PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

Evolution of the Cell Theory

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SUMMARY

The problem of the nature of life has a long history going back to the Greeks. There was little real progress until the 19th century and Aristotle may have been at home with many 18th century ideas about vital forces and basic units. Although Hooke described cells in 1665 it took a further 200 years for the significance and nature of cells to be appreciated. In the mid 18th century some considered the basic building blocks of living matter to be fibrous. Globular theories, the precursor to the cell theory, were quite popular at the beginning of the 19th century. Many workers, as microscopes improved, had described various cell types and structures including the nucleus but the idea that cells were the universal units is associated with in 1838 and that of Schwann in 1839. However, Schwann mistakenly thought that cells could form *de novo*. Cell division was established by Remak and others in the 1850s. Mitosis was first understood by Flemming in 1882. The existence of the animal cell membrane was only established by the beautiful experiments of Overton in 1895. The history of the cell theory can be used to show that progress can be based on incorrect but productive ideas. It is one of the most important ideas in all of biology.

1. INTRODUCTION

Cell theory is one of the great triumphs of biology, and its history should occupy a more central position than it currently does. One can even think of its history in evolutionary terms, new ideas and observations being selected for their 'fitness' in terms of how reliable they are and how well they describe nature (Toulmin 1967). Moreover, as will be seen, the evolution of the theory was gradual.

As with all science, ideas about the nature of life started with the Greeks. They assumed the existence of a simpler world that underlay the everyday world of experience. For example, they tried to explain the variety of everyday phenomena by theories in which matter was put together in different ways so as to generate this variety. Thales' idea that everything is made of water in different forms, in a very general way, foreshadows the cell theory.

Yet there was very little progress in understanding the nature of organisms until the late 18th century (Hall 1969). There was in biology no one equivalent to Archimedes or Galileo; perhaps biology was just too difficult and without good microscopes cell theory was impossible. It would not be unreasonable to think that Aristotle would have felt quite at home with 18th century biology. For the common idea that life was a result of some sort of vital force activating basic units, or particles, was essentially a Greek idea. Even Lamark's early ideas were couched in terms of the Greek four elements – fire, water, air and earth.

A more mechanistic approach to life did evolve in the 17th century. Robert Boyle, for example, argued that whenever matter changed form, whether living or not, physical agents were at work! '...if an angel himself should work a real change upon the nature of a body, it is scarcely conceivable to us men, how he could do it without the assistance of local motion.' By contrast George Stahl (1649–1734), inventor of the phlogiston theory, believed that living organisms were best understood as being driven by the action of a soul. This was a strong vitalist position.

Many of the problems biologists faced at that time were simply not resolvable with the techniques and knowledge of the time. For example, the controversy over preformation and epigenesis could not be settled until the cell theory had become firmly established (Wolpert 1991). Even so Buffon (1707–1785) assumed that organisms were composed of minute bodies which in turn were made up of living molecules.

2. EARLY CELL THEORY

The introduction of the microscope made the study of cells possible. It was an exciting new world. Robert Hooke (1665) writes: 'By means of telescopes there is nothing so far distant but may be represented to our view; and by the help of microscopes, there is nothing so small, as to escape of enquiry; hence there is a new visible world discovered to the understanding...in every little particle of matter, we now behold almost as great a variety of creatures, as we were able to reckon up in the whole universe itself.'

To Hooke must be given the credit for having first described cells. Examining a slice of cork under the microscope he described the air-filled spaces of dead cells and, from his examination of bones and other plants, concluded that they were channels for fluid conduction. He did not, however, appreciate the

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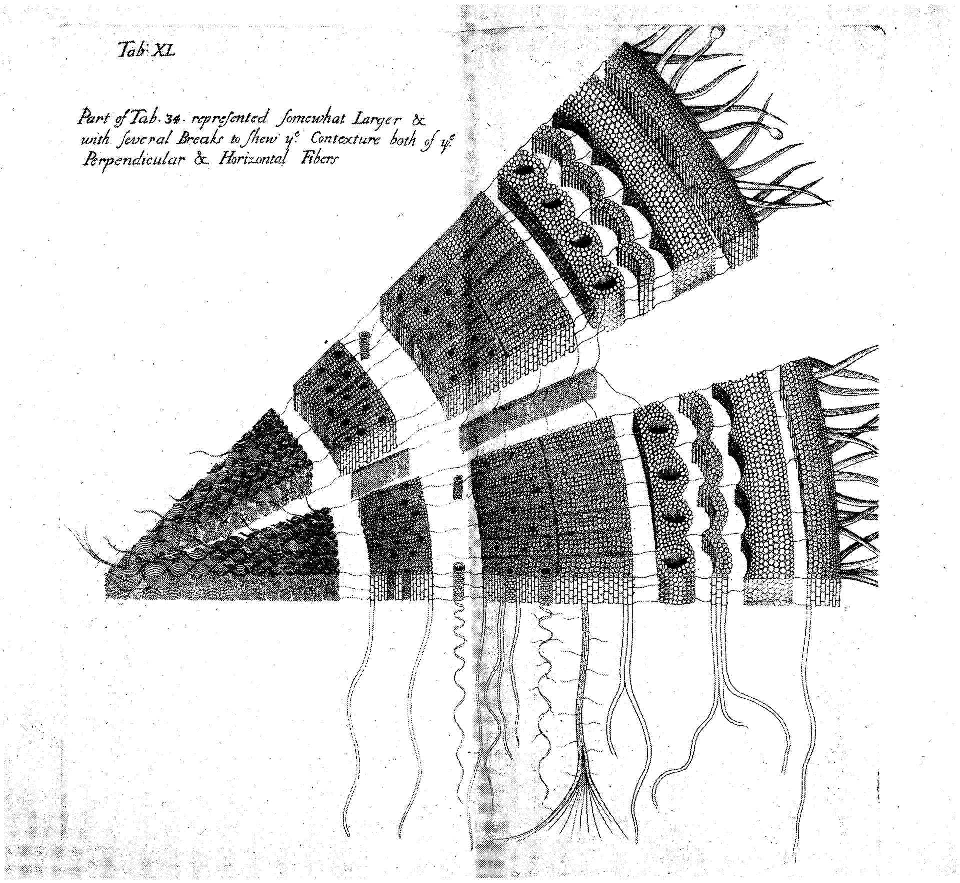

Figure 1. Grew's (1682) drawing of plant tissue. Although the cells are clearly outlined, he interpreted them as bladders woven from fibres. (Wellcome Institute Library, London.)

significance of his discovery and it is perhaps a good contrary example of Pasteur's dictum that fortune favours the prepared mind. It was to take nearly two hundred more years for the significance of this discovery to be appreciated.

Hooke was not alone in discovering cells and not realizing their significance. Nehemiah Grew, an English physician, described plant tissues as bladders clustered together. His beautiful drawings seem to outline cells but he interpreted them as vessels woven from fibres (figure 1). In the 1670s van Leeuwenhoek described his animalcules – protozoa – in pond water and also sperm but it was to take even longer to recognize that these too were cells. Leeuwenhoek also observed globules in blood and talked of the brain being made of globules.

It is an important but unsolved problem why these early investigators did not develop a cell theory. Most likely the microscopes were just inadequae together with techniques for preparing the tissues. Perhaps they could not conceive of a fundamental living unit. Again, perhaps, they focused too much on vessels and the transport of nutrients. But perhaps the real key was that, while in plants cells are easily recognized by their cell walls, this is not the case in animals. The presence of vessels and fibrous structures like tendons and muscles must have made it hard to imagine animals were constructed of units similar to those of plants.

There was also considerable interest in fibres. Albrech von Haller, probably the best known physiologist of the 18th century, defined an elementary fibre as the structural unit of the body: 'A fiber is for a physiologist what the line is for a geometer, that out of which all other figures are constructed.' He located the property of irritability – contraction following stimulation – 'in the elementary fibers of muscle'.

A different view was held by those like the embryologist Christian Wolff who thought embryos were made up of globules. William Hewson, another globulist, in 1771 confirmed Leeuwenhoek's finding of globules in the blood and that they swelled and shrank in different solutions, one of the very earliest experiments in cell biology, possibly the first. And in describing the contents of the lymphatic gland he refers to 'an almost infinite number of small cells'.

The globulists' view might be thought of as being the precursors to the cell theory. For example Brisseau de Mirbel, in the early 1800s, started 'from the principle that the entire mass of the plant is a cellular tissue' but he conceived it not as cells, but as 'a continuous structure, containing cavities like bubbles in a froth'. Oken, too, was a globulist who put forward the idea that the higher organisms were an association of simpler microscopic organisms and that this explained the emergence of 'infusoria' when animals and plants decomposed. Johann Moldenhawers' contributions of 1812 are particularly important for he macerated tissues and reported that 'When maceration is carried out with appropriate care it decomposes the cellular substance into individual bladders that persist independently'. He nevertheless believed that fibres held the globules together.

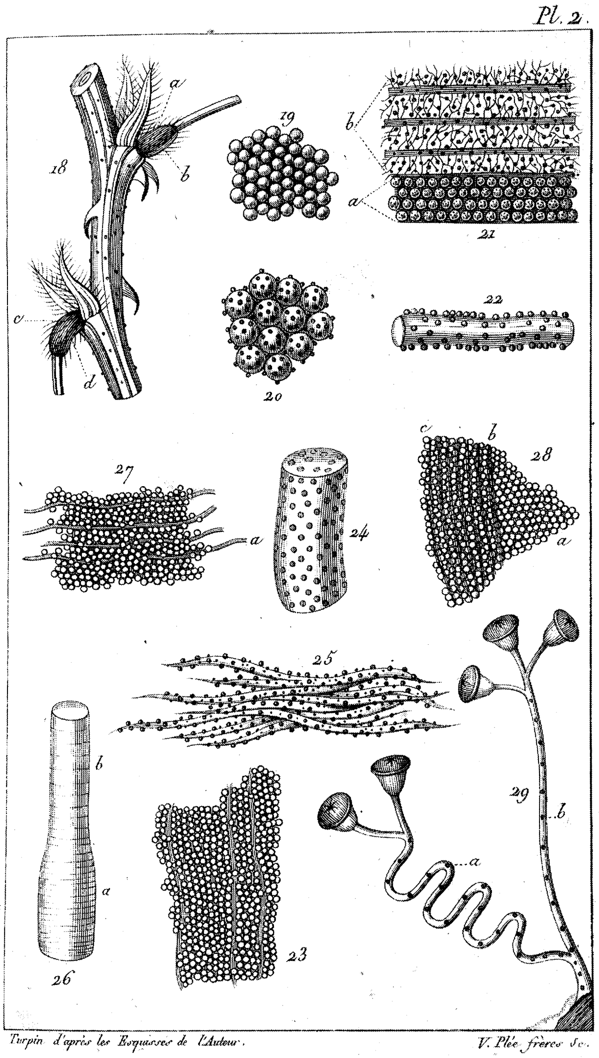

Figure 2. Dutrochet's (1824) drawings of plant and animal tissues: 19 and 20 show cells that may be from an apricot and snail respectively; 25 shows muscle fibres with corpuscles adhering to their surface. (Wellcome Institute Library, London.)

Two of the later globulists are Henri Milne-Edwards and Henri Dutrochet. Milne-Edwards reported that all the globules in animal tissue are alike with a diameter of 1/300 mm (3 μm) and concluded in 1826 that 'the most complicated animal, like the simplest, is only formed from a greater or lesser number of these corpuscles'. Dutrochet in 1824, relying heavily on Milne-Edwards' animal work, together with his own botanical observations, put forward a theory to the effect that animals and plants have a similar cellular structure (figure 2). This theory was essentially based on cells as globules or bladders that were defined by their walls. But whether he really saw animal cells clearly is disputable (Wilson 1947). Francois-Vincent Raspail put forward a similar theory in 1833 and Duchesneau (1987) suggests that he and Dutrochet are important forerunners of Schwann's cell theory. Both were critical of vitalism and adopted a physicochemical approach with crystallization as a metaphor. Raspail however did not completely dismiss some organizing force: 'This law of organization, so incompletely known, we have got into the habit of designating it by a word – vital force – and as this word is equivalent to *x* in algebra, disputes that have no other object but to replace it or to accept it, are just idle, and completely unprofitable.... What does it matter to me if you replace the term *vital force* by chemical force, if you are obliged to admit that this latter has no firm connection with the chemical properties of the unorganized world.'

It is worth noting the critique of many of these observations by Hodgkin & Lister in 1827 using the new achromatic microscope. They pointed out that many of the globules that had been observed were probably optical artefacts.

Attention had also been given to the origin and growth of these globular structures. These theories were mainly based on exogeny – the origin of cells from outside existing ones (Baker 1953). Trembley as early as 1744 had described the division of protozoa and there are descriptions of cleavage in early embryos but in no case were they regarded as being division of cells. By contrast Hugo von Mohl, in 1837, specifically set out to investigate the common assumption that 'each cell must be very small in the beginning and must only gradually grow to its full size'. He wanted to observe the process and chose a green filamentous alga where he discovered cell division by formation of a partition. This had also been described by Dumortier five years earlier in 1832.

It is thus clear that there were by 1830 quite widely held views about the cellular nature of organisms. Stephenson (1931) points out that Meyen's textbook on plant anatomy (1830) has a chapter on the structure of cells which are said to unite to form cellular tissues, and he discusses the occurrence of cells both singly and in masses. Others like Purkinje, his pupil Valentin and Muëller were, to varying degrees, assigning cells a key role in biological structure, but still distinguishing cells from fibrous structures. By 1836 the nucleus discovered by Robert Brown in 1831 was a relatively familiar structure, including the nucleolus named by Jacob Schleiden.

The main country doing biological research at this time was Germany and the romantic movement had considerable influence (Jacyna 1984). This movement proposed a research programme that looked for unity and essences in Nature and life. Evidence for the unity in nature had already been supported by the doctrine of primitive types, particularly influential being Karl von Baer's (1838) work on embryology. He had shown how 'the further back in embryogeny we go, the more we find a resemblance even among very different animals'. Comparative anatomy too was establishing similarities. It was a time when a general theory relating to the fundamental units of life would have found a warm reception. Even so it was also a time when the idea of a vital force was held by many workers.

3. CELL THEORY

The names of Schleiden and Schwann are almost as closely linked to the origin of cell theory as are Watson and Crick with DNA. There are indeed some similarities for like Watson and Crick they had quite different backgrounds and met by chance in the

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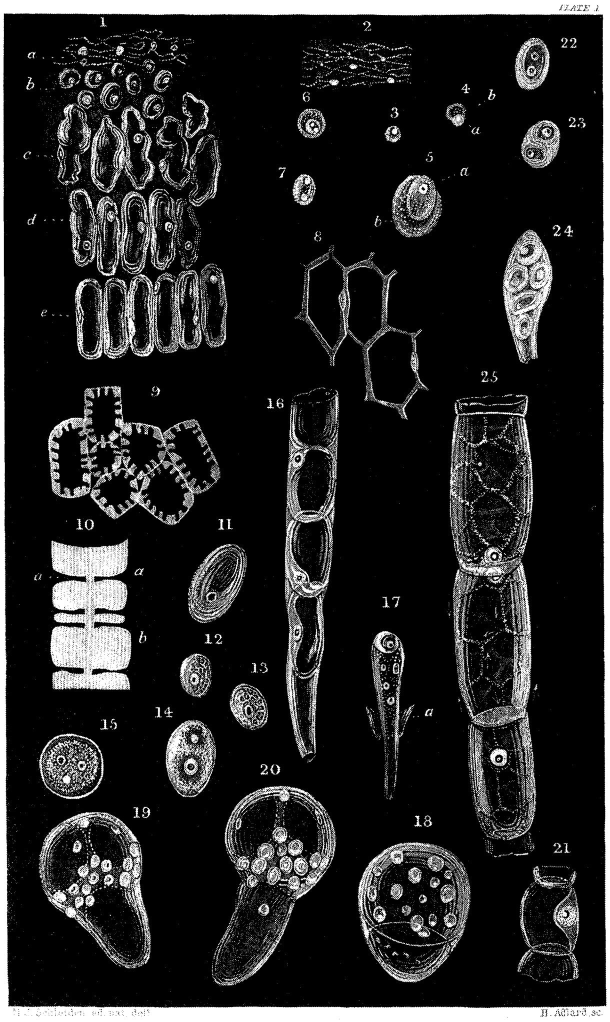

Figure 3. Schleiden's (1838) drawings of plant cells: 1 shows the *de novo* origin of cells in the endoplasm of a seed from nuclei; 25 shows three cells from a potato. (Wellcome Institute Library, London.)

laboratory of a distinguished scientist. But unlike Watson and Crick they made a major error and they never published together.

Schleiden changed from law to botany in 1833 and joined the laboratory of Johannes Muëller in Berlin. He had a clear view of organisms being made up of cells: 'Each cell leads a double life; an independent one, pertaining to its own development alone; and another incidental, in so far as it has become an integral part of a plant.' Using embryonic plant tissue, he focused his attention on the origin of cells (figure 3). He concluded (1838) that they developed *de novo* from a mass of minute granules within the cell which first form a nucleus (which he called the cytoblast) around the nucleolus. He had unfortunately been observing the endoplasm of seeds where nuclei multiply before cell walls form, and generalized from this atypical system.

Also in Muëller's lab at that time was a former medical student, Theodor Schwann, who had observed 'the beautiful cellular structure of the dorsal cord in these larvae' and noted that cartilage cells, like plant cells, had thick cell walls. In October 1837, he lunched with Schleiden: 'One day, when I was dining with M. Schleiden, 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' (Hughes 1959). On re-examination of this cartilage material he reported seeing several free nuclei within a single cell.

In 1839 he published his famous book *Microscopical researches into the accordance in the structure and growth of animals and plants*. In this book he summarizes the observations of many microscopists and systematically discusses how the tissues of both plants and animals, though appearing different, are constructed from cells. One can see how big a divide there was, for example, between Dutrochet and Schwann by comparing their drawings (figure 4). The cells and nuclei are particularly clear in the drawings by Schwann. Schwann defined a cell as having three essential elements – a nucleus, a fluid content and a wall – even if, as so often was the case in animals, no wall or membrane could be seen. And his ideas on cell multiplication were, following Schleiden, that they arose from nuclei even from outside existing cells. His most important contribution was to propose a general cell theory namely 'that there exists a general principle of construction for all organic products, and this principle of construction is cell-formation' and even more clearly (Baker 1948) 'A common principle of development is the basis of all organic tissues, however, diverse they may be, namely cell formation; that is to say nature never joins the molecules together in a fibre, tubes etc., but always first fashions a cell or first transforms this cell, where necessary, into the different elements of structure as they occur in the adult state.' He also dismissed vital forces and speculated on physicochemical processes by which cells could form, drawing again an analogy with crystallization.

It was a major achievement to try and show that all the structures in organisms were basically cellular based on the new definition. But even he had difficulty identifying the cellular nature of the early chick embryo. Again it was only in 1841 that Kölliker studying the testis found that some of the cells became sperm; and sperm were, at last, recognized as cells.

Schwann's book had an enormous impact. Muëller himself applied the ideas to his studies on cancer and his Berlin school produced such major workers in the field as Albert Kölliker, Kurt Reichert and Rudolf Virchow. But Schwann's influence was perhaps too pervasive, particularly in relation to cell multiplication.

4. CELL DIVISION

Schwann's book gave authority to the idea that cells arose either within or outside existing cells. It is somewhat puzzling to understand how this view could have been maintained in the light of von Mohl's description of cell division in algae and even more surprising that those who studied cleavage in early embryonic development should have so consistently

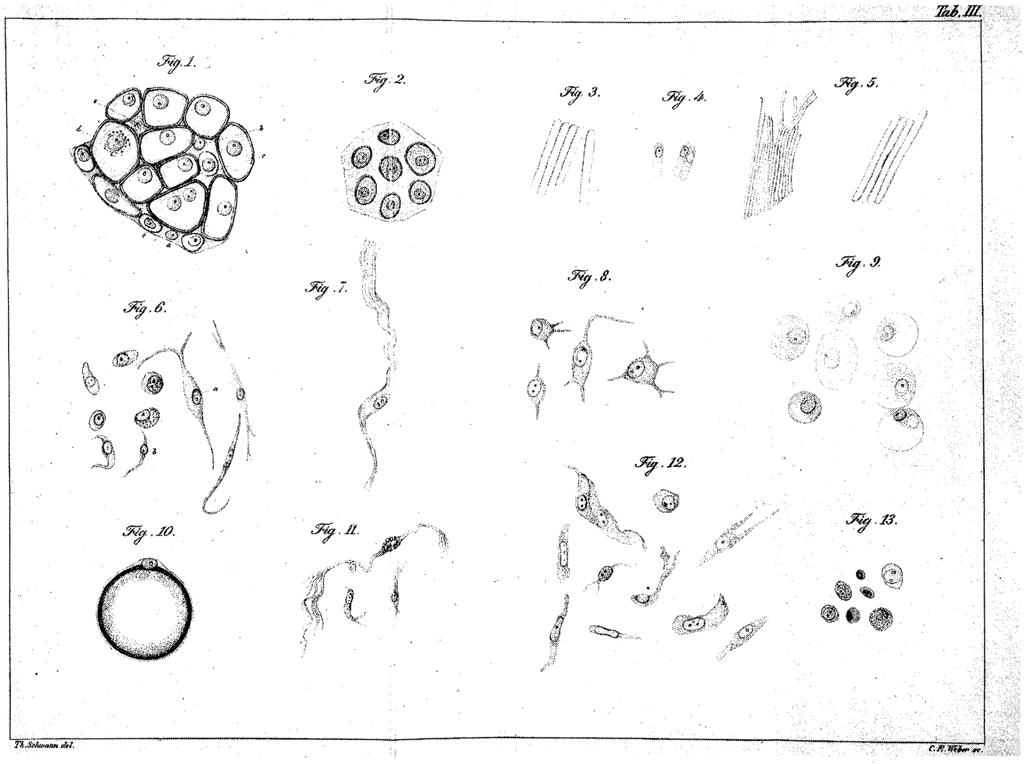

Figure 4. Schwann's (1839) drawings of animal cells: 1 is cartilage and shows *de novo* cell formation; 6 and 8 are cells from embryos. (Wellcome Institute Library, London.)

failed to recognize cell division. But then they did not appreciate that the egg was a cell.

For example, Kölliker (1843) described the cleavage of *Ascaris* very clearly and recognized that the blastomeres multiplied by division, but he thought them to be mere conglomerates of yolk granules and that the cells were later derived from the nuclei. Earlier in 1824, Prevost and Dumas also observed cleavage in the frog embryo but did not realize that the blastomeres were cells. von Baer, who correctly described the early cell divisions of sea urchin eggs, did not comment that it conflicted with Schwann's views even though he thought the tissues arose by a similar process. Reichert in 1840 did recognize that the blastomeres gave rise to the cells in the adult but still thought that they were formed endogenously within the egg, and that cleavage was merely the separation of blastomeres already present. Bergmann, in 1841, by contrast, recognized cleavage as cell division and compared it with von Mohl's algae. Kölliker by 1847 could generalize that blastomeres multiply by division yet in his *Manual of human histology* (1853), the first general textbook in the field, he continued to write that the endogenous origin of cells is a frequent occurrence, in pathological conditions free cell development occurs, that multiplication by division as seen in red blood cells was rare, and that Schwann free-cell development is 'less common than hitherto assumed'. Schwann's ideas were being modified and Busk & Huxley, the translators of Kölliker's text, comment in 1853 that cell division is common in both plants and animals.

Kölliker's reference to red blood cells stems from Robert Remak's work. Remak trained in Berlin, but as an orthodox Jew could not obtain an academic post. He, almost alone from the beginning, did not accept Schwann's view on the origin of cells: 'Ever since the cell theory became known, the extracellular origin of animal cells appeared to me to be just as improbable as the spontaneous generation of animals.' Remak traced in frog embryos the successive division of cells all the way to the appearance of specialized tissues like cartilage and muscle: 'The extracellular cell creation as postulated by Schwann cannot be proved ... The cells of which the animal germ consists, multiply by continuous division, which starts at the nucleus as I have observed it.' (Remak 1855.) Like Schwann, Remak had made a great generalization. And in 1855 Virchow probably influenced by Remak captured the new understanding with 'Omnis cellula e cellula'.

It is not clear just when it was recognized that bacteria and other microorganisms were also cells. Nevertheless, the following quotation from Pasteur in 1858 is illuminating.

'In 1835 Cagniard-Latour and Schwann, by employing a more perfect microscope, discovered that yeast consists of cells that grow and multiply. From that time on, the physical and chemical phenomena associated with fermentation have been postulated to be acts connected with the life processes of a little plant – and our subsequent researches have confirmed this.

In introducing yeasts into a sugar solution one is sowing a multitude of minute living cells, representing innumerable centers of life, each capable of growing with extraordinary rapidity. The globules of yeast are true living cells, and may be considered to have ....' (Dressler & Potter 1991).

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5. MITOSIS

An essential feature of cell division is the behaviour of the nucleus. van Baer had been able to observe what he thought was nuclear division in sea urchin eggs and Virchow considered that nuclei divided by constriction. Remak even suggested that nuclei might form *de novo* and others took the view that the nucleus disappears at cell division and then, somehow, is replaced by two new nuclei. The issue was only resolved when chromosomes were recognized as major nuclear components and mitosis described.

Baker (1955) has remarked that, in his study of the old papers in which descriptions of chromosomes appear, he found it almost impossible to give a sensible exposition of how progress in understanding mitosis was achieved. It was indeed a complex evolutionary process. In broad terms, first bodies were recognized in the nuclei, then chromosomal arrangements at mitosis, and finally the sequence of chromosomal stages during mitosis. New staining techniques made these observations possible.

It is difficult with hindsight to appreciate just how hard it was to understand what was going on. Chromosomes during mitosis bear no resemblance to anything during interphase and even prophase nuclei are hard to relate to metaphase. For example Butschli noted that when spindles became visible after disappearance of the nucleus there was a swelling in the equator. He supposed that the chromosomes were swollen regions of the spindle. And Strasburger regarded the spindle as a modified nucleus. By 1880 Strasburger believed that the metaphase plate divided in a hit or miss manner but that chromosomes that lay nearer one pole or another moved to that pole without division.

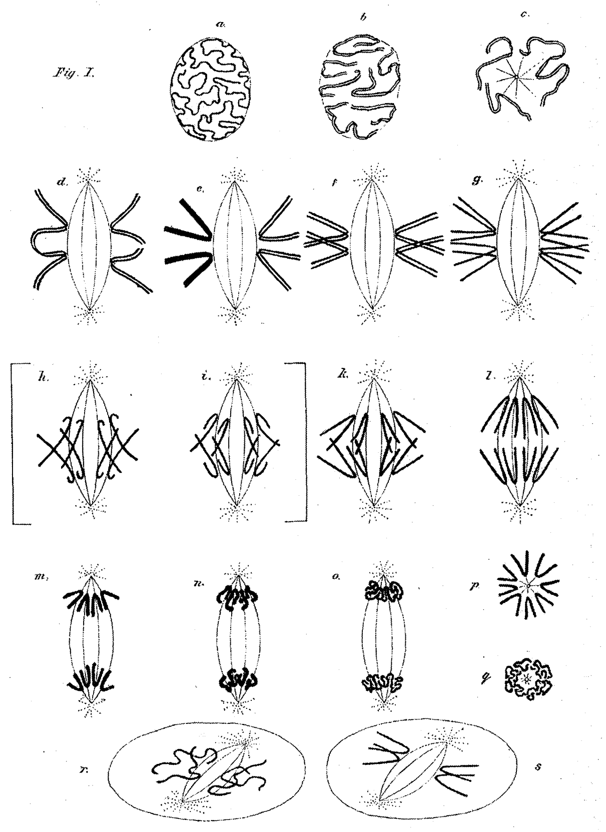

Figure 5. Flemming's (1882) diagram of mitosis. In a cell the chromosomes are linked together in prophase. The separation of the chromosomes into longitudinal halves is illustrated in *g*, *k* and *l*; *h* and *i* refer to the work of Strasburger. (Wellcome Institute Library, London.)

Walter Flemming chose to work with salamanders on account of the large size of their cells and nuclei. For the first time he established a link between the stainable substance in the interphase nucleus with chromosomes at prophase and their later arrangement at metaphase. He also describes anaphase and telophase as a reversal of the earlier stages. Most important he observed the longitudinal splitting of chromosomes at metaphase (figure 5). In 1882 he established that one longitudinal half of each chromosome went to each pole. Thus each daughter acquires a complete set of chromosome 'halves'. Rabl then established that the number of chromosomes is the same in all cells. This formed the basis of Theodor Boveri's theory of the individuality and continuity of chromosomes and August Weismann's hypothesis in 1889 to account for the constancy of genetic material from generation to generation.

6. THE CELL MEMBRANE

An attempt to generalize about the properties of the living substance was made by Purkinje in 1839 when he introduced the term protoplasm, the first created thing. He applied the term to the embryonic substance of animals. Later the term came to refer to the material that is the chief site of vital activity and T. H. Huxley, reversing an earlier opinion, called it 'the physical basis of life'.

A key question was whether this protoplasm of cells was bounded by a membrane. Since plants had clear cell walls, a general theory of cells required a similar structure in animals. The problem was of course that the membrane of animal cells is extremely difficult to see with the light microscope. Indeed workers like Max Schultz and Leydig both considered that a cell wall was not a necessary constituent of cells. This was a view that persisted until Overton (1895) demonstrated the presence of a cell membrane by beautiful physiological techniques. It was already known that a solution of cane sugar caused plasmolysis of plant cells. He showed that various alcohols, ethers and acetone of the same osmotic pressure had no such effect and so drew a clear distinction between a postulated cell membrane and a cell wall. Moreover he found that lipid-soluble substances entered the cell more easily than water-soluble ones and concluded that the membrane must contain in lipids, like cholesterol or lecithin.

7. CONCLUSIONS

The evolution of the cell theory provides a good example of the progress of science. The early globulist ideas were the forerunners of the cell theory that Schwann had propounded in 1839, which was itself quite radically transformed by the 1860s, though the central concept was still intact. As Holmes has put it, 'The development of the cell theory is as compelling an example as can be found in the history of science to demonstrate that ideas which are ultimately found to include much that is "incorrect", can nevertheless be highly productive of scientific advance.'

It is also interesting to see how difficult it was to arrive at a general cell theory – good microscopes were essential as were methods of preparing the tissues – and plant and animal tissues do not at first sight resemble each other. There was nothing in everyday experience to lead anyone to expect that all organisms were made of cells. It is also striking how powerful generalizations can be and how hard it was for some to escape from, for example, Schwann's views on the origin of cells. It is notable too how few experiments there were; the theory was almost entirely based on simple observation. The whole area is a rich one for historians.

E. B. Wilson (1892) concluded 'no other biological generalization, save only the theory of organic evolution, has brought so many apparently diverse phenomena under a common point of view or has accomplished more for the unification of knowledge'.

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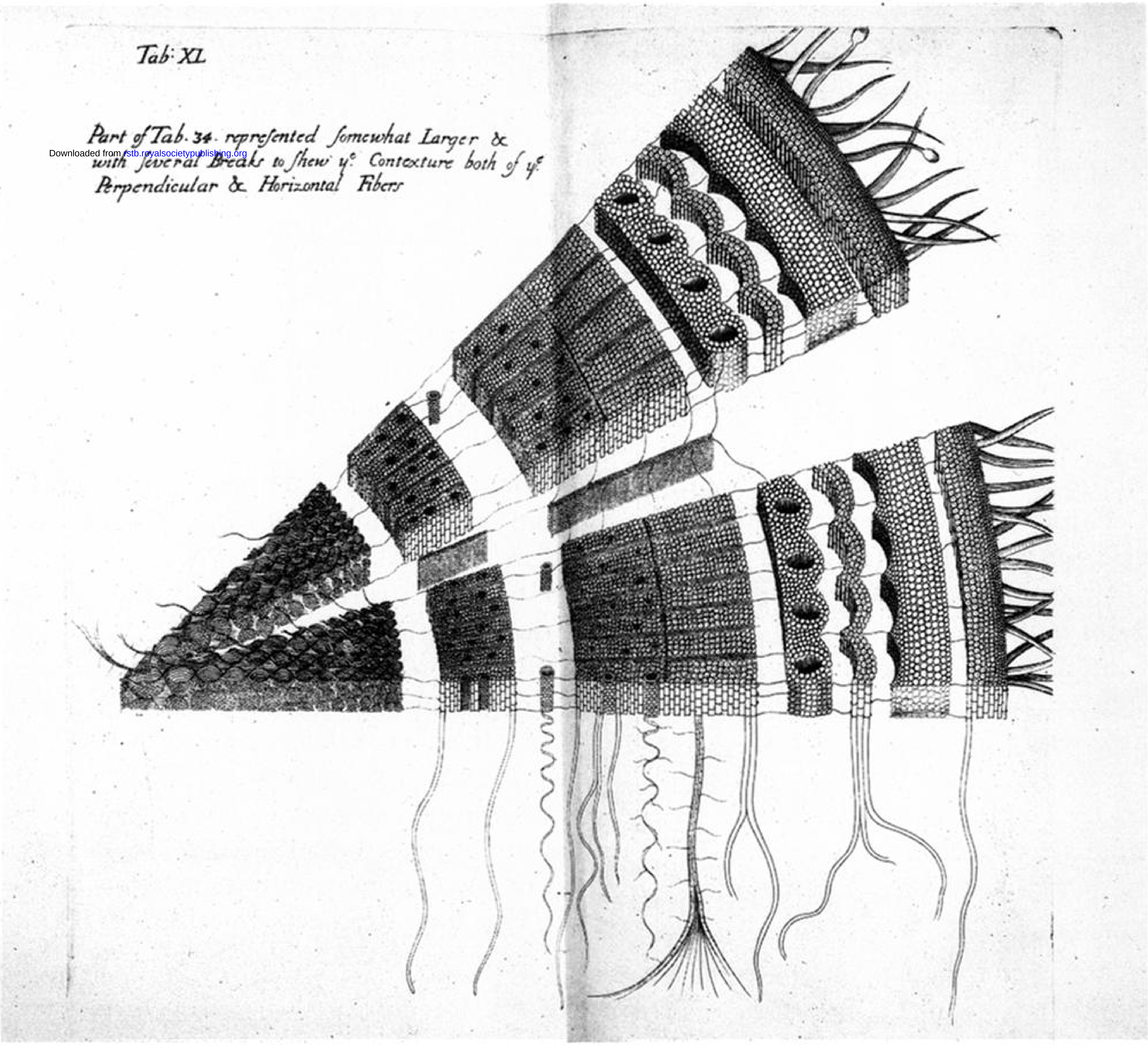

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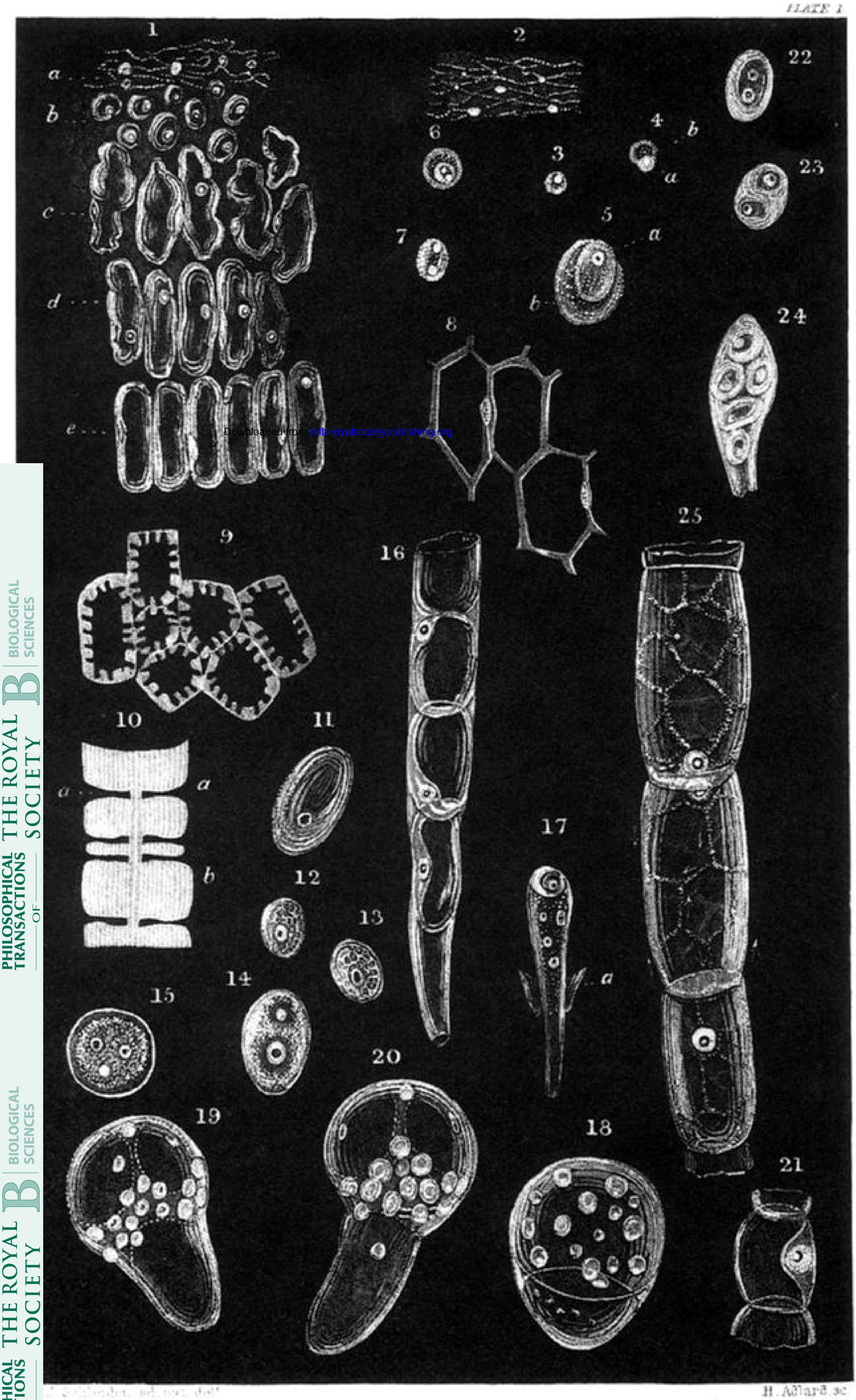

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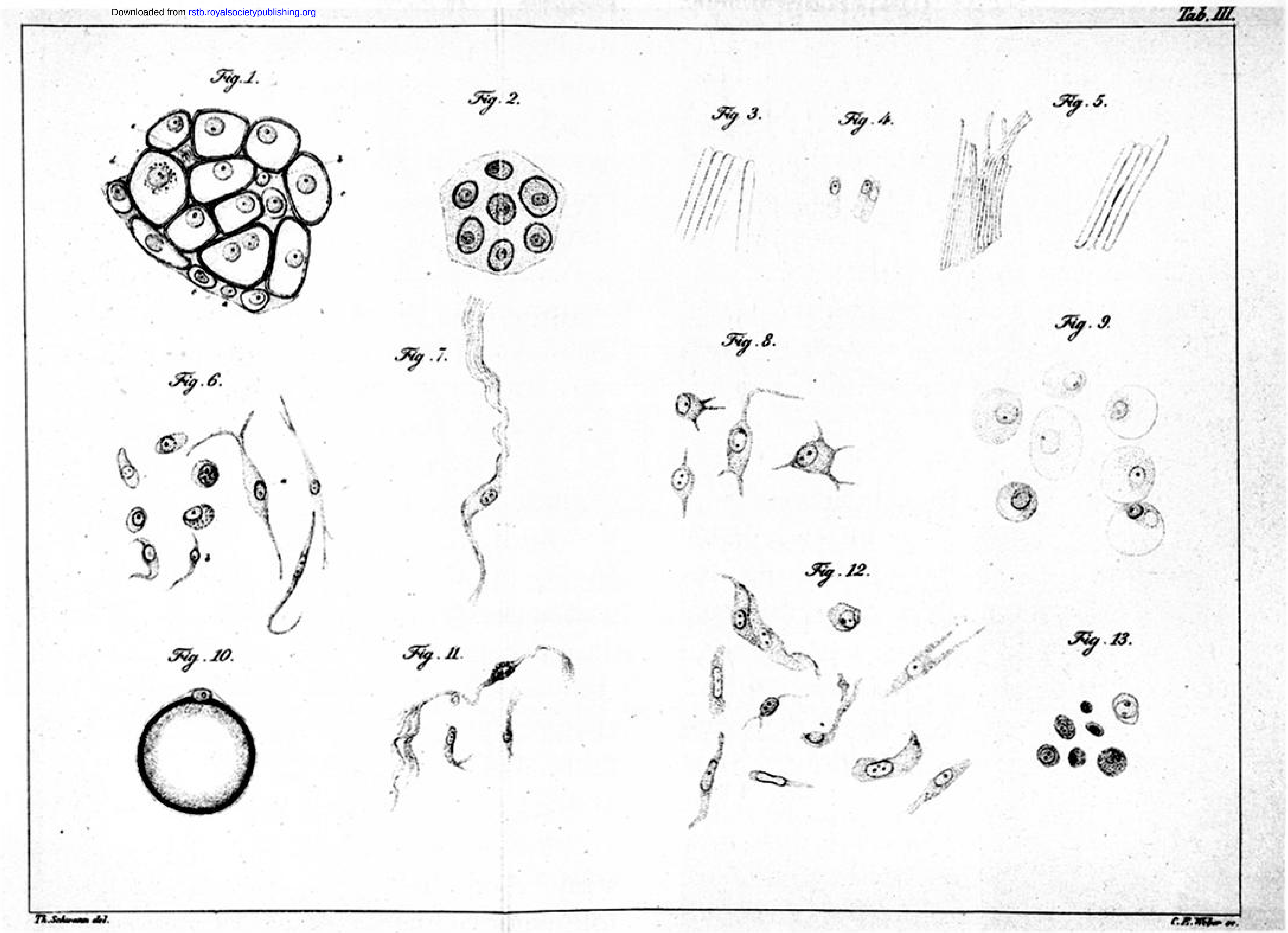

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