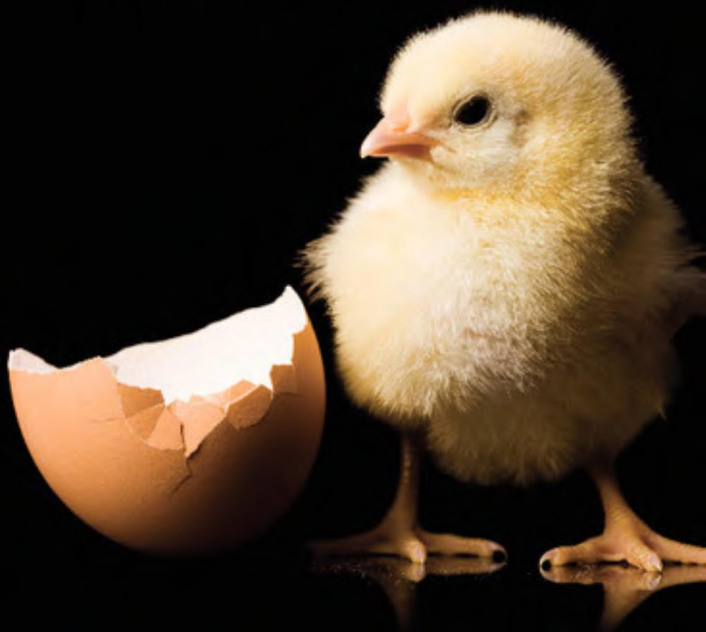


Schrödinger

What is Life?



WHAT IS LIFE?

The Physical Aspect of the Living Cell

with

MIND AND MATTER

&

AUTOBIOGRAPHICAL
SKETCHES

ERWIN SCHRÖDINGER



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Translated by Schrödinger's granddaughter Verena

WHAT IS LIFE?

THE PHYSICAL ASPECT OF THE LIVING CELL

Based on lectures delivered under the auspices of the Dublin Institute for
Advanced Studies at Trinity College, Dublin, in February 1943

*To
the memory of
My Parents*

Foreword

When I was a young mathematics student in the early 1950s I did not read a great deal, but what I did read – at least if I completed the book – was usually by Erwin Schrödinger. I always found his writing to be compelling, and there was an excitement of discovery, with the prospect of gaining some genuinely new understanding about this mysterious world in which we live. None of his writings possesses more of this quality than his short classic *What is Life?* – which, as I now realize, must surely rank among the most influential of scientific writings in this century. It represents a powerful attempt to comprehend some of the genuine mysteries of life, made by a physicist whose own deep insights had done so much to change the way in which we understand what the world is made of. The book's cross-disciplinary sweep was unusual for its time – yet it is written with an endearing, if perhaps disarming, modesty, at a level that makes it accessible to non-specialists and to the young who might aspire to be scientists. Indeed, many scientists who have made fundamental contributions in biology, such as J. B. S. Haldane and Francis Crick, have admitted to being strongly influenced by (although not always in complete agreement with) the broad-ranging ideas put forward here by this highly original and profoundly thoughtful physicist.

Like so many works that have had a great impact on human thinking, it makes points that, once they are grasped, have a ring of almost self-evident truth; yet they are still blindly ignored by a disconcertingly large proportion of people who should know better. How often do we still hear that quantum effects can have little relevance in the study of biology, or even that we eat food in order to gain energy? This serves to emphasize the continuing relevance that Schrödinger's *What is Life?* has for us today. It is amply worth rereading!

Roger Penrose
8 August 1991

CHAPTER I

The Classical Physicist's Approach to the Subject

Cogito ergo sum.

DESCARTES

THE GENERAL CHARACTER AND THE PURPOSE OF THE INVESTIGATION

This little book arose from a course of public lectures, delivered by a theoretical physicist to an audience of about four hundred which did not substantially dwindle, though warned at the outset that the subject-matter was a difficult one and that the lectures could not be termed popular, even though the physicist's most dreaded weapon, mathematical deduction, would hardly be utilized. The reason for this was not that the subject was simple enough to be explained without mathematics, but rather that it was much too involved to be fully accessible to mathematics. Another feature which at least induced a semblance of popularity was the lecturer's intention to make clear the fundamental idea, which hovers between biology and physics, to both the physicist and the biologist.

For actually, in spite of the variety of topics involved, the whole enterprise is intended to convey one idea only – one small comment on a large and important question. In order not to lose our way, it may be useful to outline the plan very briefly in advance.

The large and important and very much discussed question is:

How can the events *in space and time* which take place within the spatial boundary of a living organism be accounted for by physics and chemistry?

The preliminary answer which this little book will endeavour to expound and establish can be summarized as follows:

The obvious inability of present-day physics and chemistry to account for such events is no reason at all for doubting that they can be accounted for by those sciences.

STATISTICAL PHYSICS. THE FUNDAMENTAL
DIFFERENCE IN STRUCTURE

That would be a very trivial remark if it were meant only to stimulate the hope of achieving in the future what has not been achieved in the past. But the meaning is very much more positive, viz. that the inability, up to the present moment, is amply accounted for.

Today, thanks to the ingenious work of biologists, mainly of geneticists, during the last thirty or forty years, enough is known about the actual material structure of organisms and about their functioning to state that, and to tell precisely why, present-day physics and chemistry could not possibly account for what happens in space and time within a living organism.

The arrangements of the atoms in the most vital parts of an organism and the interplay of these arrangements differ in a fundamental way from all those arrangements of atoms which physicists and chemists have hitherto made the object of their experimental and theoretical research. Yet the difference which I have just termed fundamental is of such a kind that it might easily appear slight to anyone except a physicist who is thoroughly imbued with the knowledge that the laws of physics and chemistry are statistical throughout.¹ For it is in relation to the statistical point of view that the structure of the vital parts of living organisms differs so entirely from that of any piece of matter that we physicists and chemists have ever handled physically in our laboratories or mentally at our

¹This contention may appear a little too general. The discussion must be deferred to the end of this book, pp. 82-4.

writing desks.¹ It is well-nigh unthinkable that the laws and regularities thus discovered should happen to apply immediately to the behaviour of systems which do not exhibit the structure on which those laws and regularities are based.

The non-physicist cannot be expected even to grasp – let alone to appreciate the relevance of – the difference in ‘statistical structure’ stated in terms so abstract as I have just used. To give the statement life and colour, let me anticipate what will be explained in much more detail later, namely, that the most essential part of a living cell – the chromosome fibre – may suitably be called *an aperiodic crystal*. In physics we have dealt hitherto only with *periodic crystals*. To a humble physicist’s mind, these are very interesting and complicated objects; they constitute one of the most fascinating and complex material structures by which inanimate nature puzzles his wits. Yet, compared with the aperiodic crystal, they are rather plain and dull. The difference in structure is of the same kind as that between an ordinary wallpaper in which the same pattern is repeated again and again in regular periodicity and a masterpiece of embroidery, say a Raphael tapestry, which shows no dull repetition, but an elaborate, coherent, meaningful design traced by the great master.

In calling the periodic crystal one of the most complex objects of his research, I had in mind the physicist proper. Organic chemistry, indeed, in investigating more and more complicated molecules, has come very much nearer to that ‘aperiodic crystal’ which, in my opinion, is the material carrier of life. And therefore it is small wonder that the organic chemist has already made large and important contributions to the problem of life, whereas the physicist has made next to none.

¹This point of view has been emphasized in two most inspiring papers by F. G. Donnan, *Scientia*, xxiv, no. 78 (1918), 10 (‘La science physico-chimique décrit-elle d’une façon adéquate les phénomènes biologiques?’); *Smithsonian Report for 1929*, p. 309 (‘The mystery of life’).

THE NAÏVE PHYSICIST'S APPROACH
TO THE SUBJECT

After having thus indicated very briefly the general idea – or rather the ultimate scope – of our investigation, let me describe the line of attack.

I propose to develop first what you might call 'a naïve physicist's ideas about organisms', that is, the ideas which might arise in the mind of a physicist who, after having learnt his physics and, more especially, the statistical foundation of his science, begins to think about organisms and about the way they behave and function and who comes to ask himself conscientiously whether he, from what he has learnt, from the point of view of his comparatively simple and clear and humble science, can make any relevant contributions to the question.

It will turn out that he can. The next step must be to compare his theoretical anticipations with the biological facts. It will then turn out that – though on the whole his ideas seem quite sensible – they need to be appreciably amended. In this way we shall gradually approach the correct view – or, to put it more modestly, the one that I propose as the correct one.

Even if I should be right in this, I do not know whether my way of approach is really the best and simplest. But, in short, it was mine. The 'naïve physicist' was myself. And I could not find any better or clearer way towards the goal than my own crooked one.

WHY ARE THE ATOMS SO SMALL?

A good method of developing 'the naïve physicist's ideas' is to start from the odd, almost ludicrous, question: Why are atoms so small? To begin with, they are very small indeed. Every little piece of matter handled in everyday life contains an enormous number of them. Many examples have been devised to bring this fact home to an audience, none of them more impressive than the one used by Lord Kelvin: Suppose that

you could mark the molecules in a glass of water; then pour the contents of the glass into the ocean and stir the latter thoroughly so as to distribute the marked molecules uniformly throughout the seven seas; if then you took a glass of water anywhere out of the ocean, you would find in it about a hundred of your marked molecules.¹

The actual sizes of atoms² lie between about $\frac{1}{5000}$ and $\frac{1}{2000}$ of the wave-length of yellow light. The comparison is significant, because the wave-length roughly indicates the dimensions of the smallest grain still recognizable in the microscope. Thus it will be seen that such a grain still contains thousands of millions of atoms.

Now, why are atoms so small?

Clearly, the question is an evasion. For it is not really aimed at the size of the atoms. It is concerned with the size of organisms, more particularly with the size of our own corporeal selves. Indeed, the atom is small, when referred to our civic unit of length, say the yard or the metre. In atomic physics one is accustomed to use the so-called Ångström (abbr. Å), which is the 10^{10} th part of a metre, or in decimal notation 0.000000001 metre. Atomic diameters range between 1 and 2Å. Now those civic units (in relation to which the atoms are so small) are closely related to the size of our bodies. There is a story tracing the yard back to the humour of an English king whom his councillors asked what unit to adopt – and he stretched out his arm sideways and said: ‘Take the distance from the middle of my chest to my fingertips, that will do all right.’ True or not, the story is significant for our purpose. The king would naturally indicate a length comparable with that of his own body,

¹You would not, of course, find exactly 100 (even if that were the exact result of the computation). You might find 88 or 95 or 107 or 112, but very improbably as few as 50 or as many as 150. A ‘deviation’ or ‘fluctuation’ is to be expected of the order of the square root of 100, i.e. 10. The statistician expresses this by stating that you would find 100 ± 10 . This remark can be ignored for the moment, but will be referred to later, affording an example of the statistical \sqrt{n} law.

²According to present-day views an atom has no sharp boundary, so that ‘size’ of an atom is not a very well-defined conception. But we may identify it (or, if you please, replace it) by the distance between their centres in a solid or in a liquid – not, of course, in the gaseous state, where that distance is, under normal pressure and temperature, roughly ten times as great.

as I have called it. Therefore, the physical interactions between our system and others must, as a rule, themselves possess a certain degree of physical orderliness, that is to say, they too must obey strict physical laws to a certain degree of accuracy.

PHYSICAL LAWS REST ON ATOMIC STATISTICS
AND ARE THEREFORE ONLY APPROXIMATE

And why could all this not be fulfilled in the case of an organism composed of a moderate number of atoms only and sensitive already to the impact of one or a few atoms only?

Because we know all atoms to perform all the time a completely disorderly heat motion, which, so to speak, opposes itself to their orderly behaviour and does not allow the events that happen between a small number of atoms to enrol themselves according to any recognizable laws. Only in the co-operation of an enormously large number of atoms do statistical laws begin to operate and control the behaviour of these *assemblées* with an accuracy increasing as the number of atoms involved increases. It is in that way that the events acquire truly orderly features. All the physical and chemical laws that are known to play an important part in the life of organisms are of this statistical kind; any other kind of lawfulness and orderliness that one might think of is being perpetually disturbed and made inoperative by the unceasing heat motion of the atoms.

THEIR PRECISION IS BASED ON THE LARGE
NUMBER OF ATOMS INTERVENING.
FIRST EXAMPLE (PARAMAGNETISM)

Let me try to illustrate this by a few examples, picked somewhat at random out of thousands, and possibly not just the best ones to appeal to a reader who is learning for the first time about this condition of things – a condition which in modern physics and chemistry is as fundamental as, say, the fact that organisms are composed of cells is in biology, or as

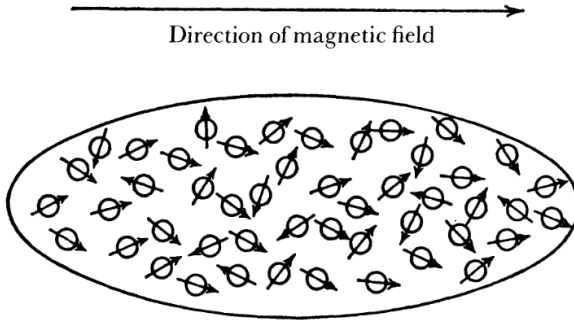


Fig. 1. Paramagnetism.

Newton's Law in astronomy, or even as the series of integers, 1, 2, 3, 4, 5, . . . in mathematics. An entire newcomer should not expect to obtain from the following few pages a full understanding and appreciation of the subject, which is associated with the illustrious names of Ludwig Boltzmann and Willard Gibbs and treated in textbooks under the name of 'statistical thermodynamics'.

If you fill an oblong quartz tube with oxygen gas and put it into a magnetic field, you find that the gas is magnetized.¹ The magnetization is due to the fact that the oxygen molecules are little magnets and tend to orientate themselves parallel to the field, like a compass needle. But you must not think that they actually all turn parallel. For if you double the field, you get double the magnetization in your oxygen body, and that proportionality goes on to extremely high field strengths, the magnetization increasing at the rate of the field you apply.

This is a particularly clear example of a purely statistical law. The orientation the field tends to produce is continually counteracted by the heat motion, which works for random orientation. The effect of this striving is, actually, only a small preference for acute over obtuse angles between the dipole axes and the field. Though the single atoms change their

¹A gas is chosen, because it is simpler than a solid or a liquid; the fact that the magnetization is in this case extremely weak, will not impair the theoretical considerations.

orientation incessantly, they produce on the average (owing to their enormous number) a constant small preponderance of orientation in the direction of the field and proportional to it. This ingenious explanation is due to the French physicist P. Langevin. It can be checked in the following way. If the observed weak magnetization is really the outcome of rival tendencies, namely, the magnetic field, which aims at combing all the molecules parallel, and the heat motion, which makes for random orientation, then it ought to be possible to increase the magnetization by weakening the heat motion, that is to say, by lowering the temperature, instead of reinforcing the field. That is confirmed by experiment, which gives the magnetization inversely proportional to the absolute temperature, in quantitative agreement with theory (Curie's law). Modern equipment even enables us, by lowering the temperature, to reduce the heat motion to such insignificance that the orientating tendency of the magnetic field can assert itself, if not completely, at least sufficiently to produce a substantial fraction of 'complete magnetization'. In this case we no longer expect that double the field strength will double the magnetization, but that the latter will increase less and less with increasing field, approaching what is called 'saturation'. This expectation too is quantitatively confirmed by experiment.

Notice that this behaviour entirely depends on the large numbers of molecules which co-operate in producing the observable magnetization. Otherwise, the latter would not be constant at all, but would, by fluctuating quite irregularly from one second to the next, bear witness to the vicissitudes of the contest between heat motion and field.

SECOND EXAMPLE

(BROWNIAN MOVEMENT, DIFFUSION)

If you fill the lower part of a closed glass vessel with fog, consisting of minute droplets, you will find that the upper boundary of the fog gradually sinks, with a well-defined velocity, determined by the viscosity of the air and the size

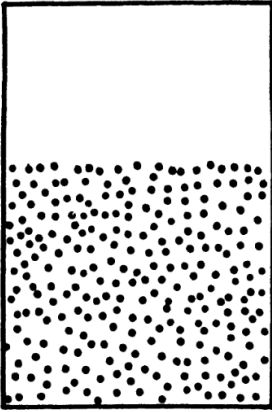


Fig. 2. Sinking fog.



Fig. 3. Brownian movement of a sinking droplet.

and the specific gravity of the droplets. But if you look at one of the droplets under the microscope you find that it does not permanently sink with constant velocity, but performs a very irregular movement, the so-called Brownian movement, which corresponds to a regular sinking only on the average.

Now these droplets are not atoms, but they are sufficiently small and light to be not entirely unsusceptible to the impact of one single molecule of those which hammer their surface in perpetual impacts. They are thus knocked about and can only on the average follow the influence of gravity.

This example shows what funny and disorderly experience we should have if our senses were susceptible to the impact of

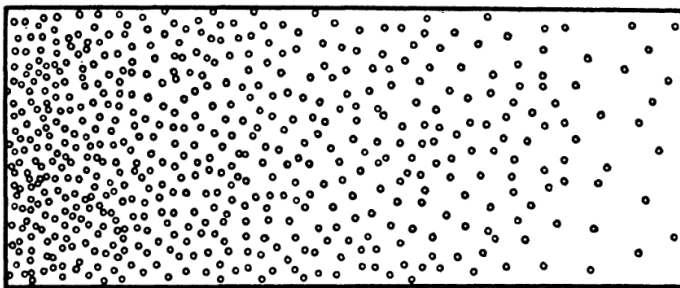


Fig. 4. Diffusion from left to right in a solution of varying concentration.

a few molecules only. There are bacteria and other organisms so small that they are strongly affected by this phenomenon. Their movements are determined by the thermic whims of the surrounding medium; they have no choice. If they had some locomotion of their own they might nevertheless succeed in getting from one place to another – but with some difficulty, since the heat motion tosses them like a small boat in a rough sea.

A phenomenon very much akin to Brownian movement is that of *diffusion*. Imagine a vessel filled with a fluid, say water, with a small amount of some coloured substance dissolved in it, say potassium permanganate, not in uniform concentration, but rather as in Fig. 4, where the dots indicate the molecules of the dissolved substance (permanganate) and the concentration diminishes from left to right. If you leave this system alone a very slow process of ‘diffusion’ sets in, the permanganate spreading in the direction from left to right, that is, from the places of higher concentration towards the places of lower concentration, until it is equally distributed through the water.

The remarkable thing about this rather simple and apparently not particularly interesting process is that it is in no way due, as one might think, to any tendency or force driving the permanganate molecules away from the crowded region to the less crowded one, like the population of a country spreading to those parts where there is more elbow-room. Nothing of the

with the effect of the force to be measured and makes the single deflection observed insignificant. You have to multiply observations, in order to eliminate the effect of the Brownian movement of your instrument. This example is, I think, particularly illuminating in our present investigation. For our organs of sense, after all, are a kind of instrument. We can see how useless they would be if they became too sensitive.

THE \sqrt{n} RULE

So much for examples, for the present. I will merely add that there is not one law of physics or chemistry, of those that are relevant within an organism or in its interactions with its environment, that I might not choose as an example. The detailed explanation might be more complicated, but the salient point would always be the same and thus the description would become monotonous.

But I should like to add one very important quantitative statement concerning the degree of inaccuracy to be expected in any physical law, the so-called \sqrt{n} law. I will first illustrate it by a simple example and then generalize it.

If I tell you that a certain gas under certain conditions of pressure and temperature has a certain density, and if I expressed this by saying that within a certain volume (of a size relevant for some experiment) there are under these conditions just n molecules of the gas, then you might be sure that if you could test my statement in a particular moment of time, you would find it inaccurate, the departure being of the order of \sqrt{n} . Hence if the number $n = 100$, you would find a departure of about 10, thus relative error = 10%. But if $n = 1$ million, you would be likely to find a departure of about 1,000, thus relative error = $\frac{1}{10}\%$. Now, roughly speaking, this statistical law is quite general. The laws of physics and physical chemistry are inaccurate within a probable relative error of the order of $1/\sqrt{n}$, where n is the number of molecules that co-operate to bring about that law – to produce its validity within such regions of space or time (or both) that matter, for some considerations or for some particular experiment.

You see from this again that an organism must have a comparatively gross structure in order to enjoy the benefit of fairly accurate laws, both for its internal life and for its interplay with the external world. For otherwise the number of co-operating particles would be too small, the 'law' too inaccurate. The particularly exigent demand is the square root. For though a million is a reasonably large number, an accuracy of just 1 in 1,000 is not overwhelmingly good, if a thing claims the dignity of being a 'Law of Nature'.

CHAPTER 2

The Hereditary Mechanism

Das Sein ist ewig; denn Gesetze
Bewahren die lebend'gen Schätze,
Aus welchen sich das All geschmückt.¹

GOETHE

THE CLASSICAL PHYSICIST'S EXPECTATION, FAR
FROM BEING TRIVIAL, IS WRONG

Thus we have come to the conclusion that an organism and all the biologically relevant processes that it experiences must have an extremely 'many-atomic' structure and must be safeguarded against haphazard, 'single-atomic' events attaining too great importance. That, the 'naïve physicist' tells us, is essential, so that the organism may, so to speak, have sufficiently accurate physical laws on which to draw for setting up its marvellously regular and well-ordered working. How do these conclusions, reached, biologically speaking, *a priori* (that is, from the purely physical point of view), fit in with actual biological facts?

At first sight one is inclined to think that the conclusions are little more than trivial. A biologist of, say, thirty years ago might have said that, although it was quite suitable for a popular lecturer to emphasize the importance, in the organism as elsewhere, of statistical physics, the point was, in fact, rather a familiar truism. For, naturally, not only the body of an adult individual of any higher species, but every single cell composing it contains a 'cosmical' number of single atoms of

¹Being is eternal; for laws there are to conserve the treasures of life on which the Universe draws for beauty.

every kind. And every particular physiological process that we observe, either within the cell or in its interaction with the environment, appears – or appeared thirty years ago – to involve such enormous numbers of single atoms and single atomic processes that all the relevant laws of physics and physical chemistry would be safeguarded even under the very exacting demands of statistical physics in respect of ‘large numbers’; this demand I illustrated just now by the \sqrt{n} rule.

Today, we know that this opinion would have been a mistake. As we shall presently see, incredibly small groups of atoms, much too small to display exact statistical laws, do play a dominating role in the very orderly and lawful events within a living organism. They have control of the observable large-scale features which the organism acquires in the course of its development, they determine important characteristics of its functioning; and in all this very sharp and very strict biological laws are displayed.

I must begin with giving a brief summary of the situation in biology, more especially in genetics – in other words, I have to summarize the present state of knowledge in a subject of which I am not a master. This cannot be helped and I apologize, particularly to any biologist, for the dilettante character of my summary. On the other hand, I beg leave to put the prevailing ideas before you more or less dogmatically. A poor theoretical physicist could not be expected to produce anything like a competent survey of the experimental evidence, which consists of a large number of long and beautifully interwoven series of breeding experiments of truly unprecedented ingenuity on the one hand and of direct observations of the living cell, conducted with all the refinement of modern microscopy, on the other.

THE HEREDITARY CODE-SCRIPT (CHROMOSOMES)

Let me use the word ‘pattern’ of an organism in the sense in which the biologist calls it ‘the four-dimensional pattern’, meaning not only the structure and functioning of that organism in the adult, or in any other particular stage, but the

whole of its ontogenetic development from the fertilized egg cell to the stage of maturity, when the organism begins to reproduce itself. Now, this whole four-dimensional pattern is known to be determined by the structure of that one cell, the fertilized egg. Moreover, we know that it is essentially determined by the structure of only a small part of that cell, its nucleus. This nucleus, in the ordinary 'resting state' of the cell, usually appears as a network of chromatine,¹ distributed over the cell. But in the vitally important processes of cell division (mitosis and meiosis, see below) it is seen to consist of a set of particles, usually fibre-shaped or rod-like, called the chromosomes, which number 8 or 12 or, in man, 48. But I ought really to have written these illustrative numbers as 2×4 , 2×6 , . . . , 2×24 , . . . , and I ought to have spoken of two sets, in order to use the expression in the customary meaning of the biologist. For though the single chromosomes are sometimes clearly distinguished and individualized by shape and size, the two sets are almost entirely alike. As we shall see in a moment, one set comes from the mother (egg cell), one from the father (fertilizing spermatozoon). It is these chromosomes, or probably only an axial skeleton fibre of what we actually see under the microscope as the chromosome, that contain in some kind of code-script the entire pattern of the individual's future development and of its functioning in the mature state. Every complete set of chromosomes contains the full code; so there are, as a rule, two copies of the latter in the fertilized egg cell, which forms the earliest stage of the future individual.

In calling the structure of the chromosome fibres a code-script we mean that the all-penetrating mind, once conceived by Laplace, to which every causal connection lay immediately open, could tell from their structure whether the egg would develop, under suitable conditions, into a black cock or into a speckled hen, into a fly or a maize plant, a rhododendron, a beetle, a mouse or a woman. To which we may add, that the appearances of the egg cells are very often remarkably similar;

¹The word means 'the substance which takes on colour', viz. in a certain dyeing process used in microscopic technique.

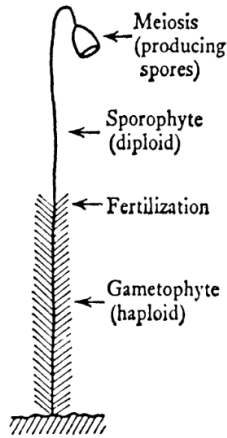


Fig. 5. Alternation of Generations.

time before syngamy is to take place. In meiosis the double chromosome set of the parent cell simply separates into two single sets, one of which goes to each of the two daughter cells, the gametes. In other words, the mitotic doubling of the number of chromosomes does not take place in meiosis, the number remains constant and thus every gamete receives only half – that is, only one complete copy of the code, not two, e.g. in man only 24, not $2 \times 24 = 48$.

Cells with only one chromosome set are called haploid (from Greek ἀπλοῦς, single). Thus the gametes are haploid, the ordinary body cells diploid (from Greek διπλοῦς, double). Individuals with three, four, . . . or generally speaking with many chromosome sets in all their body cells occur occasionally; the latter are then called triploid, tetraploid, . . . , polyploid.

In the act of syngamy the male gamete (spermatozoon) and the female gamete (egg), both haploid cells, coalesce to form the fertilized egg cell, which is thus diploid. One of its chromosome sets comes from the mother, one from the father.