly on the natural difficulties of the object, and partly also no doubt on the inexperience of the observer in this subject. Although therefore I must regret not being able to communicate more definite and satisfactory results, I yet think that I ought not to remain silent about them, even at the risk of what is brought forward here being subjected to a severe criticism from more competent authorities.

In my preliminary communication of 3rd May 1889 it was reported that the froth-drops, when between the poles of the constant current, showed streaming movements directed towards the negative side. Since, however, ordinary oil-drops also under these conditions permitted the observation of feeble streamings, soon dying away, the circumstance seemed in need of further explanation. Even at that time I had an idea that the centre of extension-currents directed towards the negative pole might possibly be only a consequence of the free alkalis formed at the negative pole by means of the electrolysis set up—an effect which would naturally produce a centre of extension-currents directed towards the negative pole as soon as they reached the surface of the drop of foam or oil (on this point see below, p. 62). Now since the glycerine, in which the drops of foam were investigated, contains potash soap in solution, a possibility of this kind ought certainly to be taken into consideration. Moreover, the water employed for diluting the glycerine is itself not free from traces of alkaline salts. The reasons which, in spite of this, caused me at that time not to ascribe the negative stream to this cause I will not go into more fully at present. My original experiments were of course performed on slides, which were provided in the usual way with electrodes of platinum foil, the electrodes being about 4 to 5 mm. apart. In order to avoid the above-mentioned source of error, in later experiments performed in the course of the summer of 1889, I made use of small, so-called non-polarisable brush electrodes, as invented by Dubois Reymond, which, wetted with 1 per cent solution of

common salt, are pushed inwards from both sides some way under the cover glass, and act perfectly well, besides being relatively easy to manipulate.

Since the negative stream did not make its appearance as a rule until after the poles had been closed for two to five minutes, this fact also pointed to its electrolytic origin. This supposition seems to me to be proved with tolerable certainty by further experiments, so that the idea of the drops being influenced by the electric current, as was stated at first, may be dismissed.

If ordinary drops of oil, placed in glycerine containing some NaCl, be exposed to a constant current between platinum electrodes on the slide, there appears almost immediately, provided the amount of NaCl contained in the glycerine be considerable, a powerful centre of extension-currents on the negative edge of the drop, with formation of soap. If the amount of NaCl in the glycerine is slight, it takes some time for a feeble system of extension-currents to be developed on the negative margin of the drop. Next there usually follows again a condition of rest lasting a short time, and then the action of the alkali soon begins to take effect very energetically at the negative margin of the drop. The drop falls into very violent streaming movements, becoming transformed into beautiful, perfectly opaque froth, so that I consider it possible to manufacture very good foam in this way.

In order to follow out this point still further, I brought drops of oil into the semi-dilute glycerine, which I usually employed, having coloured it slightly with some neutral litmus solution.[1] Then, when the constant current was passed through, employing a battery of five chromic acid elements with platinum electrodes, there immediately appeared a blue coloration at the negative electrode and a red at the positive. The blue colour gradually spread out in the form of a triangle, the base of which was at the negative electrode, while its apex was directed towards

[1] This solution I owe to Dr. K. Mays, who has already described the mode of preparing it by means of the dialytic method. See *Verh. des medic.-naturhist Vereins*, Heidelberg, N. F. Bd. iii. p. 295.

the oil-drop, placed in the middle between the electrodes. Shortly before the apex of the blue region reached the margin of the drop, the first trace of the system of extension-currents made itself noticeable at the edge of the drop. After this negatively directed extension-current had lasted a short period, a condition of rest followed for some time,—the same phenomenon which has already been mentioned above, and which was also as a rule observed under similar conditions in drops of foam investigated in glycerine. The cause of this transitory quiescent state was equally intelligible under the arrangement of the experiment that was chosen. For during the streaming of the drop the red acid fluid of the positive side spread itself out in a peculiar manner completely round the drop, so that the latter was now surrounded on the negative side as well by a narrow red zone, and the blue triangle had entirely altered its form. In consequence the cause of the negative streaming was removed, and it died down. After a short time the blue zone approached the drop again, and now called forth persistent negative streaming movements, which, after interruption of the electric current, became immediately weak, and soon died away. The phenomenon described can be reversed at will by reversal of the poles. The length of time involved up to the setting in of the persistent negative current was, with electrodes 3 mm. apart, about five minutes.

If, moreover, one takes into consideration the fact that with a slight acidulation of the glycerine by means of HCl, and the use of non-polarisable brush electrodes, a negative current could not be obtained, it is certainly a legitimate conclusion, if all these considerations are taken together, that the earlier described negative streaming of the drops of foam depended solely on the electrolytic action of alkali.

In further experiments on drops of foam, using platinum electrodes, it was soon proved, on the other hand, that, in opposition to an earlier idea, immediately after closing the current a moderately strong centre of extension-currents made its appearance at the positive margin of the drop; this fact was ascertained just as plainly and fre-

quently with non-polarisable brush electrodes also. The same phenomenon could be observed both in drops free from pressure and in those strongly compressed; and frequently not only streaming but even movement forwards towards the positive pole could be observed most plainly. I can by no means say that the phenomenon will always be produced with absolute certainty; often the experiments succeed only partially. But in quite a considerable number of cases the phenomenon was so strikingly evident that I consider its existence as proved. At the same time it was seen that this positive streaming died away immediately or in quite a short time after interruption of the electric current, and that by change of the poles it could be produced again and again and with great certainty, now on one side, now on the other.

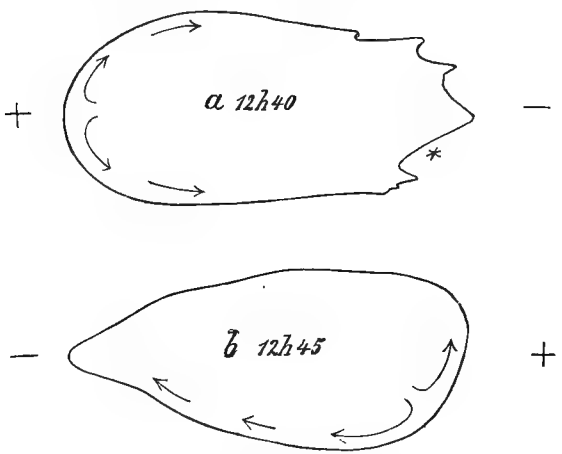

Fig. 8.

The foam-drops best suited to the experiments are such as show no streamings of their own, or only very feeble ones, since lively movements of their own act in all cases as a check to those produced by electricity. Nevertheless, even in vigorously streaming drops, the positive stream, with movement towards the positive pole, was often called forth successfully, and then with change of the poles a corresponding stream was caused very regularly, almost without

exception. Drops that were streaming and creeping well often showed most beautifully, when investigated with non-polarisable electrodes, how under the influence of the streaming caused by the electric current and the movement towards the positive side connected with it, their shape changed in a corresponding manner, similar to an Amœba, which creeps alternately in opposite directions. In the accompanying Fig. 8 two consecutive forms of the same drop are depicted: *a* shows the shape at 12.40 with the position of the poles as indicated; the peculiarly jagged hinder margin depends on the adherence of the moving drop to the slide. At 12.41 the poles were changed; the new positive centre of extension-currents made its appearance at *, and at 12.45 the shape of the drop, as it now gradually moved towards the positive side, was that of the figure *b*. The same alteration of form and streaming, however, had been already produced several times in this drop, so that the phenomenon figured could not be a mere coincidence.

At all times in drops that are streaming independently irregularities are met with, which depend principally on the fact that spontaneous streaming movements, which have arisen from other causes, disturb the regular course of events. On this account it is certainly to be recommended, in a repetition of the experiments, to employ stronger electric currents than were at my disposal.[1] This conviction impressed itself upon me more and more in the course of my experiments, and I certainly think that I should have obtained clearer and more convincing results if I had worked with stronger currents.

In the course of these experiments it occurred to me that it would be of interest to determine how ordinary oil-drops behave with regard to the electric current, when they are placed in glycerine in which some soap is dissolved. For it is quite clear that the glycerine round the drops of foam always contains some soap. As usual, finely divided lamp-black was mixed with the oil-drops, in order to render distinct any currents that might occur. In the investiga-

[1] Use was made partly of a battery of five moderately large chromic acid elements, partly of one of eight small Grove elements. The action of the two was not essentially different.

tions carried out with non-polarisable brush electrodes it was shown that under these conditions a positive streaming could be seen quite plainly, even if relatively feeble, in pure drops of oil also. Similar experiments performed at earlier dates with platinum electrodes had partly given the same results, but had more particularly shown that fairly large oil-drops in soapy glycerine obey distinctly the well-known law that small suspended particles wander towards the positive pole, which they do not do in pure glycerine.

Influence of Induction Shocks

Successfully prepared drops of foam placed in glycerine were frequently exposed to the action of single moderately strong induction shocks, from which, as a general result, the following was fairly uniformly the outcome. The shocks generally produce sudden and frequently most violent convulsive movements, which extend in good drops over the whole margin, but may appear more localised in those not so good. In such convulsions the edge of the drop takes on a more or less wrinkled appearance, and frequently shrinks back to a not inconsiderable amount. As a rule, it can be plainly observed that the shocks on closing the current have much less effect than those on breaking it. If the effect as a whole is weak, the shocks on closing frequently produce no convulsions at all, while the shocks on breaking still distinctly do so. When the experiments were continued for some time, the definite and invariable result was that the convulsions become feebler, and often cease altogether.

When vigorously streaming drops were exposed to induction shocks, it could frequently be observed that the streaming came to a stop for a moment, or even for as long as a minute, starting again after this interval, and often with increased strength. It is always streaming movements that go on fairly at right angles to the direction of the electric current, which are thus affected. Occasionally, though seldom, streaming movements which had slowed down were sup-

pressed entirely, by the formation of a new centre of streaming after a short time in their vicinity.

Several makings and breakings in quick succession always produce a fairly energetic bursting of froth vesicles in the interior of the drops—a phenomenon which naturally makes itself still more obvious with the employment of the intermittent current. By the action of the intermittent induction-current, using non-polarisable brush electrodes, it could be determined with certainty that, as a result, very violent extension-currents appear at the two spots of the edge of the drop, which face towards the poles. On interrupting the current they soon die down, and on closing it they quickly begin again. This phenomenon harmonises well with the positive streaming observed with the constant current, since in the intermittent induction-current the poles change quickly, and hence the action of the positive pole must show itself on each side.

7. *The probable Explanation of the Streaming Movements exhibited by the Drops of Foam*

In order to arrive at an explanation of the peculiar and long continuing phenomena of the streaming in the drops of foam, we must first consider their structure again. As has been remarked, they consist of a framework of very minute lamellæ of oil, the meshes of which are filled by a watery fluid. It follows from the method in which the froths are formed, that this fluid must be a watery solution of K_2CO_3 and potash soap, formed by the action of potash upon the free fatty acids of the oil, or it may be upon the glycerides themselves. If the froth-drops have been cleared up in glycerine, the alveoli then contain a solution of glycerine containing soap and K_2CO_3.

The streaming phenomena of the froth-drops take place on the whole in the fashion of the so-called superficial extension-currents (Quincke, 1888; emulsion movements, Berthold, 1886; contact movements, Lehmann, 1888), which arise regularly whenever the surface tension of a fluid (*a*), placed in air, or in a second fluid (*b*), is locally diminished

by bringing a spot in the surface of (*a*) into contact with a third fluid (*c*), with which (*a*) possesses a lower surface tension than with (*b*). This case arises, for example, if we allow a weak solution of soap to approach one side of a drop of oil, which is placed in water under a cover glass on a slide.

This experiment is best performed by the method of mixing lamp-black with the oil-drop and Indian ink with the soap solution, or by colouring the latter strongly with an aniline dye. It is then seen that at the edge of the drop, shortly before the soap solution touches it, an energetic system of radiating currents is set up, a system consisting of an axial stream from the interior of the oil-drop, which reaches the surface, and flows away on either side. In their course backwards—that is to say, towards the spot at the margin which lies diametrically opposite to the point of contact between the soap solution and the edge of the oil drop—the two down currents become continually slower. Finally, they meet at the hinder pole of the drop, to gradually turn and pass into the forward axial current. Closely studied, the relations of the currents are somewhat as seen in the accompanying Fig. 9, in which the rapidity of the local currents is roughly indicated by the length of the arrows. As the figure teaches us, at the hinder edge of the drop there is a region *x* of almost complete quiescence, which is roughly triangular in form, with the apex turned towards the so-called centre of extension. The extent of this quiescent posterior portion depends on the intensity of the streaming; the stronger are the two streams rushing backwards on each side, the farther they reach towards the hinder pole, and hence the more limited is the quiescent region *x*. Intense currents reach finally even to the hinder pole itself, and there meet. Then by the mutual interaction of the

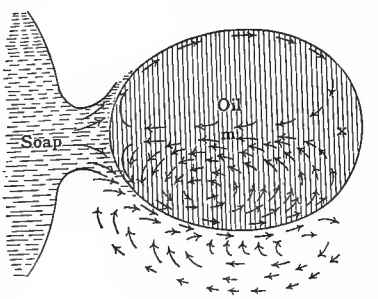

Fig. 9.

conflicting currents, there is formed only a narrow, axial, relatively quiescent streak, which is continued forwards through the entire axis of the drop, as far as the centre of the stream lines. Such a median streak (*m*, see the Fig.) is also, however, formed in the case when a more considerable quiescent region is found posteriorly, and is then an immediate continuation forwards of its forwardly-directed apex. The conditions described become much more distinct by addition of lamp-black to the oil. The further peculiar fact is then shown, that the particles of lamp-black, which were originally distributed evenly through the oil, gradually vanish completely from the posterior quiescent region, as a result of which the latter becomes transparent and clear; just in the same way the continuation of the portion *x*, which we have termed the median streak *m*, is also quite free from lamp-black. At times the lamp-black becomes more especially collected on the border of the resting portion *x*, so that two dark masses arise here.

Simultaneously, however, with these streaming processes, the drop also shows a forward movement, when the experiment succeeds well. The drop moves with more or less speed in the direction of the soap solution approaching it, and frequently creeps along for a considerable distance in this manner. Usually this forward movement commences at once on the soap solution touching the edge of the drop, and then the latter bulges out strongly and suddenly towards the soap simultaneously with the commencement of the superficial extension-current. During the continuance of the movement, the drop, as a rule, gradually assumes an oval shape, with a somewhat pointed (*i.e.* more strongly curved) anterior end and a broader posterior end.

At the same time that streamings are going on in the drop, there are naturally others, also, in the surrounding water, which can be observed in the plainest manner on addition of Indian ink to the soap solution. It is then seen that the soap solution flows backwards from the point of contact with the oil-drop along the surface of the latter, to the spot where the streaming in the oil-drop extends. At this point the current bends outwards, so that a back

current is gradually formed on each side in the surrounding water, just as in the oil-drop (see Fig. 9). The locality of this back current is marked by an aggregation of Indian ink. By degrees, the dark curved line of Indian ink reaches back to the advancing soap solution (see Fig. 10).

The physical explanation of the radiating currents described here, which Quincke and others have studied under rather different conditions, is, according to Quincke's interpretation (1888), somewhat as follows. Since the surface tension at the boundary between the olive oil and the soap solution is less than that at the boundary between the olive oil and the water, the condition of equilibrium in the tension on the surface of the oil-drop must be disturbed by contact with the soap solution on one side. Let us conceive the tension of the surface to be represented by a stretched elastic membrane. Then that part of the surface of the drop which is in contact with the water must shrink together to a certain extent, since its tension is greater than the tension in that portion of the surface which is covered by soap solution. Let us now imagine that under these conditions the limiting layer between the oil-drop and the surrounding fluid becomes torn and carried towards the hinder end of the drop, a violent movement which will naturally affect both the mass of oil and the surrounding water with equal force, and cause, to a certain depth in both, a similarly directed system of currents, leading away from the point of contact or centre of extension. But with this tearing away of the limiting zone between the oil and the surrounding fluid, a new surface of oil comes into contact with the surroundings. Since the thin layer of soap solution,

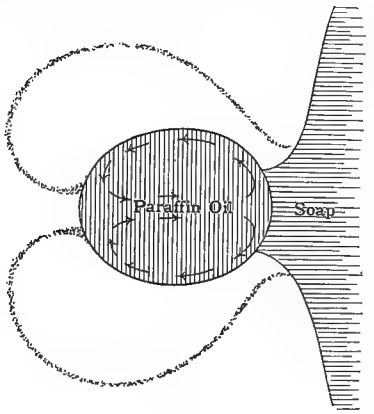

Fig. 10.

carried backwards by the so-called extension-current, immediately dissolves, or at least becomes very quickly diluted in the water surrounding the hinder region of the drop, the condition of equilibrium immediately becomes disturbed again, and in this manner a continuous extension-current results, which flows backwards on all sides from the point of contact.

In such a manner the continued duration of such currents under the conditions given is well explained. On the other hand, this mode of consideration does not seem to me to account completely for the axial current, and still less for the forward movement of the drop in the direction of the axial current. Mensbrugghe (1890-91) also has already expressed the strongest doubts as to whether the axial forward current as well as the forward movement can be effects of the surface tension, and looks upon them rather as a result of chemical attraction between the soap and the oil. It seems clear, in the first place, that the axial stream is a simple consequence of the superficial system of currents, which radiate out equally on both sides from the centre of extension, and are continued into the depth of the oil-drop. These two streams in their passage backwards must produce, as the result of friction, an eddy on each side within the oil mass, as is plainly shown in Fig. 9, on p. 62, and the combined effect of these two eddies appears as the axial current. Moreover, there is an additional factor which aids in producing the axial stream. When the oil-drop is in water, it will necessarily assume a spherical form in consequence of the surface tension being equal on all sides. Only under these conditions is there equality on all sides of the internally-directed capillary pressure. This pressure is to be regarded as the result of the surface tension, taking effect in the normal to the curvature of the surface, and inversely proportional to the radius of curvature. If then by contact of the edge of the drop with the soap solution the surface tension (*i.e.* the tension acting on the surface) is lowered, this lowering necessarily influences the shape of the drop. Since by diminution of the tension the internally-directed pressure is also lowered, the spot at the surface of the drop which is in con-

tact with the soap solution must become more strongly curved, *i.e.* arched forwards or bulged out, in order to maintain the equilibrium with the unaltered pressure of the surface in contact with water. Since as a matter of fact the internally-directed pressure is inversely proportional to the radius of the curvature of the surface, this difference of pressure will become equalised by stronger curvature of the surface of the drop. We find then, both in Quincke's experiments and in mine, that the drop actually assumes the form corresponding. Now by the phenomenon of extension the oil in the superficial region of the drop is caused to stream backwards, and at the same time the difference in tension at the surface of the drop continues to exist. The consequence of this would be, that, in order to equalise the constant diminution of the bulging out at the centre of extension which is produced by the down currents, the surface would continually bulge forwards, so that the shape of equilibrium is maintained. This bulging forwards demands, however, an afflux from within, which is supplied by the axial current, and which strengthens the latter to a certain extent.

Finally, there is the question whether the forward movement of the drop in the direction of the soap, *i.e.* in the direction of the axial stream, can also be explained as a simple result of the differences in the surface tensions of the oil-drop. Quincke affirms it to be the case, since he supposes that the capillary pressure, which is, as described, stronger behind, drives the drop forwards in the direction of the centre of the extension-currents, where the pressure is least. I cannot agree with this view, since I cannot see how this difference of pressure could produce more than the alteration in the form of the drop which has just been described. A continuous forward movement of the drop could ultimately only be explained in this manner on the assumption that the differences in surface tension became continually greater. Lehmann, on the other hand (1889, Bd. ii. p. 499), tries to refer the forward movement to the friction between the superficial currents of the drop and the surrounding fluid, as a result of which the *freely suspended* drop

is driven forwards. I think that the inadmissibility of this view is fairly clear. If the forces which are the cause of the streaming movements had their seat in the interior of the drop, then such friction at its surface would be quite possible. As a matter of fact, however, this is by no means the case, but the active forces take origin at the limiting surface between the drop and the surrounding water, and produce in the latter exactly the same streaming as they also impart to the surface of the drop. Under these circumstances, therefore, the possibility of friction between the streaming surface of the drop and the surrounding water appears excluded. Mensbrugghe believes, as has been remarked, that the forward movement, as well as the whole phenomenon in general, depends on chemical attraction, which produces, in opposition to the surface tension, forces of pressure directed outwards towards the approaching soap. Unfortunately I am as little able to agree with this opinion, since I convinced myself by numerous experiments that the whole complex of phenomena can also be called forth in the very same manner with a body so chemically unalterable as paraffin oil. Commercial paraffin oil was treated with concentrated sulphuric acid at 100° C., and well washed out, and then also showed just the same phenomena. Now since it cannot be well assumed that paraffin oil and dilute soap solution have any appreciable chemical action one upon another, it seems beyond doubt that the processes described must depend only upon purely physical causes.

The explanation of the forward movement of the oil-drop towards the soap solution may be sought, according to my idea, in something of the following kind. By the action of the extension-current some of the soap solution is being continually drawn away from its point of contact with the drop, and carried off to the hinder end of the drop. For this soap solution abstracted in front a compensation must be made by the neighbouring fluids, and this will of course be effected by the general pressure within the fluid, which works equally upon the soap solution, the water, and the oil. The easiest way of representing such a condition is

to imagine that the oil-drop is suspended in a fluid of the same specific gravity. Now since, as we have seen, the capillary pressure of the oil-drop necessitates its form remaining the same, the oil-drop itself will take part in the replacement of the soap solution that is flowing away backwards; since of course the pressure, which causes this replacement, works equally upon water, soap solution, and oil-drop. Hence the latter will wander into the soap solution or be to some extent attracted by it in the same measure as the soap solution streams backwards. For the rest, I think that it should also be possible to explain the phenomenon by a more accurate investigation of the force exerted by the lateral pressure of the currents which come into play. These forces must undergo alteration corresponding to the law that the lateral pressure in streaming fluids is diminished by an amount which is proportional to the square of the rapidity of the streaming.

In agreement with the explanation here developed of the progression forward of the drop, it may be noted that this movement is in general not set up until the phenomena of streaming reach a certain intensity. Slow or moderately strong currents may continue a long time without the edge of the drop moving forwards in the slightest. But when the streaming attains to a certain intensity, the forward movements become more and more distinct, since then the forces are sufficient to overcome the friction that is always present between the drop, the cover glass, and slide.

The superficial extension-currents described in the foregoing pages can be produced in just the same manner by allowing dilute solutions of KHO, NaHO, NH_4O, or K_2CO_3 and Na_2CO_3, to approach the drop of olive oil instead of soap solution. The efficiency of these materials depends in part on the alteration of the surface tension which they occasion directly, in part and principally upon the formation of soap, set up by their action upon the free fatty acids of the oil. The soap thus formed at the point of contact, and partly dissolved in the surrounding water, has naturally the same effect as soap solution added directly. Since, however, by the action of alkaline solutions on the oil-drops, granules of a scarcely soluble soap are also formed, which become partly collected on the surface of the drop, partly

scattered in the surrounding fluid, such experiments do not come off so clearly and distinctly as those performed with soap. The oil-drops rapidly become turbid by application of these solutions, in consequence of numerous minute drops of fluid appearing in them. These may partly arise in the way described earlier, but may partly be thrust in from the surrounding fluid by the violent streaming movements. Further, the fine granules and droplets which appear round these oil-drops may be in part very minute droplets of oil that have become split off. It was shown that during the process (oil-drops + K_2CO_3, 2·5 per cent) the fine drops of fluid, which gradually made the oil-drop turbid, collected in the posterior quiescent portion *x* (see above, p. 62, Fig. 9), as a result of which the latter soon becomes quite turbid. Without doubt the fine droplets were gradually carried to this region by the current, since the superficial streaming zone of the drop also became turbid and frothy to a small depth. Finally, the clear axial streak *m*, which in this drop was similarly well marked, also became bordered on each side by a narrow, frothy, turbid line, which no doubt took its origin from the posterior region *x*. This behaviour of the fine droplets of fluid in streaming olive oil-drops is the more peculiar since, as has already been described, the fine particles of lamp-black mixed with the drops behave quite differently, and do not penetrate into the region *x*. That this difference is not a peculiarity inherent in the particles of lamp-black themselves, follows from the fact that in streaming drops of paraffin oil they behave in just the same way as the droplets of fluid in the olive oil. Thus if a drop of paraffin oil impregnated with lamp-black is thrown into energetic streaming movements, lasting for some time, by means of soap solution or other fluids, after a relatively very short period all the particles of black collect posteriorly in the resting region *x*, which in consequence (see Fig. 11) appears as a black triangle that extends forwards more or less far into the similarly black axial streak. The remaining part of the drop usually becomes completely clear and almost quite free from black; here and there only does a particle of black emerge from the region *x* into the streaming again. I have always observed this phenomenon in the same manner in the numerous experiments performed with paraffin oil. In the streaming drops of foam also, that were prepared from olive oil containing lamp-black, the soot particles, curiously enough, showed a behaviour more as in paraffin oil. In just the same way they collected abundantly

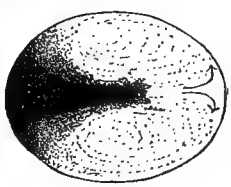

Fig. 11.

in the resting region x, and formed a black axial streak, entirely unlike their behaviour in a drop of pure olive oil. But so complete a collection of the soot at the hinder end, as is peculiar to the paraffin oil, did not occur.

I would merely point out here briefly that the currents in drops of olive and paraffin oil were also reproduced, as was to be expected, by numerous other fluids in a similar, though less energetic, manner. Since a special study of these processes from a physical standpoint was no part of my task, I only experimented on some few fluids for my own information. Absolute alcohol produces extension-currents in both the oils named, which mostly last only a short time, but can usually be called forth again by a repeated addition of alcohol. NaHO or NH_4O produce similar extension-currents in paraffin oil; in some experiments with paraffin oil and NH_4O performed in the year 1889, the currents lasted above a quarter of an hour. I have recently repeated these experiments with paraffin oil and ammonia, and, as a rule, obtained only feeble currents of short duration, but succeeded finally in reproducing the phenomenon with the duration and clearness earlier observed. Concentrated sulphuric acid produces a powerful extension-current in both oils, which can be observed very beautifully in olive oil in particular, and can, as it gradually becomes feebler, be strengthened again several times by fresh addition of sulphuric acid. No visible alteration of the olive oil by means of the sulphuric acid is observable at first; but if the drop be washed out with water its outer zone becomes turbid. Probably, therefore, minute droplets of sulphuric acid have been taken up which do not become distinct until after addition of water. In both oils the appearance of the extension-current caused by the sulphuric acid is preceded in the drop by an exactly opposite current of short duration. This has its centre in the margin of the drop farthest from the sulphuric acid, and the down current passes towards the point of contact with the acid. As has been said, this feeble current only lasts a very short time, and makes its appearance before the sulphuric acid touches the edge of the drop. I shall try to show below that this current has its cause in the rise of temperature which follows when the concentrated sulphuric acid mixes with the water.

It seemed to me of interest to try whether the experiments described could also be reversed in the following manner. The drop of oil is placed under the cover glass in the fluid with which it shows the smaller surface tension. Then the fluid with which it has the higher tension, namely water, is allowed to flow to it on one side. In this case, according to the

theory, a reversed current must be set up, which is directed towards the point of contact with the water. The centre of stream lines must lie in the edge of the drop opposite to the point of contact. Such a reversal of the experiments, however, was not very successful when the drop was placed in soap solution, which seemed to adhere rather firmly to the surface of the drop, so that the surface was surrounded by water before actual contact took place; but with alcohol, H_2SO_4 and NH_4O, good results were obtained. It was thereby shown, especially when alcohol was used, that the extension-current set up both with paraffin and olive oil, was very markedly stronger than when the drop was placed in water and approached by alcohol. For the most part the current produced is even violent, and also lasts for a fairly long time. If it becomes slower it can be strengthened again several times by repeated afflux of water. During the process minute globules of oil become split off in numbers from the surface of the drop, and carried by the current to the hinder end of the drop, *i.e.* to the end in contact with the water. Here they collect, and gradually spread out again from this point in the form of an arch on each side towards the end in contact with the alcohol. They thus form a figure exactly corresponding to that which has already been described above for the distribution of soot particles, or split off oil droplets (see above, Fig. 10, p. 64). When a drop of olive oil was used for the experiment, numerous minute droplets of the surrounding fluid penetrated into the oil, and quickly made it turbid.

An explanation for the much greater intensity of the extension-current under these conditions of the experiment can perhaps be found in the fact that here the drop has a low tension over a large portion of its surface, and a high tension over a small portion; while in the experiments first described the conditions are reversed. If, as we assume, a bursting of the surface layer of less tension takes place as a consequence of the difference of surface tension, then the whole phenomenon must of course be much more violent when a large surface is burst in this manner, than when only a small surface is dealt with.

The same reversal of the experiment can also be carried out with drops of paraffin oil which are put up in concentrated sulphuric acid or ammonia. Afflux of water then produces the reversed extension-current in the same manner. I could not, however, observe an especial strengthening of the current in these experiments. In the year 1889 some experiments made with ammonia succeeded very well, but recently they have come off badly.

Attention has been drawn above to the peculiar phenomenon that, on the oil-drops being approached by concentrated sulphuric acid, an extension-current of very short duration appears at first at the opposite pole. Since I have had an idea that this counter-current might be a consequence of the warmth produced on one side by the mixture of the sulphuric acid with water, I tried to clear up this point by some experiments. If a drop of olive oil placed under a thin cover glass in water be approached as close as possible, without, however, touching the cover glass directly, by a brass wire of 1·5 mm. thickness, heated red-hot, such a counter-current towards the heated edge of the drop can be produced very distinctly after some time. The experiment succeeded much better still with a small apparatus which Dr. C. Hilger had the great kindness to construct, consisting of a very thin platinum wire with its two halves bent parallel to one another, and heated to the glowing point by the electric current. In this way the application of warmth could be concentrated at will upon a given spot. On fixing the wire so that its recurved portion was about 1 to 2 mm. away from the drop, and then heating it to a moderate glow, the current described was beautifully shown, and lasted until the electric current was interrupted.

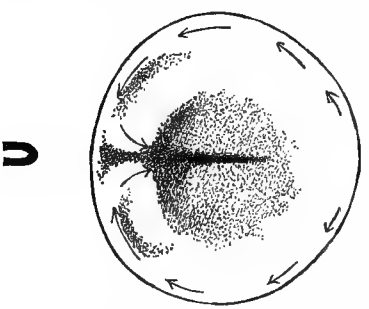

Fig. 12.

The particles of lamp-black mixed with the oil were all carried to the side that was warmed, which was the region of quiescence, and thence they extended in the form of an axial streak through the drop (see Fig. 12). It was observed very distinctly that the rapidity of the superficial current diminished steadily from the heated pole to the opposite one—that is to say, in a manner exactly the reverse of an ordinary extension-current, but in correspondence with what should occur in a reversed extension-current. If then

in this current we are really dealing with a phenomenon of extension, as appears to be the case, it would then of course follow that the surface tension between water and oil when warmed is greater than that between the two fluids when not warmed. With regard to the influence of temperature upon surface tension, it is known in general that the latter diminishes with increase of temperature; but these statements only have reference to the surface tension with air. That the process described should be produced secondarily by streamings in the surrounding water I consider very improbable.

The duration of the extension-currents described is, for the most part, relatively short, when the experiment has been arranged as prescribed, although the streamings which are produced by means of soap solution in drops of olive or paraffin oil not infrequently persist for hours, during which the drops carry out extensive migrations. Since, however, under these conditions, it is frequently rather a matter of uncertainty whether some other causes, such as pressure and the like, may not produce streamings in the drops, I arranged an experiment, which proved quite suitable, in order to obtain streamings of long duration, as follows. A fine capillary tube, partly filled with soap solution, and then sealed up at one end, is pushed towards a drop of paraffin mounted under a cover glass, until it touches the drop directly and makes an indentation in its margin. The extension-current then begins at once, and, as the accompanying Fig. 13 shows, it assumes a direction corresponding very well to the position of the end of the tube. In a preparation of this kind I followed the streaming from 1 P.M. to 7 P.M., and the next morning at nine o'clock a slight streaming could still be

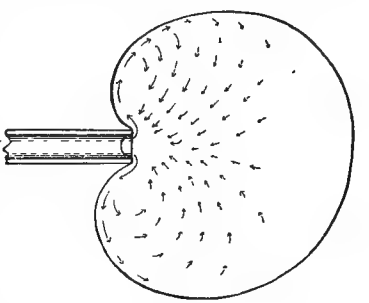

Fig. 13.

observed. In such preparations it may be occasionally observed also, that the oil-drop gets drawn deep into the capillary tube by a decrease of temperature, without the streaming suffering. In the thread of oil contained in the capillary tube a forward current then runs axially towards the soap, and a backward current runs superficially on all sides out of the tube.

Finally, I will notice here certain other experiments which were instituted with the intention of producing purely circulatory streamings by means of extension phenomena. If a thin strip of glass is fixed on a slide with Canada balsam, and then a cover glass on this in the same manner, a very shallow chamber, open on three sides, is obtained. Then if, by means of a capillary tube, a drop of paraffin oil is placed in this chamber at the edge of the strip of glass, it spreads out here to some extent between the slide, cover glass, and strip of glass. The remaining space under the cover glass is filled with water (see the accompanying Fig. 14). If now soap solution is cautiously allowed to flow along the edge of the glass strip to the drop of paraffin oil, a one-sided extension-current is set up in the latter, which, as the figure shows, causes a simple self-repeating circulation. The explanation of this phenomenon is naturally to be sought in the fact, that the contact between the soap and the oil takes place first at the point a, and since this point only presents a free edge of the oil-drop on one side, there can only be a one-sided current formed, flowing away backwards, which must result in a simple circulatory movement.

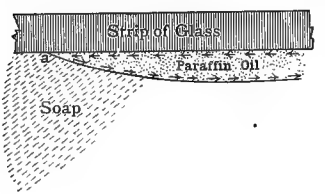

Fig. 14.

From the streaming processes hitherto described in the oil-drops, it can be plainly recognised that the currents in the drops of oil-froth spoken of earlier are of the same kind, *i.e.* extension-currents, which are produced by local diminution of the surface tension. As is evident from the mode of preparing the foams, the substance which causes

this diminution of tension can only be soap, which spreads itself out in solution upon the surface of the drop. According to the statements given above as to the origin and structure of the foams, the fluid which fills their alveoli is a watery (or after clearing them, a glycerine-containing) solution of soap. Both by diffusion and by bursting of superficial alveoli, the soap solution in the contents of the alveoli comes to the surface and produces extension-currents. I should conclude that bursting of alveoli does actually come into play from the fact that when the foams are brought into water, local eruptions of some strength frequently break out from the interior, and are accompanied by strong superficial extension-currents. That such eruptions depend upon occasional bursting of single larger vacuoles is beyond a doubt.

When we turn to details, an explanation ought first to be given for the peculiar circulatory currents, which the drops of foam, when free from pressure, usually show after being transferred to glycerine. But first of all, a word as to the influence of glycerine may not be out of place. As has been already described above, the drops move about also in water, whence it follows that glycerine does not produce the movements. On the other hand, I quite believe that it favours them to a certain degree, since, in particular, it hinders, or at least considerably diminishes, the adhesion between the drop and the glass. I am not inclined to ascribe to the addition of glycerine any other influence upon the movement.

The peculiar circulatory streaming which the drops of foam show, as a rule, after transference to glycerine may be explained, upon the basis of the results now obtained, in the following manner. If the cause of the phenomena of streaming is to be sought in the exudation of soap solution at the surface of the drop, it being a matter of indifference whether this takes place by diffusion or by bursting of alveoli, it follows that if this exudation at the surface takes place at first fairly evenly, there must be soap solution of greater concentration formed in the narrow interstices which remain between the surface of the drop and the cover glass

(D) or the slide (O) (see Fig. 15) than at the equator of the drop. Now, since soap solution of high concentration diminishes the surface tension more strongly than that which is more dilute, two centres of extension-currents will arise at the two poles *o* and *u*, since here the surface tension is lower—that is to say, the superficial layer of the drop will flow from here towards the equatorial zone *a*. At the latter region the streams meet, and thence turn horizontally inwards towards the centre of the drop, where they naturally

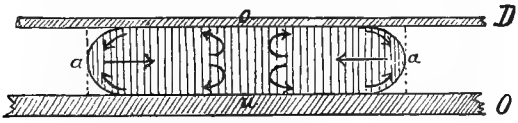

Fig. 15.

bend round into the two axial currents caused by the centres of extension *o* and *u*. Since the conditions remain constantly the same, as long as there is the same difference in the concentration of the soap solution on the surface of the drop, and since this is provided for by the constant exudation of new soap solution and its continual diffusion into the water, it is conceivable that the streaming phenomena here described may endure for a very long time.

On the same cause also depends essentially the phenomenon described above, namely, that a drop which is streaming forwards with a marginal centre of stream lines, gradually falls into more lively streaming, if it approaches one of the glass strips which support the cover glass. In this case the strip of glass lying in the way offers a hindrance to the diffusional distribution of the soap solution, which produces the centre of stream lines at the anterior end of the drop. Hence a relative concentration of the soap solution is brought about, accompanied by a strengthening both of the streaming and of the forward progress. The same thing, however, will also take place, if one drop approaches the surface of another, which then furnishes a similar hindrance to the diffusional distribution of the soap solution as does the strip of glass in the former case. But under these conditions the more concentrated soap solution which is formed

between the two drops will produce in the quiescent drop, when they have come close enough together, a centre of stream lines opposite to that of the approaching drop. I have often observed this phenomenon, and am convinced that it is to be explained in this manner, and not in any way by the friction of the streaming fluid on the quiescent drop; for the opposing centre of stream lines in the quiescent drop makes its appearance when there is a pretty considerable interval between the drops, and moreover, the strength of its streaming is too great even at quite an early period to be capable of interpretation simply as a phenomenon of friction.

The equal action of two drops upon one another is shown, of course, still more intensely when they advance upon one another with their marginal centres of stream lines foremost. For then the more highly concentrated soap solution, which is present at the centre of stream lines of each drop, comes together from the two sides, thus causing a still stronger concentration between the two drops. As has been already described, it can then be plainly observed how the streaming of two drops moving towards one another is gradually strengthened. All these circumstances bring about the result, that two drops which have come fairly close to one another, as a rule soon flow together, if their centres of stream lines do not lie exactly upon opposite sides.

It was not quite clear to me why the formation of marginal centres of stream lines, in connection with forward movement and amœboid change of shape, did not usually take place distinctly until the drops were somewhat strongly pressed. The streaming is seen to continue without pressing in the way already described, yet occasionally small drops occur which, without the help of any pressure, develop a centre of extension at their margin, and move about in a lively manner. After being pressed, one or more marginal centres of extension make their appearance, which gradually entirely overcome the first mentioned streamings, and then cause the phenomena already described. It is probable that in drops which are not pressed the causes which give rise to the two polar extension-currents have a much stronger effect than in those which are strongly pressed. In the latter the conditions causing a difference of surface tension at the poles and at the equator become less and less. When, therefore,

in a drop which is free from pressure (see Fig. 16, A), a marginal centre of stream lines arises by the bursting of some of the alveoli in the region of the equator a, it will gradually be suppressed by the strong polar centres of extension; the more so, as the soap solution which exudes into the relatively thick surrounding layer of fluid will spread abroad rapidly by diffusion. In the drop which is under pressure (see Fig. 16, B) the polar currents become more and more feeble, and since at the same time the surrounding layer of fluid is much thinner, the soap solution discharged by the bursting of some of the marginal alveoli will spread abroad much more slowly. This reasoning seems to me to make it to some extent intelligible how it is that centres of extension are gradually developed at the edge of compressed drops, leading to the phenomena already described.[1]

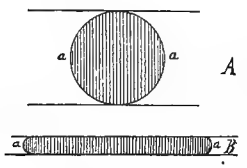

Fig. 16.

All phenomena which we observe in the streaming froth-drops, namely the posterior resting zone, the axial streak, and such like, have already come under our notice in streaming oil-drops, and are to be explained in the same way as in the latter.

The long continuance of the streaming in the drops of oil-lather is explained by the fact, that they contain a considerable store of soap solution in their alveoli, which is very gradually used up during the movement, and as gradually diffuses to the exterior. Since the froths after extinction of their movement show no alteration of appearance, the cessation of the streamings cannot be the result of an alteration in structure; it is rather the diminution of the soap

[1] It would be very important to investigate the movements of froth-drops suspended in the fluid quite free from pressure; the more so as friction against the slide and cover glass must essentially influence the movements of the strongly pressed drops. Since the drops are specifically lighter than water, such pressure could only be caused by mixing with them finely divided particles of a heavy substance, *e.g.* sulphate of baryta. I think that such experiments would not be hard to carry out and would yield important results. Unfortunately I lacked the time for putting the point to the test myself.

contained in the alveoli, and its absorption into the surrounding fluid, which must be the cause, and as soon as a complete equalisation has taken place the streaming must be definitely put an end to. Unfortunately I have not troubled to find out whether, as is probable, one can produce new streamings in drops which have streamed themselves out by replacing the soapy glycerine around them with fresh glycerine.[1] On the other hand, I tried to stir up afresh drops which had come to rest by bringing them into a 1 per cent solution of K_2CO_3. After the drops had remained some hours in this solution, and had again become quite opaque, they passed a second time into active streaming movements after being washed out and having semi-dilute glycerine added to them; the alveoli had been again filled with soap solution. On the other hand, a similar attempt to effect the renewal by means of a 1 per cent solution of Venetian soap did not succeed well, since the froth-drops were quite spoiled by it. I think, however, that one might obtain better results with a more dilute soap solution.

As we found before, a heightened temperature causes a considerable increase in the intensity of the streaming and in the forward movement. The cause of this phenomenon is to be sought in the fact that the viscid oil becomes more fluid at a higher temperature, of which fact it is easy to convince oneself with viscid oil. The greater fluidity of the oil will permit of not only an intenser current under the action of an equal force, but also no doubt of the easier bursting of the alveoli, which must favour the phenomena of movement.

Mensbrugghe is of opinion (1890-91) that the strengthening of the phenomena of movement by an increase of temperature depends on a greater intensity of the chemical reaction, which he assumes as the cause of the phenomena of streaming. For this very reason he considers the explanation given by me as erroneous. But although, as experience teaches, surface tension is in general diminished by raising the temperature, this fact is

[1] Since sending off the manuscript I have several times seen new streamings arise as the result of adding fresh glycerine to drops which had ceased to stream for a long time.

nevertheless without importance for the explanation attempted by me. My explanation does not deal with the absolute amount of the surface tension, but with its differences at different spots on the surface of the drop, and these differences may remain the same even when the absolute quantity of surface tension is diminished.

8. *Streaming Movements exhibited by Drops of Foam in Cells*

With regard to the streamings of protoplasm within plant cells, it seemed to me important to try what form the streamings might take in froth-drops which were contained in small closed spaces. This experiment was carried out as follows. Moderately thin sections of elder or sunflower pith were passed from absolute alcohol into chloroform, and then into an oil suitable for the formation of froth. The cell spaces of the pith became completely filled with oil in the process. In order to drive off the chloroform entirely, the oil was allowed to stand with the pith sections in a warm case for some time at a higher temperature. The sections soaked with oil were well washed out with water and brought into a 1 to 2 per cent solution of K_2CO_3, either under the cover glass or in a small test tube. After twenty-four to forty-eight hours the oil was milk-white, and of a fine foam-like structure throughout. The sections are again washed with water, and finally freed from any oil-foam adhering to them externally by being brushed with a paint-brush. They were then put up in semi-dilute glycerine. In successful preparations it is then observed that the oil-lather contained in each of the pith cells is in lively streaming, which persists for some hours. Since the glycerine diminishes the volume of the oil-lather, the cells are never completely full, which disturbs the approximation to the conditions of the plant cell (see Fig. 17). The phenomena

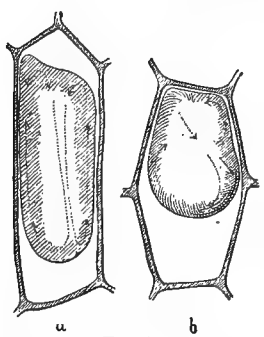

Fig. 17.

of streaming were essentially the same in all cells observed. The contents always showed but a single centre of extension-currents, situated, as a rule, at one end of the elongate cell, more rarely, however, displaced slightly towards a lateral wall, and very seldom occurring in the middle of one of the longitudinal sides. Corresponding to this arrangement, the axial current was, as a rule, directed longitudinally towards the centre of extension, more rarely obliquely, and finally very seldom transversely, to the long axis of the cell. In any case the streaming was always a double-sided one, with a flow on each side away from the centre of stream lines. Nothing was ever observed of a rotational streaming, such as occurs so commonly in vegetable cells. I lay especial stress upon this point, since I had hoped I might possibly have seen something of the sort take place under the conditions given. Isolated cases indeed occurred where the current of one side only passed a very short distance backwards, while that of the other side ran round a larger part of the circumference of the contents. Although such a state of things may be regarded as an approximation to rotation, nevertheless I found, as has been stated, no proper rotational streaming. It is not without interest to note that the streaming in a large number of the cells was directed in a similar sense; yet here and there cells were seen with the direction of the current reversed or different in some other way.

If therefore the experiments as yet performed cannot be exactly said to have yielded great results, yet their further continuation and modification might ultimately lead to conclusions upon certain phenomena of protoplasmic streaming in closed cells. It is easily understood that conclusions are possible only to a limited extent in the experiments described, since the conditions within the plant cell are without doubt quite different, as will be described with more detail in a later section.

9. *Remarks upon Frommann's Experiments on Drops of Oil-Foam*

Frommann published in 1890 some communications concerning experiments which he performed on drops of oil-lather prepared according to my directions, and upon which I feel myself bound to express an opinion. I must say beforehand, however, that I am only able to do this with some difficulty, since Frommann's statements are in great measure insufficiently clear to me. I therefore take two points in them, which at least go to the root of the author's case in his remarks directed against me. On p. 666 *et seq.*, Frommann tries to show that "in drops with non-fluid contents" a perfect alveolar structure is no longer present, and that both the walls of the alveoli and the outer limiting layer of such drops are interrupted in many places by gaps. Although Frommann unfortunately does not state more accurately what he understands by "drops with non-fluid contents," and how he manufactured them, I must suppose that he means by the expression foams which are manufactured from very much thickened and viscid oil, such as I also have described above. Since such foams spoil relatively quickly, and their framework of oil possesses at the same time a very tough consistency, I will by no means dispute that during their gradual degeneration gaps may appear in the walls of their alveoli, although I never myself observed anything of the kind in the viscid and immobile foams investigated by me (see before, pp. 20 and 44). As has been stated in the preceding sections, I have principally directed my attention hitherto to completely fluid foams, in which the formation of such gaps is simply a physical impossibility. Frommann seems inclined to dispute even this fundamental law of physics, since he states on p. 667: "Numerous gaps in the walls of the vacuoles, leading to a disappearance of the vacuolar structure, may also be obtained in drops of an emulsion which is prepared without K_2CO_3 merely by rubbing up a drop of linseed oil with water. The drops prove to be more or less regularly and thickly vacuolated, *the walls of*

the vacuoles interrupted only here and there by gaps; but if the drops are spread out flat on a slide, the walls of the vacuoles become torn in many places and are drawn out, so that at intervals in the place of vacuoles there arises only a framework of oil interrupted in many places by gaps, some smaller, some larger." I will not enter here into the obvious supposition as to what occasioned the origin of this framework of oil, when the drop of linseed oil, with droplets of water in its interior, was spread out on the slide. It is sufficient for me to have shown by the above-made quotation that Frommann actually puts forward the view, that between neighbouring drops of water suspended in fluid linseed oil gaps may exist in the fluid oil lamellæ separating them, without the partially continuous drops of water flowing together, and that similarly he entertains the opinion, that a *net-like* framework consisting of fluid oil can remain suspended in water. Since both these things are physically impossible, Frommann must have seen gaps where none were present. But this fact makes us also very doubtful as to his observations on the viscid froths, the more so as he gives us no information as to the optical means by which his investigations were carried on. We know, however, that an accurate investigation of the froths requires the strongest systems and oculars. Hence it appears to me that Frommann has not recognised the finest portions of the froths at all; at least he speaks of the fact that between the vacuoles of the froth-drops "a fine and faintly granulated substance occurs everywhere, which very probably consists of oil in a state of the finest emulsive division" (p. 665), or notices on p. 667 "a pale, finely granular, or indistinctly granulo-fibrillar material between the vacuoles." So far as I am acquainted with the froths, this material can only have been foam of the minutest structure, from which fact it is a legitimate conclusion, that the investigations were carried on with insufficient magnification.

I may take this occasion, however, to remark, that in very thinly spread out marginal portions of foam, which stick to the slide or the cover-slip, or even in very small drops of foam, where it is often possible to see larger foam

vesicles projecting beyond the edge, very sharp focussing is not infrequently necessary, to recognise the excessively thinned-out external wall of such foam vesicles.

When Frommann applies the experience which he obtained on drops with "non-fluid contents," with regard to the gaps alleged to occur in the wall of the vacuoles, in order to support his view of the net-like structure of protoplasm, he would seem to forget that the latter is to a great extent fluid.

Frommann also makes some communication upon the phenomena of streaming in drops of foam, from which, however, I can only conclude that he never observed good streaming movements. As far as I understand his communications, all that he remarks upon this subject does not refer at all to the drops of foam, but to the irregular phenomena of streaming and movement, which are shown by drops of a paste of oil and K_2CO_3, when transferred to water.

B. Investigations on Protoplasmic Structures

In the description of the drops of foam, I have intentionally avoided entering into what was the starting-point of my experiments, namely, the imitation and possible explanation of protoplasmic structures. In proceeding to this, I may first point out the really striking resemblance to protoplasm which is presented by successfully prepared drops of foam, when they have been cleared up in glycerine and are sufficiently compressed. Since the refractive index of their oily framework is greater, even after being cleared in glycerine, than that of the framework of living protoplasm, the impression made by the foam approximates more to that given by protoplasm which has been killed and fixed. I have often placed preparations of the foam before some of my colleagues, who were themselves not inexperienced in the investigation of protoplasmic structures, and were quite unbiassed in their opinions, and asked them what they believed the object to be which they were shown, and of the nature of which they were quite ignorant. One of them guessed it to be an egg cell, another thought it was Rhizopod protoplasm, or something of the sort. Although the pictorial method of representation does not fully succeed in reproducing the impression made by the natural object, yet the close resemblance may be convincingly proved by a comparison of the photographs of drops of foam, which supplement this work, with those of the protoplasm of various cells, among which I would especially draw attention to the photographs of ganglion cells from *Lumbricus* (XIII.) and of *Æthalium septicum* (XV., XVII.)

Although it was not part of my original intention to

institute studies of my own upon the structure of protoplasm, nevertheless I soon found myself forced to take this course. I therefore made use of the time and opportunity which the past two years have afforded me to collect further observations in this line, upon which I will first report briefly. It should be noted at the outset that they were all carried out with the aid of the best optical apparatus of the present day, *i.e.* with the apochromatic objectives, 2 mm. Ap. 1·30, and 1·40 of Zeiss, employed in combination with the strongest compensating oculars 12 and 18. The large amount of illumination given by the objective Ap. 1·40 permits perfectly well of the use of ocular 18.

The structural relations are in general so minute and delicate that the employment of the strongest powers seems altogether indispensable. When the daylight, as was so frequently the case, was not sufficient, a good petroleum lamp (Hinck's duplex burner) was used as a source of illumination, its light being concentrated on the mirror of the microscope by a globe filled with water slightly coloured with ammoniacal solution of copper oxide. The Abbe's condenser was used in some cases, but not in others, since I frequently remarked, as I thought, that finer structural relations came out more clearly without it. Special attention ought to be directed to regulating the strength of the illumination of the object in such investigations, since it is notorious that too intense an illumination obscures the details completely. It is therefore very advantageous to be provided with an iris diaphragm, and especially with the arrangement permitting a vertical displacement of the illuminating apparatus and of the ordinary diaphragm. I lay the more stress on these points here, since I am convinced that many results not in accordance with my own depend on insufficient attention being paid to these particulars.

1. *Investigations on Protozoa*

Since the protoplasmic structures in even the highest Protozoa can, in great part, be made out very well in the living condition, I prefer to describe these forms first.

Suctoria

The small Acinetan drawn from life on Plate III. Fig. 5 was first found by my pupil Herr Lauterborn in his fresh-water aquarium. Since I did not make a closer study with regard to its systematic position, I am unfortunately not in a position to determine it more accurately. For the most part, it recalls Claparède and Lachmann's *Acineta notonectæ*, which I referred to the genus *Solenophrya* in my work on Protozoa (*q. v.* p. 1930); our form possesses, however, in contrast to that of Claparède, a distinct, though very short stalk, and did not live on *Notonecta* but was fixed to particles of dirt. This small, very transparent Acinetan permits the structural relations of the protoplasmic body to be made out very clearly in the living condition. The protoplasm is completely reticular, and the width of the meshes of the reticulum is about the same through the whole body. The nodal points are not excessively prominent. The most external layer of meshes, that which lies under the somewhat pellicle-like external border of the surface, is everywhere directed radially to the surface, and thus forms a distinct *alveolar layer* (*alv*). Similarly, a radiate border of the same kind is also formed round the macro-nucleus (*mn*), which lies nearly in the centre of the body, as well as round the apically placed contractile vacuole (*cv*). The latter lies at some depth under the apex, opening by a relatively long efferent canal, which passes downwards from the apex into the protoplasm. The wall of this canal appears like a dark pellicle, and in any case is somewhat thicker and denser than the pellicle of the surface of the body. Small nodal points in the wall of the canal form the points of attachment for the adjacent meshes of protoplasm, which are disposed at right angles to the canal. In the protoplasm of the body, dark, strongly refractile granules are deposited, varying in size from such as are very minute to others which are coarser. These granules are more especially collected in certain spots, *e.g.* in the neighbourhood of the contractile vacuole. The largest of them show a somewhat broad, dark border. In the case of the smaller, it can always be

easily made out that they are lodged in the nodal points of the protoplasmic meshwork. The anterior edge of the house appears to pass directly into the pellicle of the anterior part of the body projecting from the shell.

The living macro-nucleus (*mn*) also shows the reticular structure very plainly, more so, in fact, than the protoplasm, since the framework of the nucleus is rather darker and its meshes are a little wider. The external limiting contour of the nucleus is somewhat dark and sharp, like the pellicle. The more external layer of nuclear meshes bordering on it is directed radially to the surface, and hence shows the relations of an alveolar layer. In the nodal points of the nuclear framework numerous dark strongly refracting granules can be made out, doubtless chromatin granules.

I did not investigate the tentacles more closely, but I was able on the same occasion to examine those of *Tokophrya* (*Podophrya*) *elongata*, Clp. and L. Their optical section gave the appearance represented on Plate XII. Fig. 5. The central circle is the optical section of the central canal, and the radially striated zone is a single layer of meshes of protoplasm which forms the wall of the tentacle.

Ciliata

On Ciliata I have recently made but few observations, although, as was known from earlier researches, they are especially suitable objects for the questions in view.

I observed the protoplasmic structure in the living condition very distinctly in a small, somewhat yellowish, undetermined marine species of *Vorticella*, which was of common occurrence on Rhizopod shells coming from Naples. If a spot at the margin, slightly behind the peristomial ridge of the living Vorticella, be studied in optical longitudinal section (Plate IV. Fig. 5), there is seen most externally the rather thick, double contoured, dark pellicle (*p*), and below this the clear alveolar layer (*alv*), the radial striation of which shows up but feebly, though it is quite recognisable. Upon this follows the internal reticular protoplasm with distinct

nodal points containing dark, strongly refractile granules in some abundance. Where the protoplasm borders on the large vacuole (*v*), which I believe to be the contractile vacuole, although I did not observe its pulsations, it again forms a very distinct radiate layer, which is separated from the vacuole by a dark margin. It is worthy of note that here the layer of meshes following immediately under the alveolar layer also shows a radiate arrangement. We thus have the same state of things before us as has already been described by Schewiakoff and myself for other Ciliata (see *Protozoa*, p. 1264, and Schewiakoff, 1889).

The alveolar framework of the internal protoplasm was in a state of incessant wave-like movement to and fro, on account of which the dark granules also appeared as if in a state of vibration.

I was able, moreover, to convince myself of the reticular nature of the living endoplasm in strongly compressed specimens of *Paramœcium caudatum* and *Stylonychia pustulata*, as well as to make out the alveolar layer in the living condition. The reticular structure of the protoplasm was very distinct in preparations of *Paramœcium bursaria*, which had been killed in a mixture of picro-sulphuric and osmic acid, and had hence become dark-brown in colour. Plate IV. Fig. 6 represents a small portion of the cortical protoplasm with the thickly-packed zoochlorellæ (*z*). Here the radiate arrangement of the meshes round the surface of the zoochlorellæ is especially noteworthy.

In *Paramœcium caudatum* and *putrinum*, in *Cyclidium*, and also in *Zoothamnium mucedo* Entz, which I was able to observe in Naples, I was struck by the fact that the entire endoplasm is crammed with an immense number of minute bodies. These bodies are present in such masses that between them only one or a few meshes of endoplasm remain (see Plate IV. Fig. 7 of *Stylonychia*, Fig. 8 *b* of *Paramœcium caudat.*) They can be easily isolated by compressing the Infusoria till they burst. I have not determined their size, but reckon it at about 1 μ in diameter. In *Zoothamnium* much larger ones also occurred. For the most part they are roughly spherical, more rarely oval or elongated. When

isolated they appear moderately refractile, with a rather broad dark border and somewhat clear interior. It would be difficult to say whether this border is a structural reality, or only an optical phenomenon such as is shown by every small globule. The bodies are remarkable for the intense readiness with which they are coloured by eosin or gentian violet, and with Delafield's hæmatoxylin also they can be tinged a light reddish colour. The protoplasmic framework is tinged very little by any of the staining fluids mentioned, most, however, by gentian violet dissolved in aniline water.

It appears that the bodies described are of widespread occurrence in the protoplasm of the Ciliata. Whether they are in part identical with the singly refracting corpuscles mentioned by Maupas appears to me doubtful. On the other hand, they can certainly be ranked with the cell granules described by Altmann.

In the above-mentioned *Zoothamnium* I devoted some attention to the strongly developed stalk muscle, since, as is well known, a fibrillar structure has often been ascribed to the muscle thread of this genus. In the living condition I could only observe a quite feeble longitudinal striation in the thread. After death, however, the fibrillar nature shows up very beautifully, and at the same time it is seen that the fibrillæ are connected in the transverse direction by numerous delicate lines, so that the structure is one composed of elongated meshes (Plate XII. Fig. 4).

I have already pointed out several times that the macronuclei of Ciliata possess a very finely meshed structure. On the occasion of the investigations on *Paramœcium caudatum* just described I was able to convince myself again of the fact. If *Paramœcia* be killed with iodine-alcohol (alcohol of 45 per cent tinged light yellowish brown with iodine), and then stained as intensely as possible with Delafield's hæmatoxylin, and broken up into little fragments in oil of cloves, particles of the protoplasm (Plate IV. Fig. 8, *a*) are found intermingled with particles of the macro-nucleus (Plate IV. Fig. 8, *b*). The latter can easily be recognised from the fact that their framework, very similar in

other respects to the protoplasm, is more finely meshed and coloured a stronger blue, and also that numerous intensely red granules are lodged in the nodal points. These granules, which correspond to the chromatin granules observed by me (1890) in numerous animal and vegetable nuclei by means of the same reaction, are much smaller than those above described in the protoplasm, and stain much more strongly.

Flagellata

Only a few have been occasionally studied by me. In living *Chilomonas paramœcium* (Plate V. Fig. 3, hinder end) I could observe with perfect distinctness the radially striated alveolar layer under the rather thick and dark pellicle (*p*), as well as the reticular structure of the adjacent internal protoplasm. Preparations which were made with osmic acid or iodine-alcohol, and stained in Delafield's hæmatoxylin, showed the alveolar layer and the reticular structure of the internal protoplasm in just the same manner, and in particular again permitted the determination of the fact that the meshes surrounding the nucleus are directed radially to its surface. The alveolar layer and reticular structure were also observed with just the same degree of perfection in preparations of *Cryptomonas*. In the same way too, in preparations of *Euglenæ* which I studied casually, a relatively thin but distinct alveolar layer, and a reticular endoplasm, frequently filled with larger vacuoles, could be well seen. The results mentioned harmonise well with the structural relations of these and other forms of Flagellata which have been observed recently (1889) and quite independently by Künstler.

As I have already remarked elsewhere (1890), there are to be found in the endoplasm of Flagellata, when they are killed with alcohol or iodine-alcohol and cautiously stained with Delafield's hæmatoxylin, larger or smaller quantities of small granules stained an intense red. They have been as yet especially observed in *Chilomonas*, *Cryptomonas*, *Euglena*, *Lepocinclis*, and *Trachelomonas*, and agree closely both in size and colouring with the chromatin

granules of the nucleus. I have already referred in an earlier publication to the distribution of corresponding granules in the protoplasm of the Bacteriacæ, Cyanophyceæ, diatoms, and certain thread algæ. To the objects enumerated before I can now add the beautiful diatom *Surirella* and the alga *Chantransia*.

Radiolaria

In this group only the intracapsular protoplasm of the large *Thalassicolla nucleata* was the object of investigation. Since the material in stock derived from Naples was quite unserviceable on account of its unsuitable preservation, I could only investigate some old, and therefore not very thin, sections of specimens which I had preserved myself in osmic acid. As a matter of fact, I have hardly seen another object which shows the meshed structure more plainly than the intracapsular protoplasm of this Radiolarian. Fig. 2, *a*, on Plate V., gives a picture of it which is in no way schematised, but as true to nature as possible. The great resemblance, in fact the really striking agreement, between this picture and the appearances presented by the artificial oil-lathers, is astonishing. The nodal points of the framework stand out very distinctly, and the radiate arrangement of the layer of meshes bordering on the vacuoles or so-called albumen spheres can everywhere be well seen. As is well known, the intracapsular protoplasm of *Thalassicolla* contains numerous large vacuoles or "albumen spheres" (R. Hertwig), some of which enclose concretions. In Fig. 2, *b*, Plate V., is drawn a portion of a large vacuole of this kind, which contains a concretion, while Fig. 2, *a*, represents the protoplasm of one of the bridges between the large vacuoles. In the sections investigated, the so-called albumen spheres showed no other contents besides the concretions, and hence gave the impression of ordinary large vacuoles. The width of the meshes of protoplasm varies to some extent. Since a direct measurement of such minute dimensions is somewhat difficult, I have counted the number of meshes round one of the vacuoles depicted on Fig. 2, *a*, and from the calculation of the circumference of the vacuole I have fixed the breadth of the

meshes at about 0·0010 mm. The figure shows, however, that meshes also occur of much smaller diameter.

Earlier observers have already found that the most superficial zone of the intracapsular protoplasm, bordering on the wall of the central capsule, is distinctly radially striated. In the sections investigated this striation was also very distinct, and at the same time it could be demonstrated with certainty that it only depended on the arrangement of the meshes in radiating series. This is plainly shown by Fig. 2, *b*, which represents the striated protoplasm bordering on the periphery of a large vacuole.

Heliozoa

As far back as 1885 I reported that the protoplasm of the large *Actinosphærium* exhibits the finely meshed structure well, after treatment with chrom-osmic-acetic acid, and that in the pseudopodia also the same structure is plainly recognisable. More recently I have found an opportunity of investigating this form, as well as *Actinophrys sol.* In both, with the optical apparatus that is now obtainable, I was able to convince myself easily as to the meshed structure of the endoplasm in the living condition, and also to observe the radiate layer of meshes distinctly present round the food vacuoles of *Actinophrys.* The protoplasm of the pseudopodia of *Actinophrys* appeared in part composed of distinct longitudinal fibres. Moreover, this fibrillar modification of the protoplasm could be followed through the coarsely vesicular ectoplasm into the finely meshed endoplasm, and at the same time it could be demonstrated that the fibrous tracts pass into the meshwork of the endoplasm.

In *Actinosphærium* also the meshed structure of the protoplasm of the pseudopodia could be made out even in the living condition (see Plate X. Fig. 3). To do so is naturally somewhat difficult on account of the continual streaming movements. Since, however, the meshed appearance shown by the protoplasm of the living pesudopodia is in no way altered by killing with picro-sulphuric-osmic acid, but only becomes sharper and plainer, this proves, as

it seems to me, that the pseudopodia killed in this manner show the normal structure. At the base of the pseudopodia the layer of protoplasm surrounding the axial thread is several meshes in thickness, and diminishes to a single layer of meshes towards the ends. For the rest, I have not yèt investigated more closely how the matter stands with the finely attenuated external ends of the pseudopodia. On killing with picro-sulphuric-osmic acid the protoplasm of the pseudopodia frequently contracts itself up into varicose swellings along the axial thread, as a result of which the latter becomes quite denuded in places (see Plate XII. Fig 1).

In the ectoplasm of the living Actinosphærium I could observe the meshed structure only very indistinctly, when the surface of the large vacuoles was focussed. It appeared most distinct in the obliquely sloping walls of the external marginal vacuoles.

After treatment, however, with the osmic mixture already mentioned, the meshed structure is everywhere easily recognisable in the ectoplasm. Whether or not the ultimate structure of the axial thread was similar, was a point not successfully determined, though it occasionally appeared to be so.

Marine Rhizopoda with Calcareous Shells and Reticulate Pseudopodia

While staying at the Zoological Station at Naples in the beginning of the year 1890, I had an opportunity of devoting some study to the above-named Rhizopoda. As objects of investigation use was made of representatives of the genera *Discorbina, Planorbulina, Polystomella, Cornuspira,* and various *Miliolidæ.* I directed my attention principally to the pseudopodia, but also investigated to some extent the protoplasm enclosed by the shell.

I will commence with the latter. If one of the Rhizopods mentioned be burst by means of pressure, or broken up with fine needles, it is easy to convince oneself that the

protoplasm which is set free has a very viscid consistency. It becomes drawn out between the broken pieces of shell into threads, which frequently stick to the glass or the needles; generally the protoplasm shows a very glutinous consistency. In *Discorbinæ* the protoplasm set free in this manner underwent in all cases immediately or very soon an essential alteration, since it neither showed movements nor had the threads that were stretched across any inclination to contract themselves together into spherical forms. The *Miliolidæ* behave differently in this respect. Here the viscid protoplasm becomes in like manner drawn out into thinner or thicker threads, in which phenomena of streaming and undulating movements are to be observed for a long time. The protoplasm also of *Miliolidæ* partially broken up can still send out pseudopodia for a long time. All this serves to prove that the protoplasm of these Rhizopods is much more tenacious of life than that of *Discorbina* and many others.

When *Miliolidæ* are broken up, larger or smaller portions of protoplasm are not infrequently separated off, which immediately assume a globular shape and form larger or smaller drops. These drops continue to show slight amœboid movements for some time; at their periphery wave-like up-and-down movements are exhibited, and thus there is a continual, though but slight, change of shape going on.

Such drops of protoplasm show with great distinctness a clear alveolar margin, which is limited externally by a somewhat strong dark border as by a pellicle. The thickness of this alveolar layer I have estimated by various measurements at about 0·0006 mm. On compressing the drops more strongly the radial striation of the marginal alveolar layer can be plainly recognised (Plate II. Fig. 5, *b*). The internal protoplasm following on this layer is very opaque on account of the numerous colourless granules and brown fat drops which it encloses; yet it can be recognised that it has usually a radially striated structure down to some depth (see Plate II. Fig. 5, *a*). The resemblance of such drops of protoplasm to the drops of oil-foam earlier described,

which frequently show a radial striation of this kind, is very striking, in addition to which the phenomena of movement described also possess a great similarity to those exhibited by uncompressed drops of foam in water. That the structure of the internal protoplasm of the drops is a meshwork can be recognised in spite of the deposits it contains, and at the same time it can be determined that the radial striation depends on the same arrangement of the meshes which has been already frequently described.

Drops of this kind remained for about three-quarters of an hour in the condition described. Then the alveolar layer suddenly disappeared over a certain extent of the periphery; the protoplasm lying beneath it burst out irregularly, and in all cases died immediately, since it retained irregular outlines, and hence must have become of a solid nature. The process of dying went on by fits and starts over the whole drop, until, having passed entirely into this condition, it appeared as an irregular lump, of much greater extent than the original drop. In the lumps the reticular structure was now shown with great distinctness.

In a squashed Miliolid the following very interesting phenomenon was displayed by the small, distinctly amœboid globules of protoplasm which were set free in great numbers. The chief portion of the squashed mass developed a rich network of pseudopodia again; as soon as a pseudopodium came in contact with a globule of protoplasm it immediately fused with it, so that in a comparatively short time the majority of the isolated globules were again united with the principal body. This observation is evidence, on the one hand, in favour of the fluid nature of the protoplasm, but on the other hand, is also not unimportant for arriving at a decision with regard to the pseudopodia, to which I shall return again below.

The protoplasm of the other Rhizopoda investigated also shows, even in the living condition, quite a distinct reticular structure, which becomes much clearer still after fixation with suitable reagents and staining with gentian violet. Very commonly portions of the network are to be met with having a fibrous structure, which is a consequence of the

arrangement of the meshes. That this is the case may also be concluded from the fact that all the bridge-like tracts of protoplasm stretching across between the broken fragments of shell have distinctly the appearance of a fibrous network, in which the direction of the fibres corresponds to the direction of the tension. Plate II. Fig. 6 shows a portion of a bridge of protoplasm from a Miliolid. The protoplasm of the bridge was in active movement, streaming to and fro, so that the network was continually being displaced. The formation of a fibrous network, running in the direction of the tension, could also be always distinctly observed when portions of the protoplasm stuck to the slide or the cover glass, forming pseudopodium-like edges as a result of the protoplasm striving to contract itself into a globular form, just as adhering oil-drops do in a similar case.

In the internal protoplasm of the *Discorbinæ* investigated occur great quantities of orange red or brown fat drops, which are viscid, since they become drawn out into the form of spindles under pressure. On addition of 70 per cent alcohol they partly flow together, but they dissolve easily in absolute alcohol. Further there also occur small colourless granules or droplets, which are frequently found in groups, as if turned out in batches. In absolute alcohol they were insoluble, in weak iodine solution they stained but slightly, in acid Delafield's hæmatoxylin not very intensely. After staining squashed Discorbinæ with eosin, there were to be found coloured granules of various sizes in addition to others such as those just described.

The study of the living *pseudopodia* of the above-named Rhizopods everywhere confirmed the result already gained with regard to the meshed structure of the protoplasm. Wherever larger masses of protoplasm make their appearance in the pseudopodial network, as in the thicker pseudopodia or in swellings of the finer ones; at the so-called web-like expansions, where a great number of threads of the pseudopodial network unite; and further in the rim-like expansion of protoplasm which emerges from the shell when pseudopodia are greatly developed, and which sends out the pseudopodia—in all these places the meshed struc-

ture is to be observed, although the continual rapid displacements of the network render the observation difficult. The thicker pseudopodial stems and the basal rim usually have the structure of a fibrous network similar to the above-described bridges of protoplasm. Naturally this fibrous structure always appears more or less confused, but the meshed structure is usually especially distinct in the webbed membranous expansions. These are, as a rule, excessively thin, since they are built up of a single layer of alveoli or meshes, and therefore they also show the structure in the clearest manner (Plate IV. Figs. 1 and 2). Fig. 1 represents such a membrane of a Miliolid in the living condition; Fig. 2, on the other hand, that of a *Discorbina* after fixation with vapour of osmic acid and very strong staining with Delafield's hæmatoxylin. It is beyond doubt that in both cases the observation yields exactly the same results. Since we are dealing with a protoplasmic layer of excessive thinness, the object is very faintly defined even in an intensely stained preparation, and demands very careful attention and study. In the figures the dark granules, staining intensely with hæmatoxylin, may also be noticed distinctly; they occur in great numbers, as is well known, in the pseudopodial network of these Rhizopods, and display the so-called granular movement. Finally in Fig. 2 the nodal points of the meshwork can also be made out very plainly.

The reticular structure shows up especially clearly in the lumps of protoplasm, which, like the granules, are carried to and fro on the fine pseudopodial threads. The distinctness of their meshed structure seems to depend principally on the fact that their protoplasm is in a condition of relative quiescence, so that the meshwork undergoes no displacements. It is remarkable that such lumps occasionally adhere to the pseudopodia in a state of complete rest, while the moving granules rush past them uninterruptedly.

The most difficult problem is presented by the fine thread-like pseudopodia, the thickness of which can scarcely be measured even when the highest magnifications are employed, and which may be so attenuated in the peripheral expansions of the pseudopodial network as even then only

to be visible as lines. No distinct meshwork structure is to be found in these pseudopodia, but there occur, on the other hand, at moderate, though, during life of course, always at variable, intervals, darker points, like faint nodules, which by their displacement along the pseudopodium are an index of the streaming movements. In their company are others which are certainly granules, as has been already mentioned; by the intense coloration which they assume in hæmatoxylin they are proved without doubt to be special structures. The question is whether the first-mentioned nodule-like points are also granules of smaller size, or whether they correspond in some way to the nodal points of the meshwork. I was not able to answer this question with certainty. The majority of the nodal points in the fine pseudopodia are very similar to the nodal points of the meshwork. It might be imagined that a fine pseudopodium of this kind is to be regarded as a row of elongated meshes of the protoplasmic framework, and the nodal points as the partitions of the consecutive meshes. This idea seems, however, scarcely permissible, since, in the preparations at least, the points in the fine pseudopodia follow one another at intervals, which correspond roughly to the usual breadth of the meshes (Plate III. Figs. 1 and 2, Plate IV. Fig. 2). Moreover, other very peculiar phenomena can be observed in the fine pseudopodia. Among them seems to me specially important and noteworthy the not infrequent impression of having observed that one or another of the granules, which rush along the pseudopodium, travels away from it for a short distance, and then fuses with it again. It strikes me that I have frequently observed granules, which were rushing along the threads, seated upon small and very pale projections of greater or less height, elevated some distance above the threads, an observation which would explain the fact that the granules can apparently leave the threads. Moreover, at times pale vesicular structures were observed, which rushed along the threads (Plate III. Fig. 1), and near them small aggregations of protoplasm, consisting of only a few meshes. Also by careful study of my best preparations (Plate IV. Fig. 2) I could to some extent make

out in the pseudopodial threads indications of very delicate expansions, which were occasionally distinctly composed of a meshwork.

All these observations awaken the suspicion that the ultimate nature of the darker pseudopodial threads, which are only just visible, is not yet exhaustively made out, but that they may yet possess extensions which are visible only with the greatest difficulty. It is conceivable that the fine pseudopodial threads really play the part of an axial thread, such as occurs in the Heliozoa and to some extent also in Radiolaria, and that on this axial thread a thin and scarcely visible coating of protoplasm is moving. Such an idea obtains some additional support from the fact that by rapidly killing the Rhizopods with the vapour of osmic acid,[1] or some other quickly acting reagent, the pseudopodia can only rarely be preserved quite intact. Usually they assume a varicose nature, since numerous and closely consecutive spindle-shaped aggregations of protoplasm form on them. These aggregations, which show the meshed structure distinctly, and sometimes a marginal alveolar layer as well, are connected with one another by a fine thread, which is for the most part quite structureless. I also frequently obtained preparations in which this thread could be followed right through the swelling. The similarity is very great between such appearances and those presented by the pseudopodia of Heliozoa after death, when the protoplasm on the axial threads runs together into varicosities. Although therefore I cannot bring forward any certain proof of a structure of this kind in the fine pseudopodia, nevertheless I regard the hypothesis which I have suggested as worthy of consideration. I only found out afterwards that M. Schultze (1863) had already been led to the same supposition by similar observations on the protoplasm of the *Miliolidæ*.

[1] The pseudopodial networks were best obtained in a state of fixation by the method of bringing the slide with the Rhizopod in a small drop of water very quickly into a glass vessel, the air in which was richly impregnated with osmic vapour by heating a 1 per cent solution on the water bath. As has been said, the pseudopodial network can be preserved in its full development in this manner, but rapid killing with fluid fixing agents under the cover glass also frequently gives good working results.

If the pseudopodia are killed more slowly, the connecting thread which has been described between the varicosities becomes destroyed or drawn in, and the pseudopodium breaks up into a series of little spheres of protoplasm, which often permit its original course to be plainly traced. A similar breaking up into isolated spherules would, moreover, only come about in a thread consisting of viscid fluid if it were liquefied rapidly. It would then necessarily break up into a great number of small droplets.

Gromia Dujardini. M. Schultze, 1854

I had numerous opportunities of observing this very large and interesting Rhizopod in Naples. Together with many other Rhizopods it was dredged on the coast of Capri, from considerable depths. It kept alive for so long a time that I was able to transport it to Heidelberg, and carry on further studies there.

Although the shell structure of this *Gromia* presents many peculiar relations, I will not enter more fully into the matter here, since I did not make a special study of it. Only, in order to comprehend the figures, it must be noted that the region of the mouth may take on a slightly different appearance, according as whether the protoplasm is issuing abundantly from the mouth-opening, or is retracted completely into the shell. In the former case the oral region projects like a nipple, as is represented on Plate I. Fig. 2. In the latter case, on the other hand, although the mouth opening usually appears very much narrowed, or even nearly closed, the nipple-like projection is quite shallow and flattened off (Plate I. Fig. 1). The fairly thick shell wall appears finely and radially striated in optical longitudinal section. At the anterior pole it gradually becomes stronger, until at the mouth opening itself it reaches a considerable thickness. Up to a certain distance from the opening the shell retains the radially striated appearance in section (Fig. 1, *b*). The thickest part of the oral region has, on the other hand, quite another structure. It appears finely granulated in the section (Fig. 1, *a*), and is marked off by a sharp,

and for the most part slightly sinuous, line from the contiguous striated portion. The oral nipple is formed from this granulated portion and from the neighbouring thicker striated portion of the shell, which, at the time when the protoplasm forces its way out and widens the oral opening, becomes raised up and pushed apart. I believe that the peculiar nature of the opening serves to supply an elastic closing apparatus, which of itself closes up the aperture again after the protoplasm has flowed back.

As a rule the opening has sticking to it a mass greater or less of various kinds of detritus, which at times may even considerably exceed the animal in circumference. This lump of dirt consists of particles of the most varied sorts, which the Protozoon has collected together by its pseudopodia, and has gathered up in front of the oral aperture. Since it can be not infrequently observed that pseudopodia apparently take their origin direct from the edge of this lump, I regard it as certain that the protoplasm extends between the particles of the mass, holds it together, and makes use of it as food. This circumstance is a great hindrance to the investigation, since the aperture, and especially the protoplasm issuing from it, is usually quite covered by the dirt. If the mass be removed cautiously the aperture usually closes at once, and even after keeping the animal for a long time new pseudopodia are only rarely sent out.

The protoplasm which fills the shell is completely opaque, since it is packed full of large brown bodies (Fig. 1, *c*) which long ago attracted the attention of M. Schultze on account of their great resistance to various reagents.

In specimens in which it was possible to watch the pseudopodia being sent out, the process observable was as follows. Through the more or less widely opened aperture a mass of protoplasm emerges which quite fills it, and which has a structure very distinctly composed of elongate meshes giving the appearance of longitudinal fibrils. This is by no means a bunch of pseudopodia projecting from the oral aperture, as M. Schultze described it, but a continuous mass, with a

structure as above said. I do not, however, wish to deny that occasionally a bunch of pseudopodia may fill the oral aperture, but the rule is what I have just mentioned. In the protoplasm passing through the oral aperture I have often convinced myself in the plainest manner of the meshed structure, and Fig. 1, Plate I. gives a picture of it as true to nature as possible. From measurements I reckon the longitudinal fibrillæ to be about 1 μ apart.

The protoplasm that is issuing forth first heaps itself up in front of the aperture into an irregular mass, which presents the appearance of a tuft composed of confused fibre-like meshes. On Plate I. Fig. 2 a small tuft of protoplasm is figured in longitudinal optical section, which plainly showed the fibro-reticular nature of the protoplasm. Larger tufts of this kind appear, as a rule, more confused, but permit it to be determined by careful investigation that their structure is a fibre-like meshwork.

From this tuft the pseudopodia now take their origin, being, as Schultze has already pointed out, usually *completely hyaline* and *free from granules*, and therefore showing no trace of streaming. In specimens with richly-developed pseudopodia they radiate out in every direction from the oral region, or apparently from the mass of dirt, becoming for the most part very long, and then also of great thickness, and sending out numerous lateral branches which usually come off at an acute angle. In very large pseudopodia the lateral branches, which may themselves branch again, sometimes also come off at a right angle, and are so numerous that the pseudopodium as a whole resembles a pine-tree. Since it was not my intention to follow out into details the general morphological relations of the pseudopodium, I will spend no more time over these matters, but merely mention that I never noticed anastomosis between neighbouring pseudopodia.

It is a striking fact that at times single pseudopodia appear sharply elbowed in certain places, a character which further increases the impression of stiffness which these pseudopodia as a rule give.

As has already been pointed out, the pseudopodia appear

completely structureless and glassy even with the strongest magnifications. The only thing to be observed distinctly in the stronger stems is a fairly thick dark border, appearing like a pellicle, and below that a clear margin. The two together remind one strongly of a marginal alveolar layer. With regard to the peculiar nature of the pseudopodia, their origin from the tuft of protoplasm, with its fibre-like meshed structure, deserves special consideration. I have frequently convinced myself definitely that the structureless protoplasmic mass of the pseudopodia arises quite directly from the fibrous meshed structure of the tuft. The protoplasmic structure of the latter can be seen to become rapidly paler, and to finally completely vanish (Plate II. Fig. 4). The fibrous structure can also be occasionally traced as far as the basal region of the pseudopodia. Hence it seems to me certain that the hyaline protoplasm takes its origin directly from that which is structured. The study of the living *Gromia*, moreover, furnishes still further proof for this immediate transition between the two kinds of protoplasm. It was occasionally observed that a hyaline pseudopodium was continued distally into a protoplasmic swelling of fibrous meshed structure, which exactly recalled the fibrous tuft at the mouth of the shell, even in the fact that from it a larger number of finer hyaline pseudopodia radiated out. This observation furnishes, on the one hand, a greatly-desired proof for the direct origin of the hyaline pseudopodia from the fibrous protoplasm, while, on the other hand, it proves just as definitely that the hyaline protoplasm can pass again into that which has a fibro-reticular structure, for in no other way can the production of the structure in question, in the course of a pseudopodium, be well explained.

There are still other observations which point to the transformation which I have just mentioned, of the hyaline protoplasm into that which has a meshed structure. In the fine pseudopodia one occasionally observes at the sides more or less irregular lumps of protoplasm, or even membrane-like expansions, which appear distinctly reticulated.

They recall similar appearances which have been described above in the reticular pseudopodia. But the clearest proof of the sudden conversion of hyaline into reticulated protoplasm is furnished by what takes place during the retraction of the pseudopodium. This process is always commenced by the pseudopodium suddenly becoming limp and flabby, and thrown into wavy curves. It may next, without further noticeable alteration, gradually diminish in size, and finally disappear entirely, or, not infrequently, it becomes bent back towards the fibrous tuft, or towards other pseudopodia, and then fuses with them. In other cases, on the contrary, the following interesting process can be observed. The pseudopodium, which has become wavy in outline, first acquires a granular appearance, as darker points make their appearance in its course. It then contracts into an irregular form, and, *pari passu*, with this process it becomes continually more distinctly reticular in structure, until it is seated finally on the hyaline larger pseudopodium, like one of the irregular reticulate protoplasmic masses already mentioned, from which it took its origin. On Plate I. Fig. 3, *a*, is depicted a pseudopodium of this kind in process of retraction, which has already become distinctly reticulate in two places, and Figs. 3, *b* and *c*, represent two stages of the retraction of the pseudopodial branch *, which became distinctly reticulated in the process, and fused with the reticulate process of the other side **, also probably a retracted lateral branch, to form the reticulated terminal appendage of Fig. 3, *c*.

If the fibrous tuft of the shell opening be pressed slightly with the cover-slip, its fibro-reticular protoplasm easily changes into protoplasm of a quite homogeneous appearance, which protrudes from the tuft in the form of lobose hyaline processes, but it undergoes a reticular modification after a short time, whereupon the tuft obtains its normal appearance again. Within the shell also, whenever the protoplasm in the region of the aperture was slightly retracted from the envelope, I frequently observed irregular, completely hyaline, amœboid protoplasmic projections of this kind. With these it was similarly possible to follow the

way in which they passed quite gradually into the fibro-reticular protoplasm of the internal body.

If from the observations described it has become very probable that the pseudopodia even when apparently quite hyaline possess a reticular structure, which has only become unrecognisable for certain reasons, this supposition receives further confirmation by treatment of the pseudopodia with reagents. Although it was not always possible to demonstrate a structure with certainty in killed and stained pseudopodia, nevertheless I obtained preparations which showed it most plainly. Fig. 3, Plate II. represents a thick pseudopodium, richly branched towards the end, which was rapidly killed with the chrom-osmium-acetic mixture and then stained with Delafield's hæmatoxylin. Throughout almost the whole pseudopodium it appears composed of longitudinally running fibres, and the structure can be distinctly recognised as made up of meshes, especially towards the base and the extremity of the pseudopodium. In the thin pseudopodial ramifications, which radiate out from the main stem, I was unable to find any structure; like the main stem, however, they everywhere show a dark, somewhat more strongly stained border.

Amœbæ

On various occasions I have studied several representatives of the genus *Amœba* and the nearly allied *Cochliopodium*. Since I directed my attention principally towards the structural relations of the protoplasm, and had no intention of studying the forms observed from all points of view, I will only report upon these questions in their proper connection, and will not enter into detailed descriptions.

In the smaller *Amœbæ* investigated, such as *A.* (*Dactylosphærium*) *radiosa*, Ehrb., in its various forms, and *A. limax*, the net-like meshwork of the granular internal protoplasm or endoplasm can frequently be plainly recognised even in the living condition. In living Amœbæ also I was often able to convince myself of the existence of a radiating layer round the contractile vacuole and of a similar layer round

the nucleus. A so-called ectoplasm of hyaline, apparently structureless consistency, is not, as I have already pointed out, by any means always present, but may be wanting in places or altogether; thus it was not to be found occasionally in the large *A. proteus*, nor as a rule in *A. limax*. Since, however, in *A. proteus* it was not infrequently beautifully distinct in places, and since also the pseudopodia of this Amœba usually showed, at least towards the end, the character of such hyaline protoplasm, it seems to me to follow beyond a doubt that the hyaline ectoplasm arises here, as in *Gromia Dujardini* just described, by modification from protoplasm with meshed structure, and can also be converted into the same again. The surface of the body, whether formed of hyaline ectoplasm or of protoplasm structurally composed of a distinct meshwork, always shows a relatively thick and dark limiting border, which has the appearance of a pellicle both in living and prepared specimens. This border can also be traced in the pseudopodia, becoming more delicate and pale towards their attenuated extremities. Under the pellicle-like margin there runs a clear narrow zone on which the reticular meshwork of the protoplasm borders directly, when a hyaline ectoplasm is not developed. The pellicle-like limiting border, together with the narrow clear zone, present exactly the appearance of a marginal alveolar layer. I have no doubt that they represent one everywhere, and do not depend in any way on optical relations. But as yet I have not been able to convince myself with certainty in living Amœbæ as to the radial striation of this marginal alveolar layer. On the other hand, I was frequently well able to do so, I may remark, in specimens preserved with picro-sulphuric-osmic acid mixture or even with iodine-alcohol. On Plate IV. Fig. 4 the radially striated marginal alveolar layer can be seen very plainly in an *A. actinophora* Auerbach, beneath the similarly striated envelope here present, upon which I shall have a few words to add later. That the radially striated envelope itself does not represent the real marginal layer of alveoli, follows from the fact that it is very clear and pale, and that the marginal alveolar layer proper

which is placed beneath it, shows at its limit towards the envelope the dark pellicle-like border, which in the absence of such an enveloping layer forms the actual surface of the Amœba. In the same preparation the protoplasm with its reticular meshwork can be seen most plainly below the marginal layer of alveoli; in *o* it is drawn as seen in surface view. Round the nucleus also the layer of radial meshes stands out very prominently. The great sharpness and darkness of the nodal points in the framework of the meshes of the endoplasm depends without doubt upon the deposition here of small strongly refracting granules.

Although the pseudopodia of Amœbæ usually consist of apparently structureless hyaline protoplasm, yet this is not always the case. The moderately long radiating pseudopodia of *A. radiosa* were seen by me even in life to be distinctly composed up to their extremities of a pale meshwork, partly fibrous to some extent. At the extremities the structure becomes paler and paler, but yet remains recognisable. At the same time the above described marginal layer of alveoli was to be traced round the whole of the pseudopodia, although its structure could not be made out. *A. radiosa*, however, frequently passed into conditions in which it exhibits large quantities of apparently hyaline protoplasm. Thus it not infrequently passes from the forms just described, with pseudopodia of moderate length and fair thickness radiating out on all sides, into a very flat and spread out condition with spiky, pointed pseudopodia, arising principally from the flat and expanded margin. This margin consists of nearly hyaline protoplasm, in which the meshwork structure can only be recognised with difficulty. Finally, I found in the same water from which the *A. radiosa* came, a considerable number of a small Amœba of a very peculiar form and mode of locomotion. As a rule it had somewhat the form of an open fan, moving with the convex edge of the fan directed forwards, and formed by a fairly broad hyaline margin, upon which followed protoplasm which showed a beautiful reticular structure, making up the pointed end of the fan, and containing the nucleus and the contractile vacuole. I

have frequently observed this Amœba, and for a long time regarded it as a peculiar species, until I noticed one day that a specimen, by throwing out a number of radiating pseudopodia, passed into the typical form of *A. radiosa*. Hence, I now have no doubt that it is only one of the forms under which the very protean *A. radiosa* may appear.

In one Amœba, which had an elongated form during movement, several finger-shaped pseudopodia of moderate length are formed, as a rule, at the anterior end, and, *pari passu*, with the movement of the Amœba forward in a straight line in the direction of its long axis, these pseudopodia travel backwards and are gradually retracted. Now as long as the pseudopodia are at the anterior end, they appear, as a rule, homogeneous and structureless, but after they have travelled backwards they become distinctly reticular throughout, even up to the outermost margin. Hence the same phenomenon would seem to be repeated here that we observed in the retraction of the pseudopodia of *Gromia Dujardini*. The pseudopodia of this Amœba showed in the preserved condition (picro-sulphuric-osmic mixture) a very pretty reticular structure usually up to the extreme tips, and the marginal layer of alveoli could at the same time be seen with great distinctness (Plate II. Figs. 7 and 8).

In the year 1878 I first drew attention to the fact that *A. Blattæ*, not uncommon in the end gut[1] of *Blatta orientalis*, offers one of the best examples of fibrous protoplasm. In this organism investigation in the living condition shows the protoplasm to be very distinctly fibrous, and the fibre-like appearances follow the direction of the movements. For this point I will refer my readers to the description formerly given by me. In recent times I have had the opportunity of again observing this interesting Amœba, but unfortunately was unable to study it in detail. Still, I am able to complete my former description in one point, namely, that the apparent fibrillæ are here also not disconnected, but united into a network. If the Amœba be followed in its movements, it is easy to convince oneself that the fibrillar appearance is only a consequence of the tensions caused by

[1] Proctodæum.

the streaming. This can be seen most beautifully at the hinder end of an Amœba of this kind when it is creeping after the manner of an *A. limax*. Corresponding to the axial forward stream towards the anterior end, an axial tract of fibrillæ traverses the Amœba, radiating out posteriorly into a tuft as a consequence of the protoplasm of the hinder end being drawn in from all sides into this forward current.

That radially disposed protoplasm may, moreover, occur occasionally in other Amœbæ is shown by the following casual observation. In one of my preparations of *A. actinophora*, I found an elongated specimen, one end of which was modified into a clear rim-like expansion. Although the characteristic envelope of *A. actinophora* could not be demonstrated with certainty in this specimen, nevertheless I consider it probable that it belonged to the species in question. The broad margin (Plate IV. Fig. 3), which without doubt represented the end of the Amœba occupied in forward movement, was radially striated in the most beautiful manner in its entire depth. Although the structure of the margin was relatively pale, it could nevertheless be most plainly made out that it was the result of a radial arrangement of the alveoli. The protoplasm bordering on the margin towards the interior appeared very sharply reticulated with very dark nodal points, resulting from the deposition of fine granules. I think the assumption, that this beautifully radially striated margin was represented in life by an apparently hyaline border, is all the more permissible from the fact that Gruber (1882) depicted on his Plate XXX. Fig. 17, an *Amœba actinophora* with a similar border, in which a radial striation is faintly indicated.

Since Greeff has recently again doubted (1891) the emptying to the exterior of the contractile vacuole of Amœbæ, I may notice that these studies gave me the opportunity of observing very clearly, in several of the Amœbæ investigated, how the vacuole does not disappear until it is in direct contact with the surface, and that during the process it collapses from within towards the exterior. Hence I have no doubt that it is emptied to the exterior.

As is well known, the endoplasm of Amœbæ contains, for the most part, numerous granular contents of very various sizes. Whenever I was successful in making out clearly the position of these granules in the meshwork of the protoplasm, I always found them deposited in the network itself, never, on the contrary, in the clear contents of the meshes. The granules constantly show an undulating, almost a dancing movement, frequently reminding one in the latter case of molecular movements. This proves in any case that the internal protoplasm is relatively very fluid. At all events the framework is in a state of continual undulating movement.

Æthalium septicum (*Fuligo varians*)[1]

It was only after the manuscript of the present work was sent off that I found an opportunity of investigating the protoplasm of *Æthalium*, an object of so great and so long a recognised importance for the study of living substance. I must regret that I had not already paid before a closer attention to this organism, for, as regards the protoplasm question, it is one of the most instructive with which I am acquainted. Hence, it seems justifiable to make in this place a brief supplementary report as to some observations on the protoplasm of this Myxomycete.

Unfortunately, I have only as yet made a cursory study of the living protoplasm, but I shall try, as soon as possible, to make up for this deficiency. The protoplasm, fixed in the way described above, with the picro-sulphuric-osmic mixture, shows the alveolar structure more distinctly and beautifully than do the majority of the objects described before. This is partly connected with the fact that it is very easy to obtain plasmodia of *Æthalium* in so thin a layer that they vie with the thinnest sections. Now, since the processes of manipulation that are performed in embedding and cutting do not in any way render the structures more but rather less distinct (as I convinced myself in *Æthalium*, of which I also made sections), it is obvious

[1] These observations on the protoplasm of *Æthalium* and *Pelomyxa* were made by the author after the text of this work had been finished and sent to the press. In the original German edition they were placed in an Appendix at the end of the work, but in the present edition these, as well as other additions of the Appendix, have been inserted in the text in their proper places.

that layers of protoplasm of such thinness, as are formed here and there by the plasmodia of Myxomycetes, are objects especially suited for investigation. In order to obtain a good preparation, it is best to proceed as follows. Some slides are thoroughly wetted and placed upon the tan, which should be in a large damp chamber in the dark. It is then necessary to wait until some plasmodia creep on to the slide and have spread themselves out in a very fine layer. Of course, only the thinnest and most branched networks should be chosen for preparations. Or, on the other hand, plasmodia which are creeping about on the walls of the vessel, or elsewhere, can be simply scraped up with a scalpel, and the lumps of protoplasm kept on damp slides in a damp chamber in the dark. I found almost always that after about twenty-four hours, such lumps of protoplasm had spread themselves out again into very beautiful networks. It is now only necessary to keep the slide in question for some time in a vertical position within a damp chamber, so that the superfluous water may run off as far as possible, and then to transfer it to picro-sulphuric-osmic acid or some other fixing fluid. When the water has been as far as possible removed from the slide in the manner stated, without, however, the plasmodium being dried up, the latter, after fixation, adheres quite firmly to the glass. If too much water has been left behind, the plasmodial network easily separates off, which renders further preparation very difficult. Plasmodia that are adhering well can, after fixation, be played upon by a strong spray from a flask without becoming loosened. Of course the preparations can be stained as desired, but all the observations described in the following were made upon unstained plasmodia, which after being washed were put up in water.

In such preparations the alveolar structure of the protoplasm, as I have often described it above, can be seen most beautifully. In the plasmodial network places may be found of such thinness that they are only formed of a single layer of alveoli. Places of this kind are of course especially suited for study, and show all the phenomena which we have observed above in similar thin layers of oil-lather. Without entering into a detailed description, I refer to the Photographs XV. and XVI., XVII., and XVIII. and XIX. Photograph XV. shows a small lobed projection at the edge of a plasmodium, which in the preparation is torn across close to its origin, probably because the principal mass, from which it arose, contracted strongly. In as accurate a focus as possible, such as was chosen in Photograph XV., the frothy framework is distinctly noticeable in the whole of the internal and thicker portion of the lobe. The

nodal points of the framework stand out very prominently in many places. Towards the edge the framework becomes paler and more finely meshed. Finally, a broad, apparently quite homogeneous border forms the exceedingly attenuated edge of the lobe, of which the outer, very delicate limiting contour is only just visible. But by careful examination distinct traces of foam-like structure can still be made out in the photograph in this apparently hyaline margin. In many cases, however, I saw this structure still better than in the present photograph, for which reason I do not doubt that an apparent absence of structure in the margin only depends on the faintness and fineness of the framework, which is caused by the excessive thinness of the margin. We shall soon see that a further fact of importance is in favour of this assumption.

Photograph XV. should now be compared with Photograph I., in order to convince oneself of the striking resemblance of the two in all the points mentioned.

We may now consider Photograph XVI., which represents *the same* lobe with a slightly higher and less sharp focus, and hence shows the false reticular image, which will be discussed more accurately and its origin examined into on p. 210 *et seq.* The distinctness of this false network here is quite striking; it is also obvious that it must be considerably more prominent, since it appears much darker than the true network does when sharply focussed. Moreover, Photograph XVI. has come out much better than XV. Now, with Photograph XVI. compare Photograph II. of the above-mentioned oil-foam in a corresponding focus, from which it is plain that in this respect also there is complete agreement between them. Hence, from the observations that have been adduced, no other conclusion can be drawn than that identical relations are here before us—that is to say, the structure of the protoplasm of *Æthalium*, like that of the oil-foams, must consist of a more strongly refractile alveolar framework, which encloses in its cavities less strongly refracting contents.

Photograph XVI. permits the corresponding faint structure to be made out much more plainly also in the margin than is the case on Photograph XV. with a sharper focus. This is easily intelligible, since the false reticular image is darker than the true one, and hence stands out more prominently. This circumstance, which in like manner holds good for the oil-lather on Photograph II., may be taken as a sufficiently sure proof that the margin has just the same structure as the interior of the lobe.

As a further confirmation of what has been stated, I have added two photographs, XVIII. and XIX., at correspondingly

different foci, which exhibit a larger portion of a very thin layer of protoplasm from the interior of a plasmodial network. The photographs were taken with a lower magnification (Obj. 4 mm.), but this is quite sufficient to make out the characteristic structure.

Finally, I refer to the very successful Photograph XVII., which in like manner shows an extremely thin portion from the interior of a plasmodium (Obj. 4 mm.). Where the protoplasm is thicker in this picture, the structure becomes, of course, more indistinct; moreover, the protoplasm is much more opaque in these places, principally on account of the large quantity of darker enclosures, varying from the finest to the much more coarse. In the photograph these enclosures can also be noticed very plainly in the thin places, and are plainly to be distinguished from the nodal points of the honeycombed framework. In some places the layer of protoplasm is interrupted by rounded gaps, so common in the network of the plasmodium. Towards the edge of such a gap the structure becomes fainter or even disappears entirely; here the edge thins out in a manner similar to the lobes of protoplasm described above. But even within the continuous thin layer of protoplasm, one sometimes comes across places where the structure is quite faint, till finally only indications of it are to be noticed. These are extremely thinned out portions in which gaps may come to be formed by dehiscence later on.

Photograph XVII. shows, however, yet another very interesting fact. When more accurately examined, one notices in the protoplasm quite a number of rounded, rather dark bodies. These are nothing more than the numerous cell-nuclei, which in such thin places can be seen distinctly without further preparation. With reference to the structure of these nuclei, I will only remark that, as a rule, they contain a central nucleolus-like structure, from which a nuclear framework, consisting of simple radiating trabeculæ, stretches across to the wall, so that in fact they possess a structure such as I have already frequently described for small nuclei. In some places it can be seen quite beautifully in the photograph that the meshes of the protoplasmic framework are directed radially to the surface of the nucleus, as has already been described above in the case of other objects.

After what has been remarked heretofore it scarcely needs to be pointed out especially that the radiate layer of alveoli is not wanting at the surface of the plasmodium. It usually shows up most clearly at the edges of the gaps which so frequently interrupt the plasmodium, granted, however, that the edges are not too thin, so as to prevent the structure from being quite visible

up to them. Unfortunately no such spot is present on Photograph XVII., but nevertheless the radiate layer of alveoli is quite recognisable as a clear border to some gaps.

The plasmodium further shows us with particular distinctness the frequent transition from the usual honeycombed into the fibrous structure. Wherever strands of protoplasm are stretched across like bridges between neighbouring branches—that is to say, in general wherever the protoplasm is subjected to a strain or tension, the structure appears fibrillar-alveolar, the direction of the fibres running constantly in the direction of the tension, and hence in bridges, for example, always parallel to their long axis. In such fibrillar bridges and strands the radiate alveolar layer can also be always plainly traced at the surface.

Bridges of this kind are often so attenuated in the middle that they consist of only a single series of alveoli, and at last, indeed, nothing more is to be seen of any structure, and they resemble the very fine pseudopodia described already in the Rhizopoda.

At the end of the plasmodial network which is occupied in creeping forwards, protoplasm quite hyaline in appearance and free from enclosures is usually to be observed during life. It can easily be established that here we are not dealing with a very thin and hence apparently structureless layer. This hyaline protoplasm at the anterior end is, on the contrary, for the most part very thick, and corresponds to the homogeneous border at the anterior end of *Amœbæ*. After fixation it proves, in like manner, to be distinctly and finely alveolar, and at times also finely radially striated; the layer of radiate alveoli can also be plainly recognised at its surface. I will, however, return again below to the question of the reality of its structure.

Fine plasmodia dried up on the slide in the air still show the honeycombed structure distinctly in thin places when examined in air; with a higher focus also the image of the false network can be made out beautifully. I set especial value upon this observation, as I have already pointed out before (1890) for the similar case of Bacteria. For since after drying up there can certainly be no question of coagulation or precipitations, the visibility of the structure in desiccated protoplasm may be taken as a definite indication that it must also be present in the living condition, and is not a product of the media of fixation.

I have made use of such dried plasmodia for deciding a further question, which is especially important. It is well known that there is as yet a lack of any sure proof as to the nature of the contents of the protoplasmic alveoli, although in my idea everything is in favour of its being a watery solution. Now if

well-dried plasmodia be brought for twelve to twenty-four hours into olive oil, and then the oil be washed off carefully with hot water, the investigation of such preparations in water teaches us that the alveoli of the protoplasm are filled, in many places at least, with oil. The preparations become still more instructive if, after the oil is washed off, they are placed for some time in 1 per cent osmic acid, which turns the oil brown. That the oil actually fills the alveoli of the protoplasmic framework in many places can be made out very plainly in thin portions, since the contents of the alveoli now show a considerably stronger power of refraction than the framework, whilst before the reverse was the case. With a rather higher focus the contents of the alveoli that are filled with oil now appear very clear and bright, while the framework becomes very dark, and hence much sharper and more distinct than in places not filled with oil. As the tube of the microscope is raised the stronger refraction of the contents of the alveoli can be definitely established, since during the process the contents of each one becomes a diminishing, glittering point, while the less refractile framework becomes darker. I possess a photograph of the alveolar framework filled with oil which shows this exceedingly well. The faint framework can also be recognised with sufficient distinctness in the neighbouring parts that are not filled with oil, and in this way it is still more definitely shown that here is really a case of the alveoli being filled with oil.

As has been remarked, I hold these results to be especially important, since they markedly support my view, that the alveolar contents are a watery solution. For if in dried or fixed protoplasm the contents can be replaced by oil, the conclusion is incontestable, and refutes more particularly the view of Schwarz, discussed below on p. 205, who explains the contents of the alveoli as being identical with the substance of the framework, only rather less refractile.

Pelomyxa palustris, Greeff

By the kind help of my respected friend and colleague Blochmann, I obtained during the past winter a considerable quantity of this highly interesting Rhizopod from Rostock. I made use of the opportunity to study the nature of the protoplasm, in addition to other observations. I must state, to begin with, that *Pelomyxa*, as I have already pointed out before (*Protozoa*, p. 99), in the normal condition possesses no cortical protoplasm or ectoplasm. At times hyaline portions, usually of

very limited extent, make their appearance as small processes or lobes on the surface. As the result of maltreatment, on the other hand, whether from pressure or from the action of chemical substances, there develops, as a rule, a layer of protoplasm of this kind over the whole surface, which gradually disappears again when these influences cease.

A clear border below the limiting contour of the surface is always very plainly noticeable even with lower powers; on the other hand, I have not succeeded as yet in observing with certainty any radial striation of this border, which in other respects possesses all the characters of an alveolar layer. In the rest of the protoplasm also I was not able to recognise distinctly a fine alveolar structure during life; the well-known coarsely frothy structure of the protoplasm of *Pelomyxa* cannot, of course, be placed on a level with the minute foam-like structure. If, however, small and rather compressed individuals be rapidly fixed with picro-sulphuric-osmic acid under the cover-slip, the entire protoplasm shows the finely honeycombed structure especially well, and the alveolar layer usually shows up on the surface with a distinctness and sharpness such as I have hardly seen elsewhere. The radiate layer is shown just as beautifully round the numerous nuclei. Also in the hyaline, and in any case very fluid protoplasm, which under the above-mentioned circumstances makes its appearance at the surface, the radiate layer of alveoli and the honeycombed structure can be made out excellently after fixation.

The protoplasm of *Pelomyxa* possesses an especial tendency to break up into a great number of spherical drops before its final death. Each of these drops shows a beautiful layer of radiate alveoli at the margin after fixation.

2. *On Protoplasmic Structures in the Bacteria and allied Organisms*

In a work which appeared in the commencement of the year 1890, I tried to show that *Bacteria* and *Cyanophyceæ* possess essentially the same structure, and that in both there could be demonstrated a nucleus of considerable size and with a beautiful alveolar structure, which at least in the larger forms of *Bacteria*, and universally in the *Cyanophyceæ*, was surrounded by a thin layer of protoplasm of alveolar structure. I would have contented myself with simply referring here to that work as a proof that these

organisms, while showing the greatest simplicity of structure in many respects, also permit the alveolar structure of living matter to be made out in them; and I might perhaps have further pointed out that Künstler also (1889) quite independently, by staining with Noir de Collin, observed, in the body of a Bacterium termed by him *Spirillum tenue*, the same alveolar structure which I demonstrated by somewhat different methods in *Spirillum undula*, Ehrb., and a number of other Bacteria; if Alfred Fischer, in a work on *The Plasmolysis of the Bacteria*, had not in the meanwhile raised some objections to the interpretation of the structure of *Bacteria* and *Cyanophyceæ* which I based upon detailed studies. I feel myself bound to consider these objections more closely. As a matter of fact, his objections seem to me to lack cogency, and on that account I would have gladly left them to be contradicted by the decision of some third person of judgment and experience in this department of knowledge; since, however, in the eyes of so many people the right seems to lie on the side of that person who has spoken the last word, and the importance of facts formerly advanced becomes forgotten, through each person scarcely finding time to master his own limited province at all thoroughly, I have made up my mind to refute in this place the somewhat peculiar method of argument adopted by Herr Fischer.

Fischer has not in any way troubled himself to study from his point of view any one of the forms investigated by me, nor one of the typical large *Bacteria*, upon the investigation of which I based my description. He has not even examined the *Oscillariæ*, which are always accessible to any one, in the least according to the methods suggested by me. Nevertheless he considers himself quite justified in declaring my views as to the structure of the organisms in question to be quite erroneous, on the ground of some experiments upon the plasmolytic contraction of the contents of certain bacterial cells. What I described as a radially striated layer of protoplasm of alveolar structure in the large *Bacteria*, such as *Chromatium okenii* and *Ophidomonas jenensis*, as well as in the numerous *Oscillariæ* investigated, is

according to him nothing else than the protoplasm which has remained sticking to certain points of the cell wall after plasmolytic contraction of the contents, and has become drawn out into threads or rays. It is therefore also impossible to speak of a special central body or nucleus in these organisms, and that which I regard as such is nothing else whatever but the central mass of the contracted cell protoplasm.

Whoever reads the interpretation put upon my observations, an interpretation which makes my qualifications for investigating such objects appear in rather a dubious light, might perhaps arrive at the obvious supposition that Fischer in his studies on the plasmolysis of the contents of the bacterial cell had observed the occurrence of some such process as he declares to be the source of my errors. It is, however, to be sought in vain. He has observed nothing more than the contraction of the contents of the cell under the action of certain solutions; in his pictures we look in vain for any trace of structural relations. The whole of his interpretation of the appearances described by me is therefore hypothetical, and is only based upon the experience that in the plasmolysis of " ordinary plant cells " single threads of protoplasm " not at all infrequently " remain sticking to the wall of the cell, and according to Fischer are continued into the pores of the cell wall. So far as I am aware, this phenomenon is by no means of common occurrence in the plasmolysis of " ordinary plant cells," but is the exception. As a rule, the contents contract on all sides without any such formation of threads, and whenever they occur, they make their appearance for the most part very irregularly here and there.

If it thus appears, from what has gone before, quite inadmissible and absurd to try to refer the radiate alveolar layer of protoplasm, observed by me quite regularly both in the large *Bacteria* and in *Oscillariæ*, to a phenomenon of such abnormal occurrence in the cells of higher plants, this is shown still further by a series of other facts. Fischer asserts, as has been said, that all the conditions described by me are deceptive appearances resulting from cells altered by plasmolysis, and supports his con-

tention by the fact that I have investigated material fixed in alcohol, which easily becomes more or less plasmolysed. Had he spent more time in attentively reading my work (which only laid claim to the importance of a preliminary communication), it would not have escaped him that I by no means used alcohol only for preservation, but employed at the same time various most excellent fixing media, such as picro-sulphuric acid, both with and without osmic acid, chrom-osmium-acetic acid, osmic acid vapour, etc., and that all these different media lead to the same results essentially. If I usually employed weak alcohol, with moreover, for the most part, an addition of iodine, as a means of fixation, this was done because I had convinced myself that it gave the same results as the remaining media, and at the same time offered the advantage that staining methods came off better and more characteristically in materials so fixed. I can also certify that with proper application of this means of fixation no plasmolysis is set up, but on the contrary there is frequently, as I remarked, rather a tendency for the membrane to burst with partial effusion of the contents.

I consider it, however, quite unnecessary to spend any more time over these things, since Fischer's quite unwarranted objections can be contradicted without difficulty by a series of facts which were just as accessible to him as to me, and which he himself ought therefore to have taken into consideration, had he thought it necessary to be better informed upon these questions, before he delivered judgment upon them. As is well known, the central body or nucleus of the *Oscillariæ* had already been observed by E. Zacharias before me, and at a later date this investigator followed up this matter further independently, but at the same time as myself. Whether Fischer knows of Zacharias's work or not remains uncertain, since he nowhere mentions it. In any case, Zacharias is as convinced as I am, that the Oscillarian cell contains a central colourless body of considerable size, and with peculiar properties. Whether this body is to be interpreted as a nucleus or not, is another question; in any case, it is satisfactory that both Zacharias and myself have obtained desirable results which agree sufficiently on this point. I can be quite content if Zacharias recognised this body as the forecast of a nucleus; for in that case it is also the representative of the nucleus

of higher cells, the light in which I consider it. Whether it possesses all the properties of the latter or not, is a question which requires further investigation, and moreover it does not seem to be absolutely necessary for this to be the case. The central body of the *Oscillariæ* is thus, according to the observations of both Zacharias and myself, which moreover are anticipated by the statements of some earlier authors, to be observed in the cell quite plainly, even during life, as a colourless central portion; just in the same way I pointed out a similar visibility of the corresponding central body of *Chromatium okenii*, and that, as a matter of fact, it may even be observed in *Bacterium lineola* while living. This being so, how any one can presume to defend the assertion, that the central body is only the central mass of the cell contents contracted by plasmolysis, is to me inscrutable, and it certainly offers a proof of the strange manner in which arguments are frequently carried on at the present day. If we consider further, that, as Zacharias and I showed at some length, the central body is marked out both by especial tingibility and by its behaviour towards digestive fluids, the untenability of Fischer's assertion becomes more and more beyond doubt. Last but not least, an additional point which is capable of absolute proof comes to our help, which I did not lay stress upon formerly, since it seemed to me impossible to raise the objection under consideration. In *Chromatium okenii*, as also in *Oscillariæ*, I frequently had opportunity to observe, in my preparations, cells in various stages of plasmolysis, *i.e.* cells in which the contents had more or less shrunk away from the cell membrane. In such specimens it could be determined in the most definite manner that, as the result of the plasmolysis, the entire radiate alveolar protoplasm had separated itself from the membrane, with a sharp, smooth, limiting surface. Of *Chromatium* in particular, I have found specimens in which the entire contents were retracted strongly from the membrane, and which, nevertheless, showed most beautifully both the protoplasmic cortex and the central body. Even in *Bacterium lineola* it was possible to observe similar conditions with certainty.

As I believe that by means of the foregoing *exposé* I have sufficiently refuted and characterised Fischer's objections, I consider it unnecessary to enter closer into the further attacks which he directs against my interpretation of the smaller Bacteria as central bodies deficient in protoplasm, or at least very poor in it.[1] Since my line of argument is in effect a simple consequence from the results which followed from the investigation of the large *Bacteria* and *Cyanophyceæ*, it may rightly be persisted in, if the objections raised by Fischer against the correctness of these observations are shown to be erroneous and unwarranted. That this, however, is the case will, I hope, have become sufficiently clear.

3. *Some Observations on the Streaming Protoplasm of Vegetable Cells*

Without having gone deeply into this subject, I have nevertheless investigated casually some of the well-known objects which show well the so-called rotational streaming of the protoplasm, such as the hairs on the stamens of *Tradescantia virginica*, the stinging hairs of *Urtica urens*, and hairs of a *Malva* sp. The results were essentially the same throughout. Almost always a very beautiful structure as of longitudinal fibrillæ can be observed in the long drawn out

[1] I seize the opportunity of correcting an error which has slipped into my work on Bacteria. On p. 34 the remark was made, that earlier observers had already occasionally compared Bacteria to the nuclei of higher organisms on account of their intense tingibility, and this was done, to my knowledge, by Klebs (*Allgem. Pathologie*, 1887, Bd. i. pp. 75, 76) more especially. Professor Hüppe had the kindness to point out to me that it was he himself who at a somewhat earlier date had already enunciated this comparison (Hüppe, *Die Formen der Bacterien*, Wiesbaden, 1886, pp. 94, 95), a correction which I here gladly make. As I was only able to give a short preliminary account of my studies on Bacteria, by reason of the work which forms the subject of the present writings, I lacked time to search carefully through the so extensive literature of Bacteria. I therefore followed Ernst in the statement in question, who made the same remark on p. 44 of his work. Besides, this historical question has no very important bearing, since both Hüppe and Klebs considered the relations indicated by them of the Bacteria to the nuclei of true cells, as quite uncertain, and did not ascribe to them any very great significance.

strands of protoplasm that traverse the cell sap in various directions. In these strands the fibrillæ always run parallel to the direction of the long axis, *i.e.* to the direction in which the strand is stretched. In favourable spots it is possible to convince oneself even in the living object, that one is not dealing with isolated fibrillæ, but with fibrillæ connected into a meshwork. The structure is everywhere the same as that which we met with in the stronger pseudopodial stems of the Rhizopods. Of course, the observation is also considerably hindered here by the continuous displacements and alterations of the extended meshwork.

In general I found the appearances more distinct in the hairs of *Malva* and *Urtica* than in *Tradescantia*. Where the streamings have temporarily slowed down, or especially where portions of the protoplasmic strands have come to rest for a time, one obtains especially favourable opportunities for studying the meshwork, which alters its structural character distinctly in the slight aggregations of protoplasm arising from stoppage of the currents. It then passes from the fibre-like meshwork into the ordinary reticulate meshwork, and *vice versa* portions with such a net-like meshwork can be observed to pass over into the fibrous condition, when they become drawn out into strands again. Fig. 9, Plate IV. represents the marginal portion of a streaming protoplasmic strand of *Malva*, into which another strand opens laterally; in the latter the streaming has come to a stop at the point of junction with the former. Hence this slightly swollen spot appears distinctly composed of a reticulate meshwork, while on the other hand the continuation of the strand, as also the strand that is streaming, exhibit to perfection a structure of fibre-like meshes. In Malva, as occasionally also in other objects, I further convinced myself completely that the structure of the protoplasmic strands, after killing with proper reagents, such as alcohol, picro-sulphuric acid, etc., undergoes no alteration, apart from the fact that it becomes sharper and more distinct. Opportunity is frequently offered of making observations on threads of protoplasm drawn out to extreme fineness, in which nothing is to be observed in the way of structure. On

the other hand, wherever these threads possess swellings the reticulate structure can be plainly recognised. On Plate XII. Fig. 2, a structureless thread of this kind is depicted with a distinct reticular swelling. The coming to a decision as to the ultimate structural relations of the thinnest threads is hindered by the same difficulties which we have already discussed for the finest pseudopodia of the Rhizopods.

In the thin layer of protoplasm lining the internal wall of the cell membrane as a continuous layer, the reticular structure is very pale, and only to be made out with difficulty, which is not to be wondered at when the excessive thinness of this layer[1] is taken into consideration. Here also, however, it is to be observed in surface view. After treatment with suitable reagents it shows up very plainly. Since, as we have seen, the places where the structure is more distinct in life undergo no alteration through the reagents employed, we have every right to consider the reticular structure of the thin layer of protoplasm lining the cell wall as a normal phenomenon, although it only becomes perfectly distinct after treatment with reagents.

In general my observations upon the structural relations of the streaming protoplasm of the vegetable cell, both in life and after treatment with reagents, prove its almost complete agreement with that of the reticulose Rhizopods, which have also a marked similarity in their mode of movement.

4. *Observations on some Egg Cells*[2]

In order to begin here also with observations on the living object, I will first mention that the ripe ova of the

[1] Although I have as yet been unable to observe in optical section the reticular nature of this layer of protoplasm clothing the wall, I am nevertheless of the opinion that it can only possess the thickness of one layer of meshes.

[2] A few remarks upon some methods of investigation, employed in the following studies, may not be out of place here. Coloration with so-called iron-hæmatoxylin was frequently employed and carried out by bringing the objects or sections first into a light brown watery solution of ferrous acetate; and then, after washing out, they were stained in a ½ per cent

very transparent Rotifer *Hydatina senta* show a reticulate meshwork most distinctly after a little pressure. At the same time it may be determined that the surface of the egg, under the thin vitelline membrane, is formed of a layer of alveoli with beautiful radial striation, which is bounded externally by a very dark and fairly thick border. Strongly compressed ova, of which the protoplasm is squeezed to bursting, show the reticulate meshwork structure exceedingly clearly, with strongly refracting granules, varying in size from minute to much coarser ones, deposited in the nodal points (Plate VII. Fig. 4). Since the protoplasm of the ovum passes into a state of lively flowing movements as soon as it is squeezed, it follows therefrom that it is completely fluid.

Very fine sections through eggs of *Sphærechinus granularis*, which have been preserved in picro-sulphuric acid and then tinged brown in 1 per cent osmic acid, show the composition

watery solution of hæmatoxylin. One obtains in this way extremely intense staining, varying from blue to dark brown, which is very necessary for the thinnest sections (1 μ). This method also gives certain differentiations of colour. Frequently, however, in order to obtain the most intense possible staining for very thin sections, aniline colours, especially gentian violet in aniline water, were used. The so-called acid hæmatoxylin, so often spoken of, is greatly diluted Delafield's hæmatoxylin, to which some drops of acetic acid are added, until the colour becomes distinctly red. This mixture gives especially good nuclear stains, which show in particular the colour differentiations of the nuclear contents described by me above. In order to prepare the thinnest sections, I cover the cut surface of the objects embedded in paraffin with a thin skin of celloidin before cutting them; this method succeeds very well for obtaining sections of 1 μ, or even considerably thinner. The investigation of the sections was first done in water, since the delicate protoplasmic structures naturally show up much more plainly in the feebly refracting water than in resins or the like. For the first investigation, therefore, this method is much to be recommended, although any one experienced in these matters can usually make out the structures in preparations mounted in Damar or Canada balsam also. The distinctness of the images is, however, so much greater in water that the use of that medium is to be strongly recommended. As has been remarked, the most intense staining is scarcely sufficient in the investigation of such fine sections, the more so as even with it the protoplasmic framework proper only stains extremely slightly, so that strong solutions of the stains seem almost indispensable for the recognition of such delicate structural elements. A section of about 0·5 to 1 μ through an object which after staining with iron hæmatoxylin appears absolutely black, is yet so faintly coloured that further staining on the slide is often necessary.

of the protoplasm very distinctly as a fine reticulate meshwork. The sections were further stained on the slide with Delafield's hæmatoxylin, as a result of which the true protoplasmic framework was, as usual, only very feebly tinged or not at all. The relatively dark coloration, which the protoplasm takes on in hæmatoxylin, depends in the main much more on the numerous fine, strongly staining granules which are lodged in the nodal points of the framework.

On the surface of the yolk a radiate alveolar layer can be made out plainly (Plate V. Fig. 1, *b*), and the eggs which were investigated after the second cleavage also showed the layer of alveoli very plainly on each side of the surfaces of contact of the two segmentation spheres.

From the investigation of eggs during the process of segmentation it was shown that the radiating appearances of the so-called asters or suns only depended on the arrangement of the meshes of the protoplasmic framework. This can be demonstrated even in entire ova killed with picrosulphuric acid (Plate V. Fig. 1, *c*), but of course much more clearly and better in sections cut as thin as possible. The similarity is very great between the arrangement of the meshes and that formerly described in the radiating protoplasm of the central capsule of *Thalassicolla*. On Plate V. Fig. 1, *b*, a fine section is figured through one of the suns of the nuclear spindle of a dividing ovum. The section passes a little obliquely with reference to the axis of the nuclear spindle, which makes its appearance in the next section, and shows a distinct equatorial nuclear plate. In the centre of the sun or aster the so-called polar or central body, which is relatively strongly stained, may be noticed. It seems to consist of three vesicles provided with strongly stained walls. This central body lies in the clear, quite unstained central area of the radiations ("sphere of attraction," Beneden; "archoplasma," Boveri), which in its turn is again enclosed by the rather intensely stained and radiating external protoplasm. The central area also is radiately disposed throughout. The central body is immediately surrounded by a zone of small extent composed of an irregular meshwork of protoplasm, which passes directly into the

radiate meshwork of the large portion of this region. That this radiate protoplasm is really composed of a reticulate meshwork can be demonstrated quite plainly. The protoplasm of the central area passes again immediately into the more strongly stained radiating external protoplasm. In this section the radiate arrangement of the external protoplasm was less strongly pronounced than is the case as a rule, but was nevertheless to be seen clearly in many places. As I have already pointed out above, the stronger tingibility of the external protoplasm certainly depends on the numerous strongly staining granules which are lodged in it, and not on an alteration in the nature of the real framework. In order to show this fact quite plainly in the figure, the section should, of course, have possessed the thickness of only a single layer of meshes. But these sections were not so thin (about 0·002 mm.), for which reason the external mass of protoplasm still shows an apparently diffuse staining.

Sections through the ovarian eggs of *Barbus fluviatilis* preserved in Müller's Fluid, especially those through larger eggs, show the fine meshwork most distinctly, as also a well-developed radially striated layer of marginal alveoli, 1 μ in thickness, under the egg membrane. In the largest eggs the radiate markings reach about four or five times deeper, which permits the supposition that we are confronted here by conditions similar to those obtaining in the peripheral zone of the protoplasm of the central capsule of *Thalassicolla*. Radiately striated protoplasm frequently occurred also round the germinal vesicle of the larger ova, which could be seen to owe its arrangement to a special arrangement of the meshes. The meshed structure of the protoplasm and the marginal alveolar layer could also be recognised in the ovarian eggs of *Dreissensia polymorpha*, on examination of some older sections, though not quite so plainly as in the eggs first mentioned.

5. *Red Blood Corpuscles of Rana esculenta*

On the occasion of some investigations upon the struc-

ture of the nuclei of these cells I was also able to make out some facts as to the structural relations of their protoplasm. Since, in the investigation of these nuclei, I was making use of hæmatoxylin to obtain the differential stain described by me on a former occasion (1890), which can only be distinctly shown in material preserved in alcohol, the observations to be described were undertaken upon blood corpuscles which were preserved in iodine-alcohol of 40 per cent, then stained in acid hæmatoxylin, and mounted in Damar. As in a large number of blood corpuscles prepared in this manner, the external form proved to be faultlessly preserved, and as from many experiments carried on directly under the cover-slip with iodine alcohol, it was known that this reagent gives good preservation of the finest structural details of the protoplasm, I have not the slightest fear that the somewhat unusual method of preservation produced abnormal alterations in the blood corpuscles.

On careful examination of a large number of well-preserved blood cells it may be recognised at the outset that they are enveloped at their surface by a pellicle-like membrane fairly thick and even distinctly double contoured (Plate X. Fig. 1, *p*), beneath which runs a clear border distinctly radially striated (*alv*). This border can be followed quite easily both in the surface view of the blood corpuscle (Fig. 1, *a*) and in optical median longitudinal section (Fig. 1, *b*). In the latter view particularly it may frequently be seen very beautifully. The pellicle-like envelope together with the radially striated border, represent, without doubt, an external layer of alveoli of similar structure to that which we described above in living Vorticellæ, for example. Beneath the marginal alveolar layer there can be seen in surface view a girdle-like zone of finely-meshed internal protoplasm, which, however, only attains from about $\frac{1}{4}$ to $\frac{1}{3}$ the width of the transverse radius of the corpuscle (*g*). This zone becomes still plainer in the optical median section, when it is seen that the internal protoplasm only forms a marginal ring or ridge (*g*), which passes down on to the flat surfaces of the corpuscle; but here it very soon thins out, so that the flattened sides throughout the greater

part of their extent are composed of the marginal layer of alveoli only, which comes into close contact with the central nucleus. The blood corpuscles possess, in addition, an internal cavity filled with cell sap, in which I occasionally observed indications of isolated radial tracts of protoplasm; I have not, however, followed up this point more closely. Studying the surface of the corpuscle by accurately focussing its superficial aspect, it may be observed that the network of the alveolar layer is more or less fibrous in nature, as is represented for a small portion of Fig. 1, *a*, at *o*.

The cell nucleus (*n*) shows a very distinct, rather delicate framework of meshes, which stains a beautiful blue with the method of preparation mentioned. In the nodal points of this nuclear framework numerous chromatin granules of a red colour are lodged, as I have briefly described already on a former occasion (1890). As the figure shows, the meshwork of the nucleus is much more open than that of the entirely unstained protoplasm, and is distinguished from the latter, therefore, not only in colour, but also in structure. Since this is also so distinct and clear in many other cases, it seems difficult to understand how it is that the theory of a direct transition between the framework of the protoplasm and that of the nucleus is continually finding new adherents.

Although it is impossible for me to enter here into the extensive literature upon the subject of blood corpuscles, I must consider some more recent observations, without setting up any pretence to completeness thereby. Leydig mentioned as early as 1876 the spongy structure of the red blood corpuscles of *Triton*: "Here also there passes out from the nucleus, in radial distribution, a fine network of threads towards the periphery of the cell." The figure of the network, which he depicted in 1885 within the blood corpuscles, is, however, much too coarse, and can scarcely represent the true network.

Frommann also observed, as far back as 1880, a reticulate structure in the red blood cells of *Salamandra maculosa*, but was of opinion that the protoplasm of the blood corpuscles was originally quite homogeneous, and only became differentiated into a network under the influence of an induction current applied to it.

Reticular structures, such as are described above, I find best described by Pfitzner (1883), especially when the figures published by him in 1886 are brought into comparison. The radiating fibre-like structure was also then partially indicated. The cell membrane mentioned by Pfitzner corresponds to the pellicula. The threads of the network, according to him, sink into this skin, and this, as a matter of fact, they do.

After I had commenced my investigations in June 1890, and had already reported briefly upon the presence of a marginal layer of alveoli (1890, 1892), there appeared a communication of Auerbach which agreed in many points with my statements. Auerbach had also observed the alveolar layer, but had not seen its radial striation. He interprets it as a cell membrane. It is interesting that in double staining with eosin and aniline blue it becomes coloured blue, while the protoplasm bordering on it stains red. Auerbach furthermore noticed the cavity in the blood corpuscle, but regarded it as a colourless and structureless protoplasm, which he terms medullary substance, in contradistinction to that which I regard as the sole protoplasm, which is termed by him cortical substance. The reticular structure of the protoplasm, which he observed after treatment with picric acid, he looks upon as an artificial product, as a vacuolisation, in fact, from which it seems to him a little strange that his medullary substance, which is at all events much richer in water, shows no such vacuolisation. All my experiences with regard to the fixation with picro-sulphuric acid (I did not use pure picric acid) of distinctly structured living protoplasm, speak against this explanation of the net-like structure. Apart from many other differences, my observations also contrast essentially with those of Auerbach in regard to the distribution of the protoplasm, or cortical layer, as he terms it. This he describes as spreading out under the whole surface of the corpuscle as a layer of even thickness, as is evident from an optical longitudinal section figured by him. This section must, however, have been taken from a deformed corpuscle, since it does not represent its true shape, and shows the nucleus separated by a thick layer of the so-called cortical substance from the marginal layer of alveoli on each side, a disposition which directly contradicts what I have observed.

Although I have not made this subject a matter of special study, I would nevertheless state my belief that the central hollow of the blood corpuscles is in reality a cavity containing cell sap, which, moreover, as has already been pointed out above, is probably traversed by delicate strands of proto-

plasm, just as in plant cells. That my description is not exhaustive in the latter respect is obvious from the fact that the nucleus must, in any case, be marked off from the central cavity by a delicate layer of protoplasm, although I have not been able as yet to observe any such with certainty.

6. *Observations on some Epithelial Cells*

Since it was known to me from former experience that the epithelial cells of the gill lamellæ of *Gammarus pulex* show a protoplasm very distinctly striated longitudinally even in the living condition, I chose this object in order to obtain further light upon the nature of its minute structure. Both the investigation of freshly cut off gill lamellæ, as well as of small and unhurt living animals, showed that the structure is not made up of fibrils, but is a distinctly reticulate meshwork. Fig. 5 on Plate VI. shows the optical section through the epithelium of a freshly cut off gill lamella, such a section as can be well seen at the edge of a lamella. Externally there is the relatively thin cuticle (*c*). Under this comes a delicate pale border, the significance of which was not clear to me. Then comes finally the protoplasm of the epithelial cells, with a very beautiful reticulate meshwork structure. As has been said, it can be clearly made out that the striation only depends upon the arrangement of the framework of the meshes. The cell boundaries were not to be made out distinctly in the optical section, while they were most conspicuous in the surface view of the gill lamellæ. Immediately round the nuclei of the epithelial cells there can be seen fairly distinctly a modification of the striated structure caused by the layer of meshes directly surrounding the nucleus being arranged radially to the surface of the nucleus.

In surface views, also, of the epithelial cells the net-like structure can be observed very beautifully during life; but from this aspect it naturally does not appear striated but irregularly reticular. The two epithelial layers of the two surfaces of the gill lamella are connected with one

another, as is well known, by peculiar pillars, which pass vertically through the blood space of the lamella. In an optical transverse section of them these pillars appear as elongated structures which contain numerous nuclei, and consist of beautifully reticulated protoplasm, on the surface of which (towards the blood space) a distinct radiate alveolar layer is formed. The optical longitudinal section of such a pillar shows that it is traversed in the middle by a distinct transverse line of demarcation, and that the pillar consists of beautifully striated protoplasm composed of a meshwork, just as are the ordinary epidermic cells of the gill lamellæ. The nuclei lie in the deeper region of the pillar, near the line of demarcation already mentioned. As far, therefore, as I can give an opinion as to the nature of the pillar from a merely cursory investigation, I believe that it is formed by the growth of epithelial cells towards the interior, which, starting from the two surfaces of the gill lamella, meet in its median plane. It is not quite clear to me why I saw no cell boundaries in the optical transverse section of the pillar in spite of its containing numerous nuclei, while the cell boundaries on the surface of the gill lamella can be traced very plainly. A more accurate investigation of sections of the gill lamellæ will, however, easily determine their structural relations.

"The striated nature" of the epithelial cells of the gill lamellæ of Asellus was observed by Leydig as far back as 1855. He pointed it out again in 1864, and represented the relations somewhat more accurately in 1878 (*Asellus*, *Porcellio*, and *Gammarus*). It seemed to him that the striation depended upon "longitudinal canals or lacunes" traversing the protoplasm. In surface view the cells appeared as if bored through by very minute, closely approximated holes. R. Hertwig,[1] in 1879, mentioned the striated nature in *Gammarus*. The pillars or trabeculæ, briefly described above, which traverse the blood space of the lamella, were also noticed by Leydig in 1878, and he seemed to be of the opinion that they consist of chitin. In the middle of the blood space fat is described as occurring, into which the trabeculæ extend, a fact of which I observed nothing whatever. It should be added, however, that he only speaks

[1] *Der Organismus der Radiolarien*, Jena, 1879, p. 112.

quite briefly of the gills of *Gammarus* in the description of a figure referring to it.

An opportunity of making some studies upon the Rotifer *Hydatina senta* enabled me to observe the very beautifully striated and fibrillar nature of the protoplasm of the large cells which carry the cilia of the two ciliated circles of the wheel organ. The cells of the posterior circlet are especially well suited for this observation. Both in animals subjected to pressure, as well as in such as had been narcotised with hydroxylamine, it is very easy to convince oneself as to this structure in the epithelial cells. As far as I could see the entire protoplasm is not differentiated into fibrils, but only a middle layer, from which the cilia arise externally. The higher and deeper layers, on the other hand, have the structure of an irregular reticulate meshwork, and at the same time contain numerous peculiar elongate or somewhat kidney-shaped bodies, which are very closely packed in the framework, and remind one greatly of Bacterioids (Plate VII. Fig. 5). The fibrils of the middle layer run down deep into the large cell until they approach the conspicuous nucleus, without, however, reaching the base of the cell. They are very distinctly knotted, and closer observation demonstrates with certainty that the nodes of neighbouring fibrils are connected by delicate transverse threads. The structure is thus seen to consist of a meshwork so disposed as to give a striated appearance, and not to be really fibrillar.

The surface of the cell is limited (at least where the cilia arise) by a radially striated border, possessing to some extent the characteristics of an alveolar layer. The striæ of this border are direct continuations of the fibrillæ, and pass, on the other hand, immediately into the cilia externally. In photographs which I have taken of such cells, I further notice at their inner circumference a fairly distinct alveolar layer, as well as a radiate layer of meshes round the nucleus.

The anterior circlet of cilia consists, as is well known, of a number of tufts of cilia. To each of these tufts corre-

sponds a bundle of fibrillæ in the underlying cell, which can similarly be well observed in the living condition.

In the investigation of the living *Hydatina* I also observed the meshed structure very plainly in the protoplasm of other cells, of which I will give a brief account. It showed up most plainly in the cells of the so-called gizzard, accompanied by the appearance of very pronounced nodal points in the framework, an appearance, however, which is partly called forth by granules deposited in it. On the surface of each cell the radiate layer of marginal alveoli was very distinct. In the cells of the gastric glands a marginal alveolar layer could also be made out. The protoplasm of these cells was either merely a reticular meshwork, or else a meshwork arranged in striæ. In the latter case the striation was directed towards the spot at which the gland opened into the mid gut. Especially in the neighbourhood of this spot the reticular structure could always be observed very plainly, which partly depends on the fact that numerous granules are lodged in the nodal points. We are dealing here, no doubt, with the secretion products of the gland, which are collected abundantly in the framework of the protoplasm in this region.

The meshwork structure frequently appeared especially distinct in the two peculiar strands which ascend forwards and obliquely outwards from the end gut. Whether these strands are glandular, or are a kind of suspensory ligament for this portion of the gut, I will not venture to decide. Finally, the cells of the foot gland show in many places the reticular structure fairly well, though not so clearly as the last-mentioned histological elements.

Very thin transverse or longitudinal sections through the body wall of *Lumbricus terrestris* show very beautifully the longitudinally striated structure of the epithelial cells which are not modified into gland cells (*i.e.* indifferent or supporting cells—Plate VI. Fig. 3). I will not go more specially into the way in which the glandular and supporting cells are arranged with regard to one another, since that has already been recently described in detail elsewhere. Fine longitudinal sections through the supporting cells (see the

figure) show very plainly the meshwork of the protoplasm arranged to form longitudinal striations. In the nodal points of the meshwork very small granules are lodged, which can only be seen with difficulty. In material preserved in iodine alcohol and stained with acid Delafield's hæmatoxylin, it can, however, be made out plainly that these granules are tinged reddish. Corresponding to their small size the colour is naturally not very intense, but still quite recognisable. Since the chromatin granules of the cell nucleus also show the red coloration excessively plainly with this method of staining, in sharp contrast to the blue tinge of the framework, the granules of the nucleus and of the protoplasm may be directly compared, and their great similarity in staining and in other respects established. I have no doubt that both are nearly allied structures, and that here conditions are presented to us similar to those which have been described already for Flagellata, Diatoms, etc. (see above, p. 91). I would particularly emphasise the fact that the nuclei of the epithelial cells of *Lumbricus terrestris* show the distinction between the staining properties of the framework and of the chromatin granules with special distinctness, just as well as, in fact even more distinctly than, I saw them in *Cyanophyceæ*, *Euglenæ*, etc. The nuclei of the gland cells also show the same relations, but their framework is arranged rather more densely, and in a different way from that of the supporting cells. It is very similar to that of the nuclei of Euglenoids, which I described briefly on a former occasion (1890-91).

In the longitudinal section of a supporting cell figured on Fig. 3, Plate VI., it can be further observed fairly well that the layer of meshes following directly under the cuticle forms a kind of radiate alveolar layer, inasmuch as it is marked off from the internal meshwork by a fairly straight line, which of course only depends on the fact that this most external limiting layer consists of meshes nearly equal in size. It can further also be seen pretty clearly that the layer of meshes surrounding the nucleus is arranged radially to the surface of the latter.

In tangential sections which pass through the outermost

zone of the epithelium, and therefore have not as yet passed through the body of the gland cells, but only through their efferent tubules, which run up between every two contiguous supporting cells, it is possible to make out in addition the following state of things. Each transverse section of a supporting cell is surrounded by a very beautifully developed radiate layer of alveoli, distinguished by staining strongly in hæmatoxylin. The alveolar layers of contiguous cells are in direct contact, so that their pellicles form only a single sharp dark limiting line. Every efferent tubule of the gland cell is therefore surrounded by the alveolar layers of two neighbouring cells, which here separate from one another to a slight extent, in order to form the lumen of the tubule. The protoplasm of the supporting cells shows a beautiful reticulate meshwork in transverse section, sometimes with a slightly radiating arrangement.

7. *Peritoneal Cells on the Gut of Branchiobdella astaci, etc.*

In very fine transverse sections of specimens of this worm preserved in picro-sulphuric acid, I have observed the protoplasmic structure very plainly, especially in the cells mentioned above, but also in numerous other cells of the body. Fig. 2, Plate VII., represents a section through a cell of this kind, which was stained intensely on the slide with gentian violet in aniline water. The thickness of the section may have been at most 1 μ, but was without doubt still less, since the investigation shows definitely that not more than a single layer of the framework of the meshes appears in the section. The appearance offered by the nucleus represents, therefore, a transverse section through it. As is shown by the figure, the protoplasmic framework stands out with excessive distinctness, and is distinguished by having numerous very intensely stained granules lodged in its nodal points. It can be seen definitely, however, that by no means all the nodal points of the framework contain granules, but that fairly extensive regions of the framework are quite free from them. In colouring and appearance no distinction can be made out between the granules of the

protoplasm and those of the nucleus. The protoplasmic framework appears almost entirely unstained, and hence very pale. The figure gives a picture of its arrangement which is as true as possible to nature, not a diagram. The meshes were drawn in exact correspondence to nature, as far as they could be traced. The gaps in the framework depend, therefore, partly on the meshwork not being distinct enough in places to permit of an accurate drawing, and partly on the existence of real gaps, which depend in their turn on the presence of large vacuoles, or here and there on local ruptures which are so easily brought about in the preparation of such thin sections.

The meshed structure of the protoplasm was further observed by me in the cells of the intestinal epithelium of *Branchiobdella*, only that here the meshes are directed longitudinally, and hence the protoplasm shows longitudinal striations. The inner ends of the cells possess a cuticular border, which stains very intensely, and is frequently distinctly striated. Finally, these ends carry numerous threads resembling cilia, which seem to bore through the cuticular border. The protoplasmic framework is in like manner stuffed quite full of intensely stained granules.

The epidermic cells of the skin also show a beautiful reticulate meshwork, with large quantities of strongly stained granules in the nodal points (Plate VII. Fig. 3, *a*).

In favourable sections of the cuticle, which did not stain in the slightest, it may be seen to consist of several layers, the height of which is about equal to the diameter of an alveolus of the framework of the cells of the epidermis. Each of the layers is distinctly vertically striated (Plate VII. Fig. 3, *a*), and therefore presents more or less the appearance of an alveolar layer. In other parts of the cuticle, on the contrary, the alternating layers differed somewhat, one being light, the other dark, and thus the total appearance being somewhat as represented in Fig. 3, *b*. In surface view the cuticle appears, as shown in Fig. 3, *c*, diagonally striated with distinct dark nodal points. From these observations it seems to me obvious that a meshed, or rather alveolar, structure appertains to the cuticle also, and that therefore

it might well have arisen by modification of the alveolar framework of the cells of the epidermis.

I take this opportunity to remark, that the much thicker cuticle of *Phascolosoma elongatum* also frequently shows the same structure and very plainly either in transverse or longitudinal section; only, corresponding to its greater thickness, the number of its layers is much more considerable.

Cuticle and so-called hooks of Distomum hepaticum.—In very fine sections of specimens of this Trematode preserved with picro-sulphuric acid, and then stained very intensely with iron-hæmatoxylin, the following details can be made out as to the structure of the cuticula. The whole cuticle stains very intensely, the cuticle proper more violet, while the hooks lying in it stain a beautiful blue. The external half of the cuticle shows, however, a rather more dirty violet tint, and the inner portion more bluish violet, which depends without doubt on large quantities of granules, staining a deep blue, and lodged in it. The whole cuticle has a distinct reticular meshed structure, in which the framework has a somewhat blue tint, the intervening matrix, on the other hand, appearing violet, for which reason the colour is violet as a whole (Plate XI. Fig. 1). In the hooks the case is otherwise, from the fact that the intervening matrix is also coloured blue, so that they appear blue throughout. The surface of the cuticle is formed of a very distinct dark border of a blue colour, appearing like a pellicle, under which extends a somewhat lighter, radially directed layer of meshes, which possesses entirely the characters of a marginal alveolar layer. The external half of the cuticle shows in its remaining parts an irregular framework of meshes, which obtains the appearance of radially directed fibres the more it approaches the internal half, this character being quite pronounced in the latter region. In addition, numerous granules, stained a very intense blue, are lodged in the nodal points of the framework of this deeper portion. Since these nodal points, and therefore the granules also, lie one behind the other, in more or less distinct rows, in consequence of the fibrillar arrangement of the meshwork, the

fibre-like structure of the deeper layer of the cuticle stands out very prominently.

The hooks also show very plainly the structure of a meshwork, and, moreover, of one that is modified into longitudinal fibres throughout its whole extent, upon which fact depends its longitudinally striated appearance. Blue granules are also deposited in its framework, although not very abundantly. Numerous lacunar spaces, resembling longitudinal clefts, appear in the substance of the hooks. The latter do not project out freely above the cuticle, but are completely embedded in it, being clothed up to their pointed external ends by a cuticular covering which gradually thins out more and more. On the other hand, the internal ends of the hooks project beyond the inner limit of the cuticle into the body. Between the circular and longitudinal muscles a protoplasmic framework extends, which carries numerous granules, stained deep blue, in its nodal points. Although I could not make out completely to what cellular elements this framework properly belongs, and especially whether the so-called gland cells, which appear so abundantly under the musculature, do not in some way belong to it, I would nevertheless draw attention to the fact that the fibrous trabeculæ of the framework of the cuticle are continued quite distinctly into the protoplasmic framework extending between the musculature. It seems to me, therefore, to follow with certainty that the cuticle, together with the hooks, has arisen by direct modification of a protoplasmic framework, although the actual origin of this covering of the Trematode body appears still as doubtful as ever.

Very remarkable relations are shown also by the peculiar and thick, so-called *bacillar lining* or *cuticular border* of the epithelial cells in the gut of this worm. The epithelial cells have a very distinct meshwork, arranged to form longitudinal fibres, and closely packed with blue granules, on which account it is relatively dark. The deep bacillar lining stains only a dirty light blue colour. If this lining be studied in the thinnest possible tangential sections through the epithelium (that is to say, in reality transverse sections

through the lining and the epithelium cells), for which opportunity is often given by longitudinal sections of the animal, the following peculiar structure can be seen (Plate XII. Fig. 3). The lining consists of rather thick and darkly stained rounded or oval bodies, which vary to some extent in diameter. These bodies have a distinct meshwork structure, and carry numerous strongly stained granules in their nodal points. They appear connected with one another by a paler, less strongly stained meshwork, which, however, also carries scattered granules in its nodes. After this composition has been made out in tangential sections, it is also possible to observe a corresponding state of things in longitudinal sections through the cuticular border. The more strongly stained portions appear in longitudinal section as conical bodies, which are united by a paler intervening alveolar meshwork. Since these conical bodies, which are pointed towards the inner surface of the lining, are not quite of equal length and thickness, they appear to differ somewhat in size in a tangential section, as the figure shows.

8. *Liver Cells of Rana esculenta and Lepus cuniculus*

Since liver cells have been made use of so often for studies on the structural relations of the protoplasm, I investigated them in the thinnest possible sections. The pieces of liver in question were hardened in the picro-sulphuric-osmic acid mixture, and then stained with iron-hæmatoxylin in the manner described. The thickness of the finest sections must certainly have been under 1 μ, and therefore, in any case, would not have been above the medium thickness of a mesh of the protoplasmic framework.

Sections prepared in such a way through the frog's liver, and, for the most part, stained still further on the slide with iron-hæmatoxylin or vesuvin, show at once a very beautiful net-like protoplasmic framework in the clearest and most convincing manner, of which Plate VII. Fig. 1, and also Photograph VIII., give a representation. I expressly point out that the figure was drawn with all

care, and is in no way a schematic representation. The actual protoplasmic framework again appears very pale and little stained: its apparently strong coloration in thicker sections depends rather on the deposition of numerous intensely stained granules in the nodal points of the network. Although these granules, as has been said, are present in great abundance, it is not by any means every nodal point that is provided with them. On the contrary, one frequently observes fairly extensive portions of the framework which are free from them. The true nodal points nevertheless stand out fairly prominently. If also a somewhat fibrous composition of the meshwork is to be seen in places, it was at all events never very pronounced in the preparations studied by me, and the thinness of the sections excludes every possibility of interpreting the structure, as in any way the result of separate fibrillæ being glued together or superposed upon one another. This possibility is still further set aside when we see that the protoplasmic framework here presents also the same peculiarities which we have met with so frequently. If the limits of the cells be more closely investigated (for which purpose, of course, the thinnest and best portions are to be chosen), it may be plainly seen that the two most external layers of meshes of cells that border upon one another are placed vertically to the line of limitation. Even in Photograph VIII. this comes out plainly in places. The line that marks the limit between two cells is always stained very darkly, which in part, at least, may depend on the abundant deposition of strongly stained granules. In any case, however, a pellicle-like modification of the most external lamella of the meshwork is also present. As Fig. 1, Plate VII. shows, this line of limitation had also frequently a distinct zigzag outline, corresponding to the contiguous meshes of the two limiting layers; at times they appear quite interrupted in places, so that the protoplasmic frameworks of neighbouring cells pass directly into one another. Since, however, to trace out in detail the relations that obtain at the boundaries of the cells is, for the present, beyond the scope of the task which I have under-

taken, I only gave quite a cursory consideration to the matter. I will, therefore, only state briefly that the dark line of demarcation sometimes appears rather thicker, and may then itself appear to have a meshed structure; it should, however, be taken into consideration, that slightly oblique sections through the limiting lamella might produce appearances of this kind, although I do not wish to deny their reality altogether off-hand.

Just as we are able to demonstrate an alveolar layer at the surface of the liver cells, so it is not infrequently possible to convince oneself that a radially arranged layer of meshes occurs round the nuclei.

The sectional width of the meshes of these liver cells I am inclined to estimate at about 1 μ.

Sections of pieces of rabbit's liver prepared in a corresponding manner showed the reticular structure of the protoplasm in the same way and very beautifully. In addition to cells, of which the protoplasmic framework was pale and finely structured, exactly as has just been described in the frog, there also occurred some with a considerably coarser and hence much more distinct structure. In these cases the trabeculæ of the meshwork were also much thicker and darker than usual. Photograph IX. gives a fairly good representation of such cells. I contented myself at the time with ascertaining the meshwork structure of the protoplasm of these cells, without entering more especially into the numerous points of detail still to be solved.

9. *Epithelium of the small Intestine of Lepus cuniculus*

Pieces of the small intestine of the rabbit, after being hardened in picro-sulphuric-osmic acid and strongly stained in iron-hæmatoxylin, show the structure of the epithelial cells very beautifully in thin sections. As in all cells of similar structure, we have also to deal here with a meshwork modified into a longitudinally fibrillar structure with numerous strongly staining granules lodged in the nodal points. As far as I investigated the structure of the protoplasmic framework, it agreed entirely in essential

points with that which has already been described above for the cells of the epidermis for *Lumbricus*. I think, therefore, that a more detailed description may be omitted, and content myself with a reference to Photograph X., which, however, both as regards the goodness of the section and the success of the photograph, still admits of being considerably surpassed.

10. *Pigment Cells of the Parenchyma of Aulastomum gulo*

I draw attention to these brown pigment cells observed by me casually, chiefly from the fact that they show the meshwork structure especially clearly and distinctly, and moreover, permit the relations of the pigment granules to the framework to be made out particularly well. The cells investigated were obtained casually when making preparations of isolated muscle cells. The maceration of small pieces of the body wall of *Aulastomum* was performed in 10 per cent iodine alcohol, and lasted two days. Plate VII. Fig. 6 gives a picture, as true to nature as possible, of a small portion of the protoplasmic framework of an isolated cell. The very small pigment granules are always lodged in the nodal points of the framework, yet on account of their staining properties it can be seen very plainly that by no means all the nodal points contain such deposits. With regard to other points, I think the figure requires no further explanation.

11. *Capillaries from the Spinal Marrow of the Calf*

In maceration preparations of the spinal cord of the calf, one frequently obtains isolations of rich networks of the finest capillaries. If one investigates more closely the finer structure of one of these capillaries (Plate IX. Fig. 1), it can be seen to possess a very thin protoplasmic wall, in which here and there large nuclei (*n*) are lodged. These nuclei cause, wherever they occur, a projection of the wall into the lumen of the capillary.

In an optical longitudinal section of the wall it may

be seen to have a reticular structure, and to consist only of a single layer of meshes. Correspondingly, the walls of the meshes are placed perpendicularly to the inner and outer limiting lamellæ of the wall. At the nucleus, the layer of meshes splits into two, so as to surround it both externally and internally by a thin layer of protoplasm, the meshes of which are placed vertically with regard to the nucleus and to the limiting lamella. If the surface of the wall of the capillary be focussed (*o*), a confirmation of the meshed structure is obtained, which, of course, can be seen in this aspect also. The result is that, corresponding to its extension in a longitudinal direction, the capillary consists of a meshwork modified into a fibrous structure. Whether or not the protoplasm belonging to the individual nuclei is separated by cell boundaries I was unable to determine in preparations of this kind, and I have not followed up this point more thoroughly.

Leydig has noticed quite correctly, as far back as 1885 (p. 15), that the cells of the blood capillaries (gills of *Salamandra*) consist in section of a single layer of alveoli, and hence appear striated. Only he draws the dark wall of the alveoli very thick, and the clear intervening spaces very narrow. From this observation, however, he wishes to infer that the thin plate-like body of these cells is porous. "Under some circumstances the fine pores might widen into larger openings, and thus permit the passage through of blood corpuscles." That this view, which would lead to consequences physiologically untenable, is also unjustifiable anatomically is evident from the description given above.

12. *Connective Tissue Cells between the Nerve Fibres of the Ischiadic Nerve of Rana esculenta*

In teased-up preparations of the ischiadic nerve, numerous elongated spindle-shaped connective tissue cells are obtained isolated, which are interpolated between the nerve fibres. By successful isolation it can frequently be seen that these cells are connected lengthways like a chain, as is shown in Fig. 4, *a*, Plate VIII., the protoplasm passing directly from one into the other. The cells have a somewhat different aspect, according to the view in which

they are studied. That is to say, they are flattened to some extent in a direction at right angles to their longitudinal extension (Fig. 4, *c*). The nucleus shows an elongated oval or sausage-like symmetrical shape when seen from this flattened side, and is always surrounded with a border formed by a single layer of meshes of protoplasm. At the ends of the nucleus the protoplasm is continued into the narrower portion of the cells, where it assumes a more or less longitudinally fibrillated structure. In the width of that portion of the cell which is drawn out like a band there do not, however, occur more than about three meshes.

In the aspect in which the cells usually show themselves, namely, at right angles to that already mentioned, as seen when lying along the isolated nerve fibres, the nucleus is asymmetrical (Plate VIII. Fig. 4, *b*) and makes the cell bulge out strongly on one side. This bulging out, so far as I have paid attention to the matter, which is beside my main subject, is always situated in the depression formed at one of Ranvier's nodes in the nerve fibre, and quite fills it up. The thread-like portion of the cell appears to be a single mesh thick in this aspect, and therefore shows the same relations as have already been described in the walls of the capillaries. On the flat side of the nucleus I could trace out the simple layer of protoplasm distinctly. Whether a similar protoplasmic envelope occurs also on the convex side was not to be made out with certainty; nevertheless I do not doubt the fact of its occurrence.

13. *Ganglion Cells and Nerve Fibres*

Ganglion Cells

I have isolated in various ways ganglion cells from the spinal cord of the calf and from the ventral nerve cords of *Lumbricus terrestris* and *Astacus fluviatilis*, and have always convinced myself in the clearest manner that their structure is a fibrous meshwork. Since there are already in existence a considerable number of sufficiently good figures that

represent such structural relations in ganglion cells, I do not for my part consider it necessary to give more. I will only refer here to the very successful photograph (XIII.) of a very thin section of a ganglion cell of *Lumbricus*, which permits the reticulate meshwork to be made out very plainly. The preparation was stained with iron-hæmatoxylin, which also rendered distinct the numerous strongly stained granules lodged in the nodal points of the network. These granules can also be observed quite plainly in isolated and unstained ganglion cells of this worm. In the latter I first observed a perfectly definite radiate layer of alveoli at the surface of the cell, as is depicted on Plate VIII. Fig. 3. Photograph XIII. also shows this layer very well in places. That the radiate layer of meshes occurs also round the conspicuous nucleus of the ganglion cell, can be definitely seen in isolated cells from the calf (Plate VIII. Fig. 2).

As I have already pointed out, the fibrous or fibrillar nature of the protoplasm only depends on the arrangement, or rather on the extension and elongation, of the meshes. There is indeed very often an appearance as if stronger and thicker fibrils or "runners" (Frommann) passed through the meshwork. In my opinion, however, this only depends, on the one hand, upon the fact that the tracts of the framework are more distinctly prominent according to the extent to which they are ranked in a straight line one behind the other, and on the other hand upon the close packing of the granules, of which we have before seen clear examples.

The processes arising from the ganglion cells always have the structure of a meshwork forming distinct longitudinal fibrils. In Fig. 1, Plate IX., I have represented the structure of a broad protoplasmic process of a ganglion cell of the calf, which was most especially clear and distinct. I reckon the breadth of the meshes at about 0·8 μ. The structure of such protoplasmic processes is always clearer and sharper than that of the axis-cylinder to be described later, which may well be the result of deposits of granules.

For the view of Nansen (1886), namely, that nerve tubules enter into the ganglion cell, spread themselves out as fibrous tracts in its reticulate protoplasm, and finally emerge again, I

have found no evidence of any kind in support, and regard this opinion as incorrect. Nansen thinks that the protoplasm of the ganglion cells is composed of two different kinds of constituent elements—first, of the reticulate so-called spongioplasma, which extends from the fibrous neuroglia sheath into the ganglion cell; and secondly, of the true nerve tubules, which, as has been stated, penetrate through the processes into the ganglion cell, and emerge again in the same manner. Every such primitive nerve tubule is supposed to be enveloped in a delicate sheath of spongioplasma, which is in direct connection with the reticulate spongioplasma of the ganglion cell. As has been said, I consider this view, viz. that the ganglion cell is built up of two different elements—a view which, if correct, would separate this structure from the typical cell series—as in no way warranted. Nansen's view is supported chiefly on the relations of the ganglion cells observed in *Homarus* and some other animals. Here bundles of such nerve tubules are said to be found cut through in sections at the periphery of the cell or even scattered through its whole body, which are distinguished from the spongioplasmic ground substance by their lighter appearance, and are proved to be transverse sections of bundles of such nerve tubules by their distinct reticular structure, resembling the peripheral nerve fibres, which are in like manner interpreted as bundles of the same kind.

Now it seems to me beyond a doubt that Nansen is deceived with regard to this supposed bundle of nerve tubules, and that they were nothing more than larger vacuoles, which not at all infrequently make their appearance in the protoplasm of ganglion cells. In the cells of the ventral nerve cord of *Lumbricus* I have frequently observed a large number of such vacuoles, and other observers also, *e.g.* Rohde (1887), have found them commonly in Polychætes, especially in the periphery of the cell. Rohde believes they should be regarded as collections of the ground substance, termed paramitome, of the protoplasm. In *Lumbricus* Nansen also has frequently seen these vacuoles, but is inclined to explain them as cross sections of nerve tubules. The correctness of my interpretation of these supposed bundles obtains still further support from the fact that Nansen himself has frequently pointed out their resemblance to vacuoles. The apparent reticulation of these vacuoles is well explained from the fact that if not focussed very sharply, at one time the reticulate meshwork of their floor, at another that of their roof, comes into view, giving the erroneous idea of reticulated contents. If it was really a matter of bundles of nerve tubules which passed through the so-called spongioplasma, they ought then to

appear with relative frequency cut longitudinally or obliquely in the sections, of which, however, very little is to be made out in Nansen's figures.

With regard to the alleged composition of the ganglion cells, *i.e.* of spongioplasma and nerve tubules, it may further be pointed out that Nansen was quite unable to demonstrate such a composition directly in by far the greatest number of cases. The greater number of the ganglion cells investigated by him consisted of a dense tangle of such nerve tubules, and the reticulation of their protoplasm hence depended on the cross sections of numerous thickly-packed tubules, together with their delicate sheaths of spongioplasma. Since, however, as I shall further explain when describing nerve fibres, the assumption both of nerve tubules and of their spongioplasmic sheath is untenable, there is left for ganglion cells of this kind only the simple and most natural interpretation still remaining, namely, that the reticulation of their substance does not depend upon special relations peculiar to nerve cells, but is the ordinary reticulate meshwork of the protoplasm, which merely exhibits modifications that can be in great part explained from the peculiarities in form possessed by these cells, and their being drawn out into processes. It is far from my intention to deal in detail here with the extended literature upon nerve cells. I merely thought it necessary to go rather more specially into the work mentioned, which in essential points approaches so near to my results.

Nerve Fibres

If pieces of the ischiadic nerve of the frog be investigated by teasing, after having been preserved in very various reagents, such as picro-sulphuric acid, picro-sulphuric-osmic acid, Müller's fluid, or weak alcohol (45 per cent), the following can be made out (with or without staining) as to the minuter structure of the axis-cylinder as a whole. It is always distinctly composed of longitudinal fibrils, which are about 0·6 to 0·7 μ apart. Since the thickness of the axis-cylinder varies, the number of the fibrillæ is naturally subject to change. I have seen axis-cylinders of such fineness that their width only contained four fibrillæ. The apparent fibrillæ are always finely punctate, *i.e.* they exhibit at fairly regular intervals, which are slightly farther apart than

the amount of their breadth, darker spots or points, which give the impression of faint node-like swellings.

Closer observation, particularly of such preparations as were coloured subsequently in the usual manner with gold chloride, shows in the plainest manner that the fibrillæ do not by any means run side by side in complete isolation from one another, but that they are connected by numerous pale threads crossing from one to another. These threads always arise from the nodal points of the fibrillæ already mentioned. The structure of the axis-cylinder is proved, therefore, in the clearest manner to be a reticulate meshwork, with somewhat elongate meshes arranged with tolerable regularity in a consecutive series, following the longitudinal direction of the nerve fibre (Plate VIII. Fig. 1, *a*, *b*).

Since it has occasionally been asserted that the fibrillar nature is limited to the external surface alone of the axis-cylinder, I must particularly lay stress on the fact that the same image can be observed both with a surface focus and in an accurate optical section of the axis-cylinder. There can, therefore, be no doubt of the fact, that the axis-cylinder possesses the structure mentioned throughout its entire mass. In connection with this, there is the transverse section to be considered, which we shall shortly describe, and which completely confirms the same fact.[1]

[1] I take this opportunity of being permitted to say a few words upon Apathy's remarks (1891) with regard to my preliminary communication upon the foam-like structure of protoplasm, and the corresponding structures of nerve and muscle fibres. I forego examining more closely here Apathy's view as to the structure of the axis-cylinder, since a complete solution of the question will not be possible until Apathy's full work is to hand, with its illustrations. On the other hand, I cannot but state that his objections have not shaken in the least my conviction as to the correctness of my statements. Apathy is willing to allow, on the one side, that foam-like structures are widely distributed in protoplasm, and has, in fact, often convinced himself of the fact. This, he says, is, moreover, nothing new, but was discovered by numerous investigators before me. In consequence, it was quite unnecessary that I should spend so much time and trouble in order to make it probable that the reticular structures so often described in protoplasm ought to be interpreted as in reality alveolar or foam-like structures; although to my knowledge no one has put forward this idea earnestly before me.

Nevertheless, however, Apathy believes that the reticular structures described by me, and later by Schewiakoff, in the contractile elements of

The structural relations described can naturally be observed most clearly in isolated axis-cylinders, such as one frequently obtains by teasing. On the surface of such cylinders there occasionally appeared to be present a radiate alveolar layer consisting of a single layer of meshes, which in surface view was distinguished by the simple net-like character of its meshes from the fibrous meshwork of the enclosed portion. Since, however, I only rarely observed this quite plainly, I do not lay any stress on the point.

On the other hand, I was frequently able to convince myself quite definitely in such isolated axis-cylinders that the apparent fibrillæ sometimes divide, or rather, that in places where the axis-cylinder becomes thinner (see Plate VIII. Fig. 1, *b*), the fibrillæ decrease in number. This seems perfectly natural if we regard the substance of the axis-cylinder merely as a modification of the ordinary net-like meshwork of protoplasm. The greatly narrowed portion of an isolated axis-cylinder, drawn in Fig. 1, *b*, corresponds most probably to the region of a ring-like constriction, where, in fact, according to most observers, the axis-cylinder becomes transitorily narrowed. With reference to this point,

muscle cells, are all to be set aside as artificial products, since, according to his view, the muscle fibril is a completely homogeneous secretion-product of the protoplasm, which has nothing to do with its structure.

He even goes so far in this respect as to declare that "Bütschli's methods of investigation present every possible means of producing an alveolar structure in an otherwise homogeneous colloid substance by swelling." I do not call to mind that I have employed any other methods than the usual ones, or than those used, at all events, by Apathy himself.

To interpret as artificial products, resulting from the swelling of colloid substances, the structures described by Schewiakoff and myself in the contractile elements of Arthropod muscles, certainly astonishes me greatly. Such an idea would not be very much out of place as regards the irregular structures of ordinary protoplasm; but to apply it to such regular structures as those of the contractile elements is somewhat strange. Without, however, entering here into a further defence of our discoveries against Apathy's assertion, I may be permitted to refer to Schäfer's work (1891, 1892, and 1893), and which at any rate confirms independently a great part of our observations, even if it interprets what has been seen in a different way.

A discussion of the conceptions as to protoplasm expressed by Apathy in the memoir referred to, and of the attacks which he takes the opportunity of directing against my theory, may, I think, be omitted, since the author's course of reasoning remains unintelligible to me in many ways, besides that many points emphasised in it appear to me of quite subordinate importance.

however, I must state unhesitatingly that, after having studied many such constrictions, I have observed, as a rule, no narrowing of the axis-cylinder, but have been, on the other hand, able to trace it as a strand of even and equal thickness right through the constriction.

I obtained preparations just as beautiful, in fact simply splendid, showing the structure described in the axis-cylinder, by making macerations of the spinal cord of the calf. The macerations were done partly in 10-15 per cent alcohol, stained yellow with iodine, partly in Müller's fluid. In these axis-cylinders, which, as is well known, can be particularly easily isolated on account of their lacking the sheath of Schwann, I have seen quite plainly that the meshes are not rectangular, but, as was to be expected, somewhat polyhedric, so that the apparent fibrillæ do not run absolutely straight, but are lines with slight zigzag bends (Plate IX. Fig. 3).

If now one takes into comparison the appearances shown in cross sections of the axis-cylinder of the frog, the structure already found is still further explained. The sections were made from material treated either with picro-sulphuric or picro-sulphuric-osmic acid, and had the thickness of about 1 μ. They were partly stained in Delafield's hæmatoxylin, partly with iron-hæmatoxylin, or in gold chloride as well, and were examined in water or methyl alcohol. In such preparations it may be made out in the plainest manner that the axis-cylinder does not at all show the dotted appearance of sections through isolated fibrils, but has a very beautiful net-like meshwork in cross section (see Plate IX. Fig. 4, *a-c*, and the Photographs XI. and XII.). The nodal points of the network stand out very prominently as a rule, and it also seems as if some fine granules were lodged in them. It is further of especial interest that the most external layer of meshes in the network are here again distinctly directed vertically to the surface of the axis-cylinder, and that the internal meshwork is by no means always quite irregular, but frequently exhibits a structure as of fibres running either perfectly straight, or slightly sinuously. The meshes are arranged just as we have frequently observed in other

objects, in definite tracts one behind the other, from which arrangement arises the fibrous structure.

I have observed very plainly exactly the same structure of the axis-cylinder in cross sections through the ischiadic nerve of the rabbit, prepared in a corresponding manner. Fig. 2, Plate X., gives a figure of such a preparation drawn with a camera lucida, taken from a section as thin as possible, which only showed fragments of the nerve.

Since in cross sections of the ischiadic of the frog some peculiarities can also be observed in the sheath of Schwann, I will describe them briefly. The sheath always stains very intensely with Delafield's hæmatoxylin, while the axis-cylinder, on the other hand, remains very pale. It can now be plainly observed that the substance of the sheath has a meshwork structure, consisting, in fact, of a single layer of meshes, the walls of which are directed vertically to the surface of the sheath (Plate IX. Fig. 4, *a-c*). At a spot where a nucleus is lodged in the sheath it becomes thickened, increasing at the same time to two layers of meshes, one of which then encloses the nucleus internally, the other externally, so that it comes to lie in the protoplasm. We thus find exactly the same relations as have been already described for the cells of the capillaries, and for the peculiar connective tissue cells of the ischiadic nerve.

As I did not make a special study of the substance of the medulla, I will merely remark briefly, that a net-like meshwork can be made out in it very well, both in entire isolated fibres, after treatment with picro-sulphuric-osmic acid, and in longitudinal and transverse sections of them. Just in the same way I have always found a dark sheath very distinct round the axis-cylinder, as is especially well shown in Photograph XIV. As to the relations of the two sheaths to one another, and to the medullary substance, I can only express an opinion by the way, that these three parts may well form together a single whole.

Fibres of the Nerve going to the Chela of Astacus fluviatilis

If fibres of this nerve are isolated by being teased up after maceration in iodine alcohol, it is possible to demonstrate, especially in those of medium size, structural relations which correspond completely to those of vertebrates. In the first place, they also possess a sheath, which agrees in all points with that of Schwann in the fibres of the ischiadic nerve. In optical section the sheath appears rather dark and glossy, permitting its composition out of a single layer of alveoli to be seen very beautifully (Plate VII. Fig. 7, *s*). Also, by sharply focussing the surface, the somewhat irregular net-like structure of the sheath can be recognised very plainly (*os*); in places, however, its superficial structure may also appear as a meshwork giving the appearance of longitudinal fibres. In the sheath there are large elongate nuclei (*n*), which project outwards only to a slight extent, but more strongly into the interior of the fibres (*n'*). Just as has been described in the case of the sheath of Schwann, the layer of meshes composing the protoplasm of the sheath divides in the vicinity of the ends of the nucleus into two, so that the internal and external surfaces of the nucleus are distinctly covered each by a layer of alveoli. In the thicker fibres, however, the sheath also appears to become stronger, sometimes to the extent of two or three layers of meshes. In such thicker fibres the axis-cylinder did not quite fill up the sheath, while this was always the case in thinner ones.

Now, although the structure of the axis-cylinder is very pale, it can still be made out clearly that it agrees completely with that already described for the vertebrates. The longitudinal fibrillæ are here also distinctly linked with one another by means of threads connecting them across (Fig. 7, *f*), and they show the nodal points at the places of union between the fibrillæ and the cross threads very beautifully.

The examination of cross sections of such nerve fibres proves that a distinct net-like meshwork exists in the axis-

cylinder, such as Nansen has already discovered and figured very well in *Homarus* and other Crustacea, for which reason I need only refer to the figures given by him.

In the literature there are two works, as far as I am aware, in which results have been attained that approach very closely to mine, namely, the investigations of Nansen (1887) and Joseph (1888). I therefore think I ought to point out particularly that I only subsequently came to know of these works, and thus attained the same results in an unbiassed manner. Both investigators observed the reticulation quite plainly in fine transverse sections of the nerve fibres: Nansen in numerous invertebrate animals, *Amphioxus* and *Myxine*; Joseph, on the other hand, in the medullated fibres of a number of vertebrata. The latter author, moreover, got one step farther than Nansen, since he also found, in longitudinal sections through axis-cylinders preserved in osmic, the fibrillæ frequently connected by cross threads. Nansen has never observed anything of the kind, but on the contrary has set up a view concerning the structure of the axis-cylinder which is incompatible with the existence of such cross threads. In agreement with Leydig's views (1885) as to the true nervous significance of the hyaloplasm, *i.e.* the clear intervening matrix of the framework of ganglion cells and protoplasm generally, Nansen arrived at the idea that the axis-cylinder consists of numerous fine tubules about 1 μ in diameter, which are formed of a "viscous," clear, structureless substance. Each primitive tubule is supposed to be surrounded by a thin sheath of spongioplasm. Now since the primitive tubules would be closely compressed in the formation of an axis-cylinder or of a corresponding nerve fibre, their spongioplasmic sheaths are united into a framework, since the spongioplasm is not to be regarded as "a quite firm and non-adherent substance." The spongioplasmic framework that had arisen in this manner would appear, therefore, in cross section as the reticulation described. I can agree with Nansen to this extent, that I consider it proved, from the comparison of longitudinal and transverse sections, that we are not dealing with isolated fibrils in the axis-cylinder, but with a honeycomb-like structure, the edges of which appear in longitudinal section as the supposed fibrillæ. On the other hand, the longitudinal sections show perfectly clearly that the cavities of this honeycomb certainly cannot be filled by continuous tubules, for they are divided by cross threads into numerous chambers arranged in a row, one behind the other.

Although it cannot of course be proved with absolute certainty by simple observation that these cross threads are parti-

tions which divide up the longitudinal cavities, and not threads merely, yet this seems to follow with great probability from the indubitable fact that the apparent longitudinal fibrillæ represent a honeycombed structure. When we then further see that the structure of the nerve fibre corresponds entirely to the structure of ordinary fibrous protoplasm, and at the same time are able to render probable, from a whole series of reasons, the fact of alveolar structure of protoplasm, it seems to me that the interpretation of the cross threads as partitions is proved to be the only plausible one. If we further take into consideration the great agreement between the structure of the processes of ganglion cells and that of the axis-cylinder, and also the fact that axis-cylinders may pass directly, in their entire mass, into ganglion cells, it seems to me certain that the axis-cylinder is nothing but a strand of protoplasm, the structure of which has become modified into a fibre-like meshwork in correspondence with the modification which tracts of protoplasm generally undergo when stretched out lengthways, and which is, as a rule, distinguished from ordinary protoplasm, including that of the ganglion cells, by its feeble staining powers in the usual colouring media. The latter circumstance may, however, depend principally on the small number and the fineness of the granules deposited in it, which are generally the cause of intense tingibility in protoplasm.

Although Joseph (1888), as has been remarked above, reached a step farther in observation, he remained, to my mind, far behind Nansen in the interpretation of what had been seen. In his view the reticulation observed both in transverse and longitudinal section of the axis-cylinder is a framework which is a direct continuation of that of the medullary sheath. We are thus concerned with a supporting framework to the axis-cylinder; the true nervous substance would be the intervening substance, just as Nansen also supposed. Now, although Joseph naturally found this substance always homogeneous and structureless, he yet thinks it possible to maintain the untenable view that it is in reality fibrillar. On this view the fibrillation in the axis-cylinder observed by M. Schultze and so many others would belong to this intervening substance; treatment with osmic acid is supposed to be unsuitable for rendering the real nerve fibrillæ visible. I think, however, that every one will allow that the longitudinal fibrillæ seen by Joseph are the same that M. Schultze and his successors termed the fibrillæ of the axis-cylinder, the more so as osmic acid was just the reagent most in favour for demonstrating these fibrillæ. I therefore consider Joseph's assumption of a special kind of nervous fibrillæ,

which run in the matrix, filling the supposed framework of the axis-cylinder, to be quite untenable, the more so as he never convinced himself of the existence of such fibrillæ. To enter into the dispute as to whether the substance of the framework of the protoplasmic axis-cylinder, or the enchylema itself, is the true nervous substance, seems to me quite superfluous in this place.

Although Leydig (1885) speaks occasionally of a spongy structure in the nerve fibres (especially in *Aulastomum* and *Lumbricus*), he yet openly defends the view that the axis-cylinder of the fibres of vertebrates is structureless, that is to say, that it consists of structureless so-called hyaloplasm (= enchylema), which collects in the centre of the medullated fibres, while the reticular spongioplasm forms the medullary sheath round the axis-cylinder.

A passage in Dietl (1878, p. 95) may well be taken to indicate that he had seen the net-like connections of the so-called nerve fibrillæ in invertebrates, while denying their existence in vertebrates. It is difficult, however, to become quite clear on this point, yet I consider this interpretation of Dietl's statements as correct.

Heitzmann also (1883, p. 296) speaks of a "delicate net-like structure" in the axis-cylinder of vertebrates, but apparently has not paid sufficient attention to these relations, since in opposition to Schultze and others he denies the longitudinal fibrillar structure. He therefore cannot raise any claim to be considered seriously in this question, the less so also as he gives no figures.

PART II

GENERAL PART

ALTHOUGH I have devoted much time to the study of the numerous works upon the structural relations of protoplasm, it seemed to me at first, after much reflection, almost advisable not to enter into a critical and historical examination of the subject, but to simply communicate my observations and the conclusions drawn from them. On the one hand, this subject has already frequently been treated in great detail from the point of view of its gradual development; on the other hand, I am somewhat doubtful as to the value of detailed expositions of this kind, especially in a question which is as yet so little ripe for final treatment; besides which, the great productiveness of the present time puts every one's power of assimilation to a severe test, so that brevity appears to be the ideal to be striven after.

Nevertheless, even at the risk of not being read, I made up my mind, after all, to give a compressed summary of the gradual development of the structural question. I have, as already stated, worked conscientiously through the works accessible to me, so far as I was able, without, however, wishing to set up any claim to completeness; this is, as a matter of fact, scarcely possible, especially for more recent times, in which such floods of literature have been poured out dealing with the subject. Since, moreover, we are in no way concerned with reporting carefully upon every single work in which anything is said concerning the

structure of the protoplasm of some cell or other, but only with trying to obtain information upon the different views as held by their chief exponents, and the most important grounds brought forward in support of them, no appreciable harm will arise from this incompleteness.

A. The Theory of the Net-like or Reticular Structure of Protoplasm

As is well known, the first observations upon the peculiar structures in the protoplasm of certain cells were made at a very early period. If we leave the muscle cells out of consideration, as has been done throughout this work, observations upon ganglion cells and the so-called axis-cylinders were what first brought peculiar structures into notice.

As far back as 1837 Remak found (p. 39, footnote) that the axis-cylinder of the medullated nerve fibres of vertebrates (Remak's so-called primitive band) appeared to be composed of very minute fibres, which occasionally showed nodular thickenings in their course. In 1843 he discovered the fibrillar structure of the axis-cylinder of the large nerve fibres in the ventral nerve cords of *Astacus fluviatilis*, but was not quite certain whether this fibrous strand was the equivalent of the axis-cylinder of the vertebrate nerve fibre. In 1844 he expressed himself more definitely upon this homology, and at the same time demonstrated the fibrillar nature of the ganglion cells of the crayfish, while Will in the same year also observed a concentric striation in the ganglion cells of *Helix pomatia*.

Since it is not our intention to describe in detail the further development of the question of the structure of ganglion cells and nerve fibres, we will confine ourselves to noting that, especially through the works of Remak (1852), Stilling (1856), Leydig (1862 and 1864), Walter (1863), Deiters (1865), and above all, those of M. Schultze (1868

and 1871), the doctrine of the fibrillar structure of protoplasm of nerve cells was confirmed and further developed.

Frommann, who, as far back as 1864 and 1865, occupied himself with the careful investigation of the fibrous structure of ganglion cells, and chiefly sought to show that the fibres of the protoplasm arise from the nucleus and nucleolus, came in 1867 to the conviction that the fibrous structures were not only a specific peculiarity of nerve cells, but probably formed a universal peculiarity of protoplasm. Since his work of 1867 is unfortunately not accessible to me, my judgment is limited to what he himself (1884) and others have reported on the subject. As has been said, Frommann had, on the one hand, observed similar fibrous structures, taking their origin from the nucleus, in numerous other kinds of cells also, but he further occasionally remarked filamentous connections between the granules of the protoplasm, and similar ones between those of the nucleus. Supported by these observations, the question seemed to him even then worthy of consideration, whether a network might not unite the granules of the protoplasm, and whether the latter might not themselves be merely the nodal points of such a network. Although, therefore, Frommann in 1867 had not, properly speaking, by any means observed the reticular structure of protoplasm, yet the real merit is due to him of having pointed out the possibility of such a structure, and of having at the same time recognised the structural relations already discovered in ganglion cells, as being probably a universal peculiarity of protoplasm.

Simultaneously and independently J. Arnold (1865 and 1867) had also observed fibres united into a network in the ganglion cells both of the sympathetic and of the spinal column, and had seen fibres running out on various sides from the minute granules of the protoplasm. He also laid stress on the connection of these fibres with the nuclear corpuscles, or rather with the fibres of the nucleus.

Fibrous or striated structures had, however, already been seen at quite an early period in certain epithelial cells. Friedrich in 1859 described the striated structure of the ciliated cells of the *Ependyma ventriculorum* of man. In

1866 a corresponding structure was also recognised in the ciliated cells of the gut of *Anodonta* by Eberth and Marchi, and it was shown most convincingly that there was an actual differentiation of the protoplasm in question. Marchi was able to observe a similar fact in the cells of the ciliated epithelium of the labial tentacles and the gills of this mussel. Since that time numerous observers have established the fact that a striation is widely distributed in ciliated cells, if not present universally. Special mention should be made of the works of Stuart (1867), Arnold (1875), Eimer (1877), Nussbaum (1877), Engelmann (1880), Gaule (1881), and Frenzel (1886).

Even before these observations upon the cells of ciliated epithelia had been collected, Leydig had already, in 1854, drawn attention to the fact that the non-ciliated epithelial cells of the gut of Isopods had a similar longitudinal striation. Henle (p. 53) and Pflüger observed in 1866 a partial fibrillation in a longitudinal direction of the protoplasm of the epithelial cells clothing the efferent ducts of the salivary glands of vertebrata. At a later period numerous investigators, especially Pflüger (1869 and 1871), and Heidenhain (1868, p. 21; 1875), occupied themselves in extending these observations. It was established thereby that the striated structure of protoplasm is a phenomenon of very widespread, in fact one might say of almost universal occurrence in the columnar epithelial cells of the skin, intestine, and numerous glands.

As has been remarked above, Frommann and Arnold had really only observed more or less isolated filaments, which here and there showed a net-like union. Frommann's more far-reaching supposition was a hypothesis, the correctness of which could only be proved by future observations. The works that appeared soon afterwards were evidence of the correctness of this supposition. Pflüger found (1869) that the protoplasm of liver cells was fibrillar, and in his detailed work the structure is even represented as a beautiful fibrous network, since the fibres are made to anastomose with one another. It is interesting also to find that he expresses himself to the effect that the fibrillar axis-cylinders, which

are stated to be in direct connection with the liver cells, expand into these cells by anastomosis of their fibrillæ. The networks drawn and described are rather coarse, as was in general the case with all the early observations upon protoplasmic structures; on which account we can only be dealing in all these observations with a part merely of the true structure, that is to say, in all probability with a coarsely vacuolar structure in certain protoplasms—a point which cannot now be decided with certainty in many cases.

In 1870 Kupffer described the protoplasm of *living* follicle cells of the egg of *Ascidia canina* as having a beautiful reticular structure, and was also able to see that the most external meshes, as well as those round the nucleus, had a radial arrangement. He regarded the structure as a breaking up of the protoplasm into "vesicles." I estimate the diameter of the alveoli figured at about 2 μ, for which reason it is probable, even if not quite certain, that he observed the true protoplasmic structure.

In 1873 I described the flat epidermic cells of the *Pilidium* as having a fine net-like structure in surface view; the study of the optical section showed that this depended on a finely-chambered or alveolar structure of the protoplasm. Although more accurate measurements of the structural relations were unfortunately not made, nevertheless I am of opinion that this was not the real minute structure of the protoplasm, but a coarser one produced by vacuolisation.

In proceeding to criticise briefly the important works published by J. Heitzmann in 1873 upon the structure of the protoplasm and the cell—in fact, of the whole organism—I find myself in rather a difficult position. For if one takes into consideration the degree of perfection which had been attained by optical apparatus at the commencement of the year 1870, and further, the great difficulties presented by the very objects, namely, small Amœbæ, which Heitzmann made the basis of his views upon the structure of protoplasm, it is difficult to overcome a certain amount of doubt which arises with reference to his observations. Heitzmann found a reticular framework in the protoplasm of small

Amœbæ during life; also in that of the colourless blood corpuscles of Astacus, Triton, and man, and in colostrum corpuscles. With regard to the observations upon blood corpuscles, I am certainly of opinion that Heitzmann, as also Frommann afterwards, has partly taken *post-mortem* appearances, of the nature of vacuolisation, for normal reticular structures; a proof of this is his statements concerning the alleged differentiation or new formation of nuclei in these blood corpuscles under the eye of the observer. For there can be no doubt in the mind of any experienced observer that this is simply a case of the nuclei becoming distinct, as happens regularly after death.

As for Amœbæ, I am inclined to believe that in the same way Heitzmann observed forms in which the protoplasm was thickly vacuolated, for I consider it scarcely possible that he was successful in tracing out in the living object the true reticular structure in the protoplasm of Amœbæ with his optical apparatus. It is also very apparent from Heitzmann's description that he schematised and speculated in a most lively manner, since he extended the mere indications of reticular structure seen by him to the whole protoplasm. I therefore cannot but ascribe a strongly hypothetical character to his work of 1873, which, moreover, received its punishment in not obtaining the consideration it deserved. In addition to this, Heitzmann forthwith expanded his observations upon the reticular structure of protoplasm into a theory concerning all living matter, which frequently clashed strongly with the facts. His description of the origin of reticular protoplasm by vacuolisation from the so-called primitive compact living matter, was altogether hypothetical, and the alleged proofs were undoubtedly entirely uncertain. His efforts to show that protoplasm, nucleus, nucleolus, and even intercellular substance, were merely modifications of the one living matter, and that therefore there was an easy transition from one to another, stood in opposition to a great number of well-established experiences, quite apart from the lack of any substratum of fact upon which such far-reaching conclusions might be built up. Hence these

comprehensive and very dogmatic assertions could only be of harm to Heitzmann's theories, however much they might be proved to be correct by later observations. In the same way the attempt to eliminate the cell entirely as an elementary unit in the building up of organisms, could only increase the hostility of his opponents. Since we must discuss more closely later on the theory of the structure of protoplasm, developed by Heitzmann as far back as 1873, and again, with greater detail, in 1883, we may content ourselves in this place with these remarks.

In 1875 Frommann also, in the investigation of the blood corpuscles of Astacus, arrived in many points at the same results as Heitzmann. Although Frommann certainly observed fine networks in the living blood cells, even if they are not very apparent in his figures, yet it appears to me just as certain that the alterations he claims to have seen in the two kinds of blood corpuscles—the gray ones and the so-called granular cells—were nothing more than *post-mortem* appearances. Thus I consider it beyond a doubt that the blood corpuscles figured by him on Plate XV., Figs. *f, g, h, k, p,* and Plate XVI., *a-g* and *k-v*, were dead, and that therefore the vacuolisation of the yellow granules of the granular cells, described already by Heitzmann, the formation of granules and networks from them, and finally the alleged new formation of a nucleus in the granular cells—that all this only depended on the gradual death of the cells. In the ganglion cells also of the crayfish Frommann was now able to clearly convince himself of the existence of a reticular structure, and he declared that the protoplasmic granules in them were only the nodal points of the network. With regard to the relations between the framework of the nucleus and that of the protoplasm, Frommann, as before, was essentially in agreement with Heitzmann, since he energetically defended their direct connection, just as Arnold also had done already.

In the same year, 1873, in which Heitzmann described the reticular structure in the protoplasm of Amœbæ, the botanist Velten, who also worked in Vienna, communicated the results of his observations on the streaming protoplasm

of the vegetable cell. More plainly than by Heitzmann there is shown in Velten's communication the influence upon the Vienna biologists of the work published by Brücke in 1861, in which is set forth the necessity of an organisation in the protoplasm, *i.e.* of its being made up of more solid and more fluid parts. Velten found the living protoplasmic strands, which traverse the cell sap (more particularly in *Cucurbita pepo*), to be frequently of a finely fibrillar structure, the spaces between the fibrillæ showing the same low power of refraction as the cell sap. His interpretation of his observations is as follows. The protoplasm is made up of a system of fine canals filled with watery fluid, which are quite shut off from the cell sap, and traversed frequently by "transverse partitions." The configuration of the chambers so formed is "constantly altered by the movement of the protoplasmic walls." The granules of the protoplasm are to be found in or on the walls, not in the intervening fluid. It may happen, however, under abnormal conditions, that granules get into the latter, where they then exhibit lively molecular movements. Velten pointed out particularly that this canal system of the protoplasm was in no way to be confused with "a spongy framework." While in 1873 he believes he has observed these structural relations only in cells subjected for some length of time to weak induction-currents, in 1876, when he also gives a figure, this is no longer definitely stated. His statements as well as the figure given in 1876 prove quite definitely that Velten really had observed the fibrillar structure of the living and streaming protoplasmic strands, and had also seen plainly the net-like connections of the fibrillæ. It appears, however, natural and beyond all doubt, that he could only have seen distinctly a few strands and threads of the meshwork, and has therefore made the width of the meshes much too great—a fact which, as remarked already, is equally true of the older observations.

Kupffer observed in 1874 the reticular structure of the protoplasm quite plainly in the salivary glands of *Periplaneta orientalis*, both in the fresh condition and after treatment with the most various reagents. Since the width of the

meshes was about 0·002 mm. after treatment with concentrated caustic potash, in which the network swells up, he very likely had the true protoplasmic structure before him. He found the epithelial cells of the efferent ducts to be of a longitudinally fibrillar structure. It seemed to him certain in the case of this object that the granulation of the protoplasm could be referred to the reticular structure. In 1875 he extended his investigations more especially to the liver cells of the Vertebrata, and saw in them a net-like framework, which frequently became more compact round the nucleus. As before, he found that the structure could be made out even in the fresh condition, and only became more distinct under the action of reagents. In fact, he thought he had observed slow movements in the threads by warming the fresh liver cells on the slide.

I think it would lead us too far if we tried to follow out step by step the gradually increasing confirmations of the reticular structure of protoplasm. In the following lines, therefore, I will proceed more cursorily, and only lay especial stress upon the more important and extended observations.

In 1876 Schwalbe became an adherent of the theory of reticular structure from his own observations on the colourless blood corpuscles of the crayfish, *Triton*, and various ganglion cells. He also traced these structural relations in objects as fresh as possible, and arrived at the important opinion, which was enunciated here probably for the first time, that the structural relations of the nerve cells observed by M. Schultze and his predecessors depend on regular arrangement of the trabeculæ of the network. "From all this it is obvious that isolated fibrillæ are not to be assumed in ganglion cells," was Schwalbe's conclusion from his experiences. It is further of interest to note that he considered net-like connections of the fibrillæ of the axis-cylinder as quite possible.

In the same year Trinchese also described the net-like structure of the protoplasm of various cells on the occasion of the anatomical investigation of an opisthobranch (*Caliphylla*), and of the connective tissue corpuscles of the frog

from preparations. Since the width of the meshes described is on the whole rather great (0·0027 mm. in the figure provided with a scale of measurement), and the contents of the meshes themselves are drawn as being finely punctate, it seems rather doubtful if the true protoplasmic structure was seen.

Doubts may also be raised with respect to the net-like structures described by Strassburger (1876) in the protoplasm of vegetable cells. Both in his treatise on protoplasm and in the second edition of his book on cell formation and cell division, it is almost exclusively the coarser vacuolated structures which are described as reticular. This follows with tolerable certainty from the size of the meshes, the width of which varies, as a rule, from 0·005 to 0·01 mm., though occasionally sinking to 0·0015 mm. The fact, therefore, of Strassburger having occasionally seen the true meshwork of the protoplasmic structure, is certainly by no means excluded. But one thing appears especially noteworthy, namely, that he especially remarks (*Zellbildung*, p. 217) that the net-like structure of the protoplasm is in reality a "dividing up of the protoplasm into chambers, in which the cavities of the chambers are filled by a more or less concentrated solution of albumen." The distinction which he seeks to draw in his treatise on protoplasm between vacuoles and chambers in the granular protoplasm is not quite clear to me. Vacuoles are said to be drops of a watery fluid in the protoplasm, but the chambers, on the other hand, are formed by the protoplasm filling up the cell fluid in the form of thin plates connected like a network. This conception of the reticular structure seems to me the more remarkable from the fact that Strassburger gave it up soon afterwards, and in its place adopted the idea of a net-like or spongy structure.

As we have seen that Schwalbe had already tried to refer the peculiar structural relations of the ganglion cells to their reticular nature, it is especially interesting to note that Eimer in 1877 brought the longitudinal striation of the ciliated cells of various objects into connection with the special arrangement of the usual reticular meshwork. That is to

say, he observed distinctly that the longitudinal fibrillæ were frequently connected with one another into a network.

As has been indicated above, as far back as 1878 I expressed the opinion that the reticular structures described might be *alveolar*, or in other words, that protoplasm has a froth-like composition.

In two memoirs of the years 1878 and 1879 Klein confirmed the net-like structure of protoplasm for very many cells of Vertebrates, and declared himself in favour of Frommann's and Heitzmann's views with regard to many points. This was especially the case with regard to the intimate connection and transition which both he and the latter authors assume between the framework of the nucleus and the protoplasm. Indeed he goes so far as to believe, with Stricker, that fusion frequently takes place between the nucleus and the protoplasm, especially in the colourless blood corpuscles. The nucleus is only a portion of the cell protoplasm marked off by a perforated membrane. This agrees essentially, as has been said, with the views developed by Heitzmann and Frommann. Although I do not wish to assert that everything which Klein describes and figures is really the true protoplasmic structure (which is frequently very doubtful, especially in the case of gland cells), yet this is the case in many of the structures described. Like Eimer, he made out quite correctly the fact of the longitudinal striation being only a modification of the ordinary reticular structure.

In opposition to these observations, Arnold (1879), in a discussion of the investigations upon cell structures which had been made up to that time, expressed himself as still doubtful upon the fundamental question whether filamentous or reticular structures were present in protoplasm or not; "whether the nuclear filaments are connected with one another; whether such a relation exists between the filaments of the body of the cell; to what extent the reticular arrangement of the filaments can be regarded as generally typical; and whether, finally, an invariable connection exists between the filaments of the nucleus and those of the pro-

toplasm; these are questions which still require the most careful observation in order to obtain a final answer." At the same time Arnold confirmed the existence of filamentous structures in the cells of numerous tumours.

On the botanical side Schmitz (1880) came forward to support energetically the universal distribution of the reticular structure of protoplasm. He observed it in material preserved with concentrated picric acid. It can be affirmed with great certainty that Schmitz had not seen the true minute structure of protoplasm, but only more coarsely vacuolated structural appearances, just as Strassburger had done. For instance, he describes the original protoplasm as being in general finely punctated, and the reticular structure as first arising in this. The frequently repeated remark that the cell sap cavity arises by flowing together of meshes of the protoplasmic network also expresses the same view. Schmitz is, however, of the opinion that the punctation of protoplasm which is not distinctly reticular is only the optical expression of a very minute net-like structure, and that, therefore, both the modifications of protoplasm pass one into the other. On the other hand, he tries to refute any interpretation of the structures observed as phenomena of coagulation, or artificial products of any other kind.

Frommann published, from the year 1879 onwards, a series of communications on his further studies of protoplasmic structures, which it would take too much time to even enumerate here. They extended to various cells of the animal body, such as cartilage, ganglion cells, epidermic cells, and blood corpuscles, as well as to various vegetable cells. In 1884 he brought together the greater part of these investigations, and set them forth with increased accuracy. We will, therefore, attempt to give a rather more exact account of the opinion which Frommann has formed upon the ground of his numerous studies, with the help of his description of 1884. It must first be pointed out that he found reticular structures everywhere in the protoplasm investigated. The network or framework was not, however, one connected together on all sides and at all points; on the contrary, isolated portions of it frequently occurred. As a

rule, it was very changeable, since spontaneous and continual alterations took place in it. Fusions of filaments and granules of the network were frequently to be observed, but on the other hand the nets might also break up into granules. Indeed it could even be observed that all the structured portions might vanish transitorily, so that the protoplasm became quite homogeneous. In the reverse way such homogeneous protoplasm could change back into reticular by reappearance of the framework. By fusions such as have been mentioned above, the walls of vacuoles, and even entire nuclei, were formed. In this way he again supported the view here that nuclei might arise under the influence of the induction-current, or spontaneously, in the protoplasm. As before, he maintained the direct connection between the framework of the nucleus and the protoplasm. The nuclear membrane is said to be interrupted by finer or coarser gaps for the passage through it of the filaments of the network. In fact, it is really, on the whole, only a thickening of the framework. In the same way the surface of the cell is not surrounded by a continuous layer or lamella of the framework, but limited in the same manner as the surface of the nucleus.

The view of Schmitz with regard to the nature of vegetable protoplasm was adopted soon afterwards by Reinke and Rodewald (1881 and 1882) for the protoplasm of *Æthalium septicum*, and supported by further proofs. From experiments which they made by compressing the objects, both investigators concluded that the protoplasm of the Æthalia, especially that of the fructifying cakes which collect on the surface of the tan, consisted of a firm ground substance and a fluid enchylema. They succeeded in obtaining 66 per cent of fluid enchylema by forcibly pressing it out, while the substance of the framework remaining behind formed a solid and rather dry cake. With a centrifugal, however, it was not possible to separate the two substances. On the ground of these and other experiments, they assumed the presence of a spongy framework of plastic and contractile nature in the protoplasm, which was permeated by the fluid, albuminous enchylema, and shut

off from the exterior by a thin enveloping layer formed of the substance of the framework. Reinke is inclined to admit that the spaces filled by the enchylema "become partitioned off here and there by delicate diaphragms of the substance of the framework," in which statement we may perceive an approach to the theory of an alveolar structure. In the figures which were added by Krätschmar to the work of 1883, the reticular structure of the protoplasm of *Æthalium* is represented rather fine and indistinct, but is quite recognisable.

From the year 1882 there come a few more contributions from other observers. Thus Freud again confirmed the presence of net-like anastomosing fibres in the ganglion cells of *Astacus fluviatilis* without, however, having seen the real minute protoplasmic network; he therefore gave his complete adherence to Schwalbe's conception of the structure of ganglion cells. Paladino found reticular structures in the cells of the endothelium of the Arachnoidea, and Schmidt in the cells of the pancreas.

Strassburger also now (1882, *Zellhäute*) came into agreement with the more recent results of observation, namely, that the structure of protoplasm was reticular, but in the work which he published at the same period upon the processes of division in the cell nucleus, etc., he represented the protoplasm as a tangle of short twisted fibres, after the manner of Flemming. Externally it was supposed to be enclosed by a so-called "cuticular layer" (Hautschicht), which arose by narrowing or obliteration of the meshes of the framework, just as Schmitz had already assumed.

1883 brought with it two works of great importance for the problem in hand; first, the extensive investigations of Leydig, which comprised observations upon very numerous histological objects, and were amplified by a work that appeared in 1885; and secondly, the investigations of E. van Beneden, which were confined to the sexual organs and sexual products of *Ascaris megalocephala*.

Leydig was able to observe distinctly the reticular or spongy structure of the framework everywhere, both in fresh

and fixed protoplasm. The so-called protoplasmic granules were in great part merely the nodal points of the framework, but there were frequently also numerous granules of various kinds present, which lay originally, at least, in the substance of the framework. The fact that the striated, radiating, and confused fibrous structures, which were frequently observed in the protoplasm of certain cells, were only modifications of the spongy framework was quite certain in his opinion, and was clearly proved by their frequent transitions into ordinary protoplasm. In consequence of this view, which was only occasionally slightly shaken by his referring to vacuolar protoplasm (1885, footnote on p. 2), he arrived, like Frommann, at the opinion that the surface of the protoplasm must be *porous*, and interrupted by finer or coarser gaps, which were subject to great change in shape and size. He therefore conceives of the surface of the cell as porous, somewhat in the same way as that of a bath sponge. With this is connected the fact that the intervening substance or contents of the framework—his "hyaloplasm"—must be "soft, clear, and semi-fluid," and in any case not capable of being mixed directly with the surrounding water, since he ascribes to it certain curious peculiarities, as a further consequence of the conception just discussed. Thus the hyaloplasm is supposed to "creep out, as it were," from the framework, and form the pseudopodia of Protozoa or other cells; it would further form in a similar manner (1) the sensory bristles, knobs or hooks, the auditory setæ, the visual rods, and the real nervous substance in general; (2) the contractile material of cilia and muscles; (3) the homogeneous substance of the cuticular layers; and (4) certain secretory masses.

From this conception it follows at once that Leydig sees in the hyaloplasma the real living, contractile, and nervous substance, while the framework—his *spongioplasma*—must only perform the function of support. But he did not remain perfectly consistent with himself, since in 1885, p. 105, he believes he has seen the cilia on the epithelial cells of the olfactory mucous membrane of the cat, arising as processes of the *spongioplasma*, and on p. 161

he even ascribes to the cilia a composition of both kinds of protoplasm.

Since we shall frequently have to discuss Leydig's views again later on, this short exposition of his opinion will suffice for the present.

E. van Beneden, in his investigation of the protoplasmic structure of ova, etc., of Ascaris, was at first, at any rate, on what is in my opinion the right tack, since he was inclined to refer the net-like structure of the protoplasm to the existence of numerous vacuoles, and pointed to *Actinosphærium* and similar forms for comparison (p. 82). But he was doubtful whether the vacuoles which produced the reticular structure were entirely shut off from one another. In the further course of his work, however, this view was withdrawn altogether, and in its place another appeared, which seems to have been put forward as the result of the study of the interesting structure of the spermatozoa. Here, as in the general part dealing with protoplasmic structures, van Beneden consistently terms the fibril the structural element of protoplasm. The protoplasm is said to consist of nodular fibrils and an intervening substance. The fibrils are orientated in the three directions of space, and their nodal points, which represent actual thickenings, are connected by finer fibrillæ. In this way there results a "protoplasmic trellis work" (treillage). The fibrils are contractile, and hence the framework is capable of alteration. It would appear doubtful whether the intervening matrix is identical with the contents of the larger vacuoles; if this is the case, a special wall with extremely narrowed meshes must be formed round the vacuole, just as Heitzmann and Schmitz had already assumed.

Pfitzner, in 1880, when giving an account of the epithelial cells of the salamander larva, described a meshwork in the protoplasm which at the surface of the cell passed distinctly into the radially striated border; and in 1883 he gave a good description of the reticular structure of the red blood corpuscles of Amphibia, publishing later (1886) a most excellent figure. At the same time he developed his theoretical views as to the origin of such structures, which

were supposed to be of two kinds, the one "passive," *i.e.* such as are produced by vacuolisation, the other "active," the result of the granules becoming grouped into filaments or nets. It will be sufficient here to have mentioned this view, since in the sequel we must return to it in more detail.

Without taking special notice of the occasional descriptions given by Affanasiew and Langley of reticular structures in liver cells, we proceed at once to the extended investigations which Carnoy in 1884, 1885, and 1886 published upon the subject of protoplasm. Since with regard to the structure his standpoint is entirely that which was developed by Heitzmann, and which has been reverted to essentially in the views of Schmitz, Leydig, and van Beneden, it does not require to be set forth in detail here. Living protoplasm was but little investigated by Carnoy; hence he nowhere discusses the very important question how the occurrence of apparently quite homogeneous protoplasm is to be explained on the general hypothesis of the reticular structure.

Carnoy also recognises the fact of fibrous and radiate structures having originated by modification of a perfectly reticular structure. The framework is definitely regarded by him as solid, or at least very viscid, and contractile; the intervening matrix, on the other hand, is supposed to be "hyaline and viscous." Nevertheless I certainly believe that Carnoy also has partly mistaken coarsely vacuolar structures for the real fine protoplasmic structure; this is quite evident from the fact that he identifies the network of coarse trabeculæ in the protoplasm of *Noctiluca* with the finer protoplasmic framework, and regards the cell sap of this Protozoon as equivalent to the enchylema or intervening matrix of protoplasm. Moreover, I also infer this from the fact that Carnoy frequently represents the enchylema finely granulated, which leads one to conclude that at times he only saw the coarser network, and regarded the finer one as granulations. In opposition to Leydig, he incorrectly makes out the granular contents of the protoplasm to be located always in the enchylema, which is supposed to frequently contain even the coarser

deposits. Since Carnoy's investigations of 1885 and 1886, upon the cells of numerous Arthropods, and the sexual products of Nematodes, did not make any essential alterations in his fundamental conceptions, but rather confirmed them for these objects in every way, there is no need to go more specially into these later works.

As has been stated already in the Introduction, in 1885-86, when giving a description of the reticular protoplasmic structures of *Noctiluca* and some Rhizopods, I defended the standpoint I had already taken up in 1878, namely, that we are not dealing with a reticular, but with an alveolar or froth-like structure.

As far back as 1882 Flemming had expressed the opinion, with regard to the reticular structure described by Klein in certain gland cells (especially the goblet or mucous cells), that the relatively coarse reticular structure of the secretion masses of these cells have in any case nothing to do with the true minute structure of protoplasm. I must declare myself entirely of this opinion. The comparison of various works which have appeared since upon this subject—such as the investigations of Schiefferdecker (1884), List (1885, 1886), Paulsen (1885, 1886), Zerner (1886)—is altogether in favour of this view. From these results it seems to me beyond doubt, as has been said, that we have to deal here with coarsely vacuolated structures, the origin of which from the finely reticular protoplasm of the original gland cells is still in need of being further cleared up. The descriptions of List especially, make it quite clear that the so-called stalk of the cells still consists of the original finely reticular protoplasm; the *theca* also seems to be merely a continuation of the latter. The chief question of which a solution is required may be stated as follows: does the mass of the secretion, with its coarsely reticular structure, arise by direct modification of the original protoplasm, or is it a secreted vacuolar mass?

As has been pointed out several times already, it is frequently, in fact as a rule, very difficult to decide, whether the reticular structures described by earlier observers were really the minutest protoplasmic structures, or whether they

depended on coarser vacuolisation. Since both have a very similar appearance, it is only possible to arrive at a true decision on this point by a knowledge of their actual dimensions, since we found throughout that the meshes of the true protoplasmic structures scarcely exceed 1 μ in width. I am, therefore, obliged to consider the reticulum, for example, drawn by Sedgwick (1886) in the egg of *Peripatus capensis* as a coarser one which does not correspond to the true structure of protoplasm, since the width of the meshes is frequently drawn very coarse, and even in the finest parts does not sink below 2 μ. I believe, therefore, that in this as in many similar cases the trabeculæ of the so-called reticulum would themselves display the finer protoplasmic structure. With regard to the general conception of the protoplasmic network Sedgwick approaches most closely to Heitzmann and Frommann.

As for Protozoa, Schuberg (1886) for *Bursaria*, etc., Bütschli and Schewiakoff (1887 and 1889) for numerous *Ciliata*, and Fabre-Domergue (1887) for the same order, have in recent times been more especially deserving of notice. With regard to the views of Künstler (1882 and 1889), who followed out carefully the reticular structure in the Flagellata, they must be gone into more closely farther on. In histology, moreover, so many statements lie scattered about in various works, that it does not seem advisable to bring them together in full. Only Nansen's work (1887) upon the reticular structure of ganglion cells, which has already been discussed above (p. 147), may here be referred to again.

B. Summary of Divergent Views

1. *The Theory of the Fibrillar Structure of Protoplasm*

In opposition to the theory of the reticular framework of protoplasm, some investigators still hold fast to the conception which was so prevalent at an earlier period of the investigations, namely, that we have to deal with fibrils which are isolated, or at least only occasionally connected secondarily, in the intervening matrix of protoplasm. In fact, we have seen already that not a few authors of the works described briefly in the foregoing section speak of fibrils of protoplasm, though at the same time admitting that these fibrils anastomose as a rule in a net-like manner, even if they occasionally occur isolated.

The assumption of a fibrillar structure in protoplasm obtained the most definite support in Flemming's book of 1882. The earlier works of Frommann, Arnold (1879) and Schleicher (1879, upon the composition of the protoplasm of cartilage cells), can also be regarded as to a certain extent precursors of such a conception. Schleicher especially gave a most definite denial to the alleged existence of reticular structures in the protoplasm of cartilage cells, in opposition to Heitzmann and others, but frequently observed, on the contrary, isolated filaments in their living protoplasm.

It cannot indeed be asserted that Flemming affirms definitely the fibrillar nature of protoplasm; his standpoint is rather a sceptical one towards Heitzmann, Klein, and others. Thus he admits a net-like connection of the filaments of the protoplasm as "fully possible for many objects, but can, however, find no certainty for the fact" (p. 58). The

objects seemed to him to be too much on the border-line of visibility to obtain a definite decision. In any case, from his numerous observations he was more inclined to the assumption of a fibrillar structure, and also considered the multiplicity of the structures too great to class them all together under the conception of a continuous reticular framework (p. 64), which seemed to him unproven and improbable. That the so-called protoplasmic granules were only the nodal points of a reticular framework hence seemed to him in like manner not proved. On the other hand, Flemming considered it certain that protoplasm shows as a rule a filamentous structure, although the temporary appearance of homogeneous protoplasm might be quite possible. Such protoplasm would originate by "the filaments . . approaching until they came in contact, and perhaps becoming fused for a time" (p. 66). The so-called intervening matrix, or his "interfilar mass," he regards as possibly fluid, but it might also possibly be "a yielding solid," since after reagents it sometimes appeared finely granular. I think, however, that the fine granulation of the so-called interfilar mass was in most cases the actual fine reticular structure, which he never definitely observed.

It may, however, be asked how Flemming, so careful an observer, and provided with the best apparatus, could frequently declare that he was "never" able to convince himself for certain of the reticular nature of protoplasm, and hence felt doubtful about it. I think, however, that, both from his chief work of 1880 and from his treatise of the same period upon the structure of the cells of the spinal ganglia, the conclusion may be drawn that Flemming reposed rather too much confidence in certain apparatus that were new at that time, namely, the Abbé's condenser. In both memoirs passages can be found from which it is obvious that Flemming as a rule conducted his investigations with very "bright" light from the Abbé's condenser, and without any diaphragm (see p. 43; spinal ganglion cells, p. 15), and he cherishes the view that the images obtained by such means quite determine the point. With "worse light," however, he saw the reticular pattern of the

protoplasm. I must say I think that Flemming was in error when he regarded the image obtained with a bright light and widely open diaphragm as the more correct; for, as has already been pointed out frequently by others, the distinctness of the structures suffers very much from intense illumination, which of course receives a natural explanation from the fact that with a strong illumination our eye is no longer able to distinguish the relatively slight differences of light and shadow.

I am therefore not at all of Flemming's opinion, that the net-like connection of the filaments or fibrillæ which becomes apparent on diminishing the illumination is a result of the image becoming indistinct, so as to produce the effect of the filaments which run over one another appearing connected together. As a rule, it certainly cannot be asserted that the microscopic image is rendered less distinct by diminishing the illumination; on the contrary, any one can easily convince himself that it thereby becomes much more distinct and sharp. In any case the filaments running at a higher or lower level could not lie simultaneously in the plane of distinct vision, while net-like connections of the threads in the same plane of focus can frequently be demonstrated with the utmost certainty. All these reasons place it beyond a doubt in my mind that Flemming's dislike to the idea of a reticular framework is to be referred in the main to a false estimation of the correctness of the microscopic image.

To this must be added a further reason, which I will proceed to discuss rather more in detail. In studying the reticular framework, a more or less confused fibrous structure is usually very prominent. This depends on the fact that now in one place, now in another, some of the walls of the meshes are arranged for a greater or less distance in a series one behind the other to form a sinuous line, and thus give the impression of lines of some length. Now it can be shown easily that the eye is better able to observe delicate lines when they are long than when they are short, so that the greater the distance for which the tracts of the network have a linear arrangement in rows, the plainer

they become. On this, therefore, depends also the fact that the pronounced fibrous structure of the ganglion cells, and the striations of the epithelial cells, axis-cylinder, etc., were discovered at such a relatively early period, while the reticular structures were not discovered till much later. If a system of long parallel lines be drawn at equal distances apart, and joined together by vertical, irregularly arranged connecting lines of equal thickness, as shown in Fig. 6, Plate XII., the following fact can be observed from a consideration of the drawing. When the figure is looked at from a moderate distance, so that it can be plainly discerned, and then the interval between it and the eye gradually increased, a distance is finally reached in which only the long parallel lines can still be plainly distinguished, while the cross connections, on the contrary, have disappeared from the vision of the observer.[1]

Just the same state of things is presented by the microscopic image of an axis-cylinder, which gives in my opinion a sufficient explanation of the fact, that the longitudinal fibrillæ were discovered here at such a relatively early period, while their cross connections were not seen till so late, and even now require to be studied carefully and to have their structure rendered very distinct, if they are to be clearly observed. The same fact is true, however, of the protoplasmic reticulum generally. If a drawing of such a structure be made, at a certain distance the true filaments of the reticulum will become more indistinct, and finally only the thicker and darker nodal points will remain, provided they are sufficiently darker than the filaments of the network, so as to produce, of course, the appearance of granulation. If, however, certain tracts of the network are ranked one behind the other in a line for some distance, they will remain distinct for a correspondingly longer time, and one

[1] It is also possible to observe at the same time the vanishing of the longitudinally directed shorter lines, from which, as has been said, it follows that, other conditions being equal, the distinctness of the lines varies with their length. The observations described are just as successful, in fact even better if anything, if the figure be approached gradually from a greater distance.

obtains the appearance of isolated filaments in a granular matrix.[1]

The same objections which I have just raised against Flemming's view of the fibrillar structure of protoplasm, must of course also apply to the corresponding descriptions of earlier and later investigators. For ganglion cells H. Schultze (1878) and Rohde (1887) declared themselves of this opinion. In the same way Pfeffer (1886) and Pflüger (1889) have assumed the fibrillar structure, without, however, having brought forward any investigations of their own upon this point. Pflüger especially expressed himself very plainly. The gelatinous condition of the cell contents represents according to him "a mixture of an absolutely fluid with an absolutely solid material." The solid substance is supposed to be partly granular, and partly, on the contrary, at any rate in its chief mass, a feltwork of very minute filaments (p. 30).

Of a similar opinion is Ballowitz (1884), who in like manner believes protoplasm to consist of interwoven, contractile filaments, which are not, however, connected together, while Rabl (1889) adopts this conception to the extent of assuming the presence of isolated fibrils at certain times at least, especially during the division of the cells, when they appear in the form of radiating systems. In the

[1] In his most recent work (1891, *Archiv. f. mikroskop. Anat.*, Bd. xxxvii. p. 736) Flemming expresses himself as follows upon protoplasmic structures: "I am one of those who, reasoning from visible phenomena, assume a real formed structure in the cell, even though it may not be fixed or permanent, and who cannot agree with the opinion that the cell is an emulsion, and the fibres that can be made out in it only the expression of streaming movements." A more detailed discussion of this casual expression of opinion, in so far as it would have reference to my conceptions, seems to me unnecessary, since the whole of the present work may be taken as a fundamental contradiction of it. Only the uncertainty of such expressions as "formed structure," which "is not fixed or permanent," may here be pointed out. I hope that Flemming will convince himself in these matters also of the correctness of my views in principle, just as he has with regard to the question of nuclear division. I must not omit to point out the fact that he frequently speaks of reticular fibres in protoplasm in the work cited, but in his figures he depicts tangles of undulating fibrillæ without distinct net-like connections, just as he has usually done. That this in no way corresponds to the reality is sufficiently obvious already from the investigations of my predecessors.

resting condition of the cell, however, these fibrils are supposed to be connected together in a network, as is also the case with the nuclear framework.

Finally, the fibrillar structure has found an eloquent defence in a work of Camillo Schneider which has appeared recently (1891). Since the considerations urged by him are especially directed against my conception of protoplasmic structures, I must examine them rather more in detail. Schneider has investigated partly the same objects as I myself studied, viz. the eggs of sea-urchins and *Ascaris*, *Vorticellæ*, *Trichoplax adhærens*, etc. He finds everywhere in the protoplasm twisted fibrils of the same thickness throughout, without a trace of nodular thickenings; in fact it even appears to him not impossible that the entire cell may consist of a single enormously twisted filament. The investigations were undertaken with Zeiss $\frac{1}{18}$ homogeneous immersion, while I worked, as has been said, with the Apochromatic 2 mm., Ap. 1·30 and 1·40, of Zeiss, and the oculars 12 and 18. Now if Schneider thinks himself in a position to assert (p. 5) that "an alveolar framework or a net-like connection of the filaments is as a matter of fact not present in *Strongylocentrotus* in the ova investigated," I must for my part reply just as definitely that both are present, and that Schneider gives an entirely false representation of the microscopic image. I will not appeal to the fact that the great majority of observers, and among them quite a number of the first rank, represent the same opinion as myself with regard to the microscopic appearance, but I prefer to subject the figures given by Schneider to a brief criticism. He remarks (p. 2) with regard to them that those first executed did not represent the framework quite correctly, and refers to the explanation of the figures with regard to this. Here I find it stated only for Fig. 19, "Framework drawn very accurately." The figure represents a section through a spermatogonium of *Ascaris*. By careful study one will find in this figure quite a number of reticular connections of fibrils, in fact they are even figured as forking. This appears still more strikingly in Fig. 21, of which it is stated that the framework is drawn correctly only in part;

here there is hardly anything to be seen of fibrils, but only a continuous reticular framework. Finally, Fig. 14 shows quite a distinct network, but it is affirmed of it that it " represents the framework as it appears from superficial observation, without taking regard to the isolation of the fibres at the points where they cross." Now it is quite certain that the figures referring to Ascaris must be the later and more accurate ones, since those which are published of the egg of *Strongylocentrotus* are diagrams such as never occur in nature. I think I shall be quite certain of the assent of all observers who have ever studied such things attentively, when I assert this definitely. The schematisation of these figures, especially that of Fig. 9, is carried to such an extent that the single fibrils, which are frequently drawn connectedly of a length nearly half that of the diameter of the egg, for the greater part cast shadows, and therefore stand out in prominent relief. On the whole, however, I must take exception to Schneider's figures, inasmuch as, with few exceptions, they give an utterly false idea of the actual relations, since they show the fibrillæ light and the intervening substance on the other hand quite dark, although, as a matter of fact, the state of things is exactly the reverse of this, as has been stated not only by me but by all other observers with the single exception of Künstler, and as is shown of course in the plainest manner in every photograph.

I will enter later on into the difficulties, in fact the impossibilities, which stand in opposition to such a view as that which Schneider brings forward. This especially holds good for the formation of vacuoles which takes place so frequently in protoplasm, the walls of which Schneider supposes to be produced from the fibrils, which are connected by a special cement in order to effect this.

From all these considerations I have not the least doubt that Schneider's view is altogether erroneous, and that he has not taken the fibrillar structure of protoplasm from the objects, but has construed it into them.

In conclusion, I must say yet a few words with regard to the remarkable view which Fayod (1890) has developed

concerning the structure of protoplasm. According to his experience, which is founded principally upon the investigation of vegetable cells, protoplasm and nucleus consist of long, hollow, spirally twisted fibrils, the so-called "Spirofibrillæ." Several of such fibrils are supposed to be usually "twisted in such a manner that they form the walls of hollow strings, which are again twisted in their turn." The last-mentioned "hollow strings" are termed by Fayod "Spirospartæ." The cavities of the Spirospartæ and Spirofibrillæ are said to be filled in the normal condition by "granular plasma." Spirospartæ pass from the protoplasm into the nucleus and *vice versa*, and also can frequently be traced from one cell into a neighbouring one, so that "the cell loses its value as a morphological and physiological unit."

These results were obtained in vegetable cells, chiefly by injection with quicksilver, by which method Fayod believes he filled the cavities of the Spirospartæ and Spirofibrillæ with metal. In animal cells, which he also investigated, he made use, as a rule, of other means. I need scarcely state that, supported by the results of my investigations, I must deny Fayod's statements altogether. It could only be a matter of clearing up *what* it was exactly that this investigator injected with quicksilver, for there can be no question that it was not protoplasmic fibrils. Since I was not in a position to repeat Fayod's experiments myself, I will not attempt to express a supposition on this point. But in order to point out the character of Fayod's views, I may refer to his remarks upon the blood of vertebrates. Fayod thinks he has convinced himself that the "blood plasma" also consists of Spirofibrillæ, and that they penetrate here and there into the "Hæmatoblasts." In this case it may be taken as sufficiently clear that Fayod has mistaken coagulations of fibrin for Spirofibrillæ.

2. *The so-called Spherular Theory of Künstler*

In the year 1882 Künstler developed a most peculiar view with regard to the structure of the protoplasm in a number

of Flagellata which he had studied closely. According to his observations, it consists of numerous protoplasmic spherules ("sphérules protoplasmiques"), which, placed in close apposition to one another, build up the protoplasm, as cells build up a cellular tissue. That an analogy of this kind was of great significance for the origin of Künstler's conception of protoplasm may be plainly seen in the description given by him. Every such protoplasmic spherule is supposed to consist of an external dense and firm wall with fluid contents; it is therefore, properly speaking, a vesicle. In consequence of this structure, protoplasm frequently appears to be composed of closely packed vacuoles of the minutest size, separated *inter se* by very delicate partitions of a denser nature (1882, p. 86).

Although this conception might well excite some surprise at the outset, in the form, *i.e.*, in which Künstler brought it forward, and in combination with his peculiar views on the anatomy and biology of the Flagellata, which would raise these Protozoa to the rank of highly complicated beings, still it appeared very probable, all things considered, that observations upon the reticular structure of protoplasm had led him to these peculiar interpretations of its nature. Hence in 1883 (*Protozoa*, p. 681) I expressed myself to that effect. More recent observations of my own upon certain Flagellata, as well as the beautiful and in many respects important studies which Künstler has recently (1889) devoted to this group, place it beyond all doubt that I was perfectly in the right when I gave this interpretation to the statements made by Künstler in 1882. In his last work Künstler gives a great number of very good representations of the honeycomb structure of the protoplasm, chromatophores, nuclei, etc., of these Protozoa—in fact, he believes, as formerly, that he can observe signs of such a structure even in the flagella, which I have never yet succeeded in doing. Thus, as regards matters of fact, there is a pleasing agreement between Künstler and myself, except on one point, which I must say I find in many respects very difficult to explain. In 1882, and again also in 1889, Künstler states that the manner in which he has drawn the honeycomb structure in his

figures, does not really correspond to its natural appearance. In his figures he depicts it, as a rule, just as has been done by me as well as by the many observers of the reticular structure of protoplasm, but he declares that in reality the contents of the alveoli appear dark and their walls light. Thus on p. 454 (1889) he says the honeycomb structure consists "of vacuoles which are enclosed on all sides by a thick white ('plus blanche') substance, which in preparations stains less, and contains a more strongly staining, darker, and probably fluid substance" (contents of the alveoli or enchylema). I must confess that to me these statements, which directly contradict both my experiences and those of all former observers, seem scarcely explicable. With too high a focus the contents of each alveolus give the appearance of a dark point, as has been described already in the case of the oil-foams (see above, p. 25), yet it seems to me hardly possible that this circumstance should have led Künstler to his view. The statement with regard to the greater staining power of the contents of the alveoli is also inexplicable to me. Since, however, I am in complete agreement upon this point with all other observers of the so-called reticular structure, I think I may leave alone these contradictory statements of Künstler.

Künstler takes this opportunity to admit (p. 454) that my comparison of the structure of protoplasm with the structural relations of a foam gives "une idée assez exacte de ce que l'observation microscopique directe révèle." Although, as has been said, he gladly accepts this comparison, yet in a footnote he combats very energetically my attempts to explain or illustrate protoplasmic structures with the help of artificially produced foams. Since his remarks on this question may serve as a prototype for similar objections, which in the course of time will certainly be put forward in opposition to my efforts, I take the liberty of quoting them here in full. "Si, pour la simplicité avec laquelle elle fait saisir cette structure, j'accepte volontiers la comparaison faite par Bütschli entre la constitution de la mousse de savon et celle du protoplasma, il n'en saurait être de même de ses expériences récentes sur les émulsions, d'après lesquelles il

prétend expliquer cette structure par le mélange de deux liquides. Quelques spécieuses que puissent paraître ses données, je m'élève contre cette interprétation. Le protoplasma est une substance vivante, hautement structurée, dont la constitution est le resultat d'une évolution particulière, qui ne saurait avoir rien de commun avec ces mixtures. Comparer ces deux ordres de faits me paraît aussi inutile, au point de vue de la compréhension réelle de cette structure, que de comparer une Méduse à une ombrelle, une Oursin à une pélote d'épingles, ou certains Bryozoaires à de la dentelle. Ce sont là des jeux d'hasard, amenant des apparences plus ou moins analogues sans qu'il y ait aucun autre point commun."

On the ground already mentioned, it may be worth while to subject the unfavourable opinion expressed in this passage with reference to my experiments to a more detailed criticism. The quintessence of Künstler's train of reasoning is, as he himself says, that protoplasm is a "living, highly structured substance, *the constitution of which is the result of a special development.*" As regards, in the first place, the significance of protoplasm as "living" substance, I am naturally as strongly convinced of this as Künstler himself; on the other hand, our paths evidently diverge when it comes to explaining the peculiar manifestations of activity which distinguish protoplasm and make it a living, as opposed to a not-living substance. Since Künstler begins his refutation of my views by laying emphasis on the fact that protoplasm is living, he evidently belongs to that not inconsiderable number of biologists who eagerly carry on investigations upon life and its products, and yet do not welcome a successful attempt to get nearer to the actual causes of the phenomena of life, *i.e.* an explanation of it as due to the interaction of physical and chemical forces under definite conditions. The veil of secrecy and the mysterious obscurity, which at the present time still hang over these processes, are the very incentives whereby investigators of this kind, whom I have met with frequently before, are drawn towards the study of the phenomena of life; in fact they not infrequently spur them on to obscure the processes and

relations, and make them still more mysterious, by introducing complications and false analogies with higher forms of development. This endeavour was very apparent in Künstler himself in his earlier work on the Flagellata. To the same category belong also the scientists that crop up from time to time, who have a preference for paradoxes, who feel a secret horror of all simple and straightforward solutions of the problem, who in fine are only content when they think they have found as extraordinary an explanation as possible, directly contradicting all other experiences.

Any one who takes exception, at the outset, to all attempts to explain the various phenomena of life, on the ground that such attempts are devoid of importance, because not made upon the living body or upon protoplasm, renounces at once all possibility of an explanation of these processes; he shows that he does not take their explanation seriously, but thinks it more correct to regard vital phenomena as the outcome of a secret and mystical cause, which it is not permissible to touch upon. Whoever, on the other hand, does not share this point of view, will as little as myself be of the opinion that I had prepared living protoplasm by means of my experiments, but will admit that bodies were successfully manufactured which not only possess a great similarity to living protoplasm in their structural relations, but also offer certain peculiarities which hitherto were only to be observed in the same manifestation, and for the same length of time, in living protoplasm. To bring these results to bear upon the explanation of the phenomena exhibited by living protoplasm seems to me not only permissible, but even imperative.

Now Künstler explains protoplasm not only as a living, but also as a "highly structured" substance. In so far as this statement has reference to structural relations actually observed, and not to such as are supposed to be hidden from us, and to be necessarily connected with the mysterious life of this substance, I can by no means agree with it. Protoplasm, as far as our knowledge extends, is in no way more highly structured than the foams artificially manufactured

by me; and if it must of necessity possess a very high degree of complexity, it may be confidently predicted that this complexity is to be sought in the province of chemistry, as I have already attempted to explain elsewhere (1891). Finally, according to Künstler, protoplasm must be "the result of a special development, which can have nothing in common with the mixtures prepared by me." Now I think that Künstler would find it difficult to reply if he were asked for a more precise account of this special mode of development, of which protoplasm is the result. I regret to say that I, at least, know nothing definite concerning any developmental history of protoplasm, although I am, of course, greatly interested in it. So far as I have heard, there has been much talk about the growth of protoplasm, and some hypotheses concerning it have been put forward, which, however, only deal with the mode in which complete molecules or micellæ of protoplasm are added to those already in existence; but, as I have said, I know nothing of any special mode of development of protoplasm which could be adduced in opposition to the validity of my attempts to explain certain phenomena of protoplasm.

Now, finally, I may be permitted to say a few words as to the illustration, not conceived in the best of taste, which Künstler brings in at the conclusion of his remarks upon my comparison between artificial froths and protoplasm. This comparison is supposed to be just as "useless" as that "of a Medusa with an umbrella." Of course if it was to be inferred that the Medusa consisted of the framework of an umbrella, covered over with silk, linen, or some other material, then the use of this metaphor would not be at all inadmissible, even if the Medusa was manufactured by nature from special materials, while the umbrella was made in X. and Co.'s workshop in the usual way. But unfortunately this is not the case; a Medusa has no more internal resemblance to an umbrella than a professor of Bordeaux to a statue. Were the resemblance between artificial foams and protoplasm of a corresponding character, I should then, of course, have every reason to strike my colours. The affair, however, is not so bad as all that.

If I may keep to the above simile of two umbrellas, the differences and resemblances between protoplasm and the artificial foams may be summed up as follows. Protoplasm from nature's workshop is essentially of exactly the same structure as the artificial protoplasm from Bütschli's workshop, only the former enjoys the agreeable advantage that the substance of its framework is not olive oil, but the peculiar substance of protoplasm, and its enchylema also contains many substances which the latter does not possess.

Any one who denies that the phenomena to be observed in the foams may be compared with those exhibited by protoplasm, and may be used for an explanation of them, may also assert with as much reason that everything which has hitherto been stated with regard to the combustion of organic substances in the metabolism of the animal machine is useless, for the animal lives, and consists of a substance—protoplasm—which is peculiar in the highest degree, while all processes of combustion, as we know, go on in not-living material and without the co-operation of protoplasm.

Künstler has, however, as was said, adopted my view as regards the general appearance of the structure of the protoplasm. Yet he does not think it necessary to give up entirely his earlier idea of protoplasm being composed of hollow spherules. Thus he tries to render it probable that the lamellæ which form the walls of the alveoli may split occasionally, so that single alveoli become isolated as spherules through the appearance of an intervening fluid matrix. This possibility he attempts to demonstrate, more especially by means of observations upon the protoplasm of a Foraminiferan with a peculiar shell, which has been dealt with already in two works dating from 1888. Without entering more closely into these observations, I should like merely to express my conviction that the little vesicle-like bodies, which Künstler observed either singly or united into groups in the endoplasm of this Foraminiferan, and described as almost fluid and granulated, have certainly not arisen in the manner alleged by him, through isolation of the alveoli of a protoplasmic network which existed before. My own observations of a former date, as

well as those recently repeated by me, on the protoplasm of marine Rhizopoda, rather tend to show that such bodies occur very commonly as deposits in the protoplasm of these Protozoa, and certainly have nothing to do with the alveoli of the distinctly honeycombed protoplasm which is also present. That Künstler's vesicles were nothing more than the similar granules or deposits of such frequent occurrence in the protoplasm of Rhizopods, seems to me to follow beyond all doubt from his remark that in well-nourished Foraminifera these granules are the seat of the red coloration. It is, however, a matter of common knowledge that the seat of the red coloration is formed, as a rule, by droplets of fat, which are impregnated with pigment in solution, as is obvious from their being readily soluble in alcohol; on the other hand, it is probably also due sometimes to bodies of the nature of Zooxanthellæ, as I attempted to show in 1886 in the case of *Peneroplis*. But in any case we are not justified in referring these deposits, as Künstler wishes to do, to the isolation of originally connected alveoli of protoplasm; his few observations are also certainly insufficient to support an assumption so difficult to comprehend. I am inclined to see in it an abortive attempt to rescue some portion of his statements of 1882, as to the protoplasm being composed of vesicle-like spherules. But after the detailed expositions in the earlier portions of this work, it is not necessary for me to state more precisely why I regard this view to be erroneous now just as before.

3. *The so-called Granular Theory of Protoplasm*

As is well known, the earliest view with regard to the constitution of protoplasm was that it consisted of a viscid or slimy ground substance, in which numerous granules were embedded. These granules, which from a long time back have been considered as an indispensable constituent, so to speak, of protoplasm, were distinguished by the term protoplasmic granules from other granular contents lodged in the protoplasm, upon the chemical nature of which, as fat, starch, pigment, etc., it is possible to arrive

at some understanding. After they had been christened "Microsomes" by Hanstein in 1882 they obtained to some extent the right of entry, as it were; for anything that is called by a Greek name at once seems to many people to be much better known, and as something which must be definitely reckoned with.

With the gradual extension of the theory of the reticular structure of protoplasm the view developed, that a great portion of these protoplasmic granules were merely the nodal points of the network, although the adherents of this theory of course pointed out frequently enough the occurrence of granular deposits in protoplasm. There was also no lack of attempts to refer the protoplasmic structures observed to a special arrangement of the protoplasmic granules.

Martin, as far back as 1882, developed the latter view very consistently. Protoplasm consists, according to him, of a ground substance, the so-called "gangue protoplasmatique," and of granulations deposited in it. The ground substance is supposed to be the true contractile matter. The granulations embedded in it may now either (1) lie without any regular arrangement whatever in the ground substance, as, for example, in leucocytes and numerous other cells; or (2) they may be arranged in longitudinal rows one behind the other, from which a striated structure arises in the protoplasm, as, for example, in ciliated epithelial cells; or (3) finally, a breaking up of the ground substance or "gangue protoplasmatique" into "rods or cylinders" may take place, each of which contains in its axis a row of such granules; this condition is said to have been evolved in numerous gland cells, as well as in smooth and striped muscle cells; it is the cause of their longitudinal striation, or rather their fibrillar nature.[1]

Finally, Martin also discusses the question, whether the granulations of the protoplasm might not perhaps be *living*

[1] Heidenhain in 1875 had already tried to refer the striation of the internal region of the pancreas cells to the deposition of fine tubules in the ground substance of the cell. Into these tubules the granules of the protoplasm were able to penetrate, for which reason the latter often appear arranged in rows.

structures, and comes to the conclusion that this view, already originated by Béchamp (1867), may well be the correct one. His remarks upon this are as follows: "La granulation proteique du protoplasme est peut-être un élément vivant, une cellule, dont la vie et la fonction réguliseraient et speciferaient dans un sens physiologique déterminé, l'être complexe, que nous désignerons encore sous le nom de cellule simple ou primitive." *His grounds for this assumption are the great resemblance of the granulations to micrococci.*

Pfitzner also tried to demonstrate theoretically in 1883 that the structures of protoplasm have arisen from the arrangement of the granules in series. In fact this idea seemed so obvious, that the radiating phenomena in division have since their first discovery usually been referred to the protoplasmic granules being arranged in rows. As has already been mentioned above, Pfitzner distinguishes between the *active* and *passive* structures of protoplasm. By the latter he understands reticular structures produced by vacuolisation. He is of the opinion that the majority of the protoplasmic structures hitherto described belong to this category. Active structures, on the other hand, would be such as are produced by attraction and repulsion of the small particles which are suspended in the protoplasm. Pfitzner conceives of these particles as viscid, and the ground substance in which they are found as fluid. If attraction prevails, the particles flow together into larger drops, as, for example, in fat cells, where they fuse into fat drops of considerable size. If, on the other hand, repulsion prevails, the minute particles become evenly distributed in the ground substance, as, for example, the pigment granules in pigment cells. But when repulsion and attraction are equal, the particles only come into contact, and range themselves alongside of one another, as a result of which certain structures arise if the particles refract the light more strongly than the ground substance. The form assumed by the filamentous framework, which is built up by the serial arrangement of the granules, depends on the "intensity of the attraction." When it has a certain strength, each par-

ticle has the power of "binding" two neighbouring particles; then filaments are formed. If, however, a particle is able to bind three others, networks arise. As examples of such active structures, he considers those of the nuclei and the fine protoplasmic structures, which he himself described in the red blood corpuscles of Amphibia (see above, pp. 130 and 173).

I think I scarcely need point out that in these speculations Pfitzner did not go upon actual physical grounds, but that the forces of attraction and repulsion brought into play were specially invented for this service. One point, however, I should like to emphasise particularly. In Pfitzner's passive reticular structures the framework is of course the true protoplasmic substance become reticular from the formation of vacuoles. But in active structures, on the other hand, the contents of the network, or the intervening matrix, would be the true original protoplasm. My view, on the contrary, regards both structures as essentially the same.

Brass (1883-85) is also of the opinion that the reticular structures occasionally observed by him were formed by a serial arrangement of the granules. Kultschitzky (1883) had the same idea with regard to the striations in the sensory cells of Gaudry's corpuscles, and Schiefferdecker (1887) with regard to the fibrillar structure of ganglion cells. Moreover, Vejdowský (1888) drew from his investigations on the formation and development of the eggs of *Rhynchelmis*, the conclusion that protoplasm is originally quite homogeneous and structureless (p. 19); that then very minute granules make their appearance in it, which "begin to group" themselves; "rather later there arise from these granules, especially in the neighbourhood of the nucleus, filaments running irregularly and crossing repeatedly"—"thus arises the reticulum of the Cytoplasma" (p. 20). In the course of the segmentation of the egg also, Vejdowský believes he has frequently seen reticular protoplasm becoming homogeneous, and differentiating again into structured. He therefore sees in the structures of protoplasm and cells, "products of the processes of nutri-

tion, assimilation, and growth" (p. 119), produced by differentiation of the primitively structureless, homogeneous protoplasm. I think I need hardly point out that the so-called protoplasmic reticulum which Vejdowsky describes in the ripe ova of *Rhynchelmis*, is not a real protoplasmic structure, but a coarse protoplasmic framework which remains free of yolk. He himself was also forced to this assumption (p. 120), without, however, being able to find the true protoplasmic structure in this reticulum. On the other hand, he certainly has observed a great deal of the real protoplasmic structure in the so-called attraction spheres, at the ends of the nuclear spindles, periplasts as he terms them. Finally, since 1886, Altmann has made thorough studies of the protoplasmic granules, in the course of which he has arrived at views similar to those already originated at an earlier period by Béchamp, and especially by Martin. It is an incontestable merit of Altmann's to have proved that in protoplasm there occur probably quite universally numerous granules, capable of being strongly stained with certain aniline colours. On the other hand, he decidedly goes too far in his conclusions concerning these so-called "granula," as well as in the theory of the constitution of protoplasm founded upon them.

If we wish to give an account of Altmann's views and their merits, we must first trace their gradual development for a little, since they have undergone certain modifications in the course of time. In 1886 Altmann first brought forward the proof that the protoplasm of almost all cells contained granules, which he himself first discovered in a number of cells. It is rather a motley collection which is here brought together under the head of granules. First come the chlorophyll granules of the vegetable cell; then pigment granules of all kinds, the granulations of the plasma cells (Waldeyer), of leucocytes (Ehrlich), the granules of the pancreas, liver, and other gland cells, the eleidin granules of cornified cells, and the yolk granules or yolk discs of the protoplasm of the egg, are all included here. On the ground of Altmann's later work we can also count fat granules and fat drops, which are supposed to be produced by modification

of the granules through "storing up of fat." The granules are embedded in a "jelly-like substance," and play the most important part in the phenomena of life exhibited by protoplasm. As far back as 1886 Altmann pointed out their analogy with Bacteria, which were supposed to be certainly not cells. The great, and indeed determining importance, which in 1886 he ascribed to them as the real agents in carrying on and bringing about the processes of metabolism, shrinks more into the background in his later works. For instance, the assumption which he set up in 1886, that they were the means of transferring oxygen, is at a later time no more to be found. This omission is no doubt in connection with the fact that the alleged activity of the granules was based, in any case, on their supposed relation to chlorophyll granules; but since the latter structures no longer appear among the granules in 1890 as the result of Altmann becoming gradually convinced that such a conception was untenable, this side of the activity of the granules was necessarily made less of.[1]

The matrix of the protoplasm chiefly plays a part, according to Altmann, in affording a vehicle for the physical phenomena of life. In 1886 and 1887 he still admits the existence in this matrix of special fibrils, which have nothing to do with the granules. Thus in 1886 he asserts that the axis-cylinder consists of fibrils, between which the granules lie in rows. In 1887 he allows the occurrence of fibrils and networks in the protoplasm in like manner, but now they are to be derived from arrangements of the granules in rows, in the same way as the filamentous Bacteria form connected threads composed of numerous single individuals. It sounds, at least to zoologists, very confusing, that Altmann should call these threads formed by serial arrangement of the granules "Nematodes."

[1] Zimmermann in two of his works has studied Altmann's method of investigating granules in the vegetable cell. He seems, however, in opposition to Altmann, to by no means regard the granules observed in them as identical things. I am also unable to find in Zimmermann anything in favour of regarding the chlorophyll granules and leucoplasts as "granula." Since these structures themselves for the greater part possess granular contents, there can be no question of any such comparison.

In 1890, finally, he retains only the fibrils, while the networks are attributed to erroneous observations. The apparent reticular structure is explained as a delusive appearance depending on the fact that the closely packed unstained granules have been overlooked, and have been interpreted as the spaces of a meshwork. I think I need only say a little here concerning this view. Altmann extends it in like manner to the nuclei, the structure of which is supposed to correspond exactly to that of the protoplasm. The reticular framework of the nucleus is also, according to his idea, a deception. But any one who has seen the granules of the nucleus and of the protoplasm in the unstained condition, when they are, of course, just as visible as when stained, knows that they are denser and darker structures, with a high power of refraction, which, therefore, could not be confused with the clear meshes of the protoplasmic network by any observer at all experienced. On the other hand, in the investigations set forth above, we have come across granules sufficiently often, and have always found that they lie in the framework of the protoplasm. In staining experiments with very various aniline colours, etc., it was always shown in the plainest manner that the meshes of the network remain colourless, while the protoplasmic framework assumes only a feeble coloration. It is the granules alone which stain intensely in the protoplasm. For confirmation of this fact, sections are of course required which have only the thickness of one or two meshes. The alleged coloration of the spaces of the meshes, which earlier observers affirmed frequently, is to be attributed to the thickness of their sections, and can be explained without difficulty; in fact it follows necessarily, if our view of the alveolar structure of protoplasm is to be regarded as correct.

But how, it will be asked, could Altmann have completely overlooked, on his part, the framework of the protoplasm? The explanation of this seems fairly obvious. He himself recommends investigating the preparations with "an open cone of illumination," *i.e.* under conditions which cause all the more minute and pale structural elements, that are stained but little or not at all, to become simply

invisible, as has already been thoroughly discussed above (p. 179). If we examine one of Altmann's figures, as, for example, the pigment cell depicted on Plate I. (1890), which is supposed to represent to a certain extent the typical structure of the cell, the remarks just made will become still more obvious. We miss throughout this figure any distinct limiting contour to the cell. Frequently little aggregations or strands of pigment granules may be noted, which lie entirely isolated, without any connection with the rest of the cell. Hence it may be inferred very definitely, that Altmann has in reality only observed the granules, and has overlooked, on the other hand, the protoplasmic framework.

A similar result is obtained, moreover, if we pay attention more especially to the alleged formation of fibrils by arrangement of the granules in rows. In most of the figures it can be plainly made out that the fibrils do not consist at all of closely packed granules, but that clear spaces intervene between the granules. Only in very few cases relatively are the fibrillæ drawn as continuous red lines, which lie rather scattered in the cell. I put aside the latter cases, with regard to which I will assume that the continuous fibrils would prove to consist of granules when more closely studied, and will linger for a moment over the more frequent instances of the kind first mentioned. In my opinion, these observations are in favour of just the very thing which Altmann wishes to deny, namely, that something must be present which maintains the rows of granules in their arrangement; in favour, that is to say, of the presence of a fibril distinct from the granules, or rather of a fibril-like tract of the meshwork of the protoplasmic framework.

For the reasons enumerated I must conclude that Altmann's objections to a reticular framework of protoplasm are futile.

Although it lies beyond the scope of the task we have undertaken to examine more closely the importance which Altmann ascribes to the granules, yet I must not pass this over altogether, since a few critical remarks on this point

would seem not out of place on this occasion. Altmann considers the granula or *cytoblasts*, as he also terms them, to be really living, and as homologous with Bacteria. We seek in vain for any decisive proof of this view, for the oft-asserted proliferation by division is nowhere proved. That they are able to continue living outside the protoplasm, and more especially to increase, is indeed directly denied by him, in opposition to Béchamp. In 1890 the function which, according to Altmann and his pupils, they perform in the metabolism of fat is cited finally as a proof of the vitality of the granules. Although this point does not seem to me by any means sufficiently clearly established, I will not go into it farther, since I am inexperienced in this line. But as long as individual constituents of the cell are not seen to persist when isolated, nor are distinct living phenomena observed in them, it is very dangerous to speak of their life as something which they possess in themselves. They are so far living, as long as the opposite is not proved, in that they are parts of a living organism, so that the granula may therefore be living in the same way as the nucleus, even though they no longer betray any sign of life after isolation.

Are we then to regard the granula as homologous on the whole with *Bacteria*, as Altmann assumes, to derive them phylogenetically from *Bacteria*, and hence to look upon the so-called matrix of the protoplasm, with Altmann, as a kind of zooglæa jelly? I think this is not permissible. I argue quite apart from the fact that the genetic connection between the numerous granular contents of the very various kinds of cells, which Altmann unites as *granula*, has first still to be proved. I depend rather on the observation made by myself and others, that the Bacteria in like manner contain granula, and, moreover, granula which we are completely justified in regarding as equivalent to the chromatin granules of cell nuclei. Besides these, however, there may be special granules, showing different relations, in the *Cyanophyceæ*, which agree so closely with the *Bacteria*. And why does not Altmann also regard the sulphur drops of numerous *Bacteria* as granula?

The chromatin granules of the nuclei are regarded by him as being quite certainly "granula," hence he will be obliged to admit that *Bacteria* may themselves contain granula. However, I have sufficiently set forth my views with regard to *Bacteria* in another place (1890), to which I may refer the reader, and I consider that I have there also refuted Altmann's view that the *Bacteria* are non-nucleated primitive organisms of a peculiar kind, comparable to the granules of the nucleus and the protoplasm. The *Bacteria*, according to my conception of them, are partly comparable to the nuclei of higher animals, without any clearly demonstrable trace of protoplasm apart from the cilium, and partly, on the other hand, to nuclei, with a scanty envelope of protoplasm. Still less, however, is Altmann's assertion justified that many other Protista also, *e.g.* Sarcodina, are non-nucleated, and that we may, to some extent, compare the process of formation of a nucleus with the encystation of such a monerous Sarcodine, as a process in which a portion of the original protoplasm becomes encapsuled as a nucleus, while another portion remains persistent round the nuclear capsule as the protoplasm of the cell. Unfortunately Altmann has omitted to specify by name any case of encystment in Protista which might appear to him to serve as a commencing nuclear formation of this kind. I am inclined to believe that what he had in his mind was not true encystment, but something like the structure of the Radiolaria or the shell-bearing Rhizopoda. Since, however, in all these cases, as also in the true encystment of the Protista, nuclei are known with sufficient certainty to be present, the entire comparison does not, on the whole, prove what it is intended to.

On the other hand, however, it is quite possible that, among the strongly staining granules of the protoplasm, there are in reality bodies which can be homologised with *Bacteria*, so-called *Bacteroids*, as they have been termed, which have been frequently demonstrated in vegetable and animal cells. I had already at an early date pointed out that the numerous granules which fill the endoplasm of the Ciliata reminded me strongly of Micrococci, and with regard

to this point I can also further adduce an observation which Dr. Säfftigen made in my laboratory in the summer of 1890 upon *Epistylis galea.* As is well known, the ectoplasm of this form, as of *Vorticellina* generally, contains numerous rounded, rather strongly refractile structures, which Leydig once regarded as nuclei. Now the fact can be established that these granules, which I regard as identical with those mentioned above in Ciliata, were found at times in a state of rapid proliferation by division, which of course greatly supports the interpretation of them as Bacteroids.

Since it seemed to me of importance to investigate the Bacteroids discovered at an earlier date in certain animal cells, with a view to their relations with the framework of the protoplasm, I have carefully studied, for my own benefit, Blochmann's sections through the cells of the fat body of *Blatta orientalis,* which were filled with such bodies. It was thus established that the Bacteroids, strongly stained by Gram's method, lay embedded in rather a scattered manner in a very pale, but distinct reticular, protoplasmic framework (Plate VI. Fig. 4). Besides the Bacteroids, no granular contents of any kind are present in the protoplasmic framework. The nuclei, and more especially their chromatin granules, are stained very intensely.

As to the works of Zimmermann (1890 and 1891), Mitrophanow (1889) and Luckjanow (1889), who agree more or less with Altmann in their conception of protoplasm, I think I need not enter into them more specially after the above discussion.

4. *Attempts to explain the Reticular Structures as Phenomena of Coagulation or Precipitation*

It is really surprising that the question whether the so-called structures of protoplasm are not produced by the coagulation or precipitation of albuminous bodies during the process of preparation, should not have been thoroughly discussed at an earlier period. That this was not done probably depends on the fact that the investigators who worked at this subject upon zoological lines were just those who, even

in early times, occupied themselves with the study of the living object, in order to ascertain the existence of structures in living protoplasm. Since, moreover, the living nuclei frequently showed still more distinct structures of a similar kind, it seemed all the more justifiable to regard the existence of the protoplasmic structures during life also as a certain fact.

As is well known, some later observers, as more especially Berthold, Fr. Schwarz, and, in connection with the latter, also Kölliker, have disputed the idea that reticular structures are present in living protoplasm. In their opinion they are artificial products, so far as they do not depend upon pathological vacuolisation, *i.e.* appearances artificially produced by precipitation or coagulation of the protoplasm. Berthold, who first expressed this view in 1886, has come forward again, as is well known, with good arguments, and in a very praiseworthy manner, to vindicate the fluid nature of protoplasm, which was taken for granted almost universally at an earlier period. It possesses, according to him, the character of an emulsion, *i.e.* it is a mixture of two or more fluids which are insoluble in one another, or only soluble to a limited extent. Of course it was also quite in accordance with his view for solid secretions in the form of granules or crystals to appear in the protoplasm. Berthold seeks very correctly to refer the emulsive character of protoplasm to the so-called processes of desolution, which have already been briefly explained above, and were found to be the true efficient cause of the formation of oil-foams. When Berthold terms his conception of protoplasm, and, more particularly, his statements as to its fluid nature, a hypothesis merely, I think he is too sceptical in this respect. I shall try to explain later on, as I have already done before, that the fluid nature of more ordinary protoplasm follows very definitely on the contrary from all the phenomena observed. It will then also be discussed how the view gradually developed that protoplasm could not be fluid, or that it must at least be a mixture of solid and fluid parts. If then Berthold, by reason of his view of the fluid and emulsive nature of protoplasm, got so far as to deny a reticular

framework altogether, his attitude is quite intelligible, for a framework of this kind could only be imagined as a firm structure, and the alleged fluid nature of protoplasm would of course have been quite irreconcilable with such a view. For a sponge soaked full of liquid, as one would have to figure to oneself from the current views upon the reticular framework of protoplasm, could not possibly exhibit the phenomena of a fluid. Nevertheless, Berthold could not deny the appearance of filaments in protoplasm, and, in fact, he has himself observed them frequently since 1882 in living vegetable protoplasm. On the other hand, he denies that these threads are connected into a network, and that they form a continuous framework; he believes that, with regard to this point, he must rank himself with Flemming, who represented the same opinion. What these filamentous "torulous" structures in protoplasm really are, is not clear from Berthold's discussions. As far as I am able to come to a decision on this point, he places them in the same category as the granular and other contents, which are separated from the fluid ground substance of the protoplasm by processes of desolution. On this point, however, he would depart widely from Flemming's view, to an agreement with whom he attaches great importance. On the whole, however, it is clear that if filamentous solid bodies occurred in such quantities in the protoplasm, as is the case according to Flemming, for instance, and numerous other observers, the fluid character of the protoplasm would certainly be completely lost. For if we represent to ourselves a heap of solid filaments, which are connected by layers of fluid about 0·5 to 1 μ in thickness, the adhesion between the fluid and the filaments must, without doubt, have the effect of causing the entire lump of filaments to assume, at most, the character of a plastic body, while protoplasm presents the nature of a viscid fluid. For the rest, Berthold (p. 62) admits that in protoplasm occasionally "products of differentiation or precipitates may occur in the form of a fine framework," although he himself never observed anything of the kind.

Opinions in many respects similar, only more indefinite,

are expressed by Fr. Schwarz (1884) upon the reticular structure of protoplasm.

What his conception of protoplasm really is, does not appear to me sufficiently clear from his extensive treatise. He declares (p. 130) that all authors are agreed upon the point "that protoplasm consists of solid and fluid parts," from which it is to be concluded that he, in like manner, supports this view. On the other hand, however, he speaks also of the "semi-fluid" nature of protoplasm. Now, since he denies in the most definite manner that the firm substance of protoplasm appears in the form of a framework, he comes to the conclusion that protoplasm must be a "mixture, which in external appearance is homogeneous, but seems nevertheless to admit the possibility of the single substances being variously distributed" (p. 130). On p. 125, also, it is said with reference to the investigations of Reinke and Rodewald, that "there might be a homogeneous mixture, of the framework and the enchylema," which was not to be separated by the action of centrifugal force. But what this "homogeneous mixture" may be in reality is not clear to me. If protoplasm is supposed to consist of solid and fluid parts, they could only be indistinguishable if they possessed exactly the same power of refraction. But since it is inconceivable that such a thing should occur universally, it is incomprehensible to me how Schwarz arrives at the statement (p. 130) that it is never possible to convince oneself of the presence of a framework in living protoplasm —an assertion which was the more unjustifiable because numerous investigators even before Schwarz had convinced themselves of its existence. Unfortunately Schwarz, while talking about protoplasm in quite a general manner, has by no means taken into consideration the numerous observations on the zoological side. He appeals, indeed, to Flemming, without, however, appreciating or paying more special attention to what is communicated by him.

What he himself has described in the way of filamentous protoplasmic structures in vegetable cells were, in my opinion, as a rule nothing of the sort, but merely networks of minute trabeculæ of protoplasm which traverse the cell

sap, or at times also form the lining of the cell wall. The real intimate structure of protoplasm, on the contrary, he has not observed, for which reason it becomes explicable how he arrived at the idea that the filamentous protoplasmic structures gradually passed into the trabeculæ of the protoplasm which usually traverse the cell sap of the vegetable cell. A cursory study of the protoplasmic structures described in such numbers in animal cells would necessarily have taught him that there are filamentous structures which pervade the entire protoplasm, and which, therefore, in no way permit of the interpretation attempted by Schwarz.

I think, however, that in the face of the numerous proofs brought forward both in this and earlier works that not only filamentous, but also reticular substances are frequently to be observed in living protoplasm, the interpretation of them as products of coagulation or precipitation requires no further refutation. It has already been shown above that the fibrillar structure of protoplasm always proves, when accurately studied, to be a modification of the reticular structure; therefore, as I have already explained earlier, the existence of the so-called reticular structure can be inferred with a high degree of probability, if not with certainty, from the demonstration of fibrillar structures in living protoplasm.

In opposition to the attempts to set aside the structures as artificial products, it would seem worth while to give a brief review of former observations which have demonstrated structures in living protoplasm. Of course these statements are not all of equal value, since occasionally without doubt deceptive appearances or *post-mortem* alterations of the protoplasm may have been seen such as may occur quite easily, especially in the case of the cells of higher organisms detached from their natural environment.

That the structures of ganglion cells can be recognised even in the freshest possible condition, has been confirmed by the majority of observers since the time of M. Schultze (1863), namely, by Schwalbe (1876), Arnold (1879), Dietl (1878, for *Helix*), Freud (1882), Leydig (1883), and

Frommann (1879-84). In living cartilage cells, filamentous or reticular structures have been described by Flemming (1870), Frommann (1879, 1880), and Schleicher (1879). For colourless blood cells, Frommann (1875, 1880), Schwalbe (1876), and Leydig (1885) have affirmed the presence of reticular structures, and Stricker (1890) has recently photographed them from life, by which photograph Schäfer was converted from the opinion he held for so many years, namely, that reticular structures were not present in leucocytes. In the salivary corpuscles Stricker (1880) described a trabecular framework. Moreover, there are numerous assertions concerning the existence of striations in epithelial cells in the living condition. Heidenhain observed them in 1875 in fresh pancreas cells, Stricker and Spina noticed striated structures in the fresh cells of the skin glands of Amphibia (1880), Nussbaum (1887) in fresh cells from the intestine of *Anodonta*, Leydig (1885) frequently confirmed the striated structure in fresh epithelial cells of insects, and Carnoy (1885) expressly declares that the reticular framework is to be made out plainly in the living cells of insects. As is well known, Kupffer had already described in 1870 a reticular framework in the living follicle cells of the Ascidian ovum, and in 1874 in the cells of the salivary gland of *Blatta;* he also saw the reticular structures of liver cells, though more faintly, in the fresh cell.

In streaming vegetable protoplasm, Velten had already (1873 and 1876) found the structures described above, and Frommann also (1879) had frequently seen them there beyond all doubt, even though many things which he describes (especially in 1884) must have been pathological, since he often investigated the cells for quite a long time in sugar water; in fact he describes processes in them similar to those which have been already mentioned, and interpreted as pathological, in the case of the blood corpuscles of the crayfish. On the other hand, the assertion of Schwarz, that " these local reticular structures observed by Frommann were nothing else than precipitates which separated out in certain places " (of course in the cell sap), " and which later

became vacuolated," seems to me to go too far, and to be in the main unfounded, since in any case there certainly could be no question of precipitates within the cell sap.

Finally, we must mention further, that van Beneden (1883) also convinced himself that the most important of the structures described by him in the sexual products of *Ascaris* were to be observed while still in the living condition.

In Protozoa, which are especially important for the structure of living protoplasm, Bütschli (1887), Fabre (1887), Schewiakoff (1889), and others, have traced the living structures.

Taking into consideration all that has been enumerated, which could certainly be further increased by a more conscientious search through the literature, as well as, on the other hand, the further proofs which I have communicated in this work, it may well be asserted that the structures in question are frequently to be observed quite plainly in the living condition, and therefore cannot be any artificially produced appearances of precipitation or coagulation.

Now Schwarz allows reticular or filamentous structures, which can be precipitated or fixed, in the case of the nuclei and chlorophyll bodies, but denies them, on the other hand, in the case of protoplasm; and why? He asserts, in fact, that in the fixed framework of the protoplasm, a chemical difference between the framework and its contents is not demonstrable. The contents of the meshes stain in the same manner as the meshes, and therefore also consist of a coagulable substance. The difference between the framework and its contents only consists in a slight difference of density; both are said to consist of plastin. The contents of the meshes is said not to be a fluid (p. 131); this contrasts very strongly with the description given on p. 140 of the same framework in fixed protoplasm, where it is stated "the cavities" (*i.e.* those of the framework) "are for the most part filled with fluid, but may, under certain circumstances, also be filled with a less dense substance." I must say I think Schwarz would find few to agree with his view of the chemical similarity between

the framework and its contents, and I can only, as before, assert in the most definite manner that in the thinnest sections, or with the intensest staining, I could never obtain any coloration whatever of the contents of the meshes or intervening matrix. As I have remarked before, the investigation of thicker sections, or even of whole layers of protoplasm, as was the method of Schwarz in all cases, proves nothing at all in this respect; for even if only a few layers of alveoli were superposed upon one another, it must naturally give an appearance as if the intervening substance also possessed a fainter colour, because both above and below a mesh which is exactly in focus there lies a quantity of coloured matter which affects the light transmitted. Exactly the same holds good, in my opinion, for the reticular precipitates prepared artificially by Schwarz, for which also he assumes a homogeneous or granulated ground substance composed of the same material. If Schwarz saw precipitation films, which were originally homogeneous, becoming afterwards granular and reticular, I assume, until further light has been thrown on the subject, that it was nothing to do in this case with structures which became formed within the homogeneous film, but it was a matter of deposits that appeared subsequently in the form of granules, networks, and crystals.

I will not follow up this subject further, since as yet I have but few observations at my command upon reticular precipitates and coagulations. Yet I agree completely with Schwarz that coagulated drops of white of egg, as also a precipitate of ferrocyanide of iron (from rather concentrated solutions), appear very finely reticular, and possess great resemblance to protoplasmic structures. In the case of a precipitate of Prussian blue, it can scarcely be doubted that it is only the result of a serial arrangement of minute stained granules, and the same will also probably hold good for the precipitates of colloidal bodies.[1] With regard to this, and also with reference to protoplasmic structures generally, it seemed to me of importance to test in what way very

[1] Upon this point see the Appendix at the end of this chapter (pp. 216-219 *infra*) for the changed opinions which I now hold.

minute granules behave which are lying closely packed together in a liquid, or which have been dried up on a slide; that is to say, what appearance they present with high magnifications.

If some Chinese ink, rubbed up into rather a thick paste, or else some sepia of the same consistency, which has been removed from the ink sac, be spread out on a cover-slip in a thin layer and allowed to dry, and then a cover-slip placed over it with damar, the thin layer of ink or sepia, when studied with the highest powers, looks as follows. A very finely meshed but distinct network is to be seen, the nodal points of which seem to be formed by the very smallest particles of ink or sepia (Photogr. VII.). It is evident that the phenomenon does not depend on the soluble matter of the ink having been dried up with it, and having formed the reticular tracts between the ink granules, from the fact that it is possible, after drawing the cover-slip with the ink on it through a flame several times, to treat it for a long time with water, concentrated hydrochloric acid, caustic soda, alcohol, and ether, etc., without the appearances being changed. Moreover, the ink or sepia when suspended in water also shows the reticular appearance distinctly, provided it is not, as usually is the case, in a state of violent molecular movement. If one investigates the ink rubbed up with water under the cover glass, it can be observed that wherever a bubble of air is shut in between the slide and the cover glass, a very thin layer of ink is found between the air and the cover glass. In this thin layer of fluid no molecular movement takes place, and there one can see very plainly that the ink granules show reticular connections.

Just the same appearances are also obtained by slightly blackening a cover glass over a flame and mounting it in damar.

By these experiments it is shown that closely apposed, and very minute granules also present the appearance of a network. That the granules of the thin dried-up layer of ink are closely packed, however, follows from the fact, that after treatment with acids, etc., the layer frequently comes away partly as a continuous membrane. On what, then, does the

appearance of a network depend, which may be of such consequence for our studies on protoplasm? It is certain that the granules are often actually directly connected to one another; one can convince oneself of this fact by rubbing up a small quantity of ink with glycerine jelly and mounting it, and also by moistening a little of the soot on a slightly blackened cover glass with oil and investigating it. Granules can then frequently be seen to be connected together, and apparently united by a dark, short filament, giving rise to a dumb-bell shaped structure. I regard, however, the latter phenomenon as to a great extent an optical one, the explanation of which will not be further attempted here. If one examines fine drops of oil, such as can be easily produced by shaking up olive oil with weak soda solution, one notices also that two drops in close contact when sharply focussed seem to pass into one another directly by means of a dark bridge at their point of contact. It is self-evident that in this case a real connection does not exist, since otherwise they would necessarily flow together. We must, I think, put a similar value upon the above-mentioned dumb-bell shaped figures of the adherent ink granules. The network described, however, can only in part depend upon this connection of the ink granules. In the main it may depend upon another *optical* phenomenon.

If single isolated quiescent ink granules be studied in glycerine jelly or oil, it may be seen that each granule, when focussed as sharply as possible, so that it appears dark and sharply contoured, is surrounded by a clear area, which has a breadth of about the diameter of the granule, or rather more, and is marked off from the rest of the field of vision by a rather darker, dull border. This is the so-called *diffraction area*, which is seen in the microscopic image round all bodies of greater or less refracting power, and which by Nägeli and Schwendener (1877, pp. 230-236) was referred partly to the direct reflection of the incident light at the edge of the body in question, partly to the interference of this reflected light with the light which comes through unreflected. If one slightly raises or lowers the tube of the microscope, the granule disappears, but in both cases the

area remains visible as a light circle. Now, if two or more granules of ink are lying close together, and the tube be raised or lowered, the granules pass into a network of just as many meshes as there were granules originally. The explanation of this appearance must be sought in what has been pointed out above, that instead of the granules appear clear diffraction circles, which partly overlap one another and by their dark edges produce the appearance of a meshwork. Now since in the examination of a layer of ink, such as has been described above, there are numerous granules not in sharp focus which must present the appearance of such a network produced by the diffraction circles, I think that the reticular appearance depends essentially on the last-mentioned optical phenomenon.

The formation of net-like structures just described, which possess no reality, but depend only upon optical phenomena connected with the peculiarities of microscopic vision, has been followed out by me still further, since a knowledge of them, which has hitherto been quite neglected, must be exceedingly important for estimating the value of reticular structures, and may indeed render it a matter of doubt whether all reticular structures are not on the whole only due to optical phenomena. It was for these reasons that I discussed the question in detail above, and, as I believe, settled definitely whether the appearance of reticular structure in the foams depended in reality upon their frothy nature or not, since the possibility that dense granular deposits might produce the appearance of a reticulum was not to be lost sight of.

If one prepares an emulsion of oil-drops as minute as possible by shaking up a little olive oil with 1 per cent solution of caustic soda, and examines it in a thin layer with the strongest magnifications, the following facts may be observed. If the layer of fluid is thick, all the droplets are found in violent molecular movement; but if the glass be pressed down more strongly by drawing off fluid, the larger drops are held still, and round them collect groups of the smallest drops, which are now in like manner quiescent. By focussing accurately the median plane of these droplets it is

shown beyond a doubt that they are in mutual contact. This is especially shown by the fact that the larger drops which are apposed to one another are distinctly flattened at the surface of contact. Round each drop the above-mentioned clear diffraction ring is to be seen, which is distinctly marked off by a darker border from the rest of the less brilliantly illuminated field of vision. If the tube be lowered just a little, the droplets diminish in size and become dark, as is the rule with strongly refractile drops; at the same time the image of the larger ones becomes distinctly polygonal, which confirms what has been remarked above concerning their direct contact and mutual flattening (see Plate X. Fig. 5, *a*, *b*). The images of the droplets now no longer touch one another, but are separated by light intervening spaces. These intervening spaces are distinctly crossed by faint, moderately dark filaments, which unite the dark images of the droplets to one another. In this way quite an exquisite network comes to be formed, with nodal points of considerable thickness. The meshes of this network are always *triangular*, the trabeculæ for the most part very fine, but occasionally also much thicker.

The origin of this network is easily explained if one studies attentively the most external drops of such groups. It is then seen that the diffraction ring with its dark border, described above, is present round each of the droplets; but since the dark borders of neighbouring diffraction rings run into one another, and at the same time pass across adjacent droplets, the connecting filaments are shown to be portions of the dark borders of the diffraction rings. As long as a border of this kind coincides with an adjacent droplet it is no more visible. The thicker connecting filaments also admit of a simple explanation. In the smallest droplets, as a rule, the dark borders of two neighbouring diffraction rings fall so close together that they give the appearance of a common connecting filament between the two drops. If, on the other hand, two such borders are farther apart, a dark connecting bridge of greater thickness comes into view, since the whole intervening space between these adjacent borders appears darker. As a rule, each one of the triangular meshes of the

network is lightened by the superposed diffraction rings of three adjacent drops. In the case discussed, however, the space between two adjacent droplets, which are a small distance apart, is only illuminated by two diffraction rings, and therefore appears a little darker—an appearance which is strengthened by contrast with the neighbouring clear meshes. The origin of the thicker bridges can, for example, be very distinctly observed, when a series of small drops is apposed to the surface of a large one (Fig. 5, *c*, Plate X.).

The observations which have just been described are a warning to exercise the greatest caution in forming conclusions about reticular protoplasmic structures; a great deal of more detailed investigation is necessary in order to test the earlier observations with a view to determining the reality of the structures described.

We have seen how reticular appearances of this kind arise in strongly refracting droplets which are thickly crowded together in a medium of less refracting power; the same thing can be shown, however, when we are dealing with closely packed droplets of less refracting power in a more strongly refractile medium, as in the earlier described oil-froths, for example. If a very thin layer of such a froth be investigated, not exceeding in thickness one layer of alveoli, exactly the same phenomenon can be observed if one places the focus a little *above* the exact median plane. With a high focus the image of every less strongly refractile droplet changes, as is well known, into that of a darker point or granule. Round each of these points, however, there exists just such a diffraction ring as round the droplets of stronger refraction, and these diffraction rings with their borders then also produce just the same reticular appearance with dark nodal points as has been described above. Photograph II. reproduces this false reticular appearance very beautifully, while Photograph I. shows the same spot at a focus slightly below the median one.

From these results it is certainly to be concluded that in the microscopical observation of a thicker layer of such a foam, there must be indications in many places of the image of the false network mixed up with that of the real

one, because here and there portions of the froth are in too high a focus, and hence show the false reticular image. In future any fine network in which the meshes are triangular throughout must in general be regarded with suspicion, and cannot be considered as the true structural image without sure proof. As has been said, it follows from what has been set forth above, that the meshes of this mock network must always be triangular. Although I have devoted much thought to the point, I at least am unable to find anything to support the idea that quadrangular or polygonal meshes may arise in this way. Of course the circumstance must be taken into account that from various reasons individual connecting filaments may appear less distinctly marked out, and therefore may easily be overlooked, in which way meshes may be formed which are apparently polygonal.

In any case it is impossible that there could be formed in the way described modifications of the network which would give the appearance of longitudinal fibrils, such as are so frequently shown by the protoplasmic framework, especially with such distinct transitions to the usual reticular framework.

From the arguments adduced I consider that the possibility of the protoplasmic framework owing its origin to an optical phenomenon of this kind is quite excluded. But there are still other facts that prove this. As we saw, the reticular appearances described arise when the drops or granules are in close contact, or when there is an extremely small interval between them. Now, if the protoplasmic network depended upon corresponding relations, the close apposition of the granules or droplets would necessarily be evident in any case with a proper focus, and therefore the image would be essentially different in such a focus. This, however, is never the case. Hence in my opinion the protoplasmic structure cannot be produced by close apposition of granules. It may, however, on the contrary, very well be the consequence of a close, froth-like crowding together of feebly refracting droplets, for such a structure gives, as has already been shown, the appearance of a network, whether

focussed clearly or not; only the two appearances are rather different. The accompanying diagrammatic figure shows the relations of these two reticular images to one another, the real one (*a*) in sharp focus, and the optical one (*b*) with a higher focus. The distinction between them lies in the fact, that the former has a wider and more irregular mesh, the latter, on the other hand, is denser and more regular, appearing in particular more as if striated diagonally. Now if we are able to show that in very fine sections of protoplasm, which have at most the thickness of one or two alveoli, the two different reticular images are actually to be observed, this may perhaps furnish the surest proof that the structure is really present as asserted by me, that is to say, that the meshed structure of the protoplasm depends upon the deposition in it of feebly refracting droplets, which are so crowded together as to form a froth-like structure. Now this is as a matter of fact the case. Both in fine sections through liver cells and elsewhere, I was at an early period struck by this strange phenomenon, without knowing its explanation, and I may well say that at that time it gave me many a *mauvais quart d'heure*. There can be noticed, as I have said, two reticular images, one with a rather deeper focus, which even at an early period I was able to decide was alone that of the exact focus, and then, a second one which comes into view with a higher focus, and is if anything more distinct than the first one, appearing finer and more striated, and thus corresponding exactly to that which is demanded both by observation upon the oil-foams and by theoretical considerations.[1]

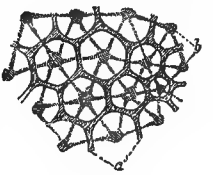

Fig. 18.

The discovery of the optical reticular images, which I did not make until nearly at the end of my investigations, of course disturbed me very much at first; indeed for some time I even considered the whole of my views, as to the reticular structure of protoplasm generally, to be entirely exploded, until, as has been described, I gradually found, by

[1] For further remarks on the false reticular image exhibited by protoplasm see the description of *Æthalium* above, pp. 111-116.

penetrating more deeply into the subject, that these observations were even of a kind to furnish additional proofs for the correctness of my theory.

The Nature of Colloid Bodies [1]

The problem of the nature of coagulated albumen and other coagulated colloids must now receive, as has already been pointed out above, quite a different solution from me from that which I gave at the time of completing this manuscript (summer of 1891). At that time I had not myself accurately investigated this subject, as I also remarked. Since, however, it is an especially important one, I attempted to obtain more detailed information upon this point after concluding the present work. That this has not been done till now is scarcely a matter to be regretted by me, but rather to be regarded as a fortunate circumstance, for I think that, probably, all the investigations communicated in the present work would have been left undone if I had taken this question in hand earlier.

To be brief, the result of the investigations hitherto undertaken by me upon the nature of coagulated white of egg, and of coagulated commercial gelatine, is, *that they present all the phenomena which we have recognised in this work as characteristic of the structure of a fine foam.* I will not describe my experiments and observations more in detail in this place, since it will be necessary to bring them out later more fully, and accompanied by photographs of the most important relations. I will only mention that coagulated white of egg and gelatine have a very beautiful, finely honeycombed structure, and since the false reticular image can be seen distinctly with a *higher* focus, the alveoli possess less refractile contents, probably consisting of a watery fluid in the honeycombed framework. In both the radiate alveolar layer can be plainly made out, both on the surface and round the larger vacuoles of the interior. In all parts which during the coagulation are subject to a pull or a tension, a fibrillated alveolar structure is shown, frequently magnificently developed, and agreeing completely with the corresponding structures of protoplasm. It is also frequently possible to see in the interior of such coagulated masses radiating appearances which quite rival those of protoplasm.

So far the appreciation of the relations of the coagulation products in question offers no special difficulties for any one who

[1] An addition made by the author in April 1892 after completion of the manuscript.

is acquainted with the optical appearance of finely frothy structures, and has more especially become sufficiently an expert by the study of coarser foam structures. On the other hand, great difficulties may be presented by the question as to what conclusions are really to be drawn from these results. Those who, like Berthold, Schwarz, and Kölliker, deny generally the existence of structures in living protoplasm, will of course be inclined to look upon the above results simply as a confirmation of their view that the alleged structures only owe their origin to processes of coagulation of this kind. In answer to this I must declare afresh that their opinion is untenable in view of the numerous cases in which the structures are distinctly demonstrable in living protoplasm. Only for such protoplasm, as in life appears quite hyaline, would their interpretation of the structures which appear in the fixed condition be possible. But it should first be decided with sufficient clearness what significance properly attaches to these foam structures of coagulated white of egg and gelatine. The subject still lies in obscurity. Two opposite possibilities confront one another here. Either fluid albumen and watery gelatine are homogeneous bodies in the sense of a solution, and at the moment of coagulation undergo a process of desolution with formation of froth, just as we have above become acquainted with an instantaneous formation of foam in suitable oil-drops; or these bodies are not homogeneous in the sense of solutions in the uncoagulated condition, but are very fine foam structures, of which the two components possess such similar powers of refraction that their structure is not recognisable. The frothy structure of their coagulation products would, in this case, not be a new formation, but it would merely be a case of their being rendered distinct, owing to the frothy framework undergoing an alteration, that is to say, becoming strongly refractile, and hence distinctly visible. Which of these two possibilities is the correct one, it is impossible to decide off-hand.

On the whole, I am more inclined, at the present time, to the latter view, without, however, being able to prove it satisfactorily, or to overcome certain difficulties which stand in the way of the assumption that it is correct.

The following points are, in my opinion, in favour of the assumption. As I have already pointed out, a layer of radiate alveoli can be observed plainly in coagulated albumen and coagulated gelatine. The gelatine was not brought into the coagulating fluid until it had stiffened to a jelly. Now, since the formation of a typical radiate alveolar layer is connected with the fluid aggregate condition, the development of such a layer in

the coagulation of solid gelatine jelly is difficult to understand; on the other hand, it is intelligible of itself, if we suppose that the foam structure already existed in the uncoagulated fluid condition, and became visible by coagulation.

The exceedingly distinct fibrillated alveolar structures alluded to (*supra*) must lead us to the same supposition. These structures are obtained when filtered albumen is sprinkled by means of a paint-brush into a drop of picro-sulphuric-osmic acid on the slide. The coagulated threads, which one commonly obtains by this method, show, as a rule, as has been said, a very beautiful fibrillated alveolar structure in their longitudinal direction. Now it seems to me most difficult to assume that the fibrillar structure of such threads is first produced by tension of the already coagulated albumen; on the contrary, I regard it as more probable that the fibrillar structure had already been produced before the coagulation by the drawing out of the fluid white of egg into threads.

If we further consider that the energetic power of swelling exhibited by albumen and gelatine would gain very much in intelligibility on the supposition of a frothy structure, and that in addition there is the fact that gelatine, at least during the process of taking up water, becomes more or less opaline, and that watery fluid can be squeezed out of gelatine jelly by strong pressure, it appears to me that there is some evidence in favour of the second of these possibilities. I will not omit to point out that neither in the fluid nor in the dried albumen, and still less in gelatine jelly, was any trace of structure to be made out. But it is noteworthy, that in drops of fluid albumen mounted in paraffin oil I was able to observe an indication of an alveolar layer, and even of its radial striation. I put no great value upon this observation, because it requires repeated investigation, and deceptions are very possible.

Now whether the question that has been raised will be decided in the future in this sense or in another, nevertheless it seems to me at the outset to be of interest, that the foregoing investigations have led me to a conception of the jelly-like distensible and coagulable bodies, which harmonises well with the opinion expressed by a physicist of experience in this subject. For Quincke has expressed himself upon this point (1890, p. 207) to the following effect: "In the same way I believe gelatinous substances, such as glue and other jellies, should be regarded as fluids in which there are numerous invisible thin partitions of firm or fluid lamellæ."[1] I may be

[1] As I see from Lehmann's *Molecularphysik* (Bd. i. p. 525 *et seq.*), similar views with regard to the physical constitution of the jellies have already been

allowed, at this opportunity, to refer also to the fact that a physicist such as Quincke names bodies of this nature "foams" without hesitation, when they are composed of two fluids. I point this out because, as is well known, it has been brought forward against me from several sides that I make an incorrect use of the word *foam;* that is to say, that the foams described by me should more correctly be termed emulsions of two fluids.

5. *The Structure of Protoplasm is Alveolar or Honeycombed (Foam-like)*

After having set forth briefly the various views held upon the structural relations of protoplasm, we must finally pass on to place upon a stronger basis the opinion which I have represented for some time, and which I am seeking to establish more firmly by means of the present investigation.

This view culminates essentially, to express myself as briefly as possible, in this, that protoplasm has a structure such as we have seen and thoroughly studied in the artificially produced drops of oil-lather, that is to say, it has a foam-like structure.

It will therefore be my first task to set forth the reasons which make it probable or certain that the spongy framework commonly assumed to exist, or fibrils connected in a net-like manner, cannot be present in protoplasm. For there is no need of any special discussion to show that the decision between these two possibilities cannot be reached from the microscopic image alone. The minuteness of the structures renders it impossible to make out off-hand whether the reticular appearance observed corresponds to a spongy framework or an alveolar meshwork, since the microscopic image, as has been said, must in such minute structures be the same in both cases.

expressed before by physicists. For instance, Guthrie (1875 and 1876) seems to have put forward the same view in the main as that represented by Quincke. Lehmann himself is also inclined to an opinion of this kind, in the chapter cited upon the jellies, even though he supposes they have a spongy instead of a frothy framework. It is not quite intelligible to me, however, how with such views with regard to the physical nature of jellies, he can interpret in a following chapter "the phenomena of swelling as due to chemical combinations" (that is to say, of the body that swells) "with the solvent medium."

(*a*) *Aggregate Condition of Protoplasm*

In order, however, to approach this question, we must first of all come to a decision with regard to the *aggregate condition* of protoplasm, since the solution of the question turns essentially upon this preliminary inquiry. The point has notoriously been much disputed, and an opinion has even been expressed that one cannot properly speak at all of an aggregate condition of protoplasm, in the same sense as of that of a homogeneous body (Brücke, 1861), for the very reasons that protoplasm is not a homogeneous body, but a mixture of solids and fluids.

I would gladly avoid entering into the historical aspect of this question, but it does not seem possible to discuss the problem clearly without such a brief review. The older observers were notoriously fairly united in their conception of protoplasm as a slimy, rather viscid fluid. This view was essentially established by the studies of prominent investigators, especially in the fifties and sixties, during which period the protoplasm question awakened a lively interest. Max Schultze's investigations on the protoplasm of Rhizopods and vegetable cells and their phenomena of movement (1854-63), on whose side Haeckel (1862, p. 90 *et seq.*) ranked himself as the upshot of his extended labours on Rhizopods, Radiolaria, etc., and finally the studies of Kühne (1864) upon protoplasm, especially confirmed this view. The principal support for it was obtained from the relations of the phenomena of streaming movement which gave the observer the impression of a substance in a state of flux, and therefore fluid; and further from the flowing together of protoplasmic processes, the taking up of solid particles into the interior of the protoplasm, and the tendency of isolated portions of protoplasm to assume a spherical form.

A reaction against this conception was started as far back as 1861 by Brücke. Brücke disputed *à priori* the possibility of fluid protoplasm being able to carry on all the complicated functions of the cell. The cell, or more properly its protoplasm, must therefore possess, in addition to its molecular structure, a "special structure" or "organisation." Hence all protoplasm must consist of solid and fluid portions. To inquire into the condition of the protoplasm in the aggregate would therefore be really just as absurd as to discuss the same question in reference

to a jelly-fish. Brücke brought forward facts, in so far that he tried to interpret the protoplasmic streamings in the hairs of *Urtica* not as simply the streamings of a liquid, but rather as giving the impression that the protoplasm, "or the contractile cell body, contained a fluid which streamed through it and contained numerous small granules." So far, therefore, as it is possible to understand the ideas briefly thrown out by Brücke, one may well assume that he imagined to himself in the protoplasm a firm contractile framework steeped in fluid, just as was described later by Heitzmann.

That Brücke's view, although it was disputed by Max Schultze (1863), found approval is obvious from the fact that the assumption of solid and fluid parts in protoplasm became more and more widely spread. Although de Bary (1862) denied Brücke's view of the processes of streaming in protoplasm, he believed it necessary to accept his opinion upon the organisation of the cell. Cienkowsky (1863), from a study of the plasmodia of Myxomycetes, arrived in like manner at the assumption of a thicker hyaline ground substance, capable of contraction and expansion, and of a fluid granular substance. How he represented to himself the mutual relations of the two substances in the building up of the protoplasm, remains, however, rather obscure, the more so as it follows from his description that he regards the contractile ground substance also as fluid. How could we in any other way understand the expression on p. 414: "The plasmodium thus gives an indubitable example of a fluid stage in the development of an organism"! Although de Bary (1864) disputed this distinction of two substances in the plasmodium, a contractile and a fluid, and regarded it with Kühne as contractile throughout its whole mass, he yet assumes a similar difference, inasmuch as he admits local differences in its "cohesion, fluidity, and mobility," which, moreover, were subject to frequent change. The plasmodium is supposed to consist therefore only of *one* substance, but its physical character is frequently liable to local variation. The protoplasm of these Protista is said to possess a "soft consistency," but in any case they would be "in no way bodies in the least of a fluid, trickling nature."

Hofmeister, who in 1867 called protoplasm a "viscid mixture of various organic substances, or a thickish slime," and often makes use of the physical properties of fluids to explain the behaviour of protoplasmic bodies, yet declared himself, as far back as 1865, and again also in 1867, in favour of a special organisation of protoplasm. He remarks on p. 8 that every attempt to obtain a conception of the phenomena of protoplasmic

movement must have as a postulate "an organisation of the protoplasm," "a peculiar structure in it, which differs essentially from the aggregate condition of viscid fluid bodies in the fact that the molecules of the protoplasm are capable of being unequally displaced in different directions." Of this alleged postulate of every explanation he makes, however, no use whatever, either in considering the phenomena of the structure, or of the movement of protoplasm; the hypothesis evolved by him with regard to protoplasmic movement contains no mention of it.

In opposition to these efforts, it must be of special interest to us that two observers so experienced in physical matters as Nägeli and Schwendener both in 1865 and later in 1877, especially point out the "viscid nature" of protoplasm, somewhat like mucilage; it may then, of course, possess an organisation with impunity. They derived their proofs chiefly from the flowing together that may frequently be observed in protoplasmic bodies, and the behaviour of swarm spores when they happened to be torn in pieces.

Brücke's views soon found further defenders. In 1870 Hanstein expressed himself to the same effect. It seemed also to him quite unthinkable that from a fluid substance a structure should have been produced which was organic, and "therefore different in itself." For the rest, his ideas of protoplasm at that time were rather obscure. He ascribes to it "a soft and plastic, and yet viscid and formed and self-forming condition." It was said to contain besides fluid parts, "soft solid" ones as well; it was not a substance but an organism.

But it was Velten especially who in his works (1873-76) tried to collect further proofs for Brücke's conception. For him also it was an established fact (1873) that protoplasm possessed in any case a complicated organisation, and was not a homogeneous fluid. But how he really represented the matter to himself is not quite clear. In 1876 he declares that protoplasm is composed of solid and fluid parts. Thus on p. 138 it is said that "in protoplasm we have a more or less coherent body, possessing the solid aggregate condition, which last may be temporarily exchanged for that of fluid substance." If the latter limitation makes the view first pronounced rather obscure, the following passage (p. 130) adds still further to the obscurity, where it is said "that protoplasm contains solid and fluid parts side by side in the smallest particles of space." Velten's view is partly based upon structures observed by him (see above, p. 165), partly upon the peculiarities of the phenomena of streaming. He makes sincere efforts to reconcile with his view the tendency of protoplasm to

assume a spherical form, which had been pointed out by the adherents of the theory of its fluid nature. When this phenomenon occurs normally, it was said to depend upon the peculiar organisation of the solid particles of the framework; he thus introduced a mock explanation in the place of a natural one. For the most part, however, the assumption of the spherical form was to be referred to an abnormal state of the protoplasm, which would hold good for the rounding off which takes place in plasmolysis, the spherical form of drops of protoplasm that have oozed out, and so forth. In these cases the protoplasm is supposed to become usually more watery; the framework of solid particles of protoplasm breaks up, but may subsequently regenerate itself. Just as little does he allow the spherical form of vacuoles to hold good as a proof, since the formation of vacuoles takes place in the abnormal condition—an assertion which betrays a certain amount of inexperience in these matters. It cannot at any rate be asserted that Velten has based his view upon sufficient grounds.

Hanstein in 1880 and 1883 set forth in still more detail the views he had already expressed in 1870. It appears from them that he had taken up to some extent the opinion already expressed by de Bary with regard to the protoplasm of the Myxomycetes. The "fluid" as well as the non-fluid parts of which protoplasm is composed are supposed to be "forms of the same *protoplastin*, which only differ from one another in the amount of water they contain" (1880, p. 163). The partitions formed by the non-fluid protoplastin, which is deficient in water, within and around that which is fluid, are explained by him as sometimes viscid, sometimes solid. The fluid part he termed *enchylema* (1882), the hyaline ground substance of the entire protoplasm, *hyaloplasma*, and the granules lodged in it the *microsomes*. His *enchylema* is, therefore, in its turn equal to hyaloplasma + microsomes. There is no need to point out specially that the use, which at a later period was made of the term enchylema, has nothing to do with the original meaning of this term in Hanstein.

We now turn to the numerous observers who have described filamentous or reticular structures in protoplasm. From the foregoing account we have learnt that theoretical deductions, as well as observations and speculations upon the phenomena of movement, had already necessitated the assumption, and finally the discovery, of such a structure. I think there is no necessity to go through the views of the numerous observers of filamentous or reticular structures in detail, as they have in part been indicated already. It is sufficient to point out that the majority have more or less plainly declared that they

represent to themselves the filaments or the network as composed of a firm substance. When the fundamental laws of physics were consulted, it was impossible for it to be otherwise, since the permanent existence of such structures was only thinkable if they consisted of a solid substance. Besides this, numerous investigators held the idea that the phenomena of contraction, or changes of form generally, such as protoplasm shows, could only be produced by solid bodies. On the other hand, it was at the same time pointed out that protoplasm behaved very like a fluid. Thus Strassburger, who still upheld the reticular structure of protoplasm, remarked (1882, p. 232) that it was "soft or semi-fluid"; that it agreed in many of its peculiarities with a colloid, but still more closely, on the other hand, with a fluid, "for it has a tendency to assume the spherical form in a condition of stable equilibrium." Such terms as soft, solid but yielding, jelly-like, semi-fluid, recur continually here and there. Those authors, however, express themselves in the most definite manner who assume, like Pflüger (1889), that protoplasm is composed of "absolutely solid and absolutely fluid" parts.

I had, for my part, expressed myself already in 1876 (p. 203) to the effect that "in spite of the objections that are raised against the idea, there are the most cogent arguments for supposing that protoplasm obeys the fundamental laws of a fluid mass." My conception of the structure also gave me no reason for departing from this view. In 1886 Berthold in his valuable book again took up the doctrine of the fluid nature of protoplasm, which had fallen very much into discredit. He did not, however, try to really support it by direct proof, but laid it down as a hypothesis upon which to base his observations and speculations upon the structure and upon the phenomena of the movement of protoplasm, in order to show the probability of the hypothesis by the ease with which the problem could be worked out.

What position Schwarz (1887) really takes up with respect to the question of the aggregate condition of protoplasm, is not quite clear to me from his work, as I have already pointed out above. As is well known, he denies the reticular framework, and speaks of a "semi-fluid aggregate condition" of the cytoplastin (p. 131). On the other hand, he says on p. 136: "In the cytoplasma no preformed networks and frameworks are present, but a part of it may modify itself into filaments and strands. In consequence of this I must assume that the cytoplasma is a mixture in which, under certain circumstances, a separation can take place of more rigid, viscous, and more fluid dissolved

substances." Hence, under certain circumstances, a framework of a firmer nature can make its appearance. Since Schwarz, on p. 139, declares that his results agree with those of Berthold, I must certainly assume that he conceives of this "mixture," which the cytoplasm is in his opinion, as a fluid one. Such expressions as "semi-fluid" are too vague to be taken definitely into account.

I had myself in 1887 advocated the fluid nature of the endoplasm of the Infusoria, and, in this connection, also that of the greater part of other protoplasm, which throughout behaves in a similar manner (p. 1392). I drew attention more especially to the constantly spherical form of the vacuoles that appear in protoplasm, a fact which would prove that both the contents of the vacuole and the surrounding protoplasm are fluid throughout. In Protozoa there is such frequent opportunity for observing vacuoles of different kinds—food vacuoles, contractile vacuoles, and ordinary fluid vacuoles—that no one can be in doubt as to their regular appearance in normal protoplasm. It is, however, just as certain, and as plain, that all these vacuoles assume the form of a spherical drop when they are not hindered by solid bodies to which they adhere, or by mutual pressure, streamings, or any other kind of special force which is acting upon them. From this positive experience, which is just as capable of proof as any other physical fact, there is only one conclusion to be drawn, namely, that expressed above, that the contents of the vacuoles, as well as the protoplasm surrounding them, must be fluid. In addition we know definitely with regard to the contents of the food vacuoles that it is water. But all other vacuoles exhibit just the same appearance and behaviour, for which reason their contents must in like manner be a watery, very dilute solution. We know further that vacuoles may flow together, and in this process behave in exactly the same way as any two drops of water in viscid oil. The study of the contractile vacuoles, which unfortunately have received very little attention from many investigators who have given vent to opinions upon such things, gives us the most beautiful instances of such fusions, and the consequent rounding off

of the product of the fusion. If we add the numerous observations made upon spherical vacuoles in protoplasm, as well as the observations upon the fusion of threads of protoplasm, and upon the drop-like shape which is assumed by pieces of protoplasm which are isolated or set free from their membrane; and, finally, the condition of things in the phenomena of streaming,—it seems to me not possible to doubt in any way the viscid or slow-flowing nature of ordinary protoplasm.[1]

This conclusion will at once obtain further confirmation when we are convinced that the assumption of a rigid network in protoplasm agrees very little with certain facts, or at least requires for its explanation complicated assumptions which render the supposition highly improbable.

[1] Pfeffer also arrived, in 1890, at essentially the same conception of the aggregate condition of protoplasm from similar grounds. Both the streaming protoplasm of the Myxomycetes, and the principal mass of the protoplasm of the vegetable cells enclosed in cell membranes, are regarded by him as "viscous fluids," and although he frequently makes use of the term "plastic," he particularly remarks that he only understands by it a condition differing in degree from the viscid condition, *i.e.* one rather more coherent, and not in any way a plastic condition like that of damp clay. Pfeffer, therefore, expressly recognises the fact that the chief mass of a protoplasmic body obeys the laws of fluid substances, and if he is forced by his acquaintance with the Myxomycetes to assume that their cortical layer possesses a greater cohesion, or even solidity, that also the external layer of other protoplasts, as well as cilia, are to be regarded as solid, yet our views agree completely in these respects also (cf. on this point below, p. 240). As regards the cortical layer of the Myxomycetes in particular, I can also only draw the conclusion from Pfeffer's investigations that it possesses a considerably greater viscosity than does streaming protoplasm, but that it is not, however, really solid, but follows, although only very slowly, the laws of fluids. This conclusion can be proved from the manner in which materials are taken up and given off from the plasmodia, as well as from the easy transition from cortical substance to the more fluid internal protoplasm. For the rest, I also consider it possible that a portion of the observations which induce Pfeffer to ascribe a relatively high cohesion to this cortical layer may depend on the fact that the plasmodia of Myxomycetes adhere to the substratum, so that their extremely thin edges have their mobility essentially diminished. In this connection I should like to adduce certain observations upon streaming oil-drops which I have made on occasions. If these drops, as sometimes happens, adhere firmly to the slide, the very striking phenomenon might frequently be well seen of the outermost edge of the froths remaining completely at rest, while streaming movements went on in a very lively manner within this quiescent margin. Since in this case there is no ground whatever for assuming a greater cohesion

(*b*) *Vacuoles*

To these certain facts belongs, in the first place, the general *formation* of *vacuoles*. There is no need of any special proof that vacuoles are drops of fluid in view of the universal agreement which prevails upon this point. On the other hand, observation teaches, in the plainest manner, that every vacuole is completely shut off by a delicate, somewhat darker, and rather shiny border, which is exactly similar to the external pellicle-like border of a naked protoplasmic body. It is, in fact, notorious that the existence of a special vacuolar membrane has been asserted again and again, without, however, any sure proof having been brought forward for the fact. The adherents of the theory of a spongy framework in

or viscidity of the margin, adhesion can alone be regarded as the cause of the phenomenon. As we have already discussed before (p. 37 above), the margin of such an adherent foam-drop is exceedingly attenuated, for which reason it seems quite possible that it is hindered in its streaming movements throughout its entire mass in consequence of the adhesion. If this conclusion is the correct one, it would follow definitely from it that protoplasm, when viscid throughout its entire mass, must always possess a very thin quiescent marginal layer, as long as it adheres to a solid cell membrane. Such a result, however, if correct, of course does not in any way exclude the fact of the external layer also possessing, in part, an actually heightened cohesion, especially after the protoplasm has become detached from the cell membrane by plasmolysis, and is also surrounded externally by a watery solution.

On the ground of his view as to the viscid nature of protoplasm Pfeffer then expresses the following opinion "that . . . in no case is a firm, continuous, permanently rigid framework admissible in protoplasm." My experience has also led to the same conclusion, while in our views upon the structural relations of protoplasm we differ very essentially from one another. The very brief remarks made by Pfeffer in 1890 (p. 255, footnote) upon this point are not very clear, and cannot in any case serve as an explanation of the structures often so distinctly observed even in living protoplasm. He says: "Possibly parts of the cytoplasm are differentiated in a retrograde manner, and it is even probable that within the cytoplasm parts of unequal cohesion and density are formed, which under certain circumstances are capable of being optically observed either directly or in fixed preparations. I suppose that in such a manner, and necessarily also with the co-operation of a different distribution in space of the microsomes, etc., a portion of the structural relations in question hitherto observed comes to be formed." Only from the circumstance that Pfeffer never occupied himself thoroughly with the investigation of protoplasmic structures am I able to comprehend to some extent how he could let fall an opinion of this kind upon these matters, which are part of the fundamental details of the protoplasm question.

protoplasm have, however, rather different views with regard to the limitation of the vacuoles. In the first place, none of them have really given any account of why the vacuoles should always be spherical, although the rigidity of their framework was yet necessarily admitted. In general the structures in question are regarded as larger collections of fluid in certain regions of the framework, which is thereby thrust apart. These views only vary on the point as to whether the contents of the vacuoles are to be considered as identical with the general contents of the matrix of the alveolar framework, or as differing from it. Thus Heitzmann has termed the vacuole "a lake in the middle of the protoplasmic body" (1883). Now, if the framework is rigid, it is not at all apparent why the vacuole when unrestrained should always possess a spherical, and not a more or less irregular outline. But it remains still more inconceivable how the adherents of the framework theory can speak of a flowing together of vacuoles, since this is simply impossible.

If the vacuole is only a collection of fluid in certain regions of the framework, there must exist, originally at any rate, a connection between the contents of the vacuole and the intervening matrix. That such a connection, however, cannot be permanent is proved not only by direct observation, which always shows a distinct and continuous limiting margin to the vacuole, but also by the common experience, that the cell sap cavity of vegetable cells, which is in reality nothing more than a very large vacuole, frequently contains a coloured fluid, while the enchylema of the protoplasm is completely uncoloured. This, as well as other observations, make it unconditionally necessary that the contents of the vacuole should be shut off from the enchylema by a closed lamella. In this way Schmitz (1881) had already assumed that the origin of the vacuoles was due to the formation of "a special continuous limiting layer" round the cavities of the framework. But this would only be possible, if the framework contracts, by closing its meshes to form a continuous membrane round the vacuole. Van Beneden also arrived, in 1883, at similar views. If, he declares, the contents of the vacuole is identical with the inter-fibrillar substance, the wall of the vacuole must possess a lattice-like structure with extremely narrow meshes. He therefore imagines in any case that this wall arises by contraction of the framework. Leydig (1883), who derives the

vacuoles from " enlargement and flowing together " of the cavities of the meshes of the framework, seems to think that they are usually not definitely shut off from the enchylema. At least he remarks that they seldom obtain a definite lining by condensation of the trabecular framework (p. 143). Finally Heitzmann also (1883) developed similar views. According to him the vacuoles always possess a special wall, which is built up in the form of a so-called " membranous layer." By such a membranous layer he understands a delicate closed membrane, which is thus formed. From the nodal points of the network, which as a rule only send out a few filaments of the meshwork, such a number of threads radiate out in one plane that they fuse into a continuous layer, while the nodal points at the same time disappear. Now, since the membranous layers formed by neighbouring nodal points become united into a continuous layer, there arises a continuous envelope round the vacuole. Frommann also states (1890, p. 10) that the vacuoles possess " for the greater part a delicate pale or somewhat shiny membrane." He even seems to regard this membrane as solid, since he remarks that the growth of the vacuoles " takes place by fusion of neighbouring vacuoles, accompanied by a tearing or liquefaction of the membrane," or by osmosis.

Finally C. Schneider (1891), whose views upon the fibrillar structure of protoplasm we described above (p. 182), has also discussed the formation of the vacuolar wall. He believes that he is able to find his fibrillæ even in the vacuolar wall. In this place they are united by a special cementing substance into a membrane. What Schneider regards as the fibrillæ in the wall of the vacuole is certainly nothing else than a surface view of the layer of alveoli which borders on the vacuole.

We have seen in the foregoing to what assumptions the representatives of the framework theory are forced in order to explain the closed vacuolar wall. If we further imagine to ourselves the apparatus of mysterious forces which bring about the condensation, or even the closure, of the meshes of the framework round the vacuoles, and on the other hand reproduce the usual condition of the network after the disappearance of the vacuole, it would seem clear that the correct explanation will be attained with some difficulty on this theory.

On the other hand, the alveolar, or foam theory of protoplasm explains the actual phenomenon, and the be-

haviour of the vacuoles, in the simplest manner, by the physical laws of fluid masses. We can completely grasp the reason why every vacuole must be surrounded by a continuous pellicle-like border, which shuts it off from the neighbouring layer of alveoli. We understand their spherical form, their occasional flowing together, etc., in the easiest manner; but we can comprehend a great deal more, which the framework theory is unable to explain. That is to say, we can understand why each vacuole is surrounded by a radially arranged layer of alveoli, as has been shown above in a series of examples. For this point the framework theory is not able to furnish a solution.

I must not leave entirely without mention in this place a theory of the vacuoles which has sprung up on botanical grounds, and has found numerous adherents among botanists, namely, de Vries's *Tonoplast Theory*. De Vries is, as is well known, of the opinion that the vacuoles are just as much independent organs of the cell as the cell nucleus, the chromoplasts, and other things. The vacuoles are the products of so-called *tonoplasts*, certain small bodies which build up strongly osmotic substances within themselves, and in this way swell up to vacuoles. The vacuoles always possess, it is supposed, a special, independent membrane, distinct from the rest of the protoplasm, which arises from the tonoplasts, and is to be regarded as the true active and living part of these structures. Admitting the correctness of this view, the difficulty would arise of explaining the continuous limitation of the vacuole. I regard, however, de Vries's theory as on the one hand unproved, in fact improbable, and on the other hand I consider the origin of the vacuoles to be completely intelligible without the tonoplast theory.

In the first place, there is a lack of any substratum of fact for the assumption of tonoplasts. No one has ever seen them in the non-vacuolated condition; there is therefore a necessity for other grounds upon which to justify the assumption. Among such it would of course be decisive to show that the vacuoles were only formed like the nucleus or the chromoplasts, by multiplication on the part of bodies like themselves. Now de Vries is actually of the opinion that this multiplication always occurs. What, however, he brings forward (1886) in the way of facts cannot be regarded as the slightest proof of an independent multiplication of the vacuoles, but would rather seem to be entirely a case of constriction of larger vacuoles into smaller ones

in plasmolysis and similar processes, in which it is evident that the division of the vacuole is effected by the surrounding protoplasm. Also what Went communicates later (1888) in this respect is not convincing. For the proof that vacuoles become constricted in two is not sufficient; it ought rather to be proved that this is effected by the proper and independent wall of the vacuole, and not by means of the surrounding protoplasm. It is just this point, however, which Went is not able to make clear. He even says himself on p. 318, "the wall of the vacuole is so thin that for the most part it is not visible," nevertheless he thinks it may be assumed "from analogy" that it takes an active part in the division. On p. 319 it is remarked: "It hence seems to me (!) that the wall of the vacuole plays an active part. This point must, however, be made clear by later investigations." This point is, however, just the most salient one in the whole question concerning the so-called division of the vacuoles, and has, therefore, in spite of his assertion to the contrary, not been solved by Went. Just as little, moreover, has Went proved that the vacuoles never appear as new formations, as he asserts. His investigations, as well as those of de Vries, only extend, as is shown by the figures, to relatively large coarse vacuoles. Now since new vacuoles are originally at any rate exceedingly minute, their statements prove nothing in this respect. What can, however, be proved, in such subtle questions, by figures so coarsely schematic on the whole as are those which accompany the works of de Vries and Went? Whoever has studied at all closely the contractile vacuoles of Protozoa cannot doubt for a moment that new vacuoles continually make their appearance, which do not owe their first origin to the division of formerly existing ones. This had already been for a long time proved to a certainty when de Vries and Went undertook their investigations.[1] Moreover, Pfeffer has

[1] In recent times Künstler (1889) has come forward energetically in defence of a "more resistant membrane" being present round the contractile vacuole of Flagellata, especially in the genus *Cryptomonas*. Both on theoretical grounds, and from the special relations of the contractile vacuole of that genus, he regards this conclusion as unquestionable. Without entering here into details, I can only refer to the much clearer relations existing in Infusoria (see on this point my book on Protozoa), in which the origin of the contractile vacuoles by fusion of numerous small ones has so often been proved, that the presence of a special and constant membrane seems quite impossible. Since a corresponding origin of the contractile vacuole has also frequently been observed in Flagellata, it is impossible that the relations should be otherwise here, unless the structure termed contractile vacuole in *Cryptomonas* corresponds in some way to the reservoir of Euglenæ, which I regard as quite improbable.

recently produced vacuoles artificially in the protoplasm of Myxomycetes by introducing small crystals of asparagin and other soluble matters into it, so that counter evidence seems to be presented from this side also.

What de Vries brings forward with regard to the independent wall belonging to the vacuoles seems to me in any case little suited to prove its existence. In the normal vacuole he has seen nothing more than the limiting margin, which is easily explained on our view; on the other hand, he and Went have observed often enough how vacuoles flow together and become rounded off again after their fusion. This, however, presupposes absolute fluidity in the membrane, if for once we admit its existence. And how does it harmonise with this view when de Vries (1886, *Dros.*, p. 33) says, "This wall must, like living protoplasm, be exceedingly extensible and elastic, and impermeable to colouring matters"? Membranes extensible and elastic, but at the same time fluid, are not very conceivable. Pfeffer (1886) has therefore remarked very correctly, that the assumption of de Vries that the wall of the large central vacuole of the plasma cells was stretched elastically to a high degree, is very improbable, since nothing can be seen of it in cutting through the cell. Now de Vries has chiefly tried to prove his view of a peculiar membrane belonging to the vacuole by plasmolytic experiments on *Spirogyra*. Under the influence of a solution of 10 per cent KNO_3 + Eosin which was used for these experiments the vacuole with its wall was said to contract strongly, and to remain living for a long time, while the protoplasm quickly dies. The latter conclusion is drawn from the protoplasm soon becoming stained with eosin, while the colouring matter does not diffuse into the contents of the vacuoles, thus proving the living condition of the wall. Now I have already remarked above that the figures of de Vries are very coarse and diagrammatic, and give no sort of information as to finer relations, on which account I consider it an admissible supposition that the author has not carefully occupied himself with finer microscopical details. It also seems to me not impossible that the interpretation of the microscopic image given by de Vries both here and in *Drosera* (1886) is incorrect. De Vries gives us in fact no clue as to what is in reality present between the wall of the strongly contracted vacuole and the frequently only very slightly contracted thin utricle of protoplasm. I should suppose that between the two lies a very strongly vacuolated protoplasm. I imagine in my own mind that through the action of the KNO_3 solution water is drawn out of the vacuole, and it therefore becomes considerably diminished in size, but at

the same time the protoplasm bordering on the vacuole becomes strongly vacuolated, and in this way the space between the apparent wall of the vacuole and the external part of the protoplasmic utricle is formed. Therefore the supposed wall of the vacuole may be explained as a thin layer of the protoplasm immediately surrounding the vacuole, which is forced apart from the remaining protoplasm by vacuolisation. It is not inconceivable that under these conditions the vacuole with its surrounding protoplasmic wall may occasionally become entirely isolated. In the same way the apparent wall of the vacuole, as being the most internal part, may well remain living the longest; but another circumstance may also be in part responsible for the non-penetration, for a long time, of the eosin into the cell sap, namely, that it becomes stored up in the external protoplasm.

As has been said, I am unable to agree with either the tonoplast theory or the view of the existence of a special membrane proper to the vacuoles. All that can be admitted in the latter respect is only that the pellicle-like limiting border of protoplasm round the vacuole may *possibly* undergo certain changes under the influence of the contents of the vacuole, just as the external limit of the protoplasm undergoes changes under the influence of the surrounding medium.[1]

[1] With regard to this modification of the limiting layer of protoplasm round the vacuole and at the external surface, *i.e.* the so-called "protoplasmic membrane" of Pfeffer and others, the more recent observations and views of Pfeffer (1890) agree very well with my ideas. I am only doubtful whether the so-called protoplasmic membrane possesses the importance for osmotic processes which Pfeffer ascribes to it; on the ground of which processes Pfeffer was really first led to assume its existence; they are now also supposed by him to prove its presence, even when direct observation shows nothing of it for certain. It seems to me rather that the protoplasm as such can well produce these osmotic processes and their peculiarities, the more so since we have found that it presents a system of the finest lamellæ, the spaces of which are filled with watery fluid. Pfeffer (1890, p. 238) also considers this possibility, which I have always held to be the most probable, but arrives at the conclusion "that for the protoplasmic membrane a greater resistance to permeability [*i.e.* than that of ordinary protoplasm] is required, for this reason, that the imbibition fluid of the protoplasm apparently also contains materials in solution, which do not pass out by exosmosis." Although this "apparently," upon which Pfeffer's argument rests, does not seem to me quite inconceivable, I yet hold to the idea that the state of the case has been essentially altered by the theory of the foam-like structure of the protoplasm, which this work attempts to prove. That which Pfeffer terms imbibition fluid and ap-

(c) *External Surface of the Protoplasm*

Considerations quite similar to those which we have put forward with regard to the vacuoles also hold good for the external surface of the protoplasmic body. Consistent adherents of the framework theory, such as Leydig (1883 and 1885) in particular, did not shrink from the assumption that the outer surface of protoplasm, the surface of the cell in general, was not formed of a continuous layer of substance, but that it was "porous," in keeping with the spongy structure of the protoplasm. Thus Leydig says (1885, p. 15) the outer surface of the cell is always porous, "inasmuch as it consists of a meshed framework and an intervening matrix enclosed by it." Even in 1883 he asserted the same thing. In this respect his interpretation of the thin stratum of alveoli, forming a single layer only in the cells of the capillaries, appears characteristic, since he explained them as porous (see above, p. 144). This strange conception of Leydig's is, moreover, intimately connected with his view of the importance of the intervening matrix as the true living substance of the protoplasm, according to which, in fact, the intervening substance was supposed to creep out of the framework in the form of the pseudopodia. For this purpose it was of course necessary that the surface should not be covered by a continuous layer of the framework.

Frommann also was constrained to put forward similar views for naked protoplasm. Thus he remarks (1880), with regard to

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parently conceives of as a fluid which permeates the protoplasm evenly and continuously, is open to an essentially different interpretation on the ground of my investigations. This imbibition fluid is in reality the enchylema contained in the alveoli, and since it is always shut off by very fine lamellæ of protoplasm, the conditions of osmosis are always present even when the external protoplasmic membrane does not exist or does not possess the significance ascribed to it. If one supposes, however, with Pfeffer, that this imbibition fluid is one permeating the protoplasm continuously, it must of course be assumed that a special protoplasmic membrane exists at the surface, which controls the osmosis of the imbibition fluid. As has been said, however, I do not regard this assumption as inevitable, but it seems to me that the protoplasm as such, *i.e.* the lamellæ of the alveolar framework, suffice for the explanation of the osmotic processes.

cartilage cells, that a few filaments (so-called limiting filaments) of the framework occur on the surface, but no continuous membrane of condensed protoplasm.

On the other hand, Heitzmann had from the first (1873), although not persistently, represented the surface of the protoplasmic framework as shut off by a continuous membrane of the skeletal substance. Later (1883) he discusses this point in more detail, and derives the membrane, in the same manner as that of the vacuoles, from the formation of a so-called "membranous layer" (see above, p. 229) from the framework.

On the botanical side the matter has received rather different treatment. The idea had notoriously prevailed among botanists for a long time that the protoplasm must be limited towards the exterior by a special *cuticular layer* (*Hautschicht*), which was distinguished by its properties from the rest of the protoplasm. This cuticular layer has often been directly observed, *i.e.* the most external non-granular hyaline protoplasm, which we usually term ectoplasm in Protozoa, was termed the cuticular layer. The assumption of an ever-present, even if not directly visible cuticular layer, was, however, first founded upon the osmotic experiments of Pfeffer and others, which in the former's opinion could only be explained on the supposition of such a protoplasmic membrane possessing special osmotic peculiarities.

Schmitz, who was the first on the botanical side (1881) to study accurately the reticular structure of protoplasm, thinks it may be assumed that the cuticular layer is specially distinguished by its more narrow meshed structure from the remaining protoplasm. Strassburger also (1882, *Zellhäute*) was inclined to agree with this view, but is of opinion that the meshes of the cuticular layer of protoplasm could also become completely obliterated (p. 195). Upon this anomalous structure of the cuticular layer its peculiar osmotic properties might well depend. On pp. 235, 236, he speaks quite definitely of the fact that he assumes the "anatomical meshes," *i.e.* the meshes of the reticular structure, to be quite closed in the cuticular layer, and that in it the so-called molecular network is more stable, and the molecules have a more definite arrangement. If the cuticular layer is wanting on occasions, "then the granular protoplasm might contract the meshes at its surface, and take on the function of the cuticular layer." In 1884 Strassburger also explains the nuclear membrane as a corresponding cuticular layer of the protoplasm, and remarks upon this point (p. 104) that, "like every cuticular layer" it is "produced by narrowing of the meshes" from the network of the cytoplasm.

Schneider (1891), a consistent representative of the theory

of the purely fibrillar structure of protoplasm, derives a continuous limiting membrane to the protoplasm in the same way as has been already described for the membrane of the vacuole, namely, by a cementing together of the fibrils by means of a special cement substance.

For the rest, the majority of investigators who have occupied themselves with protoplasmic structures do not, as a rule, touch more closely upon the question of the formation of the outer surface of the protoplasm.

From what has been brought forward it follows that the representatives of the supporting framework theory require special assumptions to explain the limitation of the framework towards the surrounding medium; for the facts of the matter are not as Leydig represented them, but every observation tends to show that a continuous non-porous limiting margin always covers the surface of the protoplasm. Now since protoplasmic bodies can often be burst by pressure or cut in pieces at will, and then still show again a sharp continuous border at their surface —an experiment which has in fact been done so often, both on the animal and vegetable side, that it seems unnecessary to bring forward special examples here—the adherents of the supporting framework theory are forced to assume either that mysterious forces immediately close the exposed meshes again and again, or that this closure is effected by a formation of cementing substance, etc.

Such assumptions are, as has been said, entirely unnecessary for the alveolar theory. According to it the constant presence of a pellicle-like continuous border is a direct consequence of the supposed structure, and every drop of protoplasm that is separated off finds itself in exactly the same conditions again as the original protoplasmic body, and will therefore in like manner possess a limiting border.

(*d*) *Alveolar Layer*

We now come to a further relation of the highest importance with regard to the external limiting layer of the protoplasm, which in my opinion is sufficient to decide the

question in favour of the alveolar theory. I have before shown that especial relations exist at the surface of the protoplasm, since the alveoli of the outermost layer are always directed vertically to the surface, in consequence of which the thin radially striated layer, termed the *marginal alveolar layer*, comes to be formed. I have demonstrated this marginal alveolar layer in quite a number of cells, etc., and may further add that Schewiakoff and myself have further proved its existence both in smooth and transversely striped muscle cells (1890, 1891).

It has, however, further been shown that this alveolar layer is in no way a special kind of membrane at the surface of the cells, for it occurs in the same manner also round the drops of protoplasm that are formed by crushing either Miliolids or *Gromia Dujardini*.

On the other hand, we also found that a marginal layer of alveoli is always marked out at the surface of artificial drops of foam, and we were easily able to explain to ourselves how and why it must always make its appearance there. This agreement between the oil-lathers and protoplasm I regard as a proof that an agreement also exists in their remaining structure. At any rate I am not aware in what way the theory of a supporting framework would give an explanation for the appearance of the alveolar layer; in any case it would need for this purpose, like every theory built up on a false foundation, certain subordinate hypotheses, by which means it would prove itself afresh to be improbable.

Since the marginal alveolar layer must be, according to our conception of the structure and physical nature of protoplasm, of quite universal occurrence, we must inquire for ourselves whether there are any statements in the earlier literature which justify the supposition. Kupffer as far back as 1870 figured the outermost meshes in the follicle cells of the Ascidian ovum as distinctly directed vertically to the surface. Since, however, as was pointed out above (p. 162), it is rather uncertain whether the alveolar structure of these cells is not a coarse vacuolisation, it remains rather doubtful whether we have here a real alveolar layer. Just as little can it be definitely determined whether the radially striated wall which he described in 1874 in the so-

called inner capsule of the salivary gland cells of *Blatta* is a true alveolar layer; but if so it is in any case a rather strongly modified one.

That the radially striated cuticular layer, which first Sachs and later Strassburger (*Zellbildung und Zelltheilung*, 2nd edition, 1876) described in the Zoospores of *Vaucheria*, must be included here, has already before been pointed out by me. I estimate the thickness of this layer from Strassburger's figures (1876, *Protoplasma*) at about 3 μ. That is rather much for an ordinary alveolar layer, since its thickness depends on the width of the protoplasmic meshwork, which does not as a rule considerably exceed 1 μ. The *Ciliata*, however, furnish us with numerous examples of similar thick alveolar layers; in fact in *Bursaria truncatella* it even reaches the thickness of 8 μ. There can therefore be no question that this layer may be subject to certain modifications, which is perhaps connected with the fact that it becomes more or less rigid, and then undergoes a special growth accompanied by considerable heightening of the meshes. I will enter rather more closely into this question presently. Strassburger without doubt gave a more correct judgment upon the alveolar layer of *Vaucheria* originally than he did later, since he at first ascribed a chambered structure to it and brought the striation into relation with the radially directed walls of the chambers. At a later period he gave this view up again, and referred the striation to minute rods, for which reason he compared the structure with the Trichocysts of Infusorians (p. 14). The rods were regarded by him as essentially supporting structures for the cilia.

It was incorrect, however, when I formerly stated (1889) that Strassburger had also observed a radially striated alveolar layer in plasmodia. What he saw there (1876, *Protoplasma*) was in any case only protoplasm drawn out into filaments, which in the shrinking which accompanied death remained sticking to the outer membrane, which was perhaps the alveolar layer. He himself interprets his observations in a similar manner.

Van Beneden (1883) figures a very beautifully developed alveolar layer in the epithelial cells of the papillæ at the lower end of the oviducts of *Ascaris megalocephala*. It is remarkable that two such layers, an external lighter one and beneath that a darker one, should occur. The state of things is therefore similar to that in certain *Ciliata* (*Vorticella*, see above, p. 88, and *Nassula*), or they remind one also of the envelope together with the alveolar layer in *Amœba actinophora* (Plate IV. Fig. 4), *Cochliopodium*, and similar forms with a shell envelope resembling the alveolar layer. For this reason I think that these rela-

tions can be similarly explained, *i.e.* that a primitive alveolar layer becomes a firm membrane as the result of chemical alteration, which leads as a consequence to the development of a new alveolar layer beneath it, since according to the already described laws governing foam, the layer of alveoli bordering on a rigid membrane must always assume the character of an alveolar layer.

In Leydig's work (1885) I can only definitely assert the radially striated border of the epithelial cells of the lingual glands of *Pelobates* to be a true alveolar layer. The outer radial zone of the epithelial cells of *Salamandra maculosa* is, on the other hand, much too thick to be regarded as an alveolar layer. This is also obvious from the later description of these cells by Tangl (1887). Pfitzner (1885) has also observed this border. It is probably a case of the meshes of the whole of this zone being radially arranged, by means of which the alveolar layer of course becomes more indistinct. Carnoy (1884) has quite certainly observed the alveolar layer, especially in the cells of the intestine of *Asellus*, but his description is rather obscure. The so-called membrane also, which he figures and describes (though without structure) in the testicular cells of *Lithobius*, without doubt belongs here. Now Carnoy considers the above-described layer at the surface of the cells as a cell membrane, and holds the view generally that all cells possess such a membrane. I think, therefore, that he must have observed frequently similar structures, and has regarded all these structures as cell membranes. As a matter of fact he has later (1885) also observed in the *amœboid motile* testicular cells of insects such a membrane, which was said to show a reticular structure, and to be occasionally raised up in places. Finally, in 1886, he described in the segmentation of Nematode eggs a so-called cell plate, which, travelling from without inwards, was found later on in the plane of separation of the two blastomeres, and within which the splitting of the cells then takes place. I am inclined to think that Carnoy is wrong when he assumes that the segmentation of the Nematode eggs goes on in two ways, *i.e.* first by means of constriction, and secondly, by splitting in the interior of this cell plate. It seems to me rather that he has overlooked the peculiar process of the so-called flattening of the segmentation cells after their constriction, and has regarded the closely appressed cells as stages of division by splitting. This alleged cell plate, however, which can hardly have anything to do with what is usually termed a cell plate, is a double alveolar layer in structure, just such as I have also observed at the limit of the appressed blastomeres of the eggs of the sea-urchin. Carnoy derives later from the two separated layers of

this cell plate the membranes of the cell. Yet he draws no distinct alveolar layer on the free surface of the segmentation cells, although it is certainly present here in like manner. That it is more plainly noticeable in the parts of the cells which border upon one another seems natural, since it possesses in this situation double the thickness, and is therefore more striking. Of course it is no concern of mine to try to clear up the matter without new investigations of my own upon the objects in question. I hope, therefore, that these conjectures will not be misunderstood.

(*c*) *Cell Membrane, Cuticulæ*

Since we have just seen that Carnoy without doubt deals with our marginal alveolar layer universally as a cell membrane, and Frommann also later (1890) refers the alveolar layer of the Infusoria to the cell membranes without one word in justification of this course, I must say a few words on this point.

The reasons for which the alveolar layer of the Infusoria cannot be placed among cell membranes in the usual sense have been set forth at length by me before (1887, p. 1268). The chief reason is that this layer is just as easily destroyed or rendered fluid by pressure, as the rest of the protoplasm from which it shows no essential difference with regard to tingibility and chemical properties, as far as this has been investigated. Besides this its behaviour in division must be taken into account, when it follows the body like an external layer of protoplasm, and during the fusion of Infusoria in conjugation. All this proves that the alveolar layer of Infusoria cannot be directly compared with an isolated, resistant membrane, of the kind which we are familiar with in typical cell membranes. Their general properties show that they must consist of a substance agreeing essentially with the rest of the protoplasm, which can have only undergone slight chemical modifications in them. On the other hand, we can trace the alveolar layer even down as far as amœboid protoplasmic bodies, in which there can no longer be any question of a cell membrane. Although, therefore, I am not inclined to allow that a mar-

ginal alveolar layer in general should be classed as a cell membrane, since, neither in the physical nor the histological sense, is it originally such, yet I consider it probable that it may frequently develop, as the result of solidification, into a firm membrane, which can be termed a cell membrane.[1]

The grounds for this assumption are, in the first place, that there is no doubt that at least the outer limiting lamella of the alveolar layer, which in Protozoa I termed the pellicle, has often, as a matter of fact, become of a firm consistence. We must always admit this where definite forms of cells occur, which are other than spherical, since they are not possible without the surface being of a firm nature. That the whole alveolar layer may become firm is a legitimate conclusion, from the circumstance that in certain Ciliata and in *Nassula* a second radiate layer occurs beneath it, which may sufficiently prove the firmness of the outer one. The radiate arrangement of the trichocyst layer (cortical protoplasm) in *Urocentrum* and *Paramœcium* also depends in part upon similar reasons.

Further there are well-formed resistant chitinous shells, which have been isolated from the protoplasmic body, and which possess the characteristic structure of the alveolar layer. This has been longest and best known for the shell of *Arcella;* similar but more flexible shells are also found in *Cochliopodium* and probably some other Rhizopods.[2] I consider it very probable that these honeycombed envelopes are derived directly from an alveolar layer. It was further shown above that the cuticle also of *Phascolosoma* and *Branchiobdella* consists of several or even numerous layers, of which each one has somewhat the structure of an alveolar

[1] Thin flat cells in which the whole body consists for a considerable distance of only a single layer of alveoli (see above, the cells of the blood capillaries, and the connective tissue cells of the ischiadic nerve), prove conclusively that not all cells can possess a cell membrane in Carnoy's sense. In such cells this simple layer of alveoli plays in itself the part of a marginal alveolar layer on both surfaces, and this fact proves most definitely, in my opinion, that the ordinary marginal alveolar layers also belong to the protoplasm, although they may assume the character of firm cell membranes.

[2] In the same way also in Flagellata, such as *Trachelomonas*.

layer, so that we could explain the origin of such stratified cuticles by the consecutive formation of several successively hardened alveolar layers. As has been pointed out, I hence consider it very probable that, as Carnoy and Frommann assume, cell membranes and cuticles might arise by hardening of the outermost layer of protoplasm, *i.e.* of the marginal alveolar layer. The suggestions of both these investigators as to the actual method in which the process takes place, namely, hardening and chemical modification of the framework, filling up of the meshes with cellulose or solid nitrogenous substance, seems to me at the present moment too hypothetical and uncertain for us to enter more closely into the subject.

On the other hand, I cannot in any way agree off-hand to regard all membranous envelopes of protoplasmic bodies in general in the same way. I am obliged rather to allow that membranes of this kind can also arise by actual secretion, *i.e.* by means of a substance which emerges at the surface of the protoplasm and hardens to an envelope. Thus I have already, at an earlier period, discussed accurately the reasons which make such an origin very probable for the cyst envelopes of the Ciliata (*Protozoa*, p. 1659). I will only refer here to the fact that certain Ciliata rotate actively by means of their clothing of cilia during the formation of this envelope, which, in my opinion, makes it quite impossible to imagine that this envelope arises by direct modification of an external layer of protoplasm. The same thing also appears very probable for the shells of the *Ciliata*, and possibly also those of numerous *Flagellata*. We may also observe many stages of transition between gelatinous coats and firm enveloping membranes, which, in like manner, point to the same interpretation; for the gelatinous coats are most certainly actual excretions, as far as we have an accurate knowledge of their origin. Moreover, we have now set foot in a region that really scarcely admitted of being investigated with profit before the nature of the protoplasm itself was accurately discovered. I hope that the further development of the view of the structure of protoplasm which has been set forth by me

will prove fruitful also for these questions, and that in fact it may even be possible to obtain experimentally in oil-foams many results explanatory of these matters.

By the foregoing discussion I think I have explained how the wide, in fact in all probability universal, occurrence of the alveolar layer testifies entirely in favour of the foam theory, since its origin can be explained by this theory, while the framework theory gives us no help in understanding it.

(*f*) *Radiate Layer of Alveoli round the Nucleus*

The case is just the same with the appearance of a similar radiating layer round the nucleus. In the descriptive part a series of examples were given of this. Heitzmann (1884) also everywhere figures very distinctly such a radiate layer round the nucleus. I think, however, it may be well assumed that it was constructed by him schematically rather than actually observed. Such a radiate arrangement of the meshes round the nucleus was indicated by Kupffer in 1870. Whether the clear area which Leydig (1883) frequently observed round the nucleus, and which was said to be traversed by radiating continuations of the framework, represents in part at least this radiate layer, seems to me doubtful; at any rate it was then in most cases considerably widened by shrinkage of the nucleus. On the other hand, Künstler (1889) has represented the radiate arrangement of the meshes towards the surface of the nucleus in *Cryptomonas* perfectly well, and at the same time was the first to observe that the outermost layer of the much finer meshes within the nucleus itself is also directed radially to its surface. In *Chilomonas* I have also observed very plainly the radiate arrangement of the protoplasmic meshes with regard to the nucleus. Now, this phenomenon is again explained very simply on our conception of protoplasm. For the very form of the nucleus shows at least in many cases that its surface at any rate must be of firm consistence.

Since it is not my intention to go here into the question

of the nuclear membrane, I will not examine how this firm surface of the nucleus is composed or takes origin. If, however, as cannot be doubted, the surface of the nucleus is actually firm, then the layer of alveoli of the protoplasm bordering on it must necessarily be arranged radially to it, and numerous discoveries confirm this, as has been said. Only one must not expect to see anything for certain of these things in shrunk or otherwise deformed nuclei. I will not attempt to show further in this place that the outermost radiate layer of the so-called nuclear framework must be regarded from the same point of view, since in this work it is not my intention to touch on the general relations of nuclei. We find, however, a further confirmation of our theory in the existence of this radiating layer round the nucleus; it can also be predicted with certainty that round every solid body which makes its appearance in the protoplasm, the same phenomenon will repeat itself, although I have not as yet found any opportunity of paying attention to this point.

Since, therefore, we have found important grounds for the correctness of our view of the froth-like nature of protoplasm, in the aggregate condition of the protoplasm, and in the appearance of the radiate layer round vacuoles, nuclei, and on the surface of the protoplasmic body, I must here once more draw attention to the very great general similarity between foams produced artificially and protoplasm. Since the figures and photographs give sufficient confirmation of this assertion, it will not be necessary to discuss the point more fully. I only point out more especially the agreement in the size of the alveoli in both instances, and enter briefly into their similarity in other points.

(*g*) *Granular Enclosures in Protoplasm, and Corresponding Position of Soot Particles in the Artificial Foams*

In describing the structure of protoplasm we found it the rule throughout that granular enclosures always lie in the framework, and in fact in the nodal points of the alveolar meshwork. Now I have tried to discover how the

froth-drops behave in this respect. When finely divided lamp-black is mixed with the oil from which the drops are prepared, it may be noticed that in the drops of foam the fine particles take up exactly the same position with relation to the foam, that is to say, that they lie in the nodal points of the meshes. It follows from that, as would have been supposed from the general relations of foam structure, that the finest granules at least, if they possess a recognisable size, are forced into the nodal points.[1] Thus this

[1] I have subsequently found that Plateau (1882) has also made an observation which in like manner confirms the aggregation of solid granules in the corners and nodal points of the alveoli of foam. If some spores of Lycopodium are scattered on a thin lamella of glycerine containing soap in solution, which is stretched out on a wire ring, and then the lamella is placed under a bell-jar, the spores gradually all become carried towards the periphery of the lamella, *i.e.* to the spot where it is fixed to the ring of wire. The granules wander, therefore, as Plateau tried to prove, to the region where the lamella is fastened to the ring by concave curvatures. Hence in a system of lamellæ the granules will collect at the edge, or at the nodal points, where, as has been described before, the lamellæ similarly pass into one another with concave curvatures. With regard to the ultimate explanation of the phenomenon the work of Plateau itself should be consulted. Since it seemed to me of no small importance with reference to the protoplasm question to obtain as certain a decision as possible of the question as to how solid granules behave in macroscopic foams, I recently performed with this object some experiments which easily and completely confirmed the supposition. If a durable froth be made in a flask by blowing air by means of a glass tube into a suitable fluid (soap solution mixed with glycerine or extract of soapwood), and at the same time there be mixed with the fluid not too small a quantity of poppy-seeds or some other suitable fine-grained seed, the little seed grains are taken up in great quantity into the framework of the soap lamellæ. By far the greatest number lie in the plainest manner at the nodal points of the framework ; a smaller number at the edges, and only an occasional seed grain is to be found perfectly isolated and contained free in a lamella. Not infrequently also a nodal point contains a group of grains, or an edge a series of them, one behind the other. When the bubbles burst it can be plainly seen how the grains immediately travel back again to the nodal points. These experiments with macroscopic foams confirm, therefore, as has been stated, our hypothesis in the most definite manner. If some rubbed-down carmine be taken instead of seed grains, one finds the same relation in respect to the coarser grains. It is interesting to note, however, that the finest carmine granules also collect by preference at the nodal points, so that the latter appear red, while the edges and lamellæ are colourless. All these observations present a certain interest, since they show us that the nodal points of the framework may appear darker or show other peculiar relations under certain conditions, even without larger or recognisable granules being lodged in them. For in protoplasm it may also happen,

peculiarity of protoplasmic structure is also easily and surely explained on the basis of the foam theory, while I am not able to understand how, by means of the theory of a supporting framework, it could be shown why the granules always take up their position in the nodal points of the framework, and do not appear in the course of its meshes.

(*h*) *Radiate Appearances in Protoplasm during Cell Division*

For a further and an important point of agreement between artificial foams and protoplasm we refer finally to the *radiate appearances* which may appear in both, and which can be demonstrated to depend upon the same structural relations, *i.e.* upon the more or less pronounced arrangement of the alveoli into consecutive rows in certain directions. As I showed before, the radiate appearances of the artificial foams very probably depend upon diffusion processes in them; that is to say, the alveoli arrange themselves in series in the direction of the diffusional exchange, and to a certain extent in the direction of the diffusion currents if this expression is permitted. This experience agrees very well with the conclusions at which I arrived many years ago with regard to the significance of radiating phenomena in protoplasm.

As far back as 1874 I found that round the contractile vacuole of the large *Amœba terricola*, during the process of diastole, a very beautiful and fine striation, radiating out on all sides, could be observed in the protoplasm. When I occupied myself later with the radiate phenomena which, as a rule, make their appearance during cell division at the poles of the nuclear spindle, I concluded, partly on the ground of this earlier experience, partly from the appearances in the protoplasm during cell division, that the suns at the poles of the nuclear spindle owe their origin on the

that granular deposits are contained in the framework, which cannot, on account of their minuteness, be plainly made out, just as, in fact, it is often impossible to decide definitely in the case of the visible granules whether they occur singly or whether they are groups of minuter granules.

whole to the same processes, which also produce a sun round the vacuole of *Amœba terricola*. Since the last-mentioned radiate appearance only exists during the growth of the vacuole, *i.e.* while the vacuole is drawing in water from the surrounding protoplasm, I concluded that the striation was an optical expression of this process. I had thus arrived at that time at an interpretation of the process, which was confirmed fifteen years later by observations upon the drops of oil-lather. Now since the radiate phenomena in cell division completely correspond in appearance with the striation round the contractile vacuole, the conclusion seemed obvious, that a corresponding migration of fluid and soluble matter in the protoplasm was also the cause of the appearances in the former case. Only at that time I thought it necessary to assume that in this process a diffusion took place in the reverse direction from the clear central area of the suns into the protoplasm on all sides, from which of course the appearance of striation would result in like manner. This train of ideas was confirmed, as has been said, by the observations upon oil-drops, for, as I explained before, radiate appearances arise in them both when diffusion is set up from the drops into the external medium, and when it is caused in the reverse direction from the latter into the drops. The striation therefore only presupposes the existence of such a diffusion movement, it being a matter of indifference whether it prevails in the one or the other direction.

In recent times our knowledge of the origin of the radiate appearances in division has, as is well known, been considerably extended. It has been shown that they are not produced by the nucleus or the protoplasm itself, as I assumed even in 1876, but they are in connection with certain peculiar corpuscles, which are permanently present near the nucleus in the protoplasm, the so-called *central bodies*. The protoplasmic rays are always formed round the central bodies, whether they have already become noticeable in the resting cell, or whether they only gradually develop at the commencement of the division round the central bodies. These facts only recently discovered necessitate of

course the modification of our former conception of the striation, inasmuch as we have to seek in the central bodies those structures which by their action on the protoplasm produce the formation of the asters. According to our view, however, this action consists in the fact, that the centrosome attracts the matters dissolved in the enchylema, or the enchylema itself partly, as the case may be, in the same way as a hygroscopic substance attracts water, and that the diffusional migration set up in this way produces the appearance of rays. That this view finds further support in the facts, follows from the observations of Boveri, who showed that in the case of *Ascaris megalocephala* the central bodies, which are very small in the resting condition of the cell, gradually increase to a considerable extent during the formation of the asters, and diminish again in the same way afterwards.[1] This observation proves directly that the central bodies take up matter from their surroundings, at the expense of which they grow in size. This observation therefore, as has been said, harmonises very well with the theory proposed. There remains only the question, whether we can also express any opinion upon the clear central area of the suns, in which the central body lies, the so-called *attraction-spheres* of van Beneden, or the archoplasm of Boveri (periplast, Vejdowský, 1888). This is not possible directly. There is, however, a physical pheno-

[1] The investigations of Vejdowský, so interesting in many respects, but in my opinion not quite continuous, and therefore in part erroneously interpreted, upon the process of segmentation of the ovum of *Rhynchelmis*, seem to prove a very considerable increase in the size of the central body during the formation of the spindle. Since Vejdowský probably overlooked the central bodies, on account of their smallness, during the resting condition, he interprets them as the forecasts of new attraction-spheres, his so-called "periplasts," which arise, at least in the first cleavage cells, endogenously within the pre-existing periplasts. From a comparison of his results with those of van Beneden and Boveri, etc., it may, as has been said, be safely concluded that Vejdowský is wrong in making the central body, observed in the swollen condition, pass over into the later periplasts or attraction-spheres. It seems to me not without interest that Vejdowský figures stages in the division of the central body which recall karyokinesis, and hence the opinion given by me elsewhere (1891), that the central bodies may perhaps correspond to the micronuclei, with karyokinetic division, of Infusoria, receives a certain amount of support.

menon which possesses a certain similarity with the formation of these areæ. It is well known that round rapidly growing crystals of coloured substance which are separating out from a saturated or supersaturated solution, there frequently arises a distinct area which is coloured slightly or not at all. This is explained by the fact, that the rapidly growing crystal attracts the dissolved substance of the surrounding fluid more quickly than it can travel by diffusion from the surrounding fluid. The formation of such an area is, for instance, always to be observed when a crystal grows in a saturated solution by means of so-called *globulites, i.e.* minute drops of strongly supersaturated solution. Then there is always found round the nucleus a clear area free from such globulites, which depends on the fact that the globulites are gradually dissolved in the solution already rendered dilute by the formation of the crystal (see on this point Lehmann, *Molecularphysik*, Bd. i. pp. 319 and 726 *et seq.*). Now in a similar manner to the growing crystal the central body draws to itself substances from its surroundings, and if this attraction goes on rapidly, it may happen, as in the growth of the crystal, that the diffusion from the surroundings does not furnish a supply with sufficient rapidity, in consequence of which the relative degree of concentration is disturbed in a certain area, and in this region chemical alterations can be effected. Whether these alterations, as in the case of the globulites, may eventually manifest themselves by the solution of granules and their attraction to the central body, I leave an open question. This certainly does not seem impossible, since the central bodies increase with every division of the cell, and do not diminish in mass, thus undergoing a gradual growth. If we consider, however, that the tingibility of the protoplasmic substance is often very considerably impaired by relatively slight influences—I will only cite in this respect the characteristic red coloration of the chromatin granules of the nucleus and protoplasm by hæmatoxylin which I have described, a reaction which almost always fails after previous fixation with acids—it may also be considered possible that the slight, or rather the special tingibility of the central

area may also be the effect of chemical alterations which are produced by the central body.[1]

Although I consider this explanation only quite hypothetical at present, nevertheless I thought it best not to omit it, since I am convinced that we shall get no farther in these matters by means of speculations upon attractions and contractions, or with the help of micellar and molecular theories, but that we must rather risk the attempt to advance upon the basis of the known phenomena of molecular physics. In any case I think that by means of this work I shall establish the conviction that in living matter there are no mysterious forces at work, but only those which also prevail in the organic world.

My interpretation of the radiating appearances which are visible during division is, however, still further supported by the fact that similar appearances are to be seen quite unconnected with division. I have already referred before

[1] See with regard to the questions here discussed a memoir by the author entitled "Ueber die künstliche Nachahmung der karyokinetischen Figur" (On the Artificial Imitation of the Karyokinetic Figure) in the *Verhandl. d. nat. med. Vereins Heidelberg*, N. F., T. V., Heft 1, where new observations have led him to somewhat changed views. It is shown that in a foam of gelatine and oil which has been warmed, a very distinct radial striation appears on cooling round little air-bubbles enclosed in it. The same occurs in the case of air-bubbles enclosed in the foam-like structures shown by albumen when coagulated by heat, and in coagulated gelatine (*vide supra*, p. 216). Each such bubble may lie in a clear space, which passes into the sun-like system of rays. This appearance is due to the contraction of the air-bubble on cooling, which causes a tension or pull to be exerted on the surrounding mass. The tension is directed from all sides towards the centre of the bubble, and modifies the foam-like structure into a system of rays. When two such systems cross each other a spindle-like figure results.

Hence the explanation of the radiate appearances round the centrosome must be somewhat as follows. The centrosome does not diminish in volume like the air-bubbles described above, but is known to increase in size during the formation of the aster. This increase can only be due to its absorbing fluid from the surrounding protoplasm. If it be supposed that the centrosome becomes chemically combined with the fluid it absorbs, it will increase in size to a less extent than the surrounding protoplasm diminishes by loss of the fluid given up to the centrosome. Then the centrosome will form the middle point of a portion of the protoplasm which is contracting and diminishing in size as a whole, and this protoplasmic area will exert radially directed tensions upon the remaining protoplasm and produce radiate appearances, just as in the case of the contracting air-bubble.

to the appearance of rays round the contractile vacuole of *Amœba terricola*. More recently I was able with v. Erlanger (1890) to observe the same thing round the contractile vacuole of *Actinobolus*. In the same way I found it also in *Nyctotherus*.[1] I need scarcely remark that this striation is not to be confused with the radiately arranged affluent canals of the contractile vacuole. I only point this out here because Frommann (1890, p. 11) seems to have fallen into this very error when he says with regard to this phenomenon: "In many Infusoria and in *Amœba terricola* there radiate out from the circumference of the contractile spaces a number of *lacunæ* (!) into the surrounding parenchyma (!) of the body, into which the parenchymal fluid (!), laden with products of metabolism, is forced by the pressure (!) of the water taken up into the body, and is thus guided to the vacuole." As is proved by the continuation of this passage, Frommann has simply confused the radiating protoplasm round the vacuole with the so-called radial canals, which occur moreover in other species, so that one is quite justified in saying of the passage quoted that it contains as many errors as there are clauses.

(*i*) *Radiate Appearances in Ova, etc.*

It is notorious that radiating appearances are a very common phenomenon in the protoplasm of egg cells. I will only recall here the observations of Leydig (1872) and Eimer on Reptilian eggs, of van Beneden (1876), Flemming (1881, 1882) and Frommann on Echinoderm eggs, of Rauber (1883) on the eggs of *Triton*, the trout, and the

[1] It is interesting that Frenzel in like manner has recently, in a so-called *Amœba cubica*, observed a very well developed radiate striation round the contractile vacuole. This discovery appears the more important, since it forms, after nearly twenty years, the first confirmation of my observation which was achieved, as it would seem, quite independently, *i.e.* without knowledge of my earlier observations. It is to be hoped that rather more attention will now be given to this important phenomenon than has been done during the relatively long time it has been known. (See J. Frenzel, "Untersuchungen über die mikroskopische Fauna Argentiniens," *Arch. f. mikr. Anat.*, Bd. xxxix. 1891, p. 9, Plate I.)

alligator, of Carnoy (1880) on the egg of *Cyprinus*, and of van Beneden on the ovum of *Lepus cuniculus* (1880) and *Ascaris megalocephala* (1883). In most of these cases it is only a superficial cortical zone of the protoplasm of the ovum which shows the radial striation; the same is usually the case, as we have already described, in the central capsule of *Thalassicolla* and many other Radiolaria. Such a radial striation can therefore hardly be brought into connection with the centrosome, situated as it is in all cases in the vicinity of the nucleus, for the radial striation, which has the centrosome as its starting-point, is always characterised by being most distinct in its neighbourhood and becoming more indistinct with increased distance from it, since it first makes its appearance close to the centrosome and commences to spread out centrifugally. The above-mentioned radiate striation of the ova, on the contrary, is in general most distinct at the surface of the cell, and diminishes in sharpness towards the centre, which, as has been pointed out, it never reaches as a rule. From this fact we must certainly conclude that the cause of the radiation has its seat at the surface of the egg cell, *i.e.* that diosmotic processes between the surrounding medium and the surface of the ovum produce the phenomenon. In harmony with this is the fact especially emphasised by van Beneden, and observed by him in *Ascaris megalocephala*, namely, that the radiate striation is *not* concentrated upon the often excentrically placed germinal vesicle. I would further point out that the drops of oil-lather often show the same appearance, which, from all that we know, owes its origin without doubt to such processes.

There are, however, also radiating appearances in the interior of the protoplasm, which, as far as we can judge of them, are not produced by central bodies, or at least are not exclusively caused by them. It is well known that the radiating appearances which arise during fertilisation round the male and female pronucleus, usually spread out evenly and on all sides round these nuclei, although it is quite certain from recent observations that they are originally produced from the central bodies. If, however, this were also

exclusively the case at a later period, that is to say, after the two nuclei have become closely apposed, it would not be possible for a system of rays streaming out evenly on all sides to be developed round them; there would rather have to be two such systems indicated if the radiation was exclusively caused by the centrosomes, as is in fact actually the case in division. I think, therefore, that the nuclei themselves take part in the production of rays, which harmonises well with the fact that the two pronuclei during the formation of the radiating suns grow to a considerable extent, and therefore absorb material from their surroundings.

That the nucleus can also cause by itself the formation of a system of rays centred upon it, seems to me from some other facts very probable, even if not certain. I refer especially with regard to this point to the observations of Schewiakoff (1887), which were controlled by me, upon the division of *Euglypha*. Here, there appears round the nucleus, while passing into the spirema stage, a regular radiate striation on all sides, having nothing to do with the two polar suns, which do not develop until much later, after the first system of rays has disappeared again. Now it is a very suggestive fact, that the nucleus during the existence of this striation increases its volume two or three times, and therefore must take up a considerable quantity of fluid from the surrounding protoplasm. The formation of this system of rays round the strongly growing nucleus of *Euglypha* again confirms therefore our view of the cause and significance of the striation. It may be not improbable that similar striations appear still oftener round the nucleus. Heuser has seen the same phenomenon round the vegetable nucleus in the spirema stage. I may refer further to the fact that, according to Strassburger's observations, a regular system of rays spreading out on all sides makes its appearance during the so-called free cell formation in the embryo sack of Phanerogams, which is to be regarded in just the same manner as the cases described above.[1]

[1] Whether the appearance of rays, which Vejdowský (1888) described round the centrally placed germinal vesicle of the ripe ovum of *Rhyn-*

(*j*) *Striated Protoplasm of Epithelial Cells*

That the radiate appearances are not always caused by the central body seems to me further to follow from the fact that there is no sharp distinction between them and the striated appearances which epithelial cells exhibit so often, perhaps even universally. Both depend, as I have already explained before, upon the same cause, *i.e.* upon a regular arrangement of the alveoli. Now this arrangement of the alveoli in parallel rows has no relation either to the nucleus or to any central body that may be present, but it always runs parallel to an axis of the cell, which is directed vertically to its outer surface. Since, however, there is no obvious reason for regarding the striated structure of the alveolar framework of these cells as a consequence of strain or tension in the direction of the striation, since the same striation is shown also by cells which are shorter in the direction of the axis than in one at right angles to it, and the fibrous appearance sometimes does not extend through the whole cell, it may be assumed that in these cases the longitudinal striation depends in the same manner as a rule upon diffusion currents. The fact that such diffusion currents are usually present in epithelial cells and especially in gland cells, and that then they must take the direction indicated by the longitudinal striation, scarcely requires any further elucidation, whether these currents move towards the exterior or towards the interior of the cell. As has been said, I therefore consider it most probable that the striation of the epithelial cells depends in general upon the same cause as the appearance of radial striation.

On the other hand, there are a large number of cases in which protoplasm exhibits striated alveolar structures,

chelmis, is to be included here, remains an open question, inasmuch as a central body is certainly present in the vicinity of the germinal vesicle. If, however, the rays are regularly centred round the germinal vesicle as Vejdowský alleges, I consider it certain that they are produced by it. There is no inherent difficulty in supposing that at one time the nucleus, at another time the central body, may be the cause of radiating appearances, or that occasionally both may manifest at the same time an activity of this kind.

that cannot be regarded in this manner, but where the phenomenon demonstrably depends upon the effect of tension or upon being stretched.

(*k*) *Fibrous Protoplasm*

In the description of the pseudopodia of Rhizopods, and of the trabeculæ and bridges of protoplasm which traverse the cell-sap of plant cells, etc., we have always found that these strands of protoplasm have a fibrous alveolar structure, and it can also be shown that in Rhizopods bridges of protoplasm drawn out by direct tension always assume this structure. Now it cannot be doubted that in the formation of pseudopodia and of protoplasmic bridges in the cell-sap a tension is exerted which draws or spins them out; the formation of such bridges or pseudopodia only depends in general upon the effect of energetic tension which is exerted at their free ends, as shall afterwards be explained more accurately in the case of the coarser pseudopodia at least. In such forms as *Amœba blattæ* it can be plainly observed during life that the extremity which is progressing (the anterior end) draws towards itself an axial stream of protoplasm, and that in this stream a most beautiful fibre-like differentiation is visible, which spreads out radially towards the posterior end, where the current receives affluent streams on all sides. In the same way the fibrillæ can be plainly traced bending round forwards in the direction of the current. On the whole, as has already been shown for the foam-drops, the state of things can be described by saying, that if the alveolar framework is sufficiently viscid, a stretching of the alveoli in the direction of the current takes place, since as a matter of fact the existence of the current always presupposes tensions in this direction.

Now since I have further shown that very viscid drops of foam show plainly the fibrous alveolar structure under pressure or tension, it cannot well be doubted that the last-mentioned category of fibrous alveolar structures owes its origin to the same causes.

We have come across, however, a considerable number of fibrous alveolar structures which cannot be brought into direct connection with the streaming phenomena of the protoplasm, but which certainly might depend upon similar causes. Here in the first place stands the fibrous alveolar structure of the axis cylinder, as well as of the elongated connective tissue cells which have been described between the nerve fibres of the ischiadic, the fibrous structure of the cells of the capillaries and of the processes of the ganglion cells, and finally, also the more or less confusedly fibrous nature of the protoplasm of the ganglion cells themselves. In these cases we are always concerned with protoplasmic bodies which have grown out very strongly in certain directions, to which the course of the fibres of the meshwork invariably corresponds. We must therefore imagine that we are dealing with a viscid alveolar meshwork, which is stretched in a definite direction by the growth of the cell. I am able to further support this by the fact that the processes of the very richly branched connective tissue cells, which occur between the longitudinal muscle cells of *Lumbricus terrestris*, also show the fibrous alveolar structure very beautifully, just like the pseudopodia of Rhizopods. The confused fibrous structure which appears chiefly in greatly branched ganglion cells, probably has its cause in the fact that during the outgrowth of the numerous processes the action of tension is exerted in various directions upon the protoplasm, which is indeed plainly expressed also in the fact that the fibrous structures of the processes always penetrate more or less deeply into the cell, and here combine with one another in the most various ways. On the other hand, however, it is by no means necessary to exclude local tensions set up within the protoplasm of the cell itself, which further complicate the structure. There are many examples of such protoplasm with a confused fibrous structure. I will here only refer to a very good one, namely, the protoplasm of the large medullary sacs of *Ascaris lumbricoides* and the medullary substance of its muscles generally.

A question of fundamental importance is raised, however,

in the descriptions of these structures, namely, how we are to regard the aggregate condition of the substance of the alveolar framework in their case. If they exist permanently, it seems quite certain at the outset that their alveolar framework must be rigid, or at least so viscid that it only alters its configuration, in obedience to the laws of fluid foams, with extreme slowness. In any case it seems beyond a doubt that structures of this kind cannot exist permanently if we have to deal with fluid substances forming the framework and the contents of an alveolar meshwork, which is itself free in a surrounding fluid. The matter, however, is not simple here, but the form of all these protoplasmic bodies proves at once that they must be surrounded by a firm membrane. Moreover, these cells are so connected in the interior of the organism with others, or even with undoubtedly solid parts, that their form will become fixed accordingly. Now how a viscid foam, which is enclosed in a firm elastic envelope, will behave during tension of this membrane, does not seem to me quite easily decided *à priori;* in fact, so far as the laws of foam formation have been investigated, it seems to me even possible that it would be converted into a foam with elongated meshes, and would persist as such if the meshes were not too much stretched.

In opposition, therefore, to my former assumption (1891) I think we must admit it to be possible that these permanently fibrous alveolar structures of the axis cylinder, etc., may be of a viscid nature.

(*l*) *Theories concerning the Causes of Radiate Appearances*

Very various views have in the course of time been set up with regard to radiating protoplasmic structures, the probable cause of which we have above sought to refer to processes of diffusion. I think there is no need to enter into a detailed discussion of all the opinions, but I will confine myself to the description of the principal points of view that have been taken up with regard to this matter. At first of course the idea was put forward that the radiate appearances in cell division must be due to a kind of attraction which was exerted by the poles of the nuclear spindle upon the particles of protoplasm, or more

particularly upon its granules, such as the so-called yolk granules of the protoplasm of the ovum. Just as fine particles of iron group themselves round the poles of a magnet in peculiar systems under the influence of its attraction, it was thought that the attractive action of the centres of the rays took effect in some way also upon the protoplasm and its particles. To such ideas were inclined Fol (1873), myself (1874), Strassburger (1875), O. Hertwig (1875), and many later investigators, who cannot be enumerated individually here. Auerbach, on the other hand, had in 1874 expressed the view that the appearance of rays was produced by the nuclear fluid streaming out into the protoplasm. In 1876, when I brought forward my view, which I still uphold even at the present time, and with much better grounds than formerly, it was particularly pointed out that I could not, with Auerbach, regard actual currents as the cause of the appearance of radiations, but rather processes which we can now best denote as migration of substances by diffusion.

Anton Schneider, at a later date (1883), derived the radiate appearances in like manner from the nuclear fluid. The nucleus, which had become amœboid, "obtained the power of sending out processes and rays" (p. 75). This was said to be an "amœboid property." It then follows from his further description that Schneider also certainly regarded the nuclear fluid as forming the rays.

The idea that streamings in the interior of the protoplasm were the cause of the appearance of rays was also maintained by Fol (1879, pp. 251-256), and was especially based by him on the accumulation at the clear central areæ, as well as on the growth of the pronuclei in fertilisation, and of the young nuclei after division, in the same way as the opinion I had already (1876) expressed upon the significance of these central areæ. Fol supposed that currents, in part centrifugal, in part centripetal, produced the radiating appearances. But it was not a question of nuclear fluid streaming outwards during these processes, as Auerbach believed, but of currents of the protoplasm itself. In any case the phenomena were supposed not to depend on an arrangement of the yolk granules, since the filaments of protoplasm passing between the rows were much too broad for that. His including me on this occasion among the representatives of the hypothesis of attraction and polar orientation of the yolk molecules is an error to be regretted, since I had refuted, as I have said, the hypothesis of attraction in 1876, and had attempted an explanation which agreed with Fol's later one in a series of essential points. The so-called central areæ, or attraction centres, as Fol terms them, he believes to be caused

by a mixture of two substances, one of which was derived from the nucleus, the other from the protoplasm.

Mark, in 1881, criticised the views of earlier investigators upon the cause of the aster formation very ably indeed, without, however, expressing a definite opinion himself upon their significance. Thus he remarks, on the one hand (p. 533), "While I concur with Hertwig in the belief that there is an attractive force exerted upon the vitelline protoplasm which emanates from the centre of radiation," and, on the other hand (p. 530), "I do not claim that there is absolutely no transfer of substance to and from the centres of attraction. On the contrary, I believe the phenomena are, on any other assumption, unintelligible; but it seems to me that the formation of a clear area, and the existence of radial striations, are far from commensurate, and that to claim that the rays are only the optical expression of currents is to associate as cause and effect two things which have not necessarily any such connection with each other." The view expressed by me he also regards not as a real explanation, but more as a description of the phenomenon. I can only accept this criticism to the extent that I did not indeed give an explanation in the mechanical sense, which, however, was not my intention, but I think, on the other hand, I established certain conditions under which the phenomena make their appearance. For the rest, Mark has understood my view very correctly, and since this was not always the case I will quote here his remarks upon this point (p. 530): "Bütschli's opinion that the asters are the optical expression of a physico-chemical alteration of the protoplasm emanating from the central area is probably incontrovertible. At least there is a physical alteration of the protoplasm, and it first becomes apparent at the centre of the star; but this is rather a description than an explanation of the appearance."

Klein had already (1879 (2), pp. 416, 417) casually expressed the opinion that the striations round the poles of the dividing nucleus only depend on a particular arrangement of the protoplasmic network, since the nuclear network probably contracts during the nuclear division, and draws the protoplasmic fibres towards itself. It is strange that Klein did not come to exactly the reverse idea, which would have corresponded much more to the processes actually taking place, and which, therefore, soon came to be held. Nevertheless, we must recognise that he first pointed out the probable origin of the radiation by rearrangement of the protoplasmic framework. Flemming, in 1879, while he admitted the mechanical connection of the two processes brought into association by Klein, was yet inclined to regard the matter as not so simple. In 1881 he pointed out in *Toxopneustes* that the radia-

tion certainly did not depend on the arrangement of the yolk granules, but that it was a "transitory" protoplasmic structure. It could also be traced in places where there were no yolk granules.

Van Beneden, in 1883, recognised that in the ovum of *Ascaris* the appearances of radiation arose throughout from radial arrangements of the framework in certain places. Since he regarded the supposed fibrillar reticular framework as the true contractile substance, he therefore as good as stated that this radiating arrangement of the otherwise irregular fibrillæ must depend on their contractions, although he did not say so in so many words.

Leydig arrived at the same opinion as to the origin of the sun-like figures by special arrangement of the framework (1883, p. 144). In 1885 he particularly pointed out that he had convinced himself of the correctness of this view by means of his own investigations upon the eggs of *Ascaris megalocephala*. Flemming, also, had in the meanwhile expressed himself to the effect that the radiation was probably founded upon an "arranging and centring of the felt work of the cell substance." At the same time he correctly criticised and refuted the opinion of Anton Schneider referred to above. Finally, Carnoy (1884), Frommann (1890), and other observers, came forward in support of the view that derives the radiations from the radial arrangement of the framework, so that it may now well be termed the one which enjoys the most universal recognition. In addition there is the fact that van Beneden, after renewed study of the so-called systems of asters or rays, which he investigated in company with Neyt, has come to the opinion that by contraction of their moniliform fibrillæ, which took origin from the protoplasmic trellis work (treillis), they mechanically caused both nuclear and cell division. The structure of such a moniliform fibril of the aster was supposed to be comparable to that of the muscle fibrils, for which reason their contractility was rendered probable. The so-called central corpuscles, which in van Beneden's work were first proved to occur in the cell near the nucleus even in the resting condition, only played in these processes the part of supporting organs for the contractile fibrils of the aster, among which were also reckoned the whole of the fibres of the nuclear spindle, just as is usually done now, in spite of numerous observations to the opposite effect, and indeed of contradictory experiences of his own. At about the same time Boveri arrived at a very similar conception of the part played by the fibrils of the systems of rays in division—in fact he even asserted that the fibrils, or archoplasmic filaments as he termed them, could, by

reason of their "power of lengthening and shortening themselves, be characterised as muscular fibrillæ, and all the laws that obtain for muscles might be applied to them" (ii. p. 99). After such an opinion it seems astonishing when Boveri defends (ii. p. 80) on the other hand the view, or at least declares it to be the most probable one, that the fibrils of the aster do not permanently exist as such in the protoplasm, and that they are not, as van Beneden and others correctly recognised, produced from the meshes of a framework existing in the protoplasm, but that they are first formed *ad hoc* by connection of the otherwise separate microsomes of the archoplasma. As far as I understand Boveri, he seems to represent the view that it is especially the microsomes of the so-called archoplasma, *i.e.* of the so-called central areæ, that produce the filaments, which then commence to grow from the archoplasm outwards into the surrounding protoplasm by elongation. I scarcely think that any one will be strongly in favour of this view, according to which alleged muscle fibrils arise at one time from the union of microsomes, and at another time break up again into such bodies.

Rabl (1889) has recently fallen in with the interpretation of the systems of rays as contractile fibrillæ, which play in cell division the part assigned to them by van Beneden. He assumes that the framework of the cell protoplasm and nucleus is permanently centred round the central corpuscle—a view which is in fact favoured by observations upon the radiate arrangement of the protoplasm round the central bodies of certain resting cells. He is further inclined to believe that the reticular framework of the protoplasm is transformed into fibrils during division, like those of the nucleus, by a breaking up of the cross connections of the filaments; consequently the systems of rays only consist of isolated fibrils, which later become modified again into networks by the formation of anastomoses.

Finally, Fol has attempted recently (1891) to demonstrate in the egg of the sea-urchin a different mode of formation for the radiations which appear primitively round the sexual nuclei and the segmentation nucleus derived from them, and for the so-called suns or asters at the poles of the nuclear spindle. The former are stated to depend only on the arrangement of the yolk granules and of the "tracts of sarcode" by which they are suspended. The true asters, on the other hand, are formed of actual rays, *i.e.* fibrillæ which are just as distinct and capable of being isolated as the connective tissue and muscular fibrils. I am unable to agree at all with this view, either from my own observations, or from the experience of other investigators. The possibility of isolating the fibrils is not, in my opinion, in any

way decisive in this matter, since tracts of the hardened alveolar meshwork may quite well be isolated by teasing like fibrils in certain places. I think that possibly special accumulations of the granules in certain radial tracts may have been the cause of the distinction laid down by Fol.

Although I am willing to admit that the course of the phenomena in the division of the nucleus and the cell harmonises fairly well with the theory set up by van Beneden and Boveri concerning the contractile nature and action of the so-called fibrillæ of the systems of rays, I am not inclined to consider my explanation of these processes as improbable on that account. Apart from the structure of the protoplasm not being, as a matter of fact, spongy or fibrillar, a great number of important facts, which have been detailed above, are in favour of it. It will be the subject of a special investigation, based on the results of this work, to discover whether there are not other points of view for the processes occurring in cell and nuclear division, which bring them into unison with my view of the significance of the systems of rays. I entirely put aside for the present the hypothetical, and in itself inexplicable, contractility of the fibrils, since I shall treat of this point more in detail later. On the other hand, I should like to point out that I still consider the opinion developed by me at an earlier date (1876) upon the forces that come into action in cell division to be the probable one, at least in principle.

6. *The Homogeneous Protoplasm and the Alveolar Theory*

As we have frequently pointed out in the descriptive portion of this work, the living protoplasm of certain organisms occasionally appears entirely homogeneous and structureless in parts, without even a trace of granular contents. *Gromia Dujardini* in particular supplied us with a good example of this, in its often very large pseudopodia. The pseudopodia and the so-called ectoplasm of the fresh-water Rhizopods, however, very often show the same condition, as has often been pointed out by earlier investigators.

The fact is therefore beyond doubt that living protoplasm occasionally exhibits no trace of alveolar structure.

Among the representatives of the framework theory some have not discussed this difficulty at all, while others have tried to cope with it in various ways. Heitzmann (1883) thinks the apparent homogeneity of such protoplasm can be explained by the fact that the meshes of the framework are so strongly stretched and widened that their nodal points vanish entirely, *i.e.* pass into filaments of the framework which at the same time become no longer visible on account of their attenuation. This view obtained a certain amount of support from the fact that it is just those pseudopodia which are stretched out, or to a certain extent pressed out over the surface, that often appear homogeneous; and it therefore harmonised with Heitzmann's view, to be discussed later, as to the causes of pseudopodial formation.

Frommann was also quite aware of the existence of homogeneous protoplasm. Since he cherishes the idea, as has already been described, that the frameworks can be dissolved in the protoplasmic matrix just as easily as they can be formed anew in it, this phenomenon did not in his opinion present any essential difficulty. Flemming (1882), on the other hand, had rather a different conception of the matter. He considers the origin of homogeneous protoplasm possible by the filaments becoming densely crowded together or being temporarily fused.

Leydig (1883, 1885) was the representative of an essentially different view. As has already been discussed on a former occasion, the homogeneous protoplasm of the pseudopodia of Rhizopods was the same in his opinion as the structureless matrix of the protoplasm, his so-called *hyaloplasm*, which was supposed to have the power of creeping out of the stiff framework of the *spongioplasm*.

This summary practically exhausts the opinions expressed upon this point, which in any case has a very important bearing upon the protoplasm question. As has been said, the majority of the representatives of the theory of a framework or of fibrillæ have not approached the question at all. Künstler also has expressed no opinion upon it. In the same way I do not find any discussion of it in Altmann's granular theory, though such a discussion would have great importance, since granules are certainly wanting in homogeneous protoplasm.

As has frequently been pointed out in the descriptive part of this work, it can be demonstrated with certainty that the apparently homogeneous protoplasm of the pseudo-

podia and cortical layer of Rhizopods is produced from alveolar protoplasm, and is capable in like manner of re-conversion into it. The investigation of the pseudopodia of *Gromia Dujardini* furnished a decisive proof of this fact. Moreover the fibrous alveolar structure, which is distinctly exhibited by these apparently homogeneous pseudopodia here and there after suitable fixation and coloration, is a sure proof that they do not lack the honeycombed structure, but only that as the result of special conditions it is no longer to be observed in life, nor even to a great extent after fixation.

Hence arises the question whether it is possible to supply a more or less plausible explanation for the disappearance of the structure. At an earlier date (1890) I had already suggested, as a possible explanation of this phenomenon, that the alveoli became widened, whilst there was a consequent thinning out of their walls to such a degree of fineness that they ceased to be visible. I also pointed out upon physical grounds that a foam, which as a matter of fact manifests a great similarity to solid bodies in its appearance, would do so the more the thinner its walls became. I did not see until later that this suggestion also obtains a certain amount of support from the observations of Mensbrugghe (1882) upon the tension of thin fluid lamellæ. Mensbrugghe has shown that the tension of these lamellæ increases when their thickness sinks below a certain limit, and that the lamellæ then behave as firm elastic membranes, whose resistance to further stretching constantly increases (see on this point Lehmann, *Molecularphysik*, Bd. i. p. 257).

This would agree with the fact that the homogeneous protoplasm which occurs in Rhizopods seems to possess a greater viscidity or firmness than the more fluid and distinctly reticular internal protoplasm. It is usually sought to explain this fact by ascribing a somewhat greater density to the homogeneous ectoplasm—a notion which, as a matter of fact, obtains no support from its optical appearance.

From Plateau's calculations on soap-bubbles, it follows that the thickness of the lamellæ of macroscopic soap-foams may be very small. From the interference colours which

they exhibit he could establish the fact that the thickness of the fluid lamella at the summit of a soap-bubble may sink to 0·0001 mm. A lamella of such thinness nevertheless exhibits great durability, since it maintains itself under favourable circumstances for many days (Bd. ii. pp. 4, 5). Hence there is theoretically nothing to oppose the notion that the walls of the microscopic alveoli of protoplasm might under certain circumstances become thinned out to invisibility. To effect this a comparatively slight attenuation would be quite sufficient, since when they are visible in the living condition they are already so delicate and faint that, if attenuated to a relatively small extent, they would disappear from vision.

This interpretation of the apparent homogeneity and absence of structure in certain protoplasms is to a certain degree strengthened by the observations that have already been briefly described upon artificial froths. I pointed out above that in a froth-drop sticking to the cover glass or slide, the structure at the edges, where the drops spread out into a perfectly flat thin layer, becomes so faint and indistinct that it is at last no longer recognisable (p. 38; see Photographs I. II.). The perfectly gradual diminution of distinctness towards the edge, as well as slight traces of structure which are still visible even in the apparently homogeneous edge, prove that the nature of the edge is not really homogeneous, but is also alveolar, and that the structure has merely become too faint and delicate to show up distinctly any more. I formerly tried to refer this phenomenon to the great tenuity of the marginal border, and it is not without importance in this respect that the homogeneous pseudopodia, as well as the homogeneous marginal layer of Rhizopods, are mostly portions of the protoplasm which are very thinly spread out upon the surface over which they are creeping, although homogeneous protoplasm certainly occurs, for which this statement does not hold good.

In any case this discussion may serve to show that the occasional transition of alveolar protoplasm into that which is apparently quite homogeneous, is quite compatible with the theory, and that on the ground of this fact no

exception can be taken to it. On the contrary, I have described above a number of facts with regard to *Gromia Dujardini* from which it follows quite necessarily that homogeneous protoplasm also possesses an alveolar structure, for otherwise it would not be explicable how it could arise so suddenly from alveolar protoplasm, or how, on the other hand, it could be again converted into the latter.

In this phenomenon it remains for the present still unexplained why the granular contents of the interior do not penetrate into the homogeneous protoplasm. There is no intrinsic reason why this should be so. Schwarz (1887) has observed that granules which are suspended in a viscid fluid usually keep at a certain distance from the surface, and hence he thinks that the hyaline non-granular marginal protoplasm, such as is often seen in vegetable cells also (the so-called "Hautschicht" of the botanists), may be referred to this physical phenomenon. Apart from the fact that I never observed the phenomenon described by Schwarz in my numerous experiments on oil-drops with which finely-divided lamp-black had been mixed, I cannot accept this explanation for the further reason that in Amœbæ one frequently notices that when the marginal border is wanting the granules penetrate as far as the surface, or at least as far as the alveolar layer, which could not well take place if the explanation given by Schwarz was correct. On the other hand, however, from the fact that non-granular homogeneous protoplasm as soon as it passes into the alveolar condition becomes distinctly granular (that is to say, that the nodal points of the alveolar framework which have now become visible, impart this character to it), the view already stated may be proved with certainty, namely, that the granular appearance of the protoplasm depends to a great extent on the alveolar structure, since both the nodal points and the optical properties which have already been pointed out in the case of artificial foams cause the same appearance in them.

7. *The Phenomena of Protoplasmic Movement in their Relation to the Alveolar Structure*

(*a*) *Theories as to the Causes of the Phenomena of Movement*

In my review of 1891 I had already pointed out that the great similarity between the phenomena of movement of the foam-drops and the simpler locomotory phenomena of protoplasmic structures, is further evidence for the correctness of my view with regard to the structure of protoplasm. For these and other reasons it therefore seems necessary that we should give some attention to these relations; that is to say, that we should consider rather more closely both the phenomena of movement and previous attempts to explain them.

(*b*) *So-called Contractility*

For a long time back the view has been consciously or unconsciously held that all the phenomena of movement exhibited by protoplasmic bodies are to be referred to the same fundamental property. Under these circumstances it was natural that the form of movement hitherto most familiar to us, namely, the contraction of muscle protoplasm, should be claimed as this fundamental property, and an attempt be made to derive all phenomena of movement from it. Since, therefore, the older attempts to explain the phenomena of streaming and movement in simple protoplasmic bodies as the result of electrical or chemical forces, etc., did not lead to a successful issue, it was thought that the key to the comprehension of these protoplasmic movements was to be found in the so-called *contractility* of protoplasm, which itself was not to be further explained. From the facts of the genetic development of organisms it might perhaps have been predicted that a correct explanation ought rather to take the opposite path, since the typically contractile protoplasmic structures are undoubtedly not the most primitive, but have developed at a much later stage. The solution of the problem would, as has been said, have

appeared *à priori* more hopeful, if the explanation of the so-called sarcode or protoplasmic movements had been chosen as the starting-point, and contraction proper had been treated as a special or subordinate case, which attains its full development under certain conditions.

Investigation was, however, pursued, as has been remarked, in the opposite direction from the fifties onwards, since it was thought necessary to make use of contractility as a general property of protoplasm for the explanation even of the processes of movement and the streamings of simple protoplasmic bodies, such as Rhizopods, protoplasm of plant cells, etc.

Amongst those who took up this standpoint were both M. Schultze (1863) and his opponent Reichert (1862, 1863), Brücke (1861), Cienkowsky (1863), de Bary (1862 and 1864), Haeckel (1862, p. 90 *et seq.*), Kühne (1864), and numerous others.

If the process of movement in an Amœba, or the process of streaming in the protoplasm of a plant cell, was to be explained on the basis of contraction, it was, of course, necessary to assume some kind of organisation in these protoplasmic bodies which would offer a certain analogy to the organisation of higher organisms, since obviously the whole mass could not be contracted evenly if phenomena of locomotion and streaming were to be brought about. The contraction then was confined chiefly to a cortical layer of the protoplasm, which, like a layer of integumental muscles, was supposed to set the remaining protoplasm in movement by local contraction, or to this contractile and therefore changeable cortex a contractile framework or felt work was superadded, which traversed the entire protoplasmic body (Brücke, 1861; Cienkowsky, 1863, etc.). In general, however, the adherents of the contraction theory scarcely made any attempt to explain or to analyse at all more accurately the locomotory phenomena of simple protoplasmic bodies on the basis of their theory. They contented themselves rather with referring in a general way to contractility as the cause. If they had gone more accurately into the individual cases, the untenability of the theory would have been earlier apparent.

(*c*) *Contractility of the alleged Reticular Framework*

As has been mentioned, Brücke had already actually postulated a contractile internal framework of firmer consistence for the explanation of the phenomena of movement and streaming in protoplasm. When, therefore, Heitzmann in the seventies had described the reticular framework of protoplasm, he concluded at once that it was a contractile framework of this kind, by alterations in which all the movements of protoplasm could be explained. In his opinion this framework alone is contractile; the intervening matrix, on the contrary, is a "non-contractile fluid." During the contraction of the framework the filaments which connect neighbouring nodal points shorten, owing to the latter at the same time swelling and approaching one another. In accordance with this view Heitzmann was forced to imagine that the substance of the filaments is absorbed by the nodal points as they swell. When the framework is relaxed the reverse process takes place. In addition to this Heitzmann further assumes the occurrence of a condition of extension of the framework, which arises by a squeezing out of the intervening fluid of one region of the protoplasmic body, which is contracted, and its being driven into another, thereby causing the framework to become stretched beyond the normal condition. As a result of this expansion of the meshes the filaments are said to become greatly elongated, the nodal points reduced to the vanishing point, and the whole meshwork finally so attenuated that it becomes quite invisible, as in the pseudopodia of Amœbæ, etc. The protrusion of the latter, as well as phenomena of protoplasmic movement in general, he thus explains by a local stretching of the framework in this manner as the result of local contractions.

Most of the adherents of the framework theory were, on the whole, in agreement with Heitzmann, to the extent at least that they in like manner considered the framework, or the fibrillæ of the protoplasm, as the contractile elements, and sought in them the seat of the locomotory phenomena, changes of form, processes of division, etc. A more precise analysis of the processes was

not undertaken by any of the investigators whom we shall shortly mention. The perfectly natural idea, that phenomena of contraction were only conceivable in solid substances, was, to a certain degree, the determining one in this conception; it was not, as a rule, definitely expressed—only in Reinke (1881, ii. p. 96) do I find a direct reference to it—yet this train of reasoning at any rate formed the chief ground for considering the framework, conceived of as being solid or at least very viscid, as the contractile substance. The following authors professed themselves more or less definitely as being of the opinion which has just been mentioned: Schleicher (1879), Klein (1879), Reinke and Rodewald (1881 and later), van Beneden (1883 and later), List (1884), Carnoy (1884), Marshall (1887), Fabre (1887), Ballowitz (1889), Boveri (1889), Rabl (1889), and many others.

In more recent times, as we have seen, some authors even went so far as to ascribe the properties of muscle fibrils to ordinary protoplasmic fibrils (see above, p. 260).

(*d*) *Objections to the Theory of Contractility*

Even at quite an early period strong objections have been raised to the contractility theory, which were directed just as much against the older conception of it as against the turn which it took under the influence of the framework theory.

With regard to the movements of Amœbæ and plasmodia, Wallich (1863) had already drawn attention to the important fact, quite decisive as to the untenability of the contraction theory, that the commencement of a current does not take place in the interior or at the hinder end of the Amœba, and then advance from this region towards the portion of the surface that was streaming forwards, as would be required by the contraction theory, but that, on the contrary, the current first makes its appearance in exactly the opposite manner at the surface that was moving forwards, and from thence gradually extends backwards. De Bary (1864) also found this observation confirmed in plasmodia, to this extent, that he certainly observed such currents, which he termed centripetal; but in addition, he believed

he had also observed so-called centrifugal currents moving in the opposite direction, which would agree with the contraction hypothesis. He thus saw himself forced to assume causes of two kinds to explain the two streams; the former would arise by an "expansion" of the peripheral protoplasm at the edge of the plasmodium, the latter, on the contrary, by a contraction of it.

Hofmeister (1865, 1867) and many recent investigators have seen the streams in plasmodia and Amœbæ always arise at the forwardly moving edge. For my own part I drew attention to this fact in 1873 for the large *Amœba terricola*, and for this reason declared myself opposed to the contraction theory. Hofmeister (1865 and 1867) was also able to convince himself that in the hair cells of *Tradescantia* the currents extend from before backwards.

This observation caused him to turn against the contraction theory just as Nägeli and Schwendener (1865) had also done. The latter authors remarked with reference to protoplasmic streamings in plant cells that contractility really explained nothing, the more so as this conception was obscure and unintelligible for protoplasmic bodies. Under such circumstances streamings could only arise according to the analogy of a blood circulation. We see also, as a matter of fact, that the further development of the contraction theory did necessitate this idea.

(*e*) *Hypotheses of Hofmeister, Sachs, and Engelmann*

Hofmeister, therefore, attempted to found a special hypothesis of protoplasmic movements, and in particular of the protoplasmic streaming in plant cells, the identity of which with those of Rhizopods was recognised on all sides. He thought (1865) that these phenomena of streaming might be referred to the very varying *power of imbibition* of the protoplasm, which was chiefly manifested in the play of the contractile vacuoles. With regard to the contractile vacuoles, however, he held erroneous ideas. The individual "particles" of protoplasm were supposed to possess a very different and varying power of imbibition. If this power

possessed by the particles within the protoplasmic body were to increase constantly in a certain direction, the water would necessarily be set in movement in this direction, since it would be attracted by the particles with the greater power of imbibition; thus a streaming movement would be brought about, with which an increase in the volume of the particles with stronger powers of imbibition would at the same time be connected. In 1867 he put the latter point more in the foreground, without, however, basing the actual explanation of the streamings on it, which was given in just the same way as in 1865. In 1867 Hofmeister more specially declares that, as a result of the increase or decrease in the thickness of the envelope of water round each molecule of protoplasm endued with different powers of imbibition, changes of place must be produced in the molecules, and their middle points brought closer together or carried farther apart. Although he now remarks that this conception of the alteration in the position of the molecules, as the result of different degrees of imbibition, is completely sufficient for the "demonstration" ("Versinnlichung") of the "mechanics of protoplasm," yet, in the further course of his description, he gives exactly the same explanation of the currents again which he had already put forward in 1865, where he speaks, indeed, of the above-mentioned water currents, but does not try to refer the streaming movements to alterations of this kind in the position of the molecules.

Hofmeister, when he thought that the mechanics of protoplasm could be interpreted by the idea that the watery envelopes of the molecules possess a variable thickness, had yet overlooked one important point, namely, the observed fact that a muscle cell when it contracts becomes thickened in correspondence with its shortening, which his hypothesis in the form put forward by him was not able to explain.

Sachs also (1865) came forward as an opponent of the contraction theory in the case of vegetable protoplasmic movements. He regards Hofmeister's theory as admissible in general, but in need of still further elaboration in order to lead to a clearer understanding, since it did not explain the actual causes of the varying imbibition of the particles

of protoplasm, which is supposed to bring about the processes of movement. Sachs attempted, therefore, to complete the theory in this direction by introducing a number of further hypotheses, which gave it such a complicated form that there was little hope at the outset of arriving in this direction at a clearer comprehension of the processes. He bases his view upon four assumptions with regard to the nature of the molecules, or rather molecular complexes, of the protoplasm: (1) That they must possess a definite, but not spherical form; (2) that they mutually attract one another in proportion to their mass and their distance apart; (3) that each molecule possesses a strong affinity for water, which, however, decreases more rapidly with distance than does the attraction of the molecules for one another, so that each molecule is surrounded by a relatively thick envelope of water; and (4) that the molecules, in addition to their general attraction for one another, also possess so-called directive forces, which depend upon their form, *i.e.* a sort of polarity, and that these forces tend to bring the molecules into certain definite positions with regard to one another. By the combined effect of all these forces and conditions, a state of unstable equilibrium of the molecules to one another is produced, the consequence of which is that any local disturbance in it immediately spreads throughout the entire mass. He is of opinion in particular that as soon as the distance between two molecules is increased through any circumstance, their watery envelopes become thickened by attraction of water from the neighbouring "molecular interstices," and thus a streaming movement is set up which is continued backwards from the point towards which it is directed. If, now, it is to be admitted, on the ground of the hypothesis put forward, that by an increase in the distance between two molecules their watery envelopes are able to grow, as the result of a diminution in the hindrance which the mutual attraction of the molecules opposes to this growth in thickness of the water envelopes, it is yet in no way intelligible, as far as I am able to judge, why these molecules should then necessarily absorb water from the

neighbouring ones, for the water envelopes depend on the force of the affinity for water possessed by the molecules remaining *in statu quo;* and since this force is not disturbed or altered in the adjacent molecules, I do not see how a current of water can be brought about in the manner alleged. I am hence of opinion, both from these and other reasons, that a comprehension of the most simple protoplasmic movements is not to be arrived at in the way which Sachs considers possible, and still less so in the case of the more complicated instances of pseudopodial development, etc.[1]

In 1879 Engelmann put forward the hypothesis that the cause of the phenomena of movement exhibited by protoplasm was to be sought in the contraction of its minutest particles, the so-called "Inotagmas," which are to be conceived of as "combinations of molecules." These inotagmas are supposed to possess an elongated form when in a state of rest, and during the contraction following upon stimulation to approach a spherical form more or less. Their contraction itself is supposed to depend upon an alteration in their state of turgidity, since it is probable that with increased turgidity they would tend to shorten, or on the other hand, after giving off fluid, to become stretched again. The latter assumption, therefore, brings Engelmann's theory near to that of Hofmeister and Sachs to a certain extent, from which it differs essentially with regard to the mechanical explanation of the processes of movement. I am, however, of the view that Engelmann's

[1] A special micellar theory of the movements of protoplasm was also developed by the botanist C. Kraus in 1877. I think I need not discuss it here more particularly, but will content myself with the remark that Kraus starts from the assumption that the attraction of the micellæ, both among themselves and for the water of their envelopes, depends on the relation of their volume to their surface. With diminution of the volume of the micellæ their mutual attraction diminishes more rapidly than their affinity for water; hence the protoplasm becomes more watery. During the increase in size of the micellæ, on the other hand, their mutual attraction would increase to a relatively greater extent, which would necessitate an approximation of their middle points, and at the same time a contraction, which would be able to produce phenomena of movement, changes of shape, processes of division, formation of vacuoles, etc.

theory does not justify the expectations of its founder, and I will attempt to explain this rather more fully.

Engelmann wishes to refer the spherical form assumed by naked protoplasmic bodies, consequent upon stimulation, to the fact that all the inotagmas become spherical at the same time, that is to say, become contracted, as a result of which "the surface attraction which they exert upon one another, that is to say, the cohesion of the entire mass, must become sensibly equal everywhere and in all directions." He thus introduces a new assumption, namely, that the mutual attraction of the inotagmas in the resting condition is different in different directions, corresponding to their elongated form, without, however, paying closer attention to this subordinate assumption. Now even if, as postulated by the above explanation of Engelmann, the mutual attraction of the inotagmas becomes equal everywhere and in all directions, there will, in my opinion, only result a tendency towards the spherical form if the protoplasm at the same time obeys the general laws of fluid bodies; and the cause of this tendency to a spherical form can only be, as Engelmann himself also formerly assumed, the surface tension, which, with equal cohesion throughout, only attains to equilibrium under this condition.

If the mass be not fluid, it seems self-evident that the rounding off of the inotagmas and the equality of their cohesion cannot produce a tendency to a spherical form, but at most slight alterations of form. If, on the other hand, the mass is fluid, the same point really holds good, only then, as soon as the cohesion becomes equal on all sides, the surface pressure necessarily produces the spherical form. If we imagine to ourselves an irregularly-shaped *Amœba*, or even the richly-branched pseudopodial network of many *Sarkodina* and *Myxomycetes*, it is, in my opinion, quite inconceivable how these structures should contract into a spherical form merely as the result of the inotagmas becoming rounded off, and of their mutual attraction being equalised on all sides; for these processes, as has been said, could only produce certain alterations in form, since there is no reason at all for the assumption of a spherical form as

a whole as long as the surface tension does not come into play.

The formation of a simple pseudopodium of an Amœba, Engelmann thinks, can be referred to "a general contraction of all the inotagmas of the portion of the hyaline cortical layer which is bulging forwards." To me, however, the origin and gradual elongation of a larger pseudopodium does not seem to be intelligible in this manner. If we assume that the inotagmas of the hyaline cortical layer are all directed parallel to the surface of the region in question, of the body of the Amœba, and if we then imagine them contracted to the fullest extent, so that they become greatly thickened in a direction at right angles to the surface,[1] there will of course result a thickening of the cortical layer of the portion of the surface in question, which may produce a moderate bulging forward of it, but with that the process will have reached its limit. For since we know that the cause of the elongation of the pseudopodium, and of the current that passes through the protoplasm, has its seat at the tip of the pseudopodium, and that here, at all events, the contraction of the inotagmas reaches its maximum at the commencement, a further contraction does not seem to be possible at this spot. The theory, therefore, gives indeed an explanation for the first slight bulging forwards, but is not able to explain the further growth of the pseudopodium. For it seems inadmissible that the inotagmas in question should continually contract further. If, on the other hand, it was thought necessary to assume in some way that the layer of contracted inotagmas at the tip of the pseudopodium finally became ruptured and the protoplasm lying beneath, which had come to the surface, now contracted in its turn, this view would also seem to be inadmissible, quite apart from the improbability of such assumptions, since a rupture will not in any case occur at the spot where contraction is taking

[1] Although Engelmann makes no exact statements with reference to the power possessed by the inotagmas of becoming shortened or thickened, yet it seems to me beyond a doubt, that he must imagine the degree of shortening to be a relatively moderate one, namely, of about the same extent as he has become acquainted with from the shortenings that can be observed in muscular contractions.

place. Now if we consider that many simple *Amœbæ* move forward for long distances at a time in exactly the same way that a pseudopodium is protruded, *i.e.* that they really represent a single creeping pseudopodium, this fact is still more definite evidence than the case upon which we based our argument above, against the complete applicability of Engelmann's explanation. There is also the further fact, that while it explains the stream of protoplasm forwards into the pseudopodium, it does not account for the lateral back currents at the ends of the pseudopodium.

Engelmann believes, however, that the formation of pseudopodia is produced by other causes still. He is, with de Bary, of the opinion that pseudopodia can be pressed forwards, and streaming movements set up, also by a *vis à tergo*, which depends on local contractions. Finally, he does not wish to refer the origin of the fine filamentous pseudopodia to contraction, but on the contrary to relaxation of contracted rows of inotagmas. The latter explanation, the mechanical representation of which in itself presents very great difficulties, if one thinks of the considerable length to which pseudopodia of this kind frequently attain, may also be rejected for the reason, that it is improbable in the highest degree that the development of pseudopodia, in which very gradual transitions can be traced so beautifully in the Rhizopod series, should owe its origin to two completely opposite causes.

Just as unsatisfactory as the explanation of the formation of pseudopodia it seems to me is Engelmann's view as to the causes that produce rotational currents in plant cells. He says on this point (p. 378): "A current of this kind must be brought about when the inotagmas of the layers in motion are, on the whole, orientated with their longitudinal axes parallel to the direction of movement, and the spontaneous stimulation continues to move forward in this direction. The motile protoplasm then creeps upon the non-motile layer of the wall just as the foot of a snail upon the substance beneath it."

In opposition to this explanation it may be urged that, in the first place, there is certainly a continuous connection

and a gradual transition between the non-motile layer of the wall and the streaming protoplasm, and that therefore the relations are here, as a matter of fact, essentially different from the case of a snail's foot, which moves upon a firm substance completely separated from itself. Further, if the relations were as supposed, one would expect to observe in the rotating protoplasm something of the wave of contraction that would move forward, which would, of course, be marked out towards the cell-sap cavity as projections, just in the same way as distinct waves of contraction are to be traced in the snail's foot. Finally, the observation of these streaming processes teaches us quite definitely that there is certainly no creeping substance present in the way in which Engelmann's explanation supposes, but that we are dealing with a substance which is flowing—a fact which can be traced very plainly in the movements, displacements, torsions, etc., which the particles contained in the streaming protoplasm go through.

Hence, as has been said, the hypothesis of Engelmann also seems to me to give no satisfactory idea of the causes and mechanical relations of protoplasmic movements, just as little as the two before-mentioned molecular hypotheses were able to do. On the whole, I believe that, as Berthold has declared already, nothing profitable is to be obtained by setting up peculiar molecular hypotheses to explain certain processes in the organic world. At any rate it seems to me much more promising and satisfactory to seek for the causes and conditions of these processes among the known physical forces than to have recourse to special molecular forces constructed *ad hoc*. It is only necessary to call to mind, for example, the complication of the assumptions made by Sachs—and those of Engelmann are in like manner very complicated, since he also postulates an increase and decrease of the attractive forces of his inotagmas corresponding to the decrease and increase of their water of imbibition, that is to say, of the watery envelopes of the inotagmas—in order to convince oneself that it would be difficult to attain to satisfactory explanations in this direction.

(*f*) *Electrical Hypotheses of Velten and Fol*

The opinion frequently expressed by older observers, namely, that protoplasmic movements depend upon electrical forces, was defended again by Velten in 1876. According to him it is electrical forces, which reside in, and take origin from, the individual cells, that cause the streamings. Velten supported this supposition, and his view cannot be termed anything else, since he is not able to elucidate either the origin or the mode of action of these forces in bringing about protoplasmic movements, by his observations upon the effect of strong induction-currents on plant cells after death. Under these conditions he was able to call forth streamings and rotations in the dead contents, or rather on their granular enclosures (starch granules, etc.), which were very similar to the natural streamings of protoplasm. The fact that we are dealing with phenomena in dead cells, and further also the possibility that these processes of movement produced by strong electric currents might be in part at least the result of a considerable increase in temperature in the cellular tissue subjected to the currents—which Velten does not take into account at all, although he himself estimated the rise of temperature at 65° or more,—this fact in itself makes the value of these observations seem very little for forming an opinion upon the streaming phenomena of living protoplasm. It was without doubt in consequence of this that Velten's view met with no support at all. Reinke in 1882, by means of a series of interesting experiments, sought to directly contradict the basis of Velten's supposition, namely, the presence of electric currents crossing one another in the cell, in the same way as Becquerel (1837) had already undertaken to do by means of other methods in the case of *Chara*. Reinke showed, for instance, that the closely approximated poles of a strong electro-magnet, between which are brought cellular filaments of *Chara* or *Nitella*, or hairs of *Urtica*, suspended freely in a drop of water, exert no directive influence upon the position of the filaments. If electric currents really moved in cells with flowing protoplasm, it might have

been expected that the cells would have assumed a definite position with regard to the poles of the magnet. But, as has been said, there was nothing to be seen of this. The magnet also proved without effect upon the arrangement of the strands of protoplasm and the streaming of the granules in the hair cells of *Tradescantia*, etc., a fact which in like manner confirms the absence of electric currents.

For the sake of completeness it should be further mentioned here that Fol (1879) set up a hypothesis as to the connection of protoplasmic movements with electric forces, which was not, however, raised above the rank of a supposition, since it did not enter at all into details. Fol's view and its significance may be made clear most simply by means of the following quotation: "Si nous supposons une pile électrique dont chaque élément soit de la grosseur d'un de ces granules que le microscope dévoile au sein du sarcode sous formes de petits points grisâtres, la quantité totale d'électricité produite dans une pile de quelques millions de ces éléments réunis en tension pourra être considérable sans qu'il se dégage aux extrémités de la pile une quantité d'électricité bien appréciable à l'aide de nos galvanomètres. Néanmoins, suivant la manière dont cette force se répartit à la surface de chaque granulation, un mouvement imprimé à la première particule d'une série pourra se propager de l'une à l'autre et produire un déplacement mécanique considérable" (p. 269).

(*g*) *Leydig's View of the so-called Hyaloplasm*

Even at an early date there was a hypothesis framed which sought for the actual living substance, and therefore also the seat of movement, in the intervening matrix, the so-called *Enchylema*. Leydig, the principal representative of this view, had rather strange ideas concerning the matrix, his hyaloplasma, which may be briefly indicated, since they are of course the essential conditions for the possibility of such a conception. He evidently had the greatest difficulty in forming an opinion as to the nature of this hyaloplasm, as can be proved by the following passage taken from his

memoir of 1885 (p. 43). It runs thus: "We know that the hyaloplasm contains throughout an abundance of water—in fact, as far as the perceptions of our senses are concerned, hyaloplasm and water may run into one; they form, if we may assist ourselves with the expression, a solution. Where, then, is the line to be drawn between water and hyaloplasm, a line which it is nevertheless necessary to assume?"

In spite of this evident lack of any idea at all definite as to the nature of the hyaloplasm, Leydig did not hesitate to regard it both as "the primary motile substance" (p. 152) and also as the nervous, etc., although he was not even quite certain whether lymph might not be identical with hyaloplasm and with the homogeneous nerve substance, which was also supposed to be merely hyaloplasm. Since Leydig's assumption, as has been pointed out, was based principally upon the supposition that the axis-cylinders consisted of such homogeneous and structureless hyaloplasm, for which very reason the hyaloplasm was supposed to be the real nervous and generally active substance, this view of course falls to the ground, when it is proved that the axis-cylinders possess just the same honeycombed structure as the rest of the protoplasm. Even with the modification which Nansen (1887) has given to Leydig's view, the latter is no longer tenable, since, as we saw, the assumption that the axis-cylinders are composed of continuous hyaloplasmic nerve tubules is incorrect, because the hyaloplasm, or in our terminology the enchylema, is really discontinuous, and distributed in the substance of the axis-cylinder in the form of numerous chambers or alveoli separated by delicate partitions. If, however, this view is correct, it seems absolutely necessary to consider the substance of the framework as the substratum of nerve conductivity, for it alone extends continuously through the axis-cylinder, and is therefore in a position to be instrumental in conduction. The arguments brought forward by Pflüger (1889) against Leydig's view seem to me also important. Pflüger remarks that this assumption is improbable from the fact that the nerve fibres are only stimulated by currents directed longitudinally, and not by those directed transversely,

for which reason the fibrillæ must be the really active and irritable components. This observation also seems consistent with our view relative to the constitution of the axis-cylinder, since the cross connections which we have found are throughout discontinuous, and are therefore essentially distinct from the longitudinally directed tracts of the framework. Pflüger further declares it to be unthinkable that images of memory, such as we must ascribe to the ganglion cells of the brain, could be retained by a fluid substance such as the hyaloplasma; rather that this would only be possible in a solid substratum. So far as a conception of these things is generally possible in the present time, his conclusion seems to me perfectly justified. Now, since my interpretation of the structure of the ganglion cells quite admits of their framework becoming partially or entirely firm, it can be brought very well into harmony with these physiological requirements.

We have already learnt before that some investigators, such as Brass (1883 and 1885), Schäfer (1887), and Rohde (1890 and 1891), have ranked themselves more or less definitely on the side of Leydig's hypothesis. Schäfer alone, however, in more recent times has attempted to support the opinion alleged by further investigations. In white blood corpuscles of Amphibia, after fixing and staining, he believes he has convinced himself that the pseudopodia are always structureless and homogeneous, while the rest of the corpuscle appears more or less distinctly reticular. At the same time, the homogeneous substance of the pseudopodia stains very little or not at all, and is thus sharply marked off from the strongly staining reticular substance of the rest of the corpuscle. In these results Schäfer sees, as has been said, a decisive proof of the correctness of Leydig's hypothesis. He also especially declares the derivation of the apparently homogeneous protoplasm of pseudopodia, etc., from that of an alveolar structure—an idea expressed by me in 1890, and followed up more thoroughly in the present work—to be very improbable and contrary to experience. Since the other arguments, which are in opposition to the hypothesis of Leydig and Schäfer, are not touched upon at all in Schäfer's

dissertation, I need merely confine myself here to a brief discussion of the objections set forth above. My view, that the alveolar structure is not wanting even in apparently homogeneous protoplasm, but is only no longer traceable owing to the fineness of the walls of the alveoli, is held by Schäfer, as has been remarked, to be contradicted by the alleged sharply-defined limit between the reticular and the homogeneous protoplasm. With regard to this point I may simply refer to the investigations upon the apparently homogeneous pseudopodia of *Amœbæ* and of *Gromia Dujardini* which are described in an earlier part of this work. Moreover, I may lay especial stress on the fact that, in the pseudopodia investigated by me, I never observed a sharp boundary between the reticular and the apparently homogeneous protoplasm, but could always see a transitional zone both in life and in preparations. In fact, it may frequently be observed in the pseudopodia, that the structure becomes fainter at the extremity, or even becomes indistinct before reaching the extremity, which causes the latter to appear homogeneous. I do not believe, moreover, that the pseudopodia of the blood corpuscles investigated by Schäfer behave differently in this respect; on the contrary, even in Schäfer's Fig. 4 (1891, 1893), it can be seen in many places that the reticular structure gradually becomes blurred towards the lobed or rim-like pseudopodia, and insensibly passes into them. If in other places a very sharp limit seems to exist between the homogeneous protoplasm and the reticular central portion of the corpuscle, this can be explained by circumstances of another kind. Schäfer specially mentions that the homogeneous substance of the pseudopodia, which in accordance with his view he regards as *enchylema* (hyaloplasm) which has crept or flowed out, stains much more feebly than the granular reticular central protoplasm, and that therefore the two must also differ chemically, *i.e.* that the strongly staining spongioplasmic framework can only be present in the reticular portion. Now we have frequently found that the spongioplasmic framework, *i.e.* the framework substance of the alveolar protoplasm, stains, as a rule, very feebly, and that the apparently intense coloration of it,

which can be obtained so often, is always, upon more exact investigation, to be referred to the granules which it usually lodges in great abundance. Now, since we know that the granules, also very numerous in Amœbæ, do not pass into the hyaline protoplasm of the pseudopodia, its feeble staining powers are explained easily by this fact. This explanation will, at any rate, hold good for the white blood corpuscles, since granules are, in like manner, present in them in abundance. An apparently very sharp limit between the darkly stained reticular central protoplasm and the hyaline protoplasm of the pseudopodia may, however, in addition to being caused by this circumstance, be also an illusive appearance due to the fact that the real origin of a pseudopodium which is creeping flat upon an underlying surface, may be covered, to some extent, by a bulging out of the more or less raised central portion of the corpuscle. This frequently occurs in the case of Amœbæ creeping upon a flat surface. Under these circumstances a sharp boundary between the substance of the pseudopodia and the central protoplasm is then, of course, apparently visible, since the origin of the pseudopodium cannot be plainly traced in objects of such small size.

I think, however, that it is scarcely necessary to discuss these objections more in detail, but that it will be sufficient to refer to the above described observations upon the sudden conversion of the apparently homogeneous protoplasm of the pseudopodia into reticular protoplasm, which the hypothesis of Leydig and Schäfer is altogether unable to explain, while it is perfectly compatible with my view. As has been said, I consider my view with regard to the homogeneous protoplasm to be the more probable for these reasons, which were developed by me in 1890, without Schäfer having paid any heed to them. There is furthermore the additional fact, to which I will again call attention here, that as evidence against the Leydig and Schäfer hypothesis, which of necessity assumes the existence of a spongy framework, there are, of course, all those arguments which have already been enumerated above against the possible existence of such a framework. Schäfer expresses himself rather indefinitely

with regard to the aggregate condition of the actual spongioplasmic framework when he says (i. p. 175), "It is firmer than the hyaloplasm (but perhaps not actually solid), and is, in all probability, highly extensile and elastic." But a highly elastic substance which is not actually of a solid nature seems to me to be a physical impossibility, which we cannot well make use of to found a hypothesis upon living matter.

In recent times Rohde has specially come forward as a very zealous adherent of Leydig's theory. His investigations upon the nervous elements of the Annelids convinced him also that the hyaloplasm alone must be the nervous element, and that the spongioplasm, on the contrary, performs functions of support exclusively throughout the entire nervous apparatus. I think that the reasons for the opposite view, which have been enumerated already, are not shaken in the least by the investigations of Rohde, and on that account I will not try to discuss them more thoroughly here, the less so as his last work (1891) only became known to me after the completion of my manuscript. I might, however, point out the fact that the fibrillar structure of ganglion cells, nerve fibres, etc., which Rohde alleges, does not exist in the sense in which he interprets it. Rohde takes up, in fact, about the same position as Flemming. In opposition to him I hold my view of the structure of ganglion cells, etc., to be entirely correct, and I think I am the more justified in doing so as Rohde, in a photograph of a section through one of the so-called peripheral ganglion cells (Plate VII. Fig. B), has furnished, in my opinion, a very valuable proof of the correctness of my view.

The photograph in question shows the honeycombed structure of the protoplasm very plainly almost everywhere, and enables us to make out exceedingly well how the appearances of fibres and striations arise solely by a modification of the alveolar framework. If one compares this photograph with the drawing of one of these cells which Rohde gives at the same time (Plate VI. Fig. 12), it is very obvious not only how little the latter corresponds to nature, and to what a high degree it is schematised, but also that the drawing

does not contain many details of structure which the photograph represents very well. In this regard I may refer, by way of example, to the nucleus alone, the contents of which are described and depicted as granular, while the photograph shows distinctly that the granules are lodged in a honeycombed framework. I regard, therefore, as has been said, Rohde's photographs, as well as those of a ganglion cell from an earthworm which accompany the present work, as good evidence of the alveolar structure. The photograph in question teaches us still more, however. Rohde describes and figures the fibrillæ of the ganglion cells as being of very different thicknesses, and asserts that in certain zones of the protoplasm very strong fibrils make their appearance, while in other regions there are only very fine ones. In a former section I have already pointed out that the stronger fibrils, or "runners" (Reiser), so often described, are quite certainly only the result of densely deposited granules. Now Rohde's photograph, already mentioned, also seems to me to bring forward the strongest proof in favour of this explanation, for it can be plainly made out in it in many places that the apparent stronger fibrillæ arise by a more or less dense crowding together of such granules, and it can further be seen with the same distinctness that the differences between the five zones of protoplasm which Rohde distinguishes depend in the main, at any rate, upon differences of the degree to which they contain granules lodged in them, together with, however, special modifications of the framework here and there. On the other hand, the width of the meshes does not seem to me to be subject to any very considerable amount of variation in the different zones. The fact that the zones, with very numerous granules, appear in general more finely structured, may rather depend essentially on all the nodal points being sharply marked out by the granules lodged in them, while in the zones poor in granules many nodal points are so pale that they are only slightly prominent, or even partly left out in the photograph.

Now since, as has been said, I find in this photograph of Rohde's an involuntary support for my interpretation of the structure of ganglion cells and of protoplasm generally, I

consider it the less necessary to contradict again the doctrine, accepted by Rohde also, of the nervous nature of the hyaloplasm, since it must appear untenable in and for itself, as soon as the correctness of the view concerning protoplasmic structure, put forth by me, is admitted.

(*h*) *Montgomery's Hypothesis*

I must say a word or two, in passing, relative to the hypothesis developed by Montgomery (1881 and 1885) with regard to protoplasmic movements. It is not easy to obtain a clear idea of this view, since its founder has conceptions of protoplasm and of the forces at work in it, which depart completely from what are usual; in fact they are on the whole difficult to grasp. Without wishing to attempt a more exact proof of this assertion, I content myself with a reference to the following sentence, which concludes Montgomery's work of 1881, and contains, as it were, his confession of faith with regard to living matter. "Itself sempiternal, an indivisible specific totality, bringing back the past to the present, it is in opposition throughout all time to the remainder of transitory nature. It, the living substance, is in the world the truly permanent, and not the dead formless matter." Starting from such conceptions, which recall strongly the past times of the nature-philosophy, Montgomery arrives at the strange view that ordinary physical forces play on the whole no part in protoplasm, and that the living substance is in fact governed only by chemical forces. For this reason, according to him, it is out of the question to talk of an aggregate condition of protoplasm. If any definite idea is to be connected with these assertions, it seems to me to follow from them that Montgomery conceives of the entire protoplasm of an organism, in fact even the whole body of a higher animal, as would appear from certain of his applications, as a large chemical molecule, which is in a state of constant decomposition and reconstruction, within which also only chemical forces exert their activities and not the usual forces of molecular physics.

Montgomery's hypothesis concerning the processes of

movement is hence also a chemical one. The movements of an Amœba which is flowing in a simple manner are supposed to proceed as follows. At the anterior end of the Amœba, under the influence of the external medium, a decomposition of the hyaline protoplasm is continually taking place, a "disgregation," as he calls it; in consequence the hyaline protoplasm of the anterior end shrinks together and becomes granular, being at the same time carried towards the sides and finally towards the posterior extremity. This granular shrunken protoplasm then gradually re-enters the current, to become again restored, under the influence of nourishment, to the former condition of hyaline protoplasm, its natural condition. During this process of reconstitution, however, it "stretches," and this stretching, which has its seat chiefly at the anterior end of the Amœba, where the hyaline margin occurs, is the cause of the forward movement and, of course, of the streaming generally. The continual play of disgregation and reconstitution thus causes the streaming of the Amœba and similar protoplasmic movements. Montgomery tries to extend this hypothesis to explain also the contraction of muscles, but I will not attempt to represent here his views with reference to this point.

Frommann has recently (1890) pronounced a very shrewd critique upon Montgomery's hypothesis; elsewhere I have not seen it made the subject of earnest criticism, either favourable or otherwise. I think that I may also omit any discussion of it, the more so because, in my view, it is, in the first place, altogether hypothetical, being in fact, as is even asserted at the outset, not based at all upon physical forces. Moreover, I am of opinion that, even if we accept the postulates that are made, the regular protoplasmic movements of Amœba or of plant cells could never be brought about by the alternate action of shrinking and stretching which is asserted to occur. The fact, moreover, that any explanation is lacking as to why the protoplasm should, as a matter of fact, shrink after decomposition, and should stretch when reconstituted, need not be brought forward by me here as an objection.

(*i*) *Hypotheses relating to Surface Tension—Berthold, Quincke*

It has already been occasionally pointed out here and there, that in bringing about protoplasmic movements the phenomena of the so-called *surface tension* of the fluids may play a part.

Hofmeister attempted, as far back as 1867, to interpret the so-called rounding off of drops of protoplasm, which has often been regarded as a phenomenon of contraction, as a property identical with the tendency to assume a spherical form in ordinary drops of fluid, that is to say, as an effect of the surface tension.

Engelmann also, on the ground of his idea that protoplasm becomes fluid by electrical stimulation, arrived (1869) at the view that the forces which cause the contraction of protoplasm "may be just the same as those which tend to make every non-spherical free drop of fluid become spherical"; that would, of course, be the surface tension. He is, with Hofmeister, completely convinced of the fact that contractions, in the ordinary sense, are not the cause of movements, and agrees entirely with the view of the latter concerning the extension of the currents backwards. At a later date, however, Engelmann did not recur again to this, in my opinion, very correct idea, but developed, as we have seen, a theory of movement based on essentially other grounds.

In 1876 I tried to make use of surface tension hypothetically as the efficient cause in the explanation of cell division. As I have already remarked, I regard the explanation given then as still suitable in its main points, and indeed as having become considerably more probable from recent observations with regard to the great part played by surface tension as an important cause of the processes of movement in protoplasm. Since the time when I first arrived at the conviction that this property of fluid bodies must be of pre-eminent importance for the explanation of the changes in form exhibited by fluid protoplasm, I have

always kept this problem in view; and the firm conviction that there was in this direction a prospect of arriving at a comprehension of protoplasmic movements was one of the main incentives of the investigations described in this work.

In 1880 Rindfleisch published his ideas upon the supposed causes of protoplasmic movements, which have certain points in common with the view that surface tension comes into play in this process. Rindfleisch adopted the theory of the reticular framework of protoplasm, and sought to show that the intimate interpenetration of two different substances, *i.e.* the framework and the intervening matrix, which follows from such a structure of protoplasm, was of fundamental importance for the origin of processes of movement. His hypothesis asserts that the *adhesion* of the two interpenetrating substances forms the active principle in the origin of processes of movement; alterations of their adhesion necessarily produce small movements, the sum total of which bring about the observed effect. He tries to support this assumption by reference to the phenomena of movement in fluids. For instance, he refers to the movements which a drop of glacial acetic on a slide, or a fine layer of oil on water, shows when warmed. In these cases, however, there is no doubt that surface tension is the cause of the changes of form and phenomena of movement, so that it may well be supposed that Rindfleisch had in reality imagined this to be if anything the efficient cause. Besides, it scarcely requires any special discussion to show that no explanation is possible in the way indicated by him, since the hypothesis of a reticular framework, which nevertheless must be fluid, in order to exhibit changes of form and phenomena of movement under the assumed conditions, does not seem possible.[1]

In the year 1886 Berthold arrived at the view that the protoplasmic streamings in vegetable cells had their cause in

[1] It may be mentioned here quite briefly that Geddes (1883) developed a hypothesis which seeks to refer amœboid movement and the contractions of striped muscles to the so-called phenomena of aggregation, such as Darwin observed in the protoplasm of insectivorous plants. Geddes's view is not, however, perfectly intelligible to me.

local alterations of the surface tension between the fluid protoplasm and the cell-sap. Weber in 1855 had already pointed out the similarity between the streamings observed in certain drops, and produced by surface tension, and the protoplasmic streamings in plant cells. It is without doubt a great merit on the part of Berthold to have recognised correctly the importance of these relations, and to have ventured an attempt to follow them up consistently. Even in 1865 Nägeli and Schwendener had very rightly declared that the true seat of the motor forces in the streamings of plant cells must be the surface of the protoplasm turned towards the cell-sap; on the other hand, they formed an incorrect judgment upon the state of affairs, inasmuch as they considered that this movement of the surface of the protoplasmic body obtained its point of support in the surrounding water, "just in the same way as a bird in the air or a fish in the water," and that in this way the forward movement took place. They concluded, therefore, that the adjacent cell-sap must always be in a condition of streaming "in an opposite sense to" the movement of the protoplasm. This erroneous idea, founded upon incorrect views as to the nature of the streamings, was especially contradicted by Velten (1873), who showed that the movement of the adjacent cell-sap, as far as can be judged from the fine granules occasionally occurring in it, always took place *in the same sense* as that of the protoplasm. From these undisputed observations it also follows with certainty that the streaming of the protoplasm reaches as far as its limit on the side of the cell-sap, a fact which may also frequently be directly observed, so that no resting skin-like layer exists at this spot. It seems to me quite impossible to assume with Wakker (1888), who also observed this movement in the cell-sap, that the protoplasmic streaming sets the membranous layer lining the cell-sap vacuole or cavity in rotation by means of its friction; especially if we consider that in cell-sap cavities, which are spanned by bridges of protoplasm, such displacements of the vacuole would necessarily be very obvious.

According to Berthold's hypothesis it is a case of differences in the surface tension, at the limit between cell-sap

and protoplasm, which produce the streaming movements in the plant cell. In this point I think Berthold has hit the mark; on the other hand, I cannot consider as satisfactorily grounded his efforts to explain, by means of these processes, isolated cases of movement in vegetable protoplasm. The very important case of the so-called rotation of the protoplasm in a constant direction remains, in my opinion, unexplained. For the remarks that Berthold makes upon this point on p. 118 can scarcely be considered as a sufficient explanation. He thinks that the rotational streaming has gradually arisen from numerous irregular streamings, such as occur in the so-called circulation, in the following way. "The stronger currents will gradually suppress the weaker, and draw them along in their direction, and thus in the struggle for existence (!) only a single rotational current will be left remaining among them, for only in this way would the principle of least resistance be satisfied." Berthold further supposes that a special increase of the fluidity of the protoplasm is a condition for the development of the simple rotatory current. An explanation such as the above can hardly be considered a physical one, although Berthold means to give one of this kind, for such principles as the "struggle for existence" are here quite inadmissible and do not explain anything. A system of numerous streams will always remain as such when the causes persist which produce them; if no change takes place in the causes, a single stream cannot possibly be formed. With regard also to the principle of least resistance I am very sceptical, since I freely confess that I do not quite understand what Berthold really pictures to himself by it. In order to explain rotation currents on the ground of Berthold's hypothesis, which, as I have said, I regard as the only correct one, even after all the observations of my own which are detailed in this book, it is necessary to show why, when, and in what way there arises a single powerful current of this kind, which, as we have already been convinced by the streamings in the foam-drops, can suppress feeble local streams with perfect ease by gradually removing the cause of their origin; and we must

further show how, above all, it comes about that this current only attains development on one side, for, as we saw before, every extension-current radiates out on all sides from the place of its origin. Later on it will be a subject of inquiry whether it is possible to find an explanation for the one-sided nature of the rotational stream. For the rest, Berthold has clearly recognised that the weakest point of his explanation of the circulatory streamings consists in the fact that in them true centres of extension, such as the hypothesis postulates, are scarcely to be made out with certainty. He seeks the cause of this fact in the thinness of the protoplasmic lining of the wall, but I hardly think that the matter is to be cleared up thus.

It is curious, however, that Berthold is of the opinion that the movements and streamings of Amœbæ and plasmodia do not depend on the same causes that produce the streamings of the protoplasm of plant cells, although the forces that are at work are the same in principle. He believes that it is not extension-currents, depending on local diminution of surface tension, and the forward movements that appear in consequence, such as our drops of oil or foam show under suitable conditions, which form the cause of amœboid movement, but that the protoplasm of the Amœba behaves in much the same manner as a fluid which spreads out upon a solid body. In order, therefore, to be able to understand Berthold's view with regard to these processes, it is necessary to pay a little attention to the conditions of the spreading out of fluids upon solid bodies. Quincke, upon whose views Berthold supports himself, has attempted in 1887 to give a theoretical foundation to the proposition that the spreading out of fluids upon solid bodies is governed by the same conditions which also determine the spreading out of one fluid upon the surface of another, or rather upon the limiting surface of two others. He holds it admissible to assume that even at the limit between a fluid and a solid body, in fact even at the surface of a solid body, a surface tension exists, and that it is the ratio of the magnitudes of the three surface tensions, *i.e.* of the surface

tension of the fluid which is brought upon the solid body (a_2), of that of the limiting surface between this fluid and the solid body (a_{12}), and of that of the solid body (a_1), which determines the spreading out of the fluid; that is to say, that the latter will continually spread out, if $a_1 - a_{12} \geqq a_2$. Now, if we are not dealing, as was supposed in the above case, with the surface of a solid body (1) which is bounded by air, but with a surface covered by a fluid (3), so that the fluid (2) is brought upon the limiting surface between the solid body (1) and the fluid (3), the spreading out of (2) will take place here theoretically when the condition is fulfilled that $a_{13} - a_{12} \geqq a_{23}$. The theory further requires that in any drop of fluid which does not spread out upon the surface of a solid object, its surface should form, at each point of its line of contact with the latter, a constant marginal angle with the surface of the solid object—an angle which is independent of the geometrical form of the surface of the drop, and is only dependent on the ratio of the three surface tensions which act at every point of the line of contact.

These theoretically-obtained determinations have only been partially confirmed by experience. Thus, for example, the marginal angle of a drop of water adhering to a glass plate does not remain constant if water be gradually drawn away from the drop; the area which the drop covers remains the same, while its volume diminishes, and at the same time the marginal angle becomes smaller, while theoretically it ought not to change, or at the most it might increase, if one takes into account the decreased height of the drop. Quincke was just as little successful in causing an essential change in the marginal angle of an adhering drop of this kind, by altering the surface tension a_{23} (or a_2), by means of placing some oil on the drop, though he succeeded perfectly with drops which were lying on the surface of a fluid. In any case these results seem to indicate that in adhering drops relations come into play which are not yet sufficiently known to us; for which reason it seems very unsafe to make Quincke's theory the basis of a hypothesis relative to the phenomena of movement

of Amœbæ, and to class the latter as adhering drops of this kind, as Berthold does. His hypothesis starts, as has been said, from the view that the Amœba adheres to the solid substratum of the underlying surface and, being a fluid drop, is subject to the above-mentioned conditions, in accordance with which its marginal angle must also remain constant as long as the chemical composition of the protoplasm is constant.

Now if, at a point of the edge of the Amœba, a chemical alteration takes place, whereby a lowering of the surface tension (a_{12}) between the protoplasm and the underlying surface is brought about, or, as Berthold usually expresses it, the adhesion between the substance of the Amœba and the substratum is increased, there then results an extension of this margin, until the marginal angle is sufficiently diminished, to compensate for this change of the surface tension or of the adhesion. If we have already reason to doubt this explanation, on account of Quincke's experience to the effect that surface tension has no influence upon adhering water drops, there are in addition a considerable number of further points which, in my opinion, are evidence against it. In the first place, I consider it incorrect to suppose that Amœbæ really adhere to the solid substratum. I do not entirely dispute the fact that local adhesions at the hinder end, or occasionally also in the pseudopodia during their retraction, may come under observation. On the other hand, I consider it certain that an extensive adhesion is absent. Any one who has been frequently occupied with Amœbæ knows that even very feeble currents of water are usually sufficient to wash them away from the surface on which they are creeping, while really powerful forces would in any case be necessary for this, if an actual adhesion existed. In addition to this there is the fact that some Amœbæ, which certainly do not adhere, but swim freely in the water, develop pseudopodia, and their power of changing their shape is in no way impaired.[1]

[1] A very suitable object upon which to convince oneself of the non-adherence of very motile Amœbæ is *Pelomyxa*. With some good motile

Finally it is known that many Amœbæ can to some extent send out their pseudopodia free into the water, so that Berthold sees himself constrained, in the case of the formation of pseudopodia of this kind, which in other respects is precisely similar to that of creeping pseudopodia, to accept the old theory of the pressure brought about from behind by local contractions, and thus to assume two entirely different causes at the same time in order to explain amœboid movement.

Berthold finds a proof of the correctness of his hypothesis with regard to amœboid movement in the well-known phenomena of movement shown by drops of water adhering to a glass plate, if some ether or alcohol is brought near them at their edges. As is well known, the drops retreat from the ether or alcohol. Berthold thinks that this phenomenon is to be explained in exactly the same way as he supposed amœboid movement to be, that is to say, by the marginal angle of the drops becoming increased on the side towards the alcohol, since the surface tension is greater between water mixed with alcohol, and glass, or rather its adhesion is less; and he believes, as has been said, that the conditions are the same as in the Amœba, for which he postulates, in like manner, polar differences of adhesion, *i.e.* a preponderance of adhesion at the pole which is advancing forwards. Now, in the first place, I regard the explanation given by Berthold of the drop of water retreating from alcohol, etc., as only partially correct. Its edge shrinks back on the approximation of the alcohol with an increase of the marginal angle, and this may rightly be referred to the cause alleged by Berthold. But with this shrinkage the movement would be exhausted, and a continuous retreating movement, or, in other words, a spreading out of the edge turned away from the alcohol, would not be intelligible, since, after a corresponding

specimens in a watch-glass, it is easily proved by slightly inclining the glass that they do not adhere to it. On the slide it is possible to displace an actively-streaming *Pelomyxa* by means of a light touch with a fine glass rod. Only the hinder end, which in *Pelomyxa*, as in other Amœbæ, is distinguished by special peculiarities, sometimes adheres to a slight extent.

increase in the marginal angle, a condition of equilibrium would be established. The retreat or progression of the drop must therefore have another cause, which has, in fact, long been known. Since the alcohol greatly lowers the surface tension of the water drop towards the air, a violent extension-current is of course set up at once on the surface of the drop, which has, as its consequence, a transfer of fluid of the drop from the alcohol edge to the opposite one. Here the alcohol rapidly evaporates again, for which reason the extension-current persists, in the same way as we have already seen similar currents persist for a long time. By this continual flowing away of liquid from the edge of the drop nearest the alcohol, it is caused to shrink away before the alcohol.[1]

Berthold has paid no attention to these necessary and so often described currents, and hence has also not noticed that they are direct evidence against his explanation of amœboid movement. For instance, if we wish to apply the phenomenon of the retreating drop to an Amœba, we should be obliged, on the contrary, to imagine that we had an adhering drop of alcohol or some other fluid of relatively

[1] A drop of this kind adhering to glass and retreating before alcohol, moves therefore in exactly the opposite manner to that in which a drop that is suspended in a second fluid, or at least is only very slightly adherent, would move forwards under the same conditions; for we know of old that the lowering of the surface tension at the free surface of such a drop produces a forward movement in the direction from the centre of the drop towards this point of the surface. That this phenomenon is not exhibited in an adhering drop of water is in any case a consequence of adhesion and of its being in air. Even when the drop of water is in a fluid, and adheres strongly, the relations may take a similar course. In my experiments with drops of oil and oil-foam, I sometimes made the strange observation that in spite of the existence of an energetically streaming centre of extension, they did not, as usual, move forward in its direction, but in precisely the opposite direction. Hence the course of events was exactly the same as for the drops of water, on the supposition, that is to say, that the oil streaming away from the centre of extension was not sufficiently replaced by the current streaming towards it; and in this way a continual abstraction from the drop at the extension centre, and a continual addition to it at the opposite margin, was going on, which produced a progression of the entire drop away from the centre of extension. Formerly I was unable to explain this phenomenon satisfactorily; I now think that I was dealing with drops which adhered strongly, and for which the relations were similar to those for water drops on a glass plate when approached by alcohol.

low surface tension, which was brought into contact on one side with water or another fluid of higher surface tension; since water is less volatile than alcohol, the experiment could not be carried out in the same manner as the reverse one. Now, if the adhesion was increased, or, in other words, the surface tension of the drop towards the glass was diminished, by the surface of the drop of alcohol taking up water on one side, so that this edge of the drop spread itself out with diminution of the marginal angle, then, by reason of the difference of tension on the free surface of the drop, which would necessarily result, a superficial extension-current would at once arise, whose centre of course would be situated at the opposite edge of the drop. If this current was continuous, as would of course be the case if the polar difference of the surface tensions in the drop was maintained—that is to say, if water was more volatile than alcohol,—a movement forwards of the drop towards the side of the water would be the natural consequence.

From these reflections it seems to me obvious that, if amœboid movement had as its cause what Berthold ascribes to it, a system of currents ought to be set up in an Amœba exactly the reverse of what actually exists. The currents should flow away from the hinder end of an Amœba on each side and carry protoplasm to the anterior end. But since it is notorious that the streaming takes exactly the opposite course, I consider Berthold's hypothesis unsuitable. Now, Berthold has well remarked that the currents in an Amœba run, in the main, just as if an extension-current existed as the result of the surface tension being diminished at the anterior end, as is the case in our drops of oil or oil-foam. Nevertheless, he considers it incorrect to accept this obvious hypothesis as a means of explaining amœboid movement. He is more inclined to think that the successive spreading out of protoplasm at the anterior end of an Amœba takes place with considerable force, and that thereby not only the axial up current, but also the back currents on each side, are to be explained. In opposition to this idea I must point out that it seems to me quite

impossible to explain both the back currents and the regular circulation of the protoplasm as a whole in a simple Amœba by means of such a spreading out at the anterior end, and all the less since we have found that the theory necessarily demands an exactly opposite current.

Against the admissibility of the explanation which I have put forth, Berthold finds an objection of great moment in the fact which he claims to have established, namely, that in the water surrounding an Amœba, after mixing carmine with it, no system of currents was to be observed at its anterior end such as is required by the explanation. With reference to this point I may remark that I regard the observation of such currents as very difficult, when the extent, for the most part very slight, of the currents of Amœbæ is taken into consideration, and that, therefore, in the meanwhile, I still regard their presence as possible. Unfortunately I have hitherto delayed inquiring into this question myself.[1] Yet I may refer to an observation which shows that the apparent absence of currents in the surrounding water is not decisive with regard to the correctness of the explanation. In small drops of oil, which were yet considerably larger than most Amœbæ, and which crept and moved about very energetically under the influence of surface tension, I could not demonstrate the existence of currents of any kind in the surrounding water, with which Indian ink had been mixed. This observation astonished me very much at the time, since such currents are always very distinct and strong in the vicinity of large oil-drops. Hence, without attempting to explain the reasons of this deviation from the rule, it seems to me of sufficient importance to diminish the difficulties raised by Berthold's objections.

If, however, we take our stand upon Berthold's hypothesis, the complete absence of any phenomena of streaming in the surrounding water would be just as strong evidence against his explanation as against that put forward here. Since Berthold's hypothesis is founded exclusively upon the alterations of surface tension which are caused by

[1] See Appendix at the end of the next section (pp. 317-319 *infra*).

chemical changes at the anterior end of the body of an Amœba, extension-currents must necessarily arise, as I have pointed out already, at the surface of the body of an Amœba, in connection with these changes. Hence, if Berthold denies generally the existence of any currents in the water surrounding an Amœba, this is, in my opinion, just as strong evidence against his own theory as against the one brought forward here. I hardly think he could be of opinion that the chemical changes in the protoplasm only extend to the under side of an Amœba, *i.e.* to its adherent surface, since he regards the entire hyaline protoplasm of the anterior end as that which is chemically changed. In any case, however, this change must extend to the edge of the adhering surface, and here come into contact with the surrounding medium, so that differences of surface-tension would necessarily exist in this region, and cause currents to be set up. But, as I have already explained in discussing the drops that retreat from alcohol, I consider it as on the whole impossible that forward movements can be brought about by such a change in the adhesion without accompanying differences of tension in the free surface of the drop. On the contrary, such a change would only give rise to a single alteration in the shape of the drop.

On the ground of the foregoing explanations, therefore, I must regard Berthold's explanation of amœboid movement as unsuitable, at least in so far as it has been possible for me to rightly understand his train of argument.

It seemed to me, however, of interest to test more accurately, by means of experiment, the relations of the system of currents in the drops of water, which are theoretically postulated as necessary during their retreating movements. It was thereby proved, after some unsuccessful experiments, that the phenomena take in the main just the course that was assumed above. In order to convince oneself of this fact, it is best to proceed by placing drops of water on a glass plate cleaned as well as possible, and then causing a capillary tube, of not too great fineness, or a glass rod, with ether, to approach their margin. If some ivory black has been mixed with the drops, it can be observed

even with the naked eye, or with a lens of low power, that on the approach of the ether just the same phenomena of streaming are set up in the drop which we formerly described in detail for oil-drops, the tension of which had been lowered at one spot by soap or something of the sort. The currents are very violent, so that the eddies (A) arising on each side are shown with great distinctness. When the drops flee from before the ether, their edge, which is turned towards

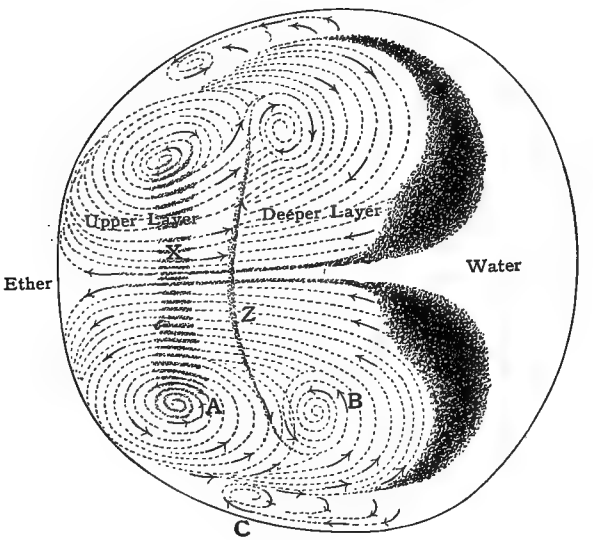

Fig. 19.

the ether, is at first rather straight, and later even concave, and with this change in the shape of the edge changes in the currents are also apparent, which modify the original appearances to some extent. An actual movement away from the ether arises most easily when the drops are very shallow; deeper drops show the streamings and the shrinking back of the edge turned towards the ether most excellently, but the movement not so well.

If a more exact knowledge of the phenomena of streaming within the drops be required, it is necessary to study the relations existing in smaller drops under the microscope.

Since the currents, as has been said, go on exceedingly energetically, the appearances to be observed in such drops with slight magnification are particularly beautiful, and very suitable to complete our knowledge gained in another way with regard to streamings in oil-drops. The appearance presented by an energetically streaming drop is in general that represented in the preceding Fig. 19. One recognises in it at once the two eddies (A) which we have already found before, but in addition to these some secondary eddies may also be observed (B and C), the positions of which, and their relations to the principal eddies, can be plainly made out from the figure, so that I will not enter into a further explanation of them here. One phenomenon, however, of particular interest, appears between the two principal eddies, and is especially distinct when the latter are placed rather far apart in the direction of their breadth. It can then be remarked that a dark and rather broad band is stretched between them, which depends on the fact that in the interval between the two eddies another eddy corresponding to the thick band extends through the whole drop. Since this eddy is seen from

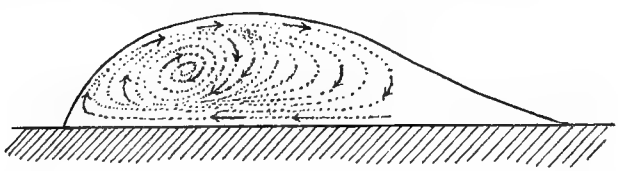

Fig. 20.

above, it necessarily appears as a dark streak. This phenomenon is explained by the fact that in the whole breadth of the drop the relations are essentially the same as are seen on the two sides as it were in longitudinal section. A median longitudinal section of the drop, of which a direct view unfortunately is not to be obtained, would therefore show something of the appearance represented in Fig. 20. The sum of all the eddies which extend transversely through the drop hence appears as the dark band. Since there is a condition of relative quiescence in the interior of these

eddies, colouring particles usually collect in them, especially the coarser ones, which form a dark streak in the middle of the band; sometimes also these particles may be distributed at quite regular intervals in the dark band. The peculiar transverse line (Z) between the two eddies, which is in continuation laterally with the secondary eddies (B), can also be explained at once from the nature of the streaming in the median longitudinal section. As we found in the drops of paraffin oil, so also in the streaming drops of water the black mixed with them for the most part gradually collects in the posterior quiescent region, and from here enters the forward current again.

Now if the ether be so closely approximated to the drop as to cause its edge to shrink away, so that it finally flees from it—which cannot be done so well with drops of water mixed with black as with pure drops—the following process is in the main exhibited. By the edge shrinking back and becoming straighter and therefore broader, the median forward current increases in breadth, and the two eddies (A) become quite separated from one another. It then appears as if there was only one very violent eddy in motion at the edge, passing above from the margin to the opposite edge of the drop, but soon descending downwards and rushing towards the edge in proximity to the ether again. This is the vortex current, which we have already become acquainted with in the form of the dark transverse band. Only at the most external portions of the edge of the drop are the eddy (A) and the lateral back currents into the forward current still to be seen. It can be easily explained how these currents owe their origin to the fact that the ether now exerts its action violently upon a broader portion of the margin.

I will take this opportunity of remarking that, in the well-known experiment, so frequently performed, of approximating a drop of ether to the surface of some water, whereby a noticeable depression is produced in it under the ether, or if the layer of water be very shallow, the bottom of the vessel is even laid bare, the same vortex movements can easily be demonstrated if ivory black be

mixed with the water. If the layer of water is fairly shallow, but not so much so as to be broken through by the depression, and if the black has already collected to some extent upon the bottom, it may be observed, on approximating a rod dipped in ether, that the colour is completely removed from a ring-like zone corresponding to the periphery of the rod, and at its inner edge is densely massed in a black ring immediately under the rod. That is to say, by the vortex current at the bottom of the vessel returning towards the rod the colouring matter is all carried inwards, and remains lying at the spot where this vortex current ascends upwards again.

As to the explanation of the retreating movement, however, it results from these observations that the retreat must depend upon the back currents in the drop being in excess of the forward currents; but this can only be due to the adhesion of the drop, which offers a hindrance to the forward current which goes on in the deeper layer. As a proof of this fact there is also the observation, which has already been mentioned above, that the retreating movement is especially pronounced when the drops are very shallow. In any case, however, all these observations confirm the view that the movements of Amœbæ cannot take place in this way.

Berthold, however, is willing to admit, as has been already remarked above, that pseudopodia are occasionally sent out by forces acting from within, somewhat in the same manner as was supposed by the older observers, namely, by contraction of the hinder part of the body of the Amœbæ (p. 102). Contractions of this kind may be produced by changes in the condition of imbibition of the protoplasm (pp. 102 and 105). Finally, Berthold adds to the three hypotheses already mentioned, concerning the causes of protoplasmic movements, yet a fourth, in order to explain the origin of fine filamentous pseudopodia, which rise up free into their surroundings; for which no one of the three detailed is sufficient. Since Berthold's ideas of these processes can scarcely be described briefly, on account of the uncertainty of the forces brought into the problem, I refer the reader to his memoir, and will confine my

remarks to a few words upon this, in my opinion, quite untenable hypothesis. The forces which Berthold draws upon to explain the development of the fine pseudopodia, are of a chemical nature, namely, those which are supposed to come into play during the solution of a solid body, as exerting attractions between its molecules and those of the solvent medium. Forces of this kind are supposed to exert their activity between the surrounding medium and the particles of the protoplasmic body, and, upon the supposition that its surface tension is very low, to be sufficient to spin it out into fine pseudopodia. As can easily be seen, this hypothesis recalls to some extent that of Mensbrugghe described earlier (p. 65) with respect to the cause of the pseudopodium-like outgrowths of oil-drops. I think, however, that Berthold's hypothesis is built upon much too uncertain a basis, *i.e.* takes forces into account which are altogether too hypothetical and uncontrollable for us to take them earnestly into consideration. If Berthold's interpretation were correct, one might well expect that pseudopodium-like processes would be seen to radiate out from a thick, coloured gum solution, upon which water was poured, which is by no means the case.

In any case, however, it would seem in the highest degree improbable that protoplasmic movements should have four different causes; it may rather be postulated with some certainty that a common cause must lie at the root of them all, even if it is not yet possible at the present time to refer all the modifications to this cause.

In 1888 Quincke developed, in connection with his observations upon superficial extension-currents as the result of local diminution of surface tension, certain views upon the explanation of the protoplasmic streams in plant cells, etc., which agree in the main with the first hypothesis given by Berthold. In its details, however, Quincke's explanation seems to me untenable, since he has not sufficiently taken into consideration the state of things that actually exists in the vegetable cell. Quincke has the following idea of the structure of a plant cell. The protoplasmic lining which occurs under the cell membrane consists of

(1) an external "protoplasmic utricle," (2) the hyaline cuticular layer (*Hautschicht*), and (3) the granular protoplasm. The so-called protoplasmic utricle is supposed to be an immeasurably thin, fluid oil membrane, for the most part invisible. Without Quincke's making any definite statement with regard to the fact, it may be assumed that he was led to suppose the existence of a so-called protoplasmic utricle by the protoplasmic membrane of Pfeffer and others. Now the streamings are supposed to arise from the formation of a saponaceous compound (the so-called albumen soap) produced by the action of the albumen of the cuticular layer upon the fatty acid set free, by the action of oxygen, from the oil of the protoplasmic utricle. This soap produces local diminutions of surface tension on the inner side of the protoplasmic utricle, and thus calls forth extension-currents. Let us pause for a moment over this fundamental conception with regard to the streamings which Quincke has put forth. I do not think that it appears admissible, and in the first place, chiefly from the following reasons. According to Quincke's view the region in which the streamings take their origin is situated close under the cell membrane, namely, at the boundary between the immeasurably fine oily utricle and the cuticular layer. Now it is known quite for certain, and has often been demonstrated, that the most external layer of protoplasm, which touches upon the cell membrane, is beyond doubt quiescent in a large series of cases, and in fact that, as in *Chara*, for example, the entire chlorophyll-bearing cortical layer of the protoplasm is in a state of rest. A similar condition is also shown by the Ciliata with cyclosis of the endoplasm, where in the same way the cortical protoplasm and the ectoplasm are in a state of rest, while the internal protoplasm streams. In these cases it is impossible that the seat of the movement should be found at the internal surface of such an external utricle of oil, but there is every reason, on the other hand, for believing that, as has already been stated above in connection with the views of Nägeli, Schwendener, and Berthold, the cause of movement has its seat at the limiting surface between the protoplasm and the cell-sap. In the cyclosis of Infusoria,

in which a cell-sap is wanting, special relations are in any case presented which cannot be gone into until later on. In addition to this difficulty, which, as it seems to me, alone suffices to prove the untenability of Quincke's explanation, there is yet a further one, namely, that since the cuticular layer is everywhere in close contact with the oily utricle, it does not in my opinion seem very clear why local extensions of the so-called albumen soap should arise, since the formation of albumen soap should go on along the whole surface of contact between the cuticular layer, which is everywhere albuminous, and the oily utricle.[1] Hence these suppositions scarcely seem to supply the conditions for the appearance of definite and often quite one-sided streaming movements.

Since also the principles from which Quincke starts in his explanation do not seem to me to be adequate, it would be unnecessary at the outset to discuss more accurately the explanations which he gives for special cases, such as circulatory streaming, development of pseudopodia, etc.

(*j*) *My own View of the Explanation of amœboid Movement*

At the commencement of this chapter it was pointed out that I should consider the possibility of an explanation, which my conception of protoplasm furnishes in the case of the simpler phenomena of movement at least, as a confirmation of the correctness of the interpretation which has been attempted of its structural relations.

In passing on to attack this question more closely, I must remark at the outset that in spite of all my efforts such an explanation seems at present feasible only for amœboid movement in the strict sense, while other modifications of it, especially the formation of the fine pseudopodia of numerous Sarkodina, obtain no explanation.

The movement of simple Amœbæ, such as *A. guttula*, *limax*, and *blattæ*, and *Pelomyxa*, is so exceedingly similar

[1] It could only be assumed in some way that oxidation, and hence the appearance of free fatty acid, took place locally in the oily membrane.

to the streaming drops of oil-lather described before—in fact so entirely their exact counterpart in all important points—that I am completely convinced of the agreement of the forces at work in the two instances. In these Amœbæ also we find an axial stream which passes through the axis towards the progressing anterior end, there bends round on each side, though certainly in other directions also,[1] flows on the exterior of the body for usually a relatively short distance backwards, and then comes to rest. The axial stream draws protoplasm to itself from all sides at the posterior end, and in the same measure that this protoplasm from behind passes into the current, the quiescent lateral protoplasm is carried farther backwards, and then by degrees passes into the axial stream again. The single essential difference, which is usually shown between such Amœbæ and streaming drops of oil-foam, is this, that the extension-current of the anterior end for the most part only extends, as has been said, a comparatively short distance backwards, and that it comes to rest relatively quickly. In the drops of oil-froth, however, the extent of the current in question also depends, on the one hand, upon the intensity of the forces at work, on the other hand, upon the viscidity of the oil. It can often be observed that feeble extension-currents are only continued a little way towards the hinder end, so that the conditions become quite similar to those of the Amœbæ described. I am hence convinced that the explanation of the phenomena of streaming in these Amœbæ must be the same as that we put forth for the froth-drops.

If we wish to apply the explanation given for foam-drops to the phenomena of movement in Amœbæ, it will be necessary, in the first place, to examine into the nature of protoplasmic substance a little. The aggregate condition has already been briefly considered above, from which it resulted that both the framework and the intervening substance must

[1] It is easy to convince oneself in Pelomyxa of the fact that the back current at the progressing anterior end, or at the tip of a pseudopodium, as the case may be, goes on over the entire free surface, and not merely at the two sides, where it usually comes into view. With a suitable focus it can always be plainly seen that the back current stretches over the whole free surface.

be fluid. It is clear, as well from all the observations which we collected upon this point as from our theoretical conception and explanation of protoplasmic structure, that the intervening substance must be interpreted as a watery solution. With this interpretation Reinke's investigations, upon the enchylema that may be squeezed out from *Æthalium septicum*, are completely in harmony. With reference to the framework substance our view requires, in the first place, that it should be a fluid substance insoluble in water. It is clear that this substance contains albuminoid bodies. From the most recent observations it becomes more and more probable that the principal component of the framework substance is an albumen compound related to the nucleins, the so-called *plastin*. Reinke has interpreted the plastin, first clearly recognised by him, in *Æthalium septicum*, and forming according to his calculation 27·4 per cent of the protoplasm when dried in air, as a combination of albumen and nuclein, possibly further accompanied by a number of molecules of a fatty acid belonging to the stearic or oleic acid series. In any case it results from these and numerous micro-chemical observations of more recent times (compare especially the works of E. Zacharias and Fr. Schwarz) that the foundation of the framework substance is not an albuminous body in the ordinary sense. All that we know of the possible nature of this substance is indeed very little, but nevertheless enough for it to be not inconceivable to us that it is insoluble in water, a fact still more intelligible if Reinke's supposition, as to molecules of fatty acid entering into its constitution, receive further confirmation. A series of reflections, based upon an entirely different foundation from Reinke's, led me to suppose, quite independently of his speculation, which I did not know of till later, that the chemical basis of the framework substance must be formed by a body which has arisen from a combination of albuminoid and fatty acid molecules. Since, as has been said, it appears quite possible for such a body to be insoluble in water, I hold the assumption of an oily membrane or something of the sort, which would protect it against the action of water, to be unnecessary; yet it

must be admitted, on the other hand, that, with the supposition of such a chemical composition for the substance of the framework, the appearance of an oil membrane as the result of the decomposing action of water is rendered possible.

If the protoplasmic framework is composed of a body of this kind, it is quite intelligible that local differences in surface tension must produce phenomena of movement similar to those which have been observed in the drops of oil-froth. It is only a question whether the enchylema also seems suited to play the part which pertains to it. With reference to this point it is now specially important that, according to the observations of Reinke and Rodewald, the enchylema has an alkaline reaction, which is observable in the fluid squeezed out. That protoplasm as such has an alkaline reaction, has been noted by a series of observers, among whom I specially mention Fr. Schwarz. Reinke and Rodewald think they may conclude that the alkalinity of the enchylema is produced by NH_3 or $NH_4NH_2CO_2$. Schwarz disputes this view, and attempts to show that compounds of alkalies with protein bodies probably cause this phenomenon. The possibility that saponaceous compounds may be the cause of the reaction has not been hitherto taken into consideration. Now whether the alkaline reaction of the enchylema depends upon the one or the other of these causes, the mere fact that there is such a reaction, as well as that fats are probably never wanting in protoplasm, and that it is not, on the other hand, improbable that fatty acids enter into the composition of the framework substance, render it very possible indeed that the enchylema must also contain saponaceous compounds in solution; that is to say, that it is perfectly capable of playing the part which pertains to it, according to our conception of the processes of movement. Since it may seem very premature to speculate upon so obscure a subject as the connection of the chemical processes in protoplasm, I content myself with these remarks.

The explanation of the processes of movement in Amœbæ is to be found, therefore, to my mind, in corre-

spondence with the interpretation of the phenomena of streaming movements in the drops of foam, in the fact that, by the bursting of some of the superficial alveoli, enchylema is poured out upon the free surface of the protoplasmic body, where it produces a local diminution of surface tension, and in this way sets up an extension centre together with forward movement.[1] In this way are explained not only simple amœboid movements, from which we started, but also more complicated movements and changes of form by means of finger-shaped pseudopodia. The formation of such pseudopodia takes place with phenomena of streaming movement corresponding perfectly to those which go on throughout the body of an Amœba which streams in a simple manner; in these pseudopodia it is therefore merely a matter of local extension-currents, reaching over a short distance only.

In Amœbæ, however, an additional circumstance seems to come into play, as has already been pointed out above, which has the effect of producing a limitation in the extension-currents. In the formation of a finger-shaped pseudopodium of *Amœba proteus* (Fig. 21) it can be seen that the current which traverses the axis of the pseudopodium and flows away on all sides from its tip, comes to rest at a very short distance behind the tip—a circumstance which in any case is extremely favourable to the rapid

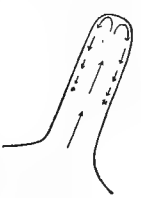

Fig. 21.

[1] A. G. Bourne has pointed out, in an investigation that has recently appeared upon the newly-discovered *Pelomyxa viridis*, that the alveoli or "vesicles," observed by him in the protoplasm of this Rhizopod, do not burst in the movement, or rather in the development of pseudopodia; he thinks that this observation opposes my view as to the causes of amœboid movements. In answer to this I must state explicitly that the "vesicles" described by Bourne certainly have nothing whatever to do with the true alveoli of the protoplasm. They are spherical structures filled with green contents, and their considerable size must alone exclude a comparison with the true alveoli of protoplasm. Of the true, and very much finer protoplasmic structure, Bourne has observed nothing. What these green "vesicles" really were I will not here further inquire, though in spite of assertions to the contrary made by the discoverer of *Pelomyxa viridis*, it is difficult, if all the other known relations are taken into account, to suppress the notion that they are nothing more or less than Zoochlorellæ.

outgrowth of the pseudopodium, in contradistinction to the relations that obtain in the drops of foam, since the protoplasm that has come to rest is heaped up and the pseudopodium grows in this way. These relations, as well as those of the simply streaming Amœbæ, evidently seem to indicate that it is only at the anterior end of the Amœba, or at the extremities of the pseudopodia, as the case may be, that sufficient fluidity exists for the extension of the current, and that farther back, on the contrary, in all probability by the action of the surrounding medium, the surface soon becomes more viscid, and the current hence dies down rapidly. That the surface of the body of the Amœba, and in particular the pellicle, is of a membranous nature, has indeed often been pointed out, and follows with tolerable certainty from other peculiarities.

In this respect the state of things at the posterior end of many Amœbæ must be taken into special consideration. It is notorious that this end frequently bears a tuft-like bundle of fine processes, which have often been compared to pseudopodia. This tuft, however, certainly bears no close relation to real pseudopodia, but is a phenomenon which almost regularly accompanies the retraction of pseudopodia, as can often be very well demonstrated in *A. proteus*, for instance. In an Amœba which simply streams along, in which the hinder end is in fact in a continual state of retraction, so to speak, the tuft must naturally attain a special development in this region. If the retraction of a pseudopodium be followed, it may be noticed that it gradually becomes covered with short papillar processes, which *pari passu* with the diminution of the pseudopodium become narrowed into fine processes, or even become, in part, split up into such, so that finally a tuft of fine processes remains in the place of the pseudopodium. These processes then fuse into a small eminence, which gradually becomes flattened down and passes into the general protoplasmic mass of the body. If numerous pseudopodia are drawn in at the same time, a considerable portion of the surface of the Amœba may be covered with such tufts.

The most probable explanation of this phenomenon which,

as has been said, so especially characterises the posterior end, is, judging from the course it takes, somewhat as follows. As has been remarked above, it is very probable that the surface of the body of the Amœba is formed by a viscid membrane-like layer. The backward flow of the pseudopodia, like the gradual retraction of the hinder end of the Amœbæ that moves forwards in a simple manner, depends, in my opinion, only upon the cessation of the forward current, and the flowing back of the protoplasm towards other directions. During this process the pseudopodium or the hinder end diminishes continually in size, and meanwhile the viscid external layer cannot flow together rapidly enough to keep pace with this diminution, in consequence of which it is thrown into folds, which appear as papillose processes. The whole phenomenon gives just the appearance of a viscid, membrane-like layer, which shrinks into folds on account of the gradual emptying of its contents. With continued emptying of the contents these folds become more numerous and fine, so that the completely shrunken layer is finally attached in the form of a tuft-like bundle of fine processes. These processes or folds then become closely apposed, and finally stick together. Meanwhile they are removed from the action of the external medium, which, as we supposed, is the cause of the cuticle-like toughness of the superficial layer; this removal, as well as the influence of the interior of the Amœba, which now makes itself felt upon the tuft, has the effect of gradually making it become fluid; and the folds or processes fuse in the above-described manner, whereupon the product of the fusion and the rest of the protoplasm finally flow together.

That the origin of the tuft is really due to shrinkage of the membrane-like external layer is also probable from the fact that by treating *Amœba proteus* with fairly concentrated NaCl solution (4 per cent), the same papillar processes can at once be produced over the whole surface, accompanied by considerable shrinkage of the Amœba, and in this case the processes certainly arise by folding of the external layer, as a result of a decrease in the volume of its contents. With 0·02 per cent caustic potash I also saw

exactly similar appearances arise over the entire surface. Moreover, it has been known for a long time back that the formation of fine processes can also be effected by salt solution over the whole surface of certain Amœbæ; processes, that is to say, such as usually compose the posterior tuft. The following observation, which I made casually upon *Amœba proteus*, is also evidence for the correctness of the explanation here attempted of the formation of the tuft. A specimen, which had been treated for a long time with 0·05 per cent solution of caustic potash, suddenly burst at a spot, as one frequently observes. Thereupon the internal protoplasm flowed out, and the membrane-like envelope shrank up together very much, at the same time assuming the bristly appearance of the tuft over its whole extent. As has been said, this observation seems to prove for certain not only the existence of the tough membrane-like enveloping layer, but also the great probability of my explanation as to the formation of those fine processes or folds. The bursting, here described, of the Amœba, together with the flowing out of the relatively fluid internal protoplasm, may frequently be observed under the action of various reagents, and also under a long-continued action of the constant current; on the other hand, a shrinking of the enveloping layer in its whole extent, which has just been described, I only saw once in this manner.

Hence if we are constrained to admit the existence of a tough, membranous layer on the surface of numerous Amœbæ, the question is then raised, in what way this layer becomes liquefied at the anterior end, or rather at the spots where the pseudopodia develop; for there can be no doubt that it must be liquefied. In this process may be traced a result of external local stimuli which concern the Amœba. That such stimuli must in the last instance be the cause of the movements, and of the development of pseudopodia, is beyond doubt. Nevertheless I do not think that the liquefaction is in direct connection with this fact, but that the outflow of enchylema, which is produced by the bursting of some of the alveoli, is the primary cause of the liquefaction of the superficial layer. This is, in fact,

quite natural, inasmuch as the internal protoplasm, which is subject to the action of the enchylema, is quite fluid, for which reason it does not seem an unwarrantable assumption that the viscid external layer would also become liquefied again if it was temporarily removed from the influence of the water by a spreading out of enchylema on its outer surface.

If, as I think, we have found in this interpretation of amœboid movement an explanation which is both very probable and harmonises well with the observations upon the froth-drops, it should nevertheless not be ignored that the same explanation cannot be applied off-hand with good results to fine reticulose pseudopodia. It is, of course, quite conceivable that here also thicker pseudopodia may possibly develop in the way described, but on the other hand I willingly admit that the explanation of filamentous pseudopodia, frequently of excessive fineness, cannot be reached in this way. It is sufficiently obvious, from the description which has been given before, that in these pseudopodia other and special relations come into the problem, which are not as yet satisfactorily cleared up. I refer in this respect more especially to the behaviour of the long filamentous pseudopodia during their retraction. It is well known that during this process they for the most part become suddenly relaxed in a peculiar manner, and even occasionally assume a zigzag or spiral form. Although we are not able to explain this peculiarity off-hand, it may be taken, as has been said, as a proof of the fact that there are here other peculiar conditions lying at the root of the matter.

It has already been shown above that Berthold's attempt at an explanation of these fine pseudopodia, which are also frequently raised up free in the surrounding medium, is in no way satisfactory. Just as little satisfactory is the explanation given by Quincke. The latter seeks to refer the origin of pseudopodium-like bridges and threads of protoplasm, such as so frequently traverse the cell sap of plant cells, to the formation of firm threads of albumen at the boundary between his protoplasmic utricle

(oil membrane) and the cuticular layer. These firm threads of albumen are supposed, on their part, to arise by the action of oxygen upon the dissolved albumen, which, as Quincke has shown in the case of egg albumen, forms a firm membrane-like envelope under the action of this gas. The firm threads of albumen which have arisen in this manner are supposed to be torn loose by the streaming movements and to be carried into the interior of the cell, where they form an internal framework traversing the cell sap. As they are torn loose the filaments take with them an envelope of oil from the oil membrane. In consequence the protoplasmic masses are then free to move upon these oil-covered filaments by means of extension-currents, in the same way as the protoplasm of the wall moves upon the external oil membrane. In the same manner Quincke thinks the fine pseudopodia of Sarcodina may also be explained, since he remarks (p. 641): "The pseudopodia appear to be just such thin filaments of albumen covered with oil, along which solid albuminous granules are carried up and down by periodic extension movements, just as in the interior of the plant cell." Although there is, perhaps, much to be said for this conception in the case of the explanation of the so-called granular movement on the pseudopodia, yet it in no way explains the formation of the fine pseudopodia themselves. For both their gradual development and the formation of bridges and filaments of protoplasm in the cell sap of plants, which, according to the statements of many trustworthy observers, frequently develop just like the pseudopodia of Sarcodina, make it impossible to refer their origin to the breaking loose of solid threads of albumen, which the streaming movements displace as pseudopodia.

As far as Quincke's interpretation, which we have just quoted, of the pseudopodia themselves is concerned, it may perhaps be justifiable to a certain extent, inasmuch as we have already seen that the study of the pseudopodia had long ago led M. Schultze, and again myself also recently, to the supposition that possibly a firm thread may form the axis of the pseudopodium—a supposition to which their analogy with the state of things in the Heliozoa adds

weight. It is well known that R. Hertwig succeeded in rendering probable the existence of such an axial thread for some Radiolaria also.

As has been remarked, however, I regard it as still premature at present to think of a final explanation for the formation of the fine pseudopodia, for we cannot, unfortunately, say even for a moment that we have obtained a satisfactory conception of the relations between their structure and movement, which must, however, be indispensably the preliminary stage of any explanation. Hence, however convinced I may be of the fact that to the explanation attempted by me of the protoplasmic movements of *Amœbæ*, etc., there attaches a further and essential significance for the processes of movement exhibited by protoplasm generally, I am equally convinced, on the other hand, that it would be very difficult to work out the explanation of the numerous special cases which exist on the basis of that principle at the present time, or at any rate that their explanation could only be achieved by the help of numerous subordinate hypotheses, which would considerably diminish the probability of the explanation. I therefore consider it not worth while to pursue this uncertain path with earnestness, but hope that with a renewed study of the processes of movement, which we shall probably not have to await very long, in connection with the ideas put forward here as to the probable causes of those processes, more sure foundations of fact may be discovered for the solution of these questions.

On the Currents in the Water surrounding Amœbæ, etc.[1]

I have already expressed my regret that I did not earlier test the important question as to the existence of currents in the water surrounding a moving *Amœba*. Having recently had an opportunity in an object so excellent for this purpose as *Pelomyxa*, I must say that the ordinary small *Amœbæ* offer very little occasion for the solution of this question. Now although during frequent observation of the processes of movement in *Pelomyxa* I invariably was astonished by the perfectly complete agreement of its movements, even in detail,

[1] An addition made by the author in April 1892.

with those of the drops of oil-lather, I was necessarily the more astounded when it was shown by observation of the *Pelomyxa* creeping in water, with which Indian ink or ivory black had been mixed, that currents, directed in the same sense as the superficial protoplasmic streaming movements, do not, as a matter of fact, exist in the surrounding water. If the streaming movements of the *Pelomyxa* are not very powerful, it really does appear as if no currents at all went on in the surrounding water, as stated by Berthold. If, however, one observes closely the anterior end of a *Pelomyxa* streaming forward very energetically, or a pseudopodium which is developing powerfully, it can be made out that currents do exist in the surrounding water, but, strange to say, currents which run in exactly the opposite direction to what was expected, and which do not pass along in the same sense as the superficial back current at the anterior end, but in a reverse direction, that is to say, they rush towards the anterior end, *i.e.* towards the supposed centre of extension. Considering the importance of the matter, I have not left it to be judged by the eye, which might easily be deceived, but have definitely traced the existence of these currents with the ocular micrometer. I will take this opportunity to state again, that in streaming drops of oil-foam of larger size I have frequently convinced myself of the presence of currents running in the same sense.

I do not underrate the consequences of these results. They necessitate the admission that the explanation of amœboid movement brought forward by me above is inadequate, *i.e.* that in it there must at least be one discordant point, in which *Amœbæ* behave differently from the drops of oil-foam. I have already remarked that the study of the movements of *Pelomyxa* shows in other respects so complete a similarity to those of the oil-foam drops—apart from the divergence that has been pointed out—that I cannot doubt as to the identity of the forces in operation in both cases. Unfortunately I am not in a position to give an explanation of this difference off-hand. In any case all that I can suppose is somewhat as follows. Perhaps the behaviour which we have described in the *Pelomyxa* points to the fact that the surface of the protoplasmic body is enveloped by an extremely fine, viscid layer of a chemically different nature, such as Quincke has assumed in the oil membrane, and that further the forces of tension which are at work make their appearance, as he supposes, at the limiting surface between this membrane and the protoplasm below. Under these conditions it may perhaps be imagined that the backward current which is necessarily present may go on in the internal zone of this fine

membrane, bordering on the protoplasm, while in its external zone, as is equally necessary, a stream runs forward to the anterior end, which is alone that which makes itself felt in the surrounding water, and thus causes the current that is so strangely reversed in the latter. It is a question whether we are justified in assuming double currents, running one upon the other, in a membrane of such extreme tenuity as that postulated must be. In this respect I would like just to refer to the following observation, which I made as far back as the seventies on the occasion of studies upon cell division, when I was induced to occupy myself a good deal with phenomena of surface tension. In the extremely thin membrane of large soap-bubbles it is possible to produce very violent streaming movements by approximating volatile substances, such as NH_3, alcohol, etc., *i.e.* by disturbance of the tension, without the membrane bursting. In this process, in spite of the thinness of the membrane, currents must pass one over the other, afferent and efferent currents, otherwise the thin membrane would burst at once. If, however, it was a question of an oil membrane, such as Quincke assumes, it would not be possible at all for it to burst under the given conditions, since its tension at the surface bounding it towards the surrounding water must in any case be considerably greater than that at the surface which limits it towards the protoplasm, for which reason it could not be made to burst from this side. I must therefore regard the double currents in a thin fluid membrane of this kind as being quite within the bounds of possibility.

For the rest, some advance may probably be made at this state of the question by means of suitable experiments.

(*k*) *Independent Movements of Granules*

Certain points in the problem of protoplasmic movements must, however, I think, be briefly touched upon now. Amongst them the question of the relations of the so-called protoplasmic granules to the streaming movements seems to me one of the most fundamental. It is notorious that the movements of protoplasm have frequently been estimated only by the movements of these granules which have served to a certain extent as indices of the streaming movements of the protoplasmic ground substance. In keeping with this there exists an almost universally occurring

idea that the granules possess no power of movement of their own, but are only carried about by the streaming movements of the protoplasm, upon or in which they are lodged. Berthold also represents this view, which has been current since M. Schultze.

When I was following out the phenomena of movement exhibited by these granules, as they can be plainly observed in plant cells (*Tradescantia* hairs, for example), I was involuntarily forced to the idea that their movements could not be in any way passive, in the sense that they were simply carried along by the streams of protoplasm as suspended corpuscles, but that they must, in a certain sense, be of an active nature, *i.e.* that the cause of movement must reside near or within the granules themselves. Although this idea was always aroused, as has been remarked, by the consideration of vegetable cells and Sarcodina, I could not come to any decision upon this question in objects of this kind, which at the same time exhibited lively protoplasmic movements. Only by the study of a peculiarly favourable object, which recently came into my hands, was a sure proof at last obtained that such an automatic movement of the granules must, as a matter of fact, take place. This object is a large diatom of the genus *Surirella*. At the limiting surface of its protoplasm turned towards the cell sap there are numerous granules in a state of incessant movement to and fro in the most various directions, which have already been mentioned before as chromatin-like granules (p. 91). It seems a point of very special interest that these motile protoplasmic granules are only to be met with in this organism at the surface of the protoplasm by which the latter is limited towards the cell sap, while I was not successful in finding corresponding granules in the interior of the protoplasm. It is also shown beyond a doubt, by tracing their movements more accurately, that they glide along the limiting surface of the protoplasm, and partly, at any rate, project from the protoplasm into the cell sap. Now since, as I have already briefly described in another place (1891), the protoplasm of this diatom is itself in a state of relative quiescence, as can

be distinctly demonstrated by the stability of its reticular and radiating structures, it follows that the granules must possess a movement of their own, and that it is impossible to suppose that they are being carried along by streams of the protoplasm.

This conception of granular movement is not so new as it might appear from the widespread belief in the contrary view. Nägeli at any rate has described, as far back as 1855, a granular movement quite corresponding to that here described on the inner surface of the primordial utricle of *Desmidiaceæ* (*Closterium* in particular); he has termed it "sliding movement" (*Glitschbewegung*). The movement also of the granules on the inner surface of the protoplasm in *Achlya*, where the cell sap is traversed by protoplasmic filaments, as frequently occurs also in *Surirella*, is regarded by Nägeli in just the same manner. This so-called sliding movement has later been comprised as a subordinate case of general protoplasmic movement (so also Berthold, 1886, for instance), in which the streaming movements of the protoplasm are very feeble and irregular. Since, at an earlier date, when protoplasmic structures had not been accurately traced, it was impossible to decide with certainty whether the movement of the granules was caused by the general streaming movements of the protoplasm or not, there was much to be said for the view, which subordinated the particular case to the more general phenomenon. Since, however, we are now able to convince ourselves, as has been said, that the protoplasm as such does not take any share in the movements of the granules in *Surirella* by means of any noticeable streaming movements or displacements, this explanation falls to the ground. On the ground of his observations upon the so-called sliding movements, Nägeli, and with him Schwendener (1865), held fast to the view that the protoplasmic granules must also possess an automatic power of movement in circulation and rotation, and that the seat of the motor forces was to be looked for in the granules themselves. Originally, in 1855, Nägeli thought of hydro-electric forces, but later (1865) he preferred to assume that the so-called sliding movements, and hence, of course, the cause of the

automatic movements of the granules in general, was a molecular movement modified by adherence to the protoplasm.

Velten (1876) held that it was quite uncertain whether the granules moved actively or passively, and has dealt with this question thoroughly in his memoir "Activ oder Passiv" (*Œsterreich. botan. Zeitung*, 1876, No. 3).

Although by reason of my own observations I must rank myself altogether on the side of Nägeli's view of the automatic movement of the granules, in so far as they are situated on the inner or the outer surface, as the case may be, which limits the protoplasm, I am nevertheless unable to share his opinion concerning the alleged cause of their movement. I incline rather to the belief that the view expressed by Quincke with regard to this cause, so far as it concerns the independent movement of the granules, comes the nearest to the truth. The granules, situated upon the limiting surface of two liquids—a viscid one, the protoplasm, and a more fluid one, the cell sap—move in all probability from the same cause from which pieces of camphor move to and fro continually on the surface of water.[1] The cause in question is that the granules continually effect a change in the surface tension at the limiting surface of the two liquids in their vicinity, as a result of which they of course move towards the direction in which the surface tension is heightened. With this change of tension feeble currents on the outermost superficial layer of the two liquids are of course connected, which, however, being very transitory and feeble, only penetrate a small distance inwards, and therefore do not call forth actual streaming movements in the protoplasm. I am of opinion that the assumption of a universal occurrence of such automatic granular movements would set aside many difficulties which have hitherto been raised in the explanation of protoplasmic movement. The sudden stoppage of these movements, their frequent reversal, the movement of granules on the finest filaments of protoplasm in exactly opposite directions, and finally, the frequent phenomenon of

[1] Compare for these and numerous allied phenomena, van der Mensbrugghe, 1869, more especially.

granules overtaking one another on very minute filaments—all these are phenomena which, as I believe, can be understood much more easily on the assumption of such an automatic power of movement, than on the hitherto current supposition that the movement of the granules is due solely to the general streaming movement of the protoplasm.

(*l*) *Causes of Internal Displacements in the Alveolar Protoplasm*

A further problem would be whether, on the same principle, corresponding granules in the interior of the protoplasm could also carry on movements. I do not consider this possibility as excluded. Since the protoplasm, according to our conception, is a system of very minute lamellæ of fluid, in which the cavities of the meshes are filled by another fluid, the enchylema, it is very possible that important consequences may result in this way affecting the internal movements of protoplasm.

In such a system of fluid lamellæ, as soon as the tension of a lamella is altered, an influence must be exerted upon the arrangement of the system. If the tension of a lamella, which meets two others, in the way earlier described, at angles of 120°, is raised, the lamella in question must contract or shorten, so that the two lamellæ will meet at an angle which is less than 120°, and the resultant of their tensions now maintains a state of equilibrium with the increased tension of the first lamella. In the opposite case, with lowering of the tension of the first lamella, there will, of course, be an increase in its size and an enlargement of the angles of the two others. That these theoretical assumptions can be proved to be correct by means of experiment has already been shown by Plateau (vol. i. pp. 368-370), who succeeded in bringing about in the lamellar framework obtained by dipping a wire cube into a glycerine solution of soap, both contraction-like shrinkings and, on the contrary, enlargements of the central lamella, as the result of altering its tension both by differences of temperature and by bringing it upon other fluids of greater or less tension. Under

these circumstances it seems certain, therefore, that in foam-like protoplasm local alterations of the tension of certain lamellæ must produce immediate changes in the shape of the alveoli, such alterations of tension being caused either by the granules of the protoplasm or by something else. In this way it becomes very probable that the granules, if they possess the properties attributed to them, may also give occasion to phenomena of movement in the interior of the protoplasm, but that numerous other causes also, which produce a change in the tension of certain lamellæ, are able to take effect in a similar manner. For it is to be expected that every chemical change in the protoplasm of the lamellæ, as well as in the contents of individual alveoli, will alter the tension of the lamellæ, and that in this way changes of shape and consequent displacements of the alveoli must continually take place.

It seems to me therefore very probable that the irregular undulating movements to and fro, which are to be observed in nearly all protoplasm, depend on the causes which have been named, and that, in fact, they are inevitable, so to speak, if the conceptions which I have developed with regard to protoplasm are admitted to be correct.

Whether these internal processes of movement, to which I have already referred in 1888 (see *Protozoa*, p. 1397), can also develop into regular streaming movements, seems to me doubtful; nevertheless I would not altogether deny this possibility in the case of the phenomena of streaming movement in the endoplasm of Ciliata. Since there is in these forms no cell-sap cavity, which in plant cells, as we saw above, is of great importance for the appearance of extension-currents, we are in this case only able to indicate the mouth opening as the region where such currents originate, since it is here that the endoplasm usually comes into contact with the surrounding water. Although I do not consider it possible that an extension-current, starting from this point, and as a rule only taking effect upon one side, is sufficient to explain the circulation of the endoplasm of the Ciliata, I do not wish to enter more thoroughly into the point, since so to do could not be productive of much result without a special

study of the individual cases. The streaming seems to take the simplest course in *Didinium*. Here an extension-current starting from the internal opening of the œsophagus would explain the circulation, if it appeared on the whole possible to refer the streaming movements of the endoplasm of Ciliata to an extension-current of so simple a nature.

(*m*) *Possibility of an Explanation of Muscular Contraction in this way*

On the other hand, I should like to point out that the above-discussed causes of the changes in shape, and the displacements in the alveolar framework, seem to me to indicate a future explanation of the contraction of muscle fibrils. Although it is not my intention, as has already been remarked before, to enter more closely in this work into muscle cells, the structure of which requires much more accurate clearing up before a satisfactory explanation of their contraction is to be thought of, I will nevertheless refer briefly to this case.[1] Let us imagine as simple a muscle fibril as possible, consisting only of a single row of protoplasmic alveoli arranged one behind the other, which are enclosed in the usual protoplasm, the sarcoplasm, of the muscle cells. The accompanying Fig. 22 is intended to represent a short extent of such a muscle fibril (*ff*), together with the contiguous sarcoplasm, in longitudinal

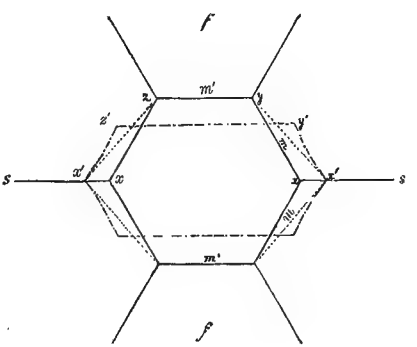

Fig. 22.

[1] In 1888, in my *Protozoa*, p. 1317, I had already pointed out the possibility of an explanation of muscular contraction, in the way which is set forth rather more accurately in the sequel here.

section. Let us also imagine that a chemical change of the enchylema suddenly takes place in the sarcoplasm enclosing the fibril, as a result of which the tension is raised at the boundary between the enchylema and the protoplasmic lamellæ: this change must influence the system of lamellæ as follows. In the transverse lamellæ *ss* of the sarcoplasm the tensions of both their limiting surfaces are heightened, while those of the lamellæ *mm* are only increased on the outer side, where they border upon the enchylema of the sarcoplasm. Hence the higher tension of the lamellæ *ss* will result in their contraction and diminution in size; but at the same time the lamellæ $m'm'$ of the fibril, since their tensions are not changed at all, must increase in size or stretch, since the lamellæ *mm* bordering upon them have their tensions heightened. Hence in any case the nodal points *xx*, *y*, and *z* must be displaced outwards from the centre of the alveolus towards the sarcoplasm. The cross section of the alveolus *xyzx* will therefore assume somewhat the shape which the figure $x'y'z'x'$ drawn in dotted lines represents, in which process it is to be expected that the side $x'y'$ will form a convex surface towards the centre of the alveolus, since only under these conditions is a state of equilibrium possible between the tensions of the lamellæ which meet in the nodal points x' and y'. In the same way, however, it is also to be expected that during this process the alveolus as a whole will widen in the transverse direction, which, since its internal volume must remain the same, can only be brought about by the height of the alveolus diminishing. Now since this will take place under the conditions given for all the alveoli of the muscle fibril, it will follow that the slight shortenings of these alveoli will be summed up, and in this way will bring about a considerable shortening of the muscle fibril as a whole. If the cause of the difference in tension vanishes again, the former condition must naturally be reverted to in the opposite way.

Without entering more closely here into the finer structure of the muscles, it will be understood that the same effect will come about when it is not a question of a fibril of the simplest kind, as was supposed, but of a plate-like

fibril, or rather a contractile column, which consists of a single layer of alveoli; the same action will be manifested in the same way, if the column consists of a double layer of alveoli. The conditions are less favourable if the muscle column is more than two layers of alveoli in thickness, because the alveoli are no longer all in contact with the sarcoplasm.

I think I have shown in the foregoing that, on the basis of our conception of protoplasmic structure, the possibility is conceded of an insight into the mechanics of muscle contraction. I am of course far from regarding what has been put forward as a theory of this process. I see only a guide-post, as it were, in the direction of a future theory, which will require the joint labours of many to follow it up or set it aside, as the case may be. Yet there appears to me to be one further point, in the supposition put forth above, which is worthy of special consideration. As is becoming more and more evident from recent observations upon the structure of muscle cells, a peculiar interpenetration of two substances, *i.e.* of the contractile elements and the so-called sarcoplasm, is especially characteristic of them. I am not aware that any one of the views that have been held hitherto upon the mechanics of contraction gives an idea of the significance of this peculiarity, while we see, on the other hand, that the hypothesis set forth above is able to explain this very point to a certain extent.

(*n*) *Rotational Currents in Plant Cells*

As we remarked before in discussing Berthold's views, the so-called *rotational streaming* movements, which occur fairly commonly in plant cells, are especially difficult to comprehend. It has already been declared above that I am unable to agree with the remarks of Berthold upon the origin of this process. Although I have not studied this subject thoroughly myself, nevertheless it seems to me worth while adding a few remarks upon this point; that is to say, to discuss the possibility, at least, of explaining this

phenomenon by means of extension-currents which have their seat at the boundary between the cell-sap and the protoplasm of the wall. We found before that it is possible to set up such a rotational current in an oil-drop, if by means of proper precautions care be taken that the extension-current only attains to development upon one side (see above, p. 74). Of course this phenomenon presupposes that there is, as a matter of fact, only a single powerful centre of extension-currents present in a state of permanent activity, which produces the current; for as I have already explained earlier, I cannot regard as correct Berthold's idea of the origin of such a rotational current by the conflict of numerous currents. If we now assume such a centre of extension-currents in a definite position, as the cause of the rotational current on the inner surface of the protoplasm lining the wall, the question arises, why the current in this case is developed only on one side, and thus leads to rotation. In reference to this point Quincke (1888) has already remarked that it must occur if, by means of solid particles or by a partial rigidity of its surface, an obstacle to the development of the current on one side is present. In our earlier described experiment the glass surface, to which the oil-drop adhered, is the obstacle. Hence if we assume that on the inner surface of the protoplasm lining the wall of a cell, somewhere at the surface of one end, near x (see Fig. 23), such an obstacle is present in the form of a narrow solid bridge, stretched out over the protoplasm of the surface of this end, then an extension-current, the centre of which is placed along one side of this solid bridge, will naturally become a one-sided rotational current, circulating in the cell in the direction of the arrows. The question now is whether arrangements really exist which make it probable that conditions of this kind are realised in rotation currents. I am only aware of one case to refer to in this respect, which at least yields the possibility of such

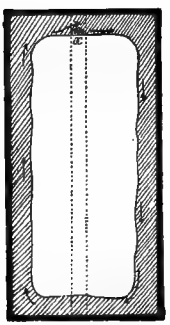

Fig. 23.

an arrangement—I mean the state of things in the *Charæ*. As is well known, there exist in the protoplasm lining the wall of the elongated thread-like cells of these algæ two so-called interference streaks, which pass along the longitudinal sides of the cells opposite to one another, and in which the chlorophyll-free protoplasm is in a resting state. Since the neighbouring protoplasm is in energetic streaming movement, it must be assumed that the protoplasm of these streaks is of a firm consistence. Now if, as seems quite possible, a rigid bridge was stretched from the ends of these interference streaks to the surfaces at the extremities of these cells (see Fig. 22), then the conditions would be to some extent realised which we postulated for the origin of the rotational current. Whether a similar state of things can be made probable in other cells also with rotational currents, remains of course an open question. Nevertheless one further difficulty may be considered here, which we meet with in the explanation attempted for the rotational current of the *Charæ*. It is to be expected that under the suppositions we have made the current might go on unaltered even after plasmolytic separation of the protoplasm from the cell wall. It is, however, well known that a long *Chara* cell can be constricted by ligatures in several places, and that when this is done, after a temporary pause a regular rotational current, corresponding to the original one, appears in each of the constricted portions. As has been said, this phenomenon presents new difficulties. Of course the two interference streaks also become constricted by the ligatures, and thus at the ends of the constricted pieces of the cell the required bridges are to a certain extent furnished by these streaks. Since, however, these firm bridges, as is easily intelligible, need not penetrate the whole lining of protoplasm, but ought to be present only at its inner surface, in order to bring about a rotational current in the required manner, the previous conditions could not be simply renewed by bending together of the interference streaks, if at least, as is probable, these streaks traverse the whole lining of protoplasm. Now whether we may picture to ourselves interruptions of the interference streaks as already present from the

outset in places, or whether after the constriction of the cell the state of things that exists at the ends of the normal cell is quickly restored at the ends of the constricted pieces, as the result of a kind of regeneration, all this may remain an open question, in order not to multiply further the number of assumptions and possibilities.

However indecisive the results may be which we have obtained with regard to the explanation of the rotation currents, it is nevertheless obvious from the preceding discussion that this case appears, under certain conditions, to admit of an explanation based upon our conceptions of the structure and the motor phenomena of protoplasm.

A few words in conclusion to this work. Unfortunately this Memoir has, while in course of preparation, considerably exceeded the limits originally prescribed for it, although I have taken pains to be as brief as possible, even at the risk of being somewhat difficult to understand in those questions which have hitherto lain beyond the province of biologists.

It gives me great pleasure to seize the opportunity of expressing my heartiest thanks to all those who have helped me in this work by their kind assistance. To my esteemed colleagues at Heidelberg, Professors Askenasy, Horstmann, Kühne, and Quincke, I am greatly indebted for much advice, and also to a great extent for assisting me with books and apparatus. I am similarly obliged to the juniors in my Institute, especially to Herrn Blochmann, von Adelung, von Erlanger, Hilger, Lauterborn, and Schewiakoff, for much assistance in the course of the last few years. During a short stay at the Zoological Station at Naples in the year 1890, the work I had in hand was greatly promoted by the most friendly attention to my wants.

All those whom I have named I beg again to accept of my most cordial thanks.

LITERATURE

SINCE it is by no means my intention to bring together a complete list of all writings that deal with the structural relations of protoplasm, only those works are cited in the following to which direct reference is made in the text. More exhaustive lists of literature are to be found in Arnold (1879), Flemming (1882), and Frommann (1890).

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EXPLANATION OF THE FIGURES [1]

SINCE I have prepared the figures for the most part without the aid of the camera, under the erroneous impression, as was afterwards found, that by its help delicate protoplasmic structures could not be recognised with certainty, I often have no sure means of determining the magnification in cases where direct measurements were not taken. In general, however, the figures relating to protoplasmic structures are drawn with a magnification of about 2500 to 3500 diameters, as is proved by those in which the magnification was actually determined. As I have said, I convinced myself at a later period that, in preparations of sufficient clearness, the protoplasmic structures can be drawn quite well by the help of the camera, using Zeiss's 2 mm. and Oc. 18; to which fact Fig. 2 on Plate X. bears witness, for example. Since the size of the alveoli varies within relatively narrow limits, that is to say, between 0·5 to 1 μ, the magnifications can be determined fairly well from this fact. Whenever it is not stated otherwise, the figures are all done with Zeiss's Apochr. 2 mm., Ap. 1·30 or 1·40, and the Comp. Oculars 12 or 18.

[1] *An Atlas of* 19 *Microphotographs* in connection with this Work can be obtained from Professor Bütschli, Zoologisches Institut, Heidelberg, by sending the sum of five shillings.

DESCRIPTION OF PLATE I

PLATE I

All the figures relate to *Gromia Dujardini* M. Schultze.

Fig. 1. Oral region of a specimen with completely retracted protoplasm, and the opening nearly closed. *a*, the finely granulated, non-striated portion of the shell, which chiefly forms the nipple-shaped elevation when the aperture is open (see Fig. 2). *b*, the portion of the shell which is radially striated in optical section. The protoplasm in the opening of the shell has a very distinct and longitudinally fibrillar, alveolar structure. *c*, the large brown bodies contained in the protoplasm. × about 1000.

Fig. 2. Aperture of a living specimen, from which a moderately large tuft of protoplasm has emerged; the protoplasm shows very distinctly a honeycomb-like structure, and sends out a number of fine hyaline pseudopodia.

Fig. 3, *a*. A pseudopodium in process of retraction, showing the alveolar structure distinctly in two places, while the rest still appears quite hyaline.

Fig. 3, *b-c*. Two consecutive stages in the retraction of a pseudopodium. The fine lateral branch * on Fig. 3, *b*, has already become relaxed and wavy, and it contracted rapidly, becoming distinctly alveolar in the process. It then united with the alveolar eminence ** to form the alveolar appendage at the end of the pseudopodium in Fig. 3, *c*.


a
1
b
c
3b
3a
3c
2
a
b

DESCRIPTION OF PLATE II

PLATE II

Figs. 1-4 relate to *Gromia Dujardini* M. Schultze.

Figs. 1 and 2. Two drops of protoplasm, appearing hyaline during life, which had been set free by pressure from the protoplasm of the oral aperture of a specimen; after treatment with picro-sulphuric acid and staining with Delafield's hæmatoxylin. Both the drops show the alveolar layer very distinctly.

Fig. 3. Large pseudopodium with numerous fine branches. Quite hyaline during life. Figured after fixing with picro-sulphuric acid and staining with Delafield's hæmatoxylin. The fibrillated alveolar structure very distinct throughout almost the whole pseudopodium.

Fig. 4. Point of origin of some thick hyaline pseudopodial stems from the protoplasmic tuft of the aperture. Note how the fibrillated alveolar nature of the tuft partly extends even to the commencement of these pseudopodia, here becoming less and less distinct, and finally vanishing entirely.

Fig. 5, *a-b*. Margin of a living drop of protoplasm, isolated by pressure from a Milliolid. It shows a very beautiful alveolar layer and a well-developed radial striation of the peripheral protoplasm generally. 5, *b*, a small portion of the margin more strongly magnified, in order to represent the alveolar layer more accurately.

Fig. 6. Living bridge of protoplasm, which was stretched across between the fragments of a squashed Milliolid. It had a distinctly fibrillated alveolar structure, and was at the same time in a constant state of undulatory streaming movement.

Figs. 7-8. Pseudopodia of *Amœba limax* after treatment with picro-sulphuric-osmic acid. The alveolar structure is perfectly distinct as far as their extremities, as also the alveolar layer.

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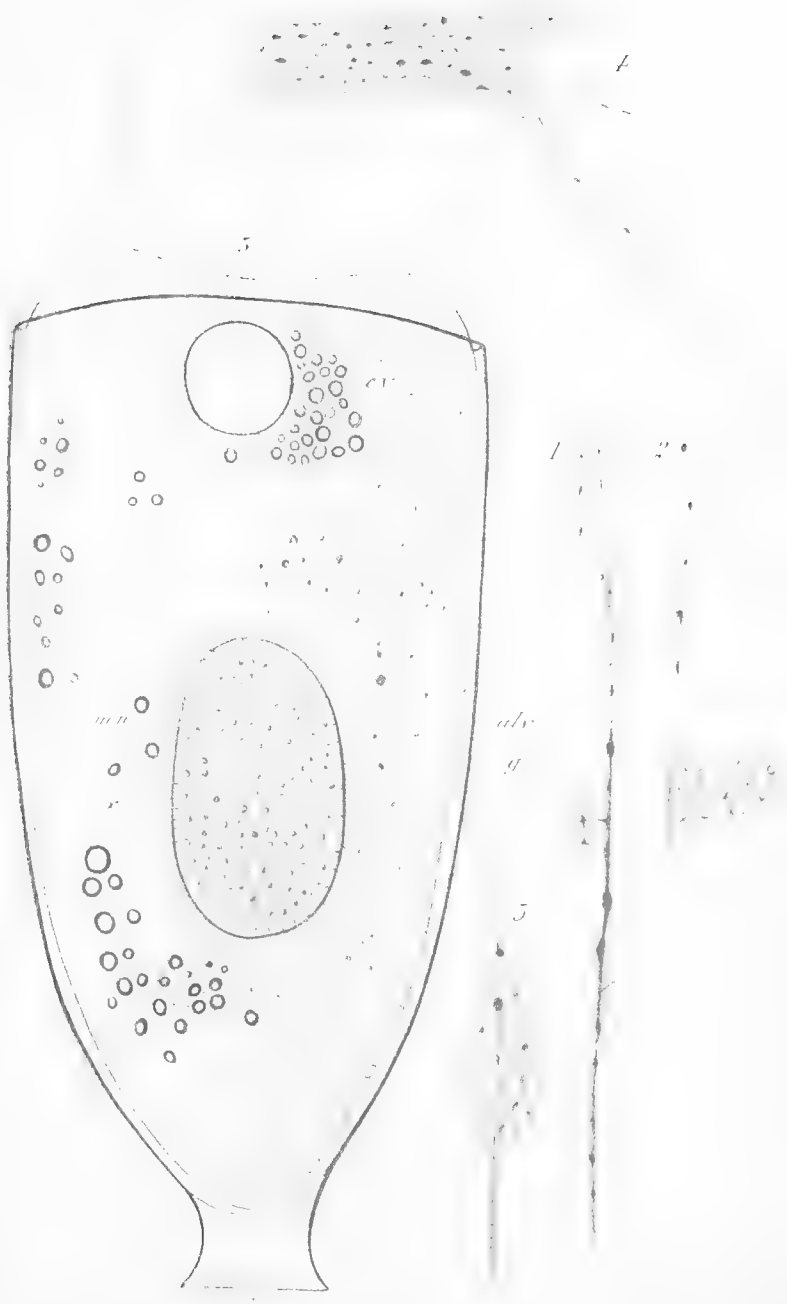
DESCRIPTION OF PLATE III

PLATE III

Fig. 1. Portion of fine pseudopodium, during life, of *Polystomella*.
Fig. 2. The same of *Cornuspira*.
Fig. 3. The same of *Discorbina*.
Fig. 4. Thicker pseudopodial stem of a living *Rotalina*, with a very distinct fibrous alveolar structure.
Fig. 5. Small *Acineta* (see the text, p. 87) from fresh water. Living. The structure of the protoplasm only partly filled in. *g*, the wall of the envelope ; *alv*, alveolar layer ; *mn*, macronucleus ; *cv*, contractile vacuole with the very distinct efferent canal ; *x*, dark bodies in the protoplasmic framework.



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DESCRIPTION OF PLATE IV

PLATE IV

Fig. 1. Membrane-like expansion, with a very distinct structure, from the pseudopodial network of a Milliolid. Living.

Fig. 2. Similar expansion from the richly developed pseudopodial network of a *Discorbina*, which was killed rapidly by being placed in the vapour of heated osmic acid and then stained with Delafield's hæmatoxylin. The drawing was made as true to nature as possible, without being schematised in the least.

Fig. 3. Marginal portion of a fresh-water *Amœba*, which was not determined with certainty, but was probably referable to *Amœba* (*Cochliopodium*) *actinophora*, although the envelope was not distinct. At the broader end the alveolar protoplasm becomes very beautifully radially striated. A more precise determination of this form was impossible, since it was only observed in a fixed preparation. Picro-sulphuric-osmic acid, damar.

Fig. 4. *Amœba actinophora* Auerbach (probably more correctly referred to *Cochliopodium* H. and L.) Picro-sulphuric-osmic acid, damar. Only a portion of the margin, with the radially striated envelope (*h*), represented. Beneath this the distinctly alveolar protoplasm, of which the most external layer immediately under the envelope has developed into an alveolar layer (*alv*). *o*, the alveolar protoplasm in surface view. *n*, the nucleus, with a very large nucleolus of a honeycombed structure, and *a* framework arranged radially to the membrane.

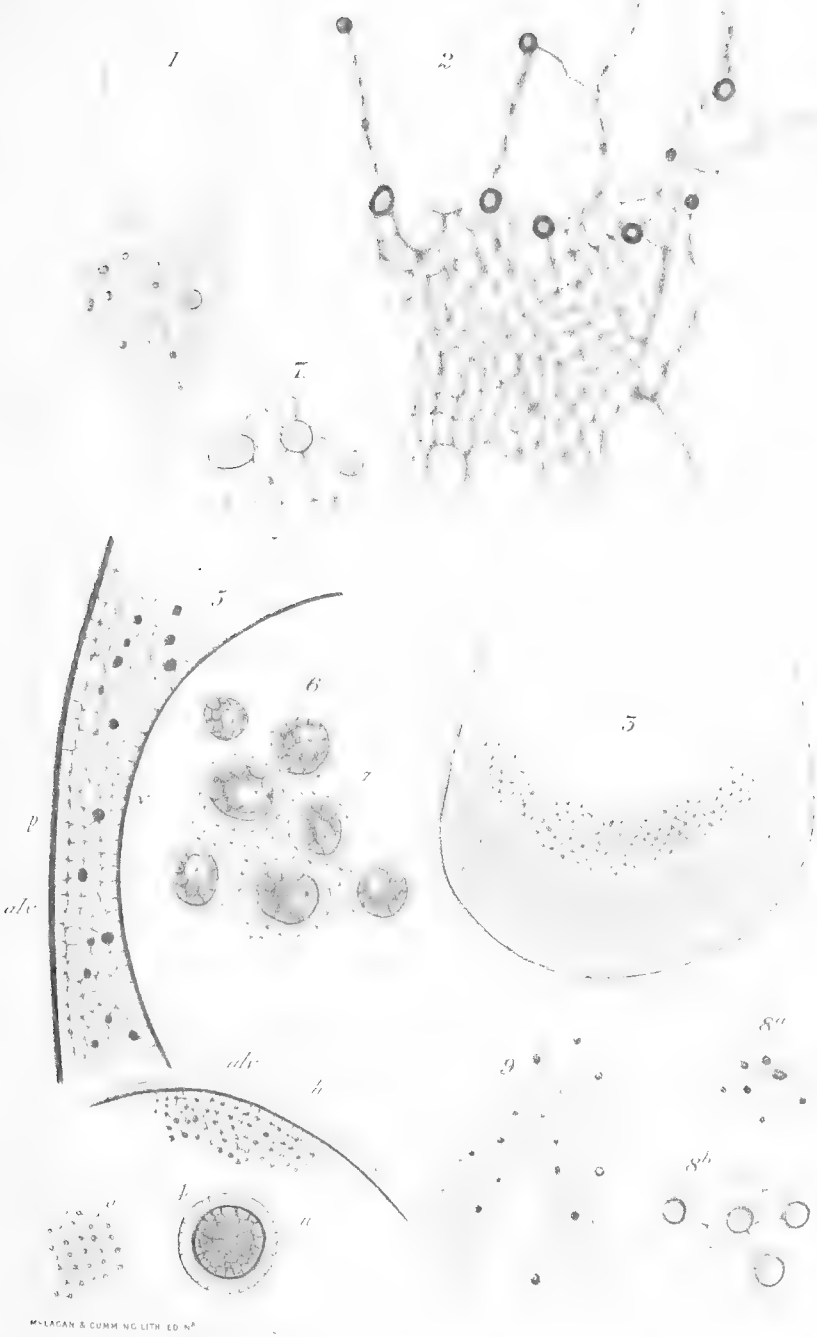
Fig. 5. Small living *Vorticella* sp. from the Mediterranean. A small portion of the edge in the region of the contractile vacuole in optical section. *p*, pellicula ; *alv*, alveolar layer ; beneath that the distinctly alveolar protoplasm, in which the most external layer of alveoli is directed radially to the alveolar layer. At the same time, a similar arrangement of the alveoli at the surface of the large vacuole (*v*), which was probably the contractile vacuole, is very distinct. Numerous strongly refracting granules in the endoplasm.

Fig. 6. Surface view of a small portion of the cortical protoplasm of *Paramœcium bursaria* Ehb. sp. with numerous *zoochlorellæ* (*z*). Picro-sulphuric-osmic acid, damar. The vertical position of the very distinct alveoli of the cortical protoplasm, with regard to the *zoochlorellæ*, is very striking.

Fig. 7. *Stylonychia pustulata* Ehb. Small portion of the alveolar endoplasm with corpuscles, strongly stained with eosin, lodged in it.

Fig. 8, *a-b*. *Paramœcium caudatum* Ehb. Killed with iodine-alcohol ; then very strongly stained in Delafield's hæmatoxylin, and transferred to oil of cloves, and there broken up. 8, *a*, small fragment of the macronucleus, showing beautifully the alveolar structure, and the fact that the small chromatin granules, stained red, are lodged in the nodal points. 8, *b*, small fragment of the endoplasm with the larger, eosinophilous granules in the nodal points of the alveoli ; the latter stain slightly reddish in hæmatoxylin.

Fig. 9. Two living strands of protoplasm from the hair cells of a *Malva* sp. ; in the strand on the left the streaming has stopped, for which reason the structure here appears irregularly alveolar ; in the neighbouring strand, on the other hand, which is in a state of streaming movement, it appears distinctly fibrillar.



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DESCRIPTION OF PLATE V

PLATE V

Fig. 1, *a-c.* Eggs of *Sphærechinus granularis* Lam.

Fig. 1, *a.* Thin section (about 1 to 2 μ), passing slightly obliquely to the axis of division, through the so-called *attraction sphere* of an egg which was in the act of dividing in two. In the centre is the centrosome, which seems to consist of three closely apposed vesicular granules. Picro-sulphuric acid, Delafield's hæmatoxylin, damar.

Fig. 1, *b.* Thin section through the surface of a similar ovum, showing very plainly the alveolar layer (*alv*), and the honeycombed structure of the protoplasm lying beneath it.

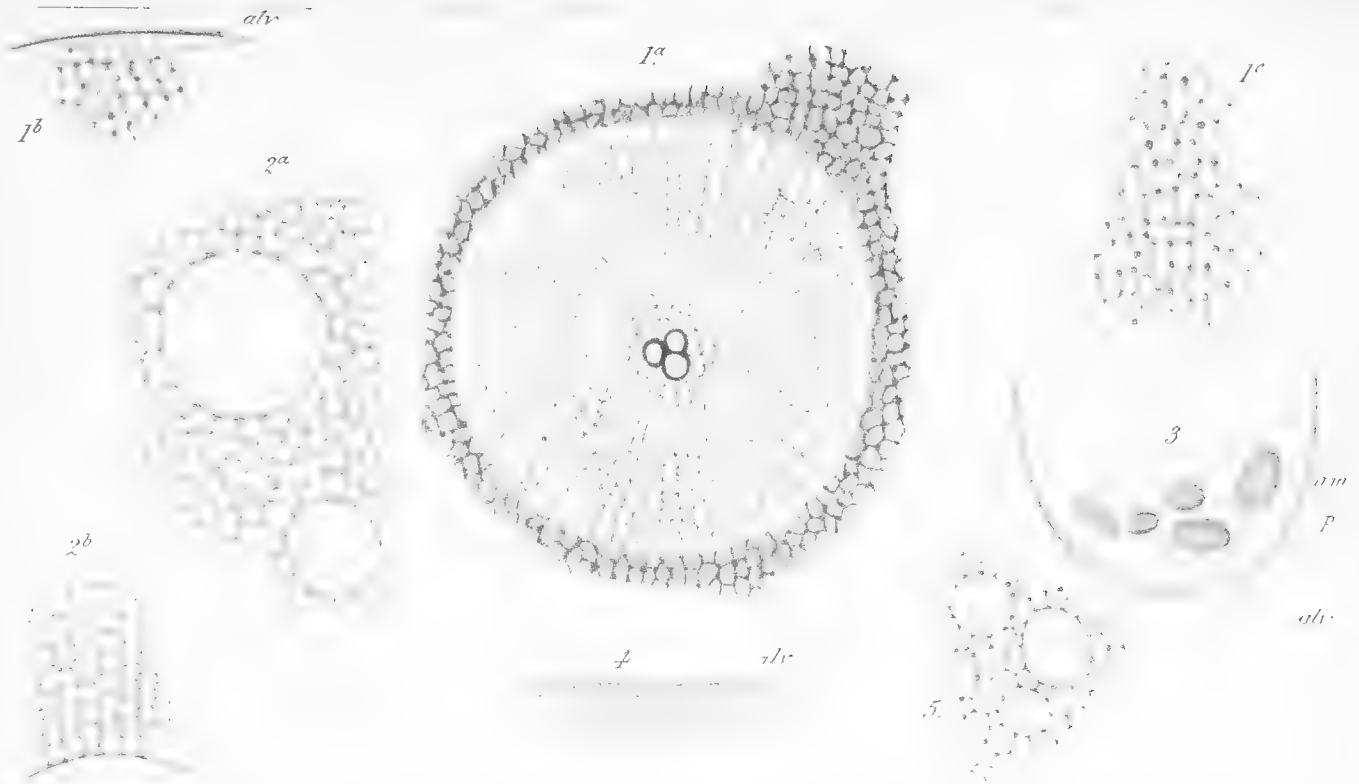
Fig. 1, *c.* Striated protoplasm during division from an entire ovum in process of division, which was investigated in water after treatment with picro-sulphuric acid.

Fig. 2, *a-b.* *Thalassicolla nucleata* Hxl. Section through the central capsule. Osmic acid, Canada balsam. 2, *a*, part of the intracapsular protoplasm with two vacuoles or albumen spheres. 2, *b*, part of the superficial, radially striated intracapsular protoplasm, bordering on an albumen sphere. × about 3100.

Fig. 3. Hinder end of a living *Chilomonas paramœcium* Ehb. Both the alveolar layer (*alv*) and the honeycombed endoplasm are very distinct. In the latter lie the large amylum granules (*am*). *p*, pellicle.

Fig. 4. Optical section of the marginal portion of a drop of oil-foam prepared from olive oil and NaCl, with a very distinct and relatively high alveolar layer (*alv*). Seibert $\frac{1}{12}$, × 1250.

Fig. 5. Foam prepared from olive oil and cane sugar. A small part of the meshwork, projected with the camera lucida. × 1200.



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DESCRIPTION OF PLATE VI

PLATE VI

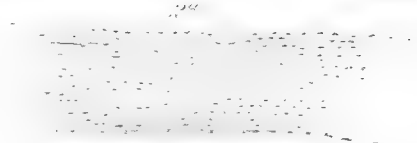
Fig. 1. Foam prepared from olive oil and NaCl. A small part of the meshwork. Camera lucida, × 1800.

Fig. 2, *a-b*. Foam prepared from very much thickened olive oil and K_2CO_3; very viscid. Drawn out by compression of the cover glass into strands, which show the fibrillated alveolar structure very beautifully. 2 *a*, a strand with low magnification. 2 *b*, a small part of this strand with greater magnification, showing the honeycombed structure distinctly.

Fig. 3. *Lumbricus terrestris* L. Longitudinal section through a supporting cell of the epidermis. Iodine-alcohol, acid hæmatoxylin, damar. *c*, cuticle. In the nucleus the framework, stained blue, is very distinct, with red chromatin granules lodged in it, and a nucleolus similarly stained. In the meshwork of the protoplasm there are similarly stained red granules, which, however, are smaller, and hence more difficult to observe.

Fig. 4. A small portion of a cell from the *fat body* of *Blatta orientalis* L. Stained by Gram's method, with subsequent staining with vesuvin. The large cavities (*f*) have arisen by fat drops becoming dissolved. *b*, the vividly stained Bacteroids, which are distinctly lodged in the pale meshwork of the protoplasmic bridges.

Fig. 5. Optical section through the epidermis (margin) of a living gill lamella of *Gammarus pulex* de G. *c*, cuticle. The striated alveolar structure of the protoplasm can be distinctly recognised.



DESCRIPTION OF PLATE VII

PLATE VII

Fig. 1. Very thin section through the liver of *Rana esculenta*. Picro-sulphuric-osmic acid, iron-hæmatoxylin, water. Region at which three cells meet. Protoplasmic structure and alveolar layer very distinct. × about 3500.

Fig. 2. Very thin section through a peritoneal cell of the gut of *Branchiobdella astaci* Od. Picro-sulphuric acid, gentian violet, water. Thickness of the section at most about equal to the diameter of a single mesh of the protoplasm. The granules in the nucleus (*n*) and protoplasm very strongly stained. Drawn as accurately as possible.

Fig. 3, *a-c*. 3, *a*, very thin section through the cuticle and epidermis cell of *Branchiobdella astaci*, showing the structure of the cuticle (*c*) distinctly. 3, *b*, section through cuticle of rather different nature. 3, *c*, surface view of the cuticle.

Fig. 4. Protoplasm of the strongly compressed living ovum of *Hydatina senta* Ehb. The alveolar structure here exceedingly distinct.

Fig. 5. Protoplasm of the living cells of the posterior circle of cilia of *Hydatina senta*, from a spot where the protoplasm has not got a fibrillated alveolar structure.

Fig. 6. Small part of the protoplasm of a pigment cell of *Aulastomum gulo* M. T. Isolated after maceration in iodine-alcohol (10 per cent). The dark granules in the nodal points of the meshwork are the pigment granules.

Fig. 7. Small portion of an isolated nerve fibre of the nerve of the chela of *Astacus fluviatilis*. Maceration in iodine-alcohol (about 10 or 15 per cent). *s*, the sheath in optical longitudinal section with the nucleus (*n*) lying entirely embedded in it. *n'*, the lateral boundary of the nucleus, drawn elsewhere in optical section. *os*, the structure of the sheath in surface view. *f*, optical longitudinal section through the axis-cylinder.


1.
2.
3a
3b
3c
4
5.
6.
n
m.
s
os
f

DESCRIPTION OF PLATE VIII

PLATE VIII

Fig. 1, *a-b*. Isolated axis-cylinder from the ischiadic nerve of *Rana esculenta*. Fixed with picro-sulphuric acid, followed by alcohol, and finally stained in the usual way with aurichloride of potassium. 1, *a*, with remains of the medullary sheath sticking to it. 1, *b*, probably from the region of a constriction. Optical longitudinal section. 1, *a*, × about 3300, 1, *b*, × about 2700.

Fig. 2. Nucleus, with surrounding protoplasm, of a ganglion cell from the spinal cord of *Bos taurus* (*juv*). Macerated in iodine-alcohol (10-15 per cent). Shows distinctly the vertical position assumed by the alveoli directly surrounding the nucleus with regard to its surface.

Fig. 3. Small portion of the margin of an isolated ganglion cell from the ventral nerve cord of *Lumbricus terrestris*, showing the alveolar layer distinctly. Maceration in iodine-alcohol (10 per cent).

Fig. 4, *a-c*. Isolated connective tissue cells from the ischiadic nerve of *Rana esculenta*. 4, *a*, several connected cells under low magnification. 4, *b*, single cells under stronger magnification in lateral view. 4, *c*, the same in surface view. Picro-sulphuric-osmic acid. *n*, nucleus.


2
n
1a
1b
5
alv.
4b
n
4a
n
4c
n

DESCRIPTION OF PLATE IX

PLATE IX

Fig. 1. Small portion of an isolated capillary from the spinal cord of *Bo taurus* (*juv*) in optical longitudinal section. *n*, two nuclei of the wall. At *o* the surface structure of the protoplasm of the cells of the wall is depicted for a short distance. Maceration in iodine-alcohol (10-15 per cent).

Fig. 2. Broad protoplasmic process of a ganglion cell from the spinal cord of *Bos taurus* (*juv*). Fibrillated alveolar structure very distinct. Maceration in iodine-alcohol (10-15 per cent). × about 2000.

Fig. 3. Isolated axis-cylinder of the gray substance of the spinal cord of *Bos taurus* (*juv*). Optical longitudinal section. Maceration in iodine-alcohol (10-15 per cent). × about 4400.

Fig. 4, *a-c*. Transverse sections of medullated nerve fibres from the ischiadic of *Rana esculenta*. Picro-sulphuric acid. Fat removed with alcohol and ether. Stained partly with hæmatoxylin, partly with gold chloride. 4, *a*, transverse section between two constrictions. 4, *b*, transverse section in the region of a constriction. 4, *c*, transverse section through a nucleus (*n*) of the sheath of Schwann. *s*, sheath of Schwann. *a*, so-called sheath of axis-cylinder which was in part very distinct. In 4, *c*, the sheath of Schwann is probably rather abnormally distorted.

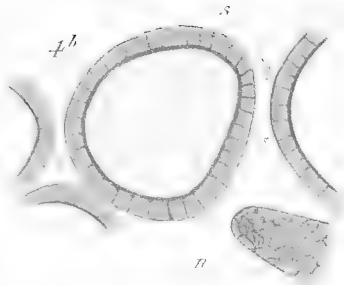
1

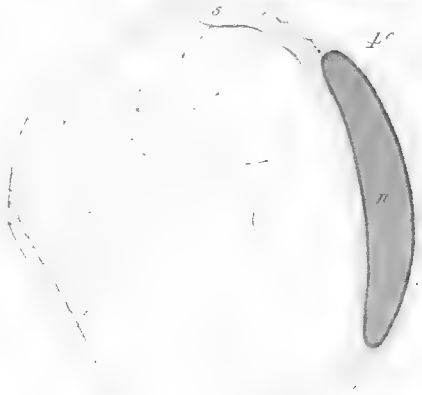
n

n

2.

3





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DESCRIPTION OF PLATE X

PLATE X

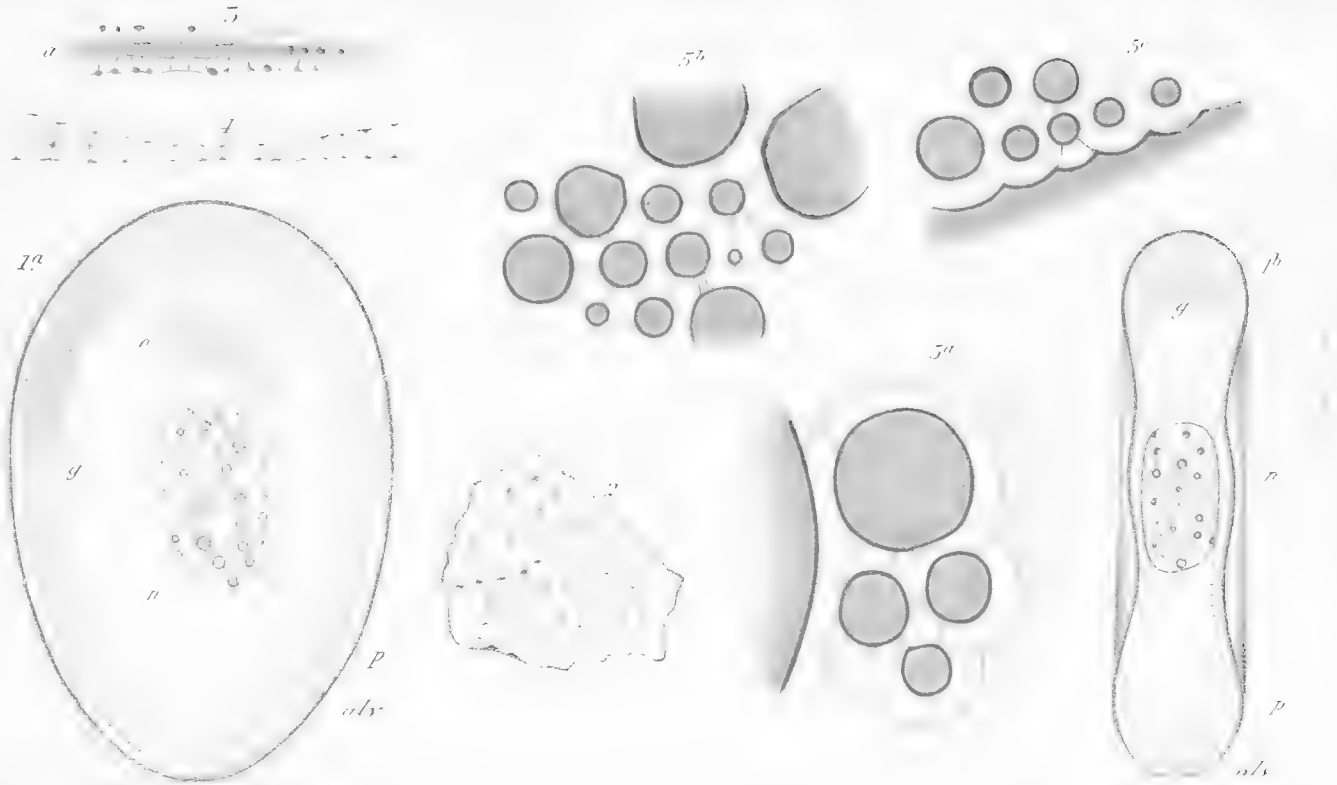
Fig. 1, *a*, *b*. Red blood corpuscles of *Rana esculenta*, iodine-alcohol, acid hæmatoxylin, damar. Only the nuclei stained. 1, *a*, view of the broad side. At *o* a small part of the surface and structure of the protoplasm is depicted. In the rest of the figure the equatorial optical section is represented. 1, *b*, view of the narrow side, optical median section. In both views the alveolar layer (*alv*) is very distinct. *g*, the limit of the protoplasm towards the cavity of the blood corpuscle. In the nucleus (*n*) the framework stained blue with the red chromatin granules can be plainly recognised. *p*, pellicle.

Fig. 2. Transverse section through an axis-cylinder, rather distorted in outline, from the ischiadic of *Lepus cuniculus*. Picro-sulphuric-osmic acid, iron-hæmatoxylin, water. × 4000. The somewhat irregular transverse section was chosen because it was extremely thin (at most 1 μ), and hence showed the structure very plainly.

Fig. 3. Small part of a living pseudopodium of *Actinosphærium eichhornii* Ehb. *a*, the axial thread, surrounded by the distinctly alveolar protoplasm, which contains numerous strongly refractile granules.

Fig. 4. Foam prepared from olive oil and sodium chloride. An outstretched lamella of foam, made up of a single layer, which it was possible to study in optical section. Unfortunately I have not taken accurate note of the special conditions under which this lamella was observed, for it is clear that it could only exist in this manner under peculiar relations, and for a short time, since the foam in question was quite fluid.

Fig. 5, *a-c*. Very small droplets of olive oil, and which are obtained by shaking up some oil with 1 per cent soda solution. The droplets are in close apposition to one another. Focussed slightly below the horizontal equatorial plane of the drops, so that the apparent network produced by the diffraction circles which is stretched out between the droplets is seen very plainly. Diaphragm drawn far down. In Fig. 5, *a*, a few small drops lie apposed to a large one, of which only a part of the edge is drawn. In Fig. 5, *c*, a number of minute droplets are similarly closely apposed to the margin of a very large one, so that the relations become rather peculiar. With reference to the interpretation of these remarkable appearances compare the text, pp. 211 *et seq.* Zeiss Apochr. 2 mm., Oc. 18.



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DESCRIPTION OF PLATE XI

PLATE XI

Fig. 1. Small portion of a very thin longitudinal section through the cuticle, and one of the hooks occurring in it, of *Distomum hepaticum* L. *f*, the hook. *a*, the dark, pellicle-like border of the cuticle; beneath this a layer, *b*, corresponding to an alveolar layer. Then follows the very distinctly alveolar outer stratum, *c*, of the cuticle, passing internally into the fibrous portion, *d*, which contains numerous granules. Below the cuticle are cross-sections of the circular muscle fibres, *e*, which are embedded in a fibrous alveolar protoplasm. Picro-sulphuric acid, iron-hæmatoxylin, water. Obj. 2 mm. 1·40, Oc. 18. Cam. luc. × 3275.

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DESCRIPTION OF PLATE XII

PLATE XII

Fig. 1. Part of a pseudopodium of *Actinosphærium eichhornii* Ehb., after treatment with picro-sulphuric acid. The protoplasm has become partly contracted in a varicose manner on the axial thread, *a*, so that the latter is laid bare in places.

Fig. 2. A very fine protoplasmic filament from a cell of a stamen of *Tradescantia virginica*. The filament becomes swollen up in its course, and the swollen portion has a very beautiful alveolar structure, while the fine filament does not permit any such structure to be made out. Unfortunately I have not noted whether this drawing was made from a living or a fixed object; the latter alternative is, however, more probable.

Fig. 3. Surface section through the bacillar border of the epithelium cells of the gut of *Distomum hepaticum*. Picro-sulphuric acid, iron-hæmatoxylin, water. *a*, the transverse sections of the more darkly-stained conical bodies, distinctly alveolar and deposited in a mass of alveoli more feebly stained and poorer in granules. Z. Apochr. 2 mm., Oc. 18. Cam. luc. × 4000.

Fig. 4. Small portion of the so-called stem filament or muscle, after fixation, of *Zoothamnium mucedo* Entz; very distinctly made up of a fibrous alveolar structure. Z. Apochr. 2 mm., Oc. 12.

Fig. 5. Optical section through a tentacle of *Podophrya elongata* Clp. and L. The central circle is the tentacle canal, the wall of which is formed by a layer of alveoli of protoplasm. Z. Apochr. 2 mm., Oc. 18.

Fig. 6. Compare the text, p. 179.

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