The Cell-Theory: a Restatement, History, and Critique

PART II

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PROPOSITION II

Cells have certain definable characters. These characters show that cells (a) are all of essentially the same nature and (b) are units of structure.

The essence of this proposition can most easily be grasped by considering what would be left of the cell-theory if it were omitted. We should then be in the same position as was Leeuwenhoek (1674), who, having found that a number of tissues consisted of ‘globules’, was not surprised to find the same structure in milk. This second proposition is concerned with the reasons for supposing that certain objects, called cells, are all to be regarded as strictly comparable with one another and not comparable with globules such as those of milk.

Very gradually, over a period of centuries, it came to be recognized that there is a fundamental living substance, the protoplasm; that this protoplasm commonly occurs in small masses, each provided with a nucleus; and that each of these masses is to some extent separated from its neighbours by a cell-membrane having special characters. Proposition II covers these discoveries and is also concerned with the reasons for supposing that cells are unitary components of organisms and that one cell corresponds with one other cell and not with several. The present paper deals with the discovery of protoplasm and the nucleus. The discussion of Proposition II will be continued in Part III of this series of papers.

The Discovery of Protoplasm

One of the most fundamental facts about cells is that they contain protoplasm as their characteristic constituent, and that, with some partial exceptions that are mentioned on p. 98, this substance never occurs except in

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cells or in objects formed by the transformation of cells. While allowing that the word protoplasm has no absolutely precise meaning, we must acknowledge that there are many substances of which it can be stated with certainty that they are not protoplasm, and that such substances occur commonly between cells, but never constitute cells; while the substance that exists in cells (and in transformed cells) and is called protoplasm has so many positive characters that it is impossible to suppose that we are lumping together under a single name utterly distinct mixtures of organic compounds. This is not the place to give a list of the physical and chemical properties of the substance; we are concerned here only to trace the history of the idea that the cells of plants and animals have a substance called protoplasm as their characteristic component.

The earliest observations and experiments on this substance were not made in connexion with cells. Trembley (1744) made a careful study of the protoplasm of Hydra without ever understanding the cellular nature of these animals. He was investigating the microscopical ‘grains’ (apparently the carotene-granules and nematocysts) that he had discovered. He noticed (p. 56) that when he had teased up a fragment of the body in a drop of water, some of the ‘grains’ remained bound together by ‘une matière glaireuse’ (literally, a substance resembling white-of-egg). Trembley stretched a fragment of the body between the points of a quill pen and saw the glairy substance spin out between them (p. 57). He was able to isolate this substance almost completely from the granules. He attributed the cohesion of the granules to the glairy substance. He was also able to stretch a tentacle and to obtain a microscopical view of the part of it lying between two ‘grains’ (nematocysts): this part consisted wholly of the glairy substance (pp. 63–4). He notes its transparency and tenacity, the latter being shown by the resistance of the tentacle against breaking when pulled. He attributes to it also the polyp’s powers of contraction and expansion.

Duhamel du Monceau (1758, p. 26), in his study of the cellular tissue of plants, mentions the ‘substance vésiculaire, ou cellulaire’ that fills, as he says, the meshes of the net (i.e. the spaces enclosed by the cell-walls). He remarks that it contracts on desiccation and that it is sometimes coloured.

The discovery of cyclosis by Corti (1774, pp. 127–200) was to play an important part some three-quarters of a century later in leading microscopists to the opinion that the living substance of plants and animals is essentially similar (see p. 95). At the time, the circulation of protoplasm was only an isolated curiosity. Corti uses the name ‘Cara’ for the various species of freshwater plants on which his observations were made; these included Chara and perhaps also Nitella. He uses the name Cara translucens minor, flexilis for the species in which he first saw the circulation of granules in the long internodal cells.

Treviranus (1811, pp. 78–95) first saw cyclosis in 1803. His observations on this subject were made on Hydrodictyon utriculatum and Nitella flexilis (which he calls Chara), among other freshwater plants. It is clear that he
had no knowledge of Corti’s discovery. He would appear to have confused cyclosis with the movement of reproductive cells set free by algae, as observed by other authors.

Treviranus calls the protoplasm of freshwater algae ‘Gallert oder organische Materie’; he notices the granules in it and mentions that he has seen them also in the cells of the cellular tissue of plants. Indeed, he found each cell of this cellular tissue ‘ganz ähnlich’ to a segment (Glied) of a conferva (1811, p. 78).

Brisseau-Mirbel (1815, p. 196) uses Grew’s word ‘cambium’ more or less as we might say ‘the protoplasm of meristematic tissues’. He describes it as a colourless mucilage that appears wherever new developments are going to occur. He did not understand that it was partitioned into cells, but considered that though a fluid, it contained the ‘linéamens’ of new structure. In his text-book of histology, Heusinger (1832, p. 41) uses the expression ‘Bildungsgewebe (tela formativa)’ roughly in the sense of what we should call protoplasm; but his style is reminiscent of Oken’s Naturphilosophie and he does not give much precise information.

Dujardin (1835) was led to the study of protoplasm by his doubts as to the correctness of Ehrenberg’s opinion that the food-vacuoles of ciliates are stomachs joined by an intestine. He was unable to see any tube joining one vacuole to another and his attention was thus directed to the intervening substance. He says that he would perhaps have abandoned these studies, if he had not solved the problem by the discovery of the properties of ‘Sarcode’. ‘I propose to give this name’, he says (p. 367), ‘to what other observers have called a living jelly—this glutinous, transparent substance, insoluble in water, contracting into globular masses, attaching itself to dissecting-needles and allowing itself to be drawn out like mucus; lastly, occurring in all the lower animals interposed between the other elements of structure.’ It is remarkable that Dujardin at once seized upon most of the important physical characters of the substance he had just named. Indeed, one could hardly improve upon his description in a short statement, except by providing the numerical data that are available to-day. He found (pp. 367–8) that sarcode decomposes gradually in water; unlike albumen, it does not dissolve, but leaves a feeble, irregularly-granular residue. Potash hastens the decomposition; nitric acid and alcohol coagulate the substance and make it white. It spontaneously produces vacuoles within itself. It refracts light much less than oil does.

Dujardin studied sarcode not only in ciliates, but also in Fasciola and Taenia, in Naïs, earthworms and other annelids, and in young larvae of insects. He seems generally to have used exudations from rents in tissues for his metazoan material.

Dujardin did not relate his sarcode to cellular structure. Various microscopists, however, began to make short remarks about the substance lying between the nucleus and the boundary of the cell. Valentin (1836), who studied it in nerve-cells, called it the ‘Parenchym’. He said that it was ‘for the most part a grey-reddish finely granular substance’, though transparent.
and clear as water in fishes (p. 138). He mentions the 'small, dispersed, separate, round particles' in the cytoplasm of various nerve-cells, and figures them (see especially his Figs. 45 and 49 of Tab. VII). These were almost certainly the vacuoles or spheroids that constitute the basis of the so-called Golgi apparatus, and he should presumably be regarded as the discoverer of this cytoplasmic element.

Schleiden (1838, pp. 143-5) seems to have used the word 'Schleim' in more or less the sense of plant protoplasm; but his attention was so much fixed upon the nucleus and cell-wall, and his ideas on the origin of cells so mistaken, that it is impossible to be sure. Certainly he did not believe his 'Schleim' to be an essential part of the cell, except in so far as the nucleus might be formed of it. He says that it occurs in irregular, granular forms without internal structure, and is stained brownish-yellow or brown by tincture of iodine. He seems to have thought that what we should call the cytoplasm of young cells was a watery fluid containing granules of Schleim.

Meyen (1839), like Dujardin, was led to the study of protoplasm by investigating the food-vacuoles of ciliates. Like Dujardin, he denied Ehrenberg's opinion that these animals have stomachs joined by an intestine: there are simply watery vacuoles (Höhlen) in a gelatinous substance. 'The true infusoria', he wrote, 'are bladder-like animals, the cavity of which is filled with a slimy, somewhat gelatinous substance' (p. 75). He mentions (p. 79) that similar vacuoles occur in the 'Schleim' of the cells of plants, particularly in the aquatic filamentous forms, but he is so much interested in the vacuoles that he omits to institute a comparison between the gelatinous substance of infusoria and the Schleim of plants.

Schwann (1839 a) added little to knowledge of the living substance. He mentions (p. 12) that the cells of the notochord of the frog-larva contain a colourless, homogeneous, transparent substance, which, he says, does not become cloudy at the temperature of boiling water; and he describes the contents of ganglion-cells (p. 182) as being a finely granular, yellowish substance. He gives some account (p. 45) of the 'strukturiose Substanz' of organisms; but this was the supposed Cytoblastem or substance in which cells originate, not the substance of cells themselves. Schwann states specifically (p. 209) that the substance that comes to surround the nucleus in the developing cell is different from the Cytoblastem. He says little about its characters, however, beyond mentioning that it is sometimes homogeneous and sometimes granular.

The first attempt to generalize about the properties of the living substance of plant and animal cells was made by Purkinje on 16 January 1839 at a meeting of the Silesian Society for National Culture. A report on his address was published the following year (Purkinje, 1840a). The intrinsic value of his remarks, and the fact that he used the word 'Protoplasma' for the first time in its scientific sense, make it necessary to reproduce a considerable part of what he said. The word Protoplasma had long been used in religious writings in the sense of the 'first created thing'; but it is a surprising—indeed
an astonishing—fact that in introducing the term into science, with a very particular and important meaning, he gives no indication that it was not already in current use in this field. He reserves the word 'Zellen' for cells that have distinct cell-walls, using 'Kügelchen' and 'Körnchen' for those that have not. He uses the word 'Cambium' in the same sense as did Brisseau-Mirbel. He wrote as follows:

'In plant-cells the fluid and solid elements have separated completely in space, the former as the inner, enclosed part, the latter as that which encloses it. In the animal development-centre, on the contrary, both are still present in mutual permeation. The correspondence is most clearly marked in the very earliest stages of development—in the plant in the cambium (in the wider sense), in the animal in the Protoplasma of the embryo. The elementary particles are then jelly-like spheres or granules, which present an intermediate condition between fluidity and solidity. With the advance of development the animal and plant structures now diverge from one another; for the former either tarries longer in the embryonic condition or remains stationary in it throughout life, while in the latter on the contrary the hardening process and the separation of the solid and the fluid progress more rapidly, and come to light first in cell-formation and then in the formation of vessels.'

It will be noticed that although he applies the word Protoplasma only to the substance of the embryonic cells of animals, yet he clearly realizes the correspondence of this substance with that of the adult cells of animals and of the meristematic cells of plants. In the case of the adult plant cell, he regards what we call simply the protoplasm as constituting the fluid part of his Protoplasma, the solid part having separated out as the cell-wall. In another paper, published in the same year, Purkinje (18406) follows up these ideas by claiming that there should be a 'Körnchentheorie' as opposed to the cell-theory of Schwann, since plants and animals originate from simpler elementary granules, which in plants become changed into cells, while in animals they either remain as they were or change into various forms of fibres. He does not use the word Protoplasma in this paper, but the idea of a substance common to plant and animal cells is implicit in what he writes.

Jones (1841) denied, like Dujardin, that the 'internal sacculi' of ciliates are connected by an intestine (pp. 56–8). He states that the lowest animals consist of a 'gelatinous parenchyma' (p. 6). He speaks of a 'semifluid albuminous matter' loosely connecting the green granules of Hydra (p. 21).

Kützing (1841) helped to direct attention towards the protoplasmic part of plant cells, but unfortunately used a confusing terminology. He claimed that each cell of a conferva consists of three elementary parts: the outer 'Gelinzelle', the 'Amylidzelle', and the 'Gonidien'. The first, from his description, was clearly the cell-wall. The second was what von Mohl was later to call the Primordialschlauch, that is the layer of protoplasm lining the cell-wall on the inside. He describes the Amylidzelle as being coloured...
brown by iodine; weak acids, alcohol, and drying cause sudden contraction, which cannot be reversed by soaking in water. Kützing made the mistake of supposing that caustic potash converts this layer into starch. The third elementary part was the granular material enclosed by the Amylidzelle (starch-grains, &c.).

A considerable advance was made by Nägeli (1844), who found (pp. 90–1) that there is a slightly granular, colourless ‘Schleimschicht’ under the whole of the inner surface of the cell-wall of the fully formed cells of green algae and of some fungi. The chloroplasts and starch-grains are attached to it. The whole of the rest of the cells is filled with a water-clear fluid. Nägeli understood that his Schleimschicht corresponded to the Amylidzelle of Kützing, but he objected to the latter’s name, firstly because it is not a Zelle (in the sense of ‘box’), and secondly on chemical grounds (p. 96). The Schleimschicht, he found, consists of granular slime, which earlier filled the whole cavity of the cell and now lies just within the cell-wall. Its outer surface is smooth, but towards the interior of the cell it forms rather irregular projections. The name ‘cell’, he insists, is not suitable for such a structure. The Schleimschicht is coagulated by alcohol, weak acids, and water; these are the properties of nitrogenous plant-slime. It is coloured brown by iodine, and it is not changed into starch by potash, as Kützing had said.

These researches of Nägeli to a large extent forestalled the more famous work of von Mohl, who gave the name of Primordialschlauch, or utriculus primordialis, to the protoplasmic layer that lines the inside of the cell-wall of plants (1844, col. 275). This primordial utricle clearly corresponds to the Amylidzelle of Kützing and the Schleimschicht of Nägeli. Von Mohl’s term conveys clearly his realization that the cell-wall is not the primary or fundamental part of the cell. He mentions (col. 276) that when a nucleus is present, it lies in the primordial utricle, generally attached to its inner wall; when the nucleus is centrally situated, it is connected to the primordial utricle by slimy threads. The cell-wall stains blue with iodine, while the primordial utricle stains yellowish-brown.

Two years later von Mohl (1846) reintroduced the word ‘Protoplasma’. He was quite obviously unaware that Purkinje had already used the word in the same sense. The importance of von Mohl’s remarks on this subject justifies rather a long extract. He remarks (col. 73) that if we study a young plant cell, we never find that it contains a watery cell-sap: a viscous, colourless mass, containing fine granules, is dispersed through the cell and is aggregated especially in the vicinity of the nucleus. He thought that this substance was present before the nucleus appeared. ‘As has already been remarked,’ he writes (col. 75), ‘wherever cells are going to be formed this viscous fluid precedes the first solid structures that indicate the future cells. We must further suppose that the development of structure in this substance is the process that initiates the formation of the new cell. For these reasons there may well be justification if, for the designation of this substance, I propose in the word Protoplasma a name based on its physiological function.’
(In this translation I have used the expression ‘development of structure' to convey the meaning of von Mohl’s word ‘Organisation'.)

In a footnote von Mohl mentions that Schleiden used the word ‘Schleim' in the same sense. Von Mohl objected to this word because it was already used on the one hand loosely for any substance whatever that is of a slimy consistency, and on the other hand in a restricted sense as a synonym for mucus.

He describes (col. 76) how in young cells the nucleus always lies at the centre, surrounded by protoplasm. He proceeds (cols. 77–8) to an account of the origin of the cell-sap. ‘Irregularly distributed spaces form in the protoplasm, which fill themselves with watery sap. . . . The older the cell becomes, the more these spaces filled with watery sap increase in size in comparison with the mass of the protoplasm. As a consequence the spaces that have been described flow together into one another.'

It will be allowed that von Mohl had now arrived at a remarkably exact idea of the general plan of a plant cell.

The next necessary step was the discovery that protoplasm is the fundamental constituent of the cells of animals as well as of plants. It might be thought that since the word had first been applied to animal tissues, this step would have been an easy one; but Purkinje's ideas had not received the recognition that was their due, nor had his word ‘Protoplasma' been accepted by students of animal cells. The ground gained by Purkinje required to be recaptured.

To Ecker (1848) is due the recovery of the idea that there might be a fundamental substance common to animals of all grades of structure. His object was to discover what there was in lower animals corresponding to the contractile substance of higher animals. He felt that Dujardin's work on sarcode had been disregarded by most histologists. There had been a mistaken tendency to look for parts corresponding to those of the higher animals in the bodies of the lower. 'The body of the Infusoria...', he writes (p. 221), 'consists throughout of a simple, homogeneous, half-fluid, jelly-like substance, in which neither cells nor fibres are perceptible—a substance that is sensitive and contractile and in which the essential properties of the animal body are thus not yet confined to particular tissues.'

Ecker concentrated a good deal of his attention on Hydra, in which animal he failed to notice the muscular bases of the epithelial cells. He gave the name 'ungeformte contractile Substanz' to the sarcode of Infusoria and the living material of Hydra. He found that both were albuminous, soft, either wholly homogeneous and transparent or finely granular; both contained bladder-like spaces or vacuoles; both were in the highest degree elastic and contractile; both insoluble in water, though altered by it; both soluble in potassium hydroxide but hardened and contracted (so he said) by potassium carbonate (pp. 237–8). He claimed to have traced the development of the true striped muscle of the Chironomus larva from a completely homogeneous, fibreless, contractile substance.
Ecker's work was important chiefly for its influence on Cohn (1850), who listed the properties of the contractile substance of animals as described by Dujardin and Ecker and then went on to show that this substance was the same as the protoplasm of plant cells. His words (pp. 663–4) are of the utmost importance for the history of the discovery of protoplasm, and must be quoted in full: 'But all these properties are possessed also by protoplasm, that substance of the plant cell which must be regarded as the chief site of almost all vital activity, but especially of all manifestations of movement inside the cell. Not only does the optical, chemical and physical behaviour of this substance correspond with that of sarcode or the contractile substance (which I had the opportunity to study in the Infusoria, Hydra, and Naids)—in particular, both substances are very rich in nitrogen, are browned by iodine and contracted by stronger reagents—but also the capacity to form vacuoles is inherent in plant protoplasm at all times. . . .

'Hence it follows with all the certainty that can generally be attached to an empirical inference in this province, that the protoplasm of the botanists and the contractile substance and sarcode of the zoologists, if not identical, must then indeed be in a high degree similar formations.

'Accordingly, from the foregoing point of view, the difference between animals and plants must be put in this way, that in the latter the contractile substance, the primordial utricle, is enclosed within a rigid cellulose membrane, which allows it only an internal mobility, normally expressing itself in the phenomena of circulation and rotation—while in the former this is not so.'

Despite this last paragraph, Cohn did not regard the cell-wall as a fundamental part of the plant cell, for he wrote (pp. 655–6): 'In general I comprehend under the expression "primordial cell" that form of the primordial utricle which assumes the aspect of a cell and appears either altogether devoid of a rigid cell-membrane, or independent and isolated from one.'

It would be difficult to exaggerate the importance of the contribution to our knowledge of protoplasm made by Cohn in the passage just quoted. The contributions made subsequently by Unger, Schultze, Haeckel, and their contemporaries, were amplifications of ideas first formulated by Cohn.

Von Mohl now devoted a book (1851) to the characteristic features of the anatomy and physiology of the plant cell. He remarks (pp. 42, 44) that the protoplasm constitutes a relatively small part of the fully developed plant cell, owing to the large size of the spaces occupied by the cell-sap, which does not mix with the protoplasm. It is difficult to be certain of the exact meaning attached by von Mohl to his word 'Primordialschlauch'. Did he mean the whole of the protoplasmic layer that lies below the wall of the plant cell, externally to the vacuole? or did he mean only the external membrane of this protoplasmic layer? There are remarks on pp. 41–4 which suggest that he was referring to the cell-membrane in the modern sense; but other passages in his writings do not confirm this view, and he does not figure the cell-membrane separately from the protoplasm. He does, however, give a remarkably good figure of typical plant cells, reproduced here as Text-fig. 1.
Ramak (1852, p. 53) now adopted von Mohl's botanical word 'Protoplasma' in referring to the substance of the egg-cell and embryonic cells of animals. The course of progress was now briefly interrupted by an extraordinary episode. T. H. Huxley (1853) made an attempt to discredit not only the view that protoplasm is the fundamental living substance, but also the cell-theory as a whole. He recognized two constituents of tissues: the endoplast (which we should call the protoplasm) and the peri-plast (intercellular material). His object was to show that life depends primarily upon the intercellular material. 'So far from being the centre of activity of the vital actions', he writes (p. 306), 'it [the endoplast] would appear much rather to be the less important histological element. The peri-plast, on the other hand, which has hitherto passed under the names of cell-wall, contents, and intercellular substance, is the subject of all the most important metamorphic processes, whether morphological or chemical, in the animal and in the plant.' The endoplast, he says (p. 312), 'has no influence nor importance in histological metamorphosis.' 'We have tried to show', he says (p. 314), 'that they [the cells] are not instruments but indications—that they are no more the producers of the vital phenomena, than the shells scattered in orderly lines along the sea-beach are the instruments by which the gravitative force of the moon acts upon the ocean. Like these, the cells mark only where the vital tides have been, and how they have acted.'

In an important paper Unger (1855) brought strong support to the views that had been formulated five years before by Cohn. After considering the properties of plant protoplasm, and especially its movements, he concludes (p. 282): 'So all this suggests that protoplasm must be regarded not as a fluid, but as a half-fluid contractile substance, which is above all comparable to the sarcod of animals, if indeed it does not coincide in identity with the latter.' Schultze (1858) next described the movement of granules in marine 'diatoms and compared it with that seen in Noctiluca and in the pseudopodia of Gromia, Foraminifera, and Radiolaria. In his oft-quoted paper of 1861, which will be considered further in Part III of this series of papers, he mentions that Remak's adoption of von Mohl's word 'Protoplasma' for the substance of animal cells has not been generally copied, and says that he himself will use it henceforth. His example was probably influential. Schultze's account of the movement of granules in protoplasm was attacked by Reichert (1862a and b), who claimed that the appearance was illusory. Schultze (1863) had little difficulty in showing that Reichert was mistaken. He proved that the granules of Gromia and other rhizopods
are real and that they display characteristic movements during life. He also studied the hairs on the stamens of *Tradescantia* and the parts of other plants in which cyclosis is observed. He found a remarkable agreement. ‘The movements in the protoplasm of plant cells’, he writes (p. 65), ‘resemble those in the pseudopodia of the Polythalamia [Foraminifera] so closely, that when the arrangement of the protoplasm is of the kind that occurs, for example, in the cells of the staminal hairs of *Tradescantia*, no difference between the two kinds of movement is to be discovered.’ Schultze also showed that chemical and physical influences had similar effects on plant and animal protoplasm.

The pseudopodia of Foraminifera and Radiolaria lent themselves particularly well to studies of protoplasm. Haeckel (1862) made a careful investigation of its properties as revealed in the latter group. He used his powerful influence in support of Cohn and his successors. He wrote (Häckel, 1868, p. 108): ‘The protoplasm or sarcode theory—the doctrine that the albuminous contents of animal and plant cells (or more correctly, their “cell-substance”) and the freely motile sarcode of the rhizopods, myxomycetes, protoplasts, etc., are identical and that in both cases this albuminous substance is the originally active substrate of all the phenomena of life—may well be characterized as one of the greatest and most influential achievements of the newer biology.’ After paying tribute to the work of Cohn, Unger, and Schultze, he continues (p. 109): ‘I have myself striven for a number of years to support and extend this doctrine by numerous observations.’

Meanwhile a strange figure had entered the field. Beale was independent to the point of perversity; he insisted on using a private terminology of his own; and his writings were marred by their polemical character. Had he understood better how to integrate his own discoveries with those of others, he would have made greater contributions to research on protoplasm. Beale first made his ideas public in a series of lectures to the Royal College of Physicians in 1861 (Beale, n.d.). He distinguished between germinal and formed matter. The former, to which he ascribed the power of infinite growth, evidently corresponds to protoplasm, while the latter is the intercellular material. He regarded an affinity for carmine as a particularly striking character of the germinal matter. Beale’s chief interest was in the synthetic function of the germinal matter, and his important contributions to this subject will be discussed under the heading of Proposition IV. The nucleus was for him the quiescent part of the germinal matter. Eventually he accepted the word protoplasm and wrote a book with that name (Beale, 1892); but, wayward to the end, he remarks in it that ‘Nowhere in the world is the essential living element a “cell” ’ (p. 203).

Brücke (1862) brought a new insight into protoplasmic studies. He insisted (p. 386) that protoplasm has ‘Organisation’. He denied (pp. 401–2) that it is either solid or fluid. He objected to its being called a slimy or jelly-like substance, for he thought that this was like the description of a medusa as a gelatinous mass by someone who was ignorant of its organization. The
cell-contents must have a complex structure in order to be able to perform the vital activities. His argument was largely deductive and seems to have had little influence on his contemporaries; but it foreshadowed the outlook of a later generation.

Although the Foraminifera and Radiolaria were well adapted for research on the living substance, yet the wholly protoplasmic nature of the Mycetozoa, combined with their fairly large size and ready availability in inland laboratories, made them of predominant importance. In the face of organisms which, in their active, plasmodial phase, contain no ‘periplast’ whatever, it was impossible any longer to maintain such views as had been put forward by Huxley in 1853. It was this that gave special importance to de Bary’s careful study of the group. His description of the protoplasm of Mycetozoa (1864, p. 41) deserves quotation. ‘The ground-substance always presents itself as a colourless, translucent, homogeneous mass, exactly similar to the homogeneous contractile substance that is known in the body of amoebae, rhizopods, etc., and is designated as *sarcode*, unformed contractile substance, and latterly, like the component of plant-cells which is in many respects analogous, as *protoplasm*. . . . As for its chemical character, rose-red colouring with sugar and sulphuric acid and with Millon’s reagent, together with yellow colouring by iodine, indicate a rich content of albuminous substances. Alcohol and nitric acid cause coagulation; in acetic acid the substance becomes thin (blass) and transparent; in potassium hydroxide solution, even when dilute, it dissolves; the same occurs in potassium carbonate solution, though often after the first action of this reagent has produced a contraction.’ It will be agreed that this is a remarkably exact short description of protoplasm.

Kühne (1864) brought strong evidence from many sources of the close similarity of plant and animal protoplasm. He studied the living substance in *Amoeba, Actinophrys, Didymium* (a mycetozoan), in the cells of the connective tissue and cornea of the frog, and in those of the staminal hairs of *Tradescantia*. He observed protoplasmic movements and noted the effects of reagents, of temperature changes, and of the passage of an electric current. He obtained protoplasm from staminal hairs (pp. 100-1) and was so struck by its resemblance to that of *Amoeba* that he called particles of it ‘vegetabilische Amoeben’.

Huxley’s rhetoric was now to be used once more on the subject of protoplasm. Without giving any indication that he had reversed his opinions or had made any observations or experiments that could cause him to do so, he plunged into powerful support of the protoplasm theory. The occasion was a Sunday evening address given in the Hopetoun Rooms, Edinburgh. According to the careful report given in the *Scotsman* (Huxley, 1868, p. 7), he described protoplasm as ‘the bases [sic] of physical life’; the expression ‘the physical basis of life’ first appeared in print as the title of his article in the *Fortnightly Review* (Huxley, 1869), which followed closely the Edinburgh address. ‘Beast and fowl,’ he wrote (pp. 134-5), ‘reptile and fish, mollusk,
worm and polype, are all composed of structural units of the same character, namely, masses of protoplasm with a nucleus. . . . What has been said of the animal world is no less true of plants. . . . Protoplasm, single or nucleated, is the formal basis of all life.' The discovery had been made by others: Huxley's contribution was first opposition and then a phrase.

It is to be noticed that the essential similarity between the living matter of plants and animals was discovered by examination of the ground cytoplasm before the existence of mitochondria in both was recognized.

A relatively small point remains. Russow (1884, pp. 578–9) discovered that in the medullary rays of certain plants there exists intercellular material that colours like protoplasm with iodine and dyes. In Acer he found thin threads connecting this intercellular with cellular protoplasm. In the same year Fromman (1884) claimed that protoplasm exists in the intercellular spaces of the hypocotyl of Ricinus. Like Russow, he said that it reacted to iodine and dyes in the same way as cellular protoplasm. He stated that it often contains single starch grains and small chloroplasts. Intercellular material had already been studied in the cotyledons of the pea by Tangl (1879), who regarded it, however, as secreted matter. The corresponding intercellular substance in the cotyledons of Lupinus was seen and figured by Michniewicz (1903), who later saw bridges connecting it with cellular protoplasm (1904). The intercellular material in the cotyledons of Lupinus was studied in considerable detail by Kny (1904a). He found that reactions for proteins were positive. He concluded from the bleaching of methylene blue solutions and the blue coloration with guaiacol and hydrogen peroxide that the intercellular material respires. Indeed, he found that it showed the same reactions as cytoplasm in all respects, except that studies with proteolytic enzymes suggested that it contained more protein. His general conclusion was that the substance was in fact intercellular protoplasm. In a second paper (Kny, 1904b) he showed that it is connected with the cells of the cotyledons by narrow bridges. Like Russow, he found that intercellular protoplasm may contain small starch grains.

This subject would be of considerable importance from the point of view of the cell-theory if it could be shown that intercellular protoplasm ever exists in the absence of any connexion with nucleated cells; but this would not appear to be so. The tissues of animals do not provide any close counterpart to the intercellular protoplasm that occurs occasionally in plants.

The Discovery of the Nucleus

Some of the older botanical writers (e.g. Balfour, 1854) call the nucellus of the ovule the nucleus. This may give rise to misunderstanding. It was stated by Meyen (1839, p. 250), for instance, that both Grew and Malpighi saw the 'Kern' of the 'Eychen' (ovule) of plants. On the same page he uses the word 'Nucleus' as equivalent to 'Kern'. Reference to the relevant parts of Grew's and Malpighi's works shows that there is no question of the
object named being-a nucleus in the modern sense (see Grew, 1682, p. 210 and Tab. 82; Malpighi, 1687, p. 71, and Fig. 233 on Tab. xxxvii).

Nuclei were in fact first seen by Leeuwenhoek, whose description of them is contained in a letter sent to the Royal Society in 1700 (see Lewenhoek, 1702, p. 556; Leeuwenhoek, 1719, p. 219). The discovery was made in the red blood corpuscles of the salmon. His description of the figure made by his draughtsman (see Text-fig. 2) is as follows:

'Fig. 2 ABCD represents the oval particles of the Blood of a Salmon that weighed above thirty pound.

'AB represents the particles that appeared flat and broad, but did not face the eye directly.

'Those about c came straight upon the eye, and for the most part had a little clear sort of a light in the middle, larger in some than in others, which the Engraver has done his utmost to imitate.'

There can be no doubt that the 'little clear sort of a light' (lumen in the Latin version (Leeuwenhoek, 1719)) was the nucleus. Leeuwenhoek also saw nuclei in the blood of a small fish which he calls 'Butt' (1702) or 'Botje'. 'Butt' was a general term in English for flat-fish; in modern Dutch 'bot' is the flounder. Figs. 3 and 4 in Leeuwenhoek's plate (reproduced here as Text-fig. 2) represent the red blood corpuscles of this fish. He refers to the nuclei as 'little shining spots' (1702, p. 557).

Nuclei were seen by some of the early students of Protozoa. Writing to Réaumur in 1744 Trembley gave some sketches of *Stentor* that show the moniliform macronucleus clearly (see Trembley, M., 1943, p. 207). The same observation was made on *Stentor* by Müller (1786, Tab. xxxvi, 8), who calls the macronucleus 'Series punctorum pellucidorum' (p. 262). Müller appears also to have seen the macronucleus in a species of *Colpoda* and a few other ciliates, but there is no indication that he recognized its homology in the different forms. Much later Ehrenberg (1838) saw the macronuclei of many ciliates (*Amphileptus, Nassula, Chilodonella ('Chilodon'), Paramecium, Spirostomum, Stentor*; see his Plates xxiii, xxiv, xxxvi, xxxix), but did not understand their nature. It is convenient to mention Ehrenberg in connexion with this early stage of the history, because his work on the subject was not related to the nuclear research of his own period, for in
accordance with his opinion that the ciliates were 'volkommene Organismen', he regarded their macronuclei as male reproductive glands (see, for example; pp. 262, 332, 352).

Hewson (1777) illustrated the nuclei in the red blood corpuscles of many vertebrates—birds, viper, slow-worm, frog, and fishes—and also saw them in the turtle. He made the understandable mistake of suggesting their presence in his figures of the red blood corpuscles of mammals. He was the first to see the nucleus in the blood corpuscle of an invertebrate. 'If one of the legs of a lobster be cut off,' he writes (p. 40), 'and a little of the blood be caught upon a flat glass, and instantly applied to the microscope, it is seen to contain flat vesicles, that are circular like those of the common fish, and have each of them a lesser particle in their centre, as those of other animals.'

Fontana (1781) would appear to have been the first to have seen nuclei in tissue-cells other than those of blood. He made a microscopical study of the slippery substance that coats the skin of eels and described the 'globules' or 'vesicules' contained in it, which were almost certainly epithelial cells derived from the epidermis. 'One saw,' he says (p. 276), 'a little body internally, situated in different parts of each globule.' He means that there is not a characteristic position for the little body within the cell. His figures (e.g. Fig. 9 of Plate 1 in Vol. 2) strongly suggest that the 'petit corps' was the nucleus. Indeed, Fig. 10 shows what seems to be a nucleolus within the nucleus. Fontana says, 'The vesicle a in Fig. 10 represents one of the vesicles of Fig. 9, in which one observes an oviform body [the nucleus], having a spot (tache) in its interior.' This 'tache' is probably the earliest illustration of a nucleolus. A life-like view was obtained of these cells because they lay in a medium of suitable osmotic pressure. The early observers were accustomed to tease up tissues in water, in preparation for microscopical examination; and it was only when nature provided a suitable medium and thus made the addition of water unnecessary that good views of tissue-cells were obtained.

When Purkinje discovered the germinal vesicle of eggs, he had no means of knowing that there was any correspondence with the 'lumen' seen in the blood corpuscles of fishes or with the 'petit corps' in the epidermal cells of eels. The discovery was not widely known until five years after it had been made. The Faculty of Medicine at Breslau had decided to congratulate Blumenbach in 1825 on the fifteenth anniversary of his taking his doctor's degree, and they wished to send him an original scientific paper to mark the occasion. Purkinje's offer to write a memoir for this purpose was accepted. It was made available to the world at large in 1830 (see Purkinje, 1830 and 1871). The germinal vesicle of the hen's egg was described in this memoir as follows (1830, p. 3):

'Thus the scar [germinal disk] of the ovarian egg contains a special part, peculiar to itself, a vesicle of the shape of a somewhat compressed sphere. This vesicle is limited by a very delicate membrane and filled with a special
fluid; perhaps connected with procreation (for which reason I might call it the germinal vesicle); it is sunk into a white breast-shaped projection composed of globules and perforated in the middle.’ This remarkable passage contains the earliest mention of the objects later to be named the nuclear membrane and nuclear sap.

Coste (1833, col. 243) showed that the egg of the rabbit contains a vesicle corresponding to that discovered in the hen’s egg by Purkinje. He later published a monograph (Coste, n.d.) giving figures of the nucleus of the rabbit’s egg. In the description of his Fig. 2 he labels the nucleus ‘vesicle analogous to that which Purkinje has demonstrated in birds’. Bernhardt (1834), who knew of Coste’s work, found the nucleus, or ‘vesicula prolifera’ as he called it, in the egg of ruminants and of the rabbit, squirrel, bitch, cat, mole, and bat. He gives figures showing the nucleus in the eggs of several of these, and remarks that with certain precautions even a ‘tiro’ could see it. He says (p. 27) that it is round or nearly round or oval and has a sharp outline. The contents are fluid.

Meanwhile, nuclei had been discovered in plant cells. Bauer made drawings in 1802 which showed them in the cells of the loose tissue lining the canal of the stigma of the orchid, *Bletia Tankervilliae*. These drawings were unfortunately not published until much later (Bauer, 1830-8; see Tab. VI). Nuclei were probably seen from time to time in plant tissues without anyone guessing that they had any general significance. For instance, Meyen (1830, Plate III) shows what look like nuclei in the pith of the stem of *Ephedra*, though he himself regarded them as consisting of resin-like material. Brown, who knew of Bauer’s drawing of *Bletia*, was the first to recognize that the nucleus is of more than sporadic occurrence, and it was he who coined the name by which this part of the cell has been known ever since. His words are as follows (Brown, 1833, pp. 710-11): ‘In each cell of the epidermis of a great part of this family [Orchidaceae], especially of those with membranaceous leaves, a single circular areola, generally somewhat more opaque than the membrane of the cell, is observable. . . . This areola, or nucleus of the cell as perhaps it might be termed, is not confined to the epidermis, being also found . . . in many cases in the parenchyma or internal cells of the tissue. . . . I may here remark, that I am acquainted with one case of apparent exception to the nucleus being solitary in each utriculus or cell.’ Brown also saw the nucleus in various cells of Liliaceae, Iridaceae, and Commelinaceae, and in a few cases also in the epidermis of dicotyledons.

The nucleolus, which had been recorded by no observer since Fontana, was now discovered by Wagner (1835) in the oocytes of various animals (*Ovis* (Fig. 2 on Tab. VIII), *Salmo, Phalangium, Anodonta, Unio*). He called it the Keimfleck or macula germinativa. The recognition of the nucleolus was important, because it helped in the identification of nuclei.

From 1836 onwards reports came repeatedly of the existence of nuclei in animal cells. Purkinje (1836) announced that the Körnchen (cells) covering the choroid plexus (apparently of man) are each provided with a small
'Körperchen'. Valentin (1836a, p. 97) introduced the word nucleus into the literature of animal cytology. Writing of the cells of the epithelium covering the vessels of the choroid plexus of the brain, he says: 'But each of them contains in the middle of its interior a dark, round kernel (Kern), a structure that reminds one of the nucleus that occurs in the plant kingdom in the cells of the epidermis, of the pistil and so forth.' Valentin classifies the epithelia, distinguishing those in which the cells are nucleated from those in which (as he supposes) they are not (p. 96). In a passage of quite extraordinary interest he makes a careful comparison between the egg and the nerve-cell. The latter he calls the formative sphere (Bildungskugel). 'But in what an astonishing way', he exclaims (pp. 196–7), 'does the basic idea of the form of the unfertilized egg correspond with the basic idea of the structure of the formative spheres!' He compares the membrane of these cells with the vitelline membrane, their 'Parenchym' (cytoplasm) with the early yolk, and their nucleus with the germinal vesicle; and he says that a 'Keimfleck' (nucleolus) occurs in both. In a second paper published in the same year (Valentin, 1836b), he again uses the word nucleus, stating (p. 143) that every cell without exception in the epithelium of the conjunctiva of man contains one. He mentions also that the nucleus itself here contains 'a perfectly spherical particle'.

The year 1837 saw the publication of a book of the first importance by Henle (1837), who now described nucleated cells in very diverse human tissues, including even the skin of the glans penis. He uses the word 'Cylindri' when referring to cells of columnar epithelium, but elsewhere uses 'Cellulae'. In describing his Fig. 4 he refers to the 'Cellulae nucleatae' of the human conjunctiva. He illustrates the nuclei of the epithelium of the trachea particularly clearly (Fig. 10). He mentions (p. 4) that the nucleus sometimes contains granules. It is not too much to say that this work, with that of Valentin (1836a), marks the beginning of an epoch in cytology, the epoch of the nucleated cell. Purkinje's name for the nucleus of the egg was, however, not readily relinquished. Siebold (1837) noticed the nuclei in the eggs and blastomeres of nematodes, but called them the 'Keimbläschen' and the 'Purkinjesche Bläschen' in the former case (p. 209) and 'hellen Flecke' in the latter (p. 212). He calls the nucleolus of the egg the 'Keimfleck'. These names, with their counterparts in other languages, persisted long afterwards, even when the homologies of the objects named were well understood.

The year 1838 brings us face to face with Schleiden and Schwann. To assess their significance in the advancement of cytology is a difficult task for the historian, and a task that has often been lightly undertaken. Too much credit has undoubtedly been given to them by some, and a reaction against exaggerated praise has produced a literature of rather superficial belittlement. It is necessary to realize in what field their chief contributions lay. They lay exactly here, in the part of this second proposition that is concerned with the nucleus. If there had been no Schleiden and no Schwann there would have been considerable delay in the general realization by
biologists that the possession of a single nucleus is a characteristic feature of most of the cells of animals and plants. Their work, taken together, provided most powerful evidence that there is a correspondence or homology ('Uebereinstimmung', Schwann called it) between the cells of the two kinds of organisms. Their ideas were far from being so original as has often been supposed; for Schleiden had his precursor in Brown, and Schwann in Purkinje, Valentin, and Henle. The three latter had made great advances in animal cytology during a period in which Brown's work on plant cells was scarcely being followed up, and Schleiden's contribution, therefore, represented a more sudden advance than Schwann's; and Schleiden was also ahead of Schwann and communicated his ideas to him in conversation. Indeed, one of Schleiden's most important functions was to act as a stimulus to Schwann: for one can scarcely read the writings of the two men without realizing that Schwann had the greater mind and made much the more massive contribution. These facts stand out even if we deliberately ignore the polemical character of much of Schleiden's writings. It must be allowed that Schleiden had too much influence on Schwann, for the latter took over, without sufficient investigation, his erroneous views as to the origin of cells. That, however, is beside the point for the present: we are here concerned with the great influence of these two men in getting the nucleated cell recognized as the fundamental building-stone of most organisms.

Schwann tells us (1839a, p. 8) that during the course of his work on the nerves of the tadpole of the frog he saw the cells and nuclei (Kerne) of the notochord. In his report on the subject (Schwann, 1837) he said nothing about the notochord; but the image of the notochordal cells remained in his mind. 'One day, when I was dining with Mr. Schleiden,' he tells us (Schwann, 1884, p. 25), 'this illustrious botanist pointed out to me the important role that the nucleus plays in the development of plant cells. I at once recalled having seen a similar organ in the cells of the notochord, and in the same instant I grasped the extreme importance that my discovery would have if I succeeded in showing that this nucleus plays the same role in the cells of the notochord as does the nucleus of plants in the development of plant cells.' The two scientists repaired at once to the anatomical institute in Berlin in which Schwann worked. There they examined together the nuclei of the notochord, and Schleiden recognized the close resemblance to the nuclei of the cells of plants.

Neither had yet published. Schwann was the first to do so, but it will be convenient to begin with Schleiden's contribution, the 'Beiträge zur Phyto-genesis' (1838). It is difficult to escape from a sense of disappointment on reading Schleiden's paper. There is nothing about a 'cell-theory' in it; it is solely concerned with plants; and it contains a great deal of error in connexion with the origin of cells, together with much that is of secondary interest. In one respect, however, it was of first-rate importance: the regular occurrence of nuclei in the young cells of phanerogams was here for the first time demonstrated. Schleiden thus focused attention on the nucleus as a
characteristic component of the cell. He was also the first to discover the nucleolus of plant cells, without realizing that it corresponded with the 'Keimfleck' already known in both germinal and somatic cells of animals. He calls it a small body (Körper, p. 141), but does not name it. He regards it as 'consistenter' than the rest of the nucleus. He shows it in several figures (see especially Fig. 25 on Tab. III). Beyond all this, Schleiden produced some ideas on cellular individuality, which will be considered under Proposition V.

Schwann's great contribution was his massive array of evidence that there is an 'Uebereinstimmung' between the cells of plants and animals. He himself concentrated upon the latter, relying on the researches of Schleiden for his knowledge of plant cells. We have already seen in the discussion of Proposition I that others had previously suggested such a correspondence between the plant and animal cell; but Schwann was struck with enormous force by the fact that each contains a corresponding object, the nucleus, itself containing a corresponding organelle, the nucleolus, which he called the 'Kernkörperchen'. It seems clear that he reached his conclusions from his own studies of animal cells and from discussion with Schleiden, before he knew of the discovery by Purkinje, Valentin, and Henle that the nucleated cell is a common constituent of animal tissues. He went much farther than these three: he found the nucleated cell to be not simply a common constituent, but the fundamental basis of structure. He founded his 'Zellen-theorie' (1839a, p. 197) chiefly on his own discoveries. His contributions to the problem of cellular individuality will be mentioned under Proposition V.

In his first cytological paper (1838a) Schwann notes the strong resemblance to the cellular tissues of plants shown by notochordal tissue and cartilage, which he had studied in the larvae of the spade-footed 'toad', Pelobates fuscus. He mentions the nuclei of both kinds of cells, each containing one or more 'Kernkörperchen'. He regards the embryo as cellular: 'Since therefore the serous and mucous layers of the blastoderm consist of cells and the blood corpuscles are cells, the foundation of all organs that appear later is composed of cells.' He mentions ganglion and pigment-cells and describes the cellular nature of the lens of the eye and of cancerous growths. This paper was published in January 1838. In it Schwann refers to the forthcoming article by Schleiden (the 'Beiträge'), and claims that the latter's statements about the way in which plant cells multiply are applicable also to animals.

Schwann begins his next paper (1838b) by stressing the importance of the nucleus in showing the correspondence between animal and plant cells. Most of the observations reported here were made on pig embryos. He records the cellular nature of horny matter, of the lining of the amnion and allantois, the surface of the chorion, the alveoli for the teeth, and the surface of tooth-pulp: all consist of cells with nuclei. He is puzzled, naturally enough, by striated muscle. He finds nuclei in the cells of the kidney, salivary and
lachrymal glands, liver, and pancreas. He notes the nucleated cells in connective tissue and considers the white fibres as projections from them. He records the cellular nature of feathers. ‘So the whole animal body, like that of plants,’ he remarks, ‘is thus composed of cells and does not differ fundamentally in its structure from plant tissue.’ In his third contribution on this subject, published in April of the same year (1838c), he deals with the cellular structure of cartilage, and shows that nail, fat, and unstriated muscle consist of or develop from nucleated cells. The paper ends with an appendix by J. Müller, in which the existence of nucleated cells in pathological growths (osteo-sarcoma, &c.) is recorded.

The valid factual part of Schwann’s great book, which was published in the following year (1839a), consists largely of a reiteration of what he had already made known in these three papers. It contains, however, a considerable amount of interesting theoretical matter, which will be discussed at the appropriate places in future parts of this series of papers.

Meanwhile, Purkinje, Henle, and Valentin had continued to make discoveries in the same field. Purkinje (1838a) mentions the ‘Centralkern’ in the ‘Körnchen’ (cells) of the liver. He also gives (1838b) an excellent figure of nerve-cells from the black substance of the cerebral peduncle of man. This is reproduced here (Text-fig. 3) so as to give a visual impression of what others were doing in the year in which Schleiden and Schwann made their results known. The nucleus, nucleolus, and pigment are well seen in the figure. Henle followed up his book (1837) with a paper (1838) in which he gave a detailed description of the cellular nature of the epithelia of the human body, including even the lining of the blood-vessels. He is, of course, familiar with the nucleus and the nucleolus; the former he here calls the ‘Kern’ and the latter, unfortunately, the ‘Nucleus’. A useful reminder of the state of knowledge at the time of Schleiden’s and Schwann’s contributions is provided by the fact that Henle’s paper occurs before Schleiden’s ‘Beiträge’ in the same volume of the journal. About the same time Valentin (1838) contributed a curious paper on the differentiation of the cells of the human embryo into their definitive forms. He tried to follow the behaviour of the nuclei (Zellenkerne) during differentiation. What he writes on this subject contains much error, but he was striking out on an important new line and at least he made it clear that the nucleus is far less liable to modification during differentiation than the rest of the cell. Next year Valentin made an unequivocal statement of the correspondence of the nucleated cells of plants
and animals (1839a, p. 133). He remarks that Schwann has completed the comparison between them.

Valentin now introduced the word 'Nucleolus', in the course of an abstract of Schwann's book (Valentin, 1839b, p. 277). He does not mention that he is coining a word, but simply says, 'In mammals the cartilage-corpuscles appear to constitute the whole cell and as such to contain nucleus and nucleolus.' (Turner (1890a, p. 11) is wrong in saying that Schwann introduced the word.)

The story of the nucleus may be rounded off by mention of Nägeli's demonstration (1844) that this organelle is a characteristic component of the cells not of phanerogams only, but of all kinds of plants from algae upwards. Thenceforth there was seldom any difficulty in recognizing nuclei; appeal was made especially to the nucleolus as a distinguishing feature in cases of doubt. The use of stains in microtechnique was repeatedly rediscovered during the years 1848–58, as I have told elsewhere (Baker, 1943), and this naturally gave a great impetus to the study of what is usually the most stainable object in cells. Huxley's attempt (1853) to discredit the nucleus is therefore all the more extraordinary. He tells us (p. 297) that Schleiden's belief in the existence of nuclei in all young tissues is 'most certainly incorrect'. The nucleus, he says (p. 298), 'has precisely the same composition as the primordial utricle.' Little attention, however, appears to have been paid to him. From the forties onwards the position of the nucleus in cytology was secure: it was regarded as an essential constituent of the cell. It is to be noted that this conclusion was reached long before there was any general agreement that protoplasm was also a necessary constituent. This may at first seem strange; but it must be recollected that the nucleus is obviously easier to recognize than protoplasm, on account of its having morphological as well as physical and chemical characters.

The discussion of Proposition II will be continued in Part III of this series of papers. I thank Prof. A. C. Hardy for his valuable criticism of the typescript of this paper, and Miss O. Wilkinson for conscientious clerical assistance.

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