MODERN BIOLOGY AND THE THEORY OF EVOLUTION

ERICH WASMANN

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Nihil Obstat

Sti. Ludovici, die 17 *Aprilis,* 1910

P. G. ROLWERK

Censor

Imprimatur

Sti. Ludovici, die 17 *Aprilis,* 1910

JOANNES J. GLENNON

Archiepus Sti. Ludovici

MODERN BIOLOGY

AND THE

THEORY OF EVOLUTION

BY

ERICH WASMANN, S.J.

TRANSLATED FROM THE THIRD GERMAN EDITION

BY

A. M. BUCHANAN, M.A.

LONDON

KEGAN PAUL, TRENCH, TRÜBNER & CO. Ltd.

DRYDEN HOUSE, GERRARD STREET, W.

1910

Motto

Nulla unquam inter fidem et rationem vera dissensio esse potest.

There can never be any real contradiction between faith and reason.

(Constitutiones Concilii Vaticani, c. 4, *De fide et ratione.*)

Cum opus, cui titulus est: 'Biologie und Entwicklungstheorie,' editio tertia, ab Erico Wasmann, Sacerdote Soc. Jesu, compositum aliqui eiusdem Societatis revisores, quibus id commissum fuit, recognoverint et in lucem edi posse probaverint, facultatem concedimus, ut typis mandetur, si ita iis, ad quos pertinet, videbitur.

In quorum fidem has literas manu nostra subscriptas et sigillo muneris nostri munitas dedimus.

Exaten, die 29 mensis Julii, 1906.

P. Carolus Schaeffer, S.J.
Prov. Germ. Præpositus.

PREFACE TO THE SECOND EDITION

At the present day it is incumbent upon every educated man to familiarise himself to some extent with the progress made and the results attained by modern science, and especially by biology. Only in this way will he be in a position to form any opinion regarding the intellectual contest that rages round certain important philosophical problems arising out of biology, namely, the comparative psychology of man and beasts and the theory of evolution. I have already dealt with the former of these two problems in two special works, intended for general reading, viz.: 'Instinkt und Intelligenz im Tierreich' ('Instinct and Intelligence in the Animal Kingdom') (third edition, Freiburg im Breisgau, 1905), and 'Vergleichende Studien über das Seelenleben der Ameisen und der höheren Tiere' ('Comparative Studies regarding the intelligence of ants and the higher animals') (second edition, Freiburg im Breisgau, 1900). My aim in the present work is to comply with wishes expressed in various quarters, and to render my articles on biology and evolution accessible to readers in general.

These sketches appeared originally as a series of articles in the magazine entitled *Stimmen aus Maria-Laach*, 1901–3. Even in their present considerably expanded form they are still sketches, with no pretensions to completeness,[1] as they are intended chiefly for readers who have no special knowledge of the departments of science with which I have dealt. I hope,

[1] The chapter on the relation between cellular division and the problems of fertilisation and heredity has been rewritten. For much information on the subject of botany I am deeply indebted to my colleague, Father J. Rompel, S.J., Professor at the Stella Matutina Gymnasium at Feldkirch. I have received very valuable suggestions from other specialists in various branches of science, and I take this opportunity of expressing my gratitude to them.

however, that these dissertations will be of some use also to students attending lectures on biology and the theory of evolution; they will find many facts presented to them from a fresh point of view, and this is particularly true of the last four sections on the modern theory of evolution. The chapter headed 'Theory of Permanence or Theory of Descent' is based almost exclusively upon the results contained in my previous 150 special articles on inquilines or guests among ants and termites, and may be of interest to my colleagues who have made a special study of zoology.

I trust that this work will be received in as friendly a spirit as were the two previously mentioned psychological works. In all three alike I have spoken as a Christian engaged in scientific research, and I am firmly convinced that natural truth can never really contradict supernatural revelation, because both proceed from one and the same source, viz. the everlasting wisdom of God. Therefore the study of modern biology and of the theory of descent, if carried on without prejudice, can tend only to the glory of God.

THE AUTHOR.

LUXEMBURG,
Feast of St. Ignatius, 1904.

PREFACE TO THE THIRD EDITION

This new edition contains many corrections and additions, which our increased knowledge of this branch of science has enabled me to make. The chapter on the physiology of evolution and the section on the history of slavery amongst ants are entirely new. The former throws some light on the problem of determination, and the latter illustrates the application of the theory of descent to the development of instinct.

In its present form the book possesses more unity than it did before. The two chief parts, those, namely, on cytology, or the study of cells, and on the theory of evolution, are now connected harmoniously with one another. The branch of science with which I had to deal is, however, vast in itself, and is being enriched almost daily by the publication of fresh works, so that it is quite impossible to give an exhaustive account of it in a limited space. Similar considerations led even E. B. Wilson to have the new editions of his classical work ' The Cell ' (1900 and 1902) reprinted without alteration, and so I may, perhaps, be forgiven for having made only the most absolutely necessary corrections and additions.

I wish to emphasise the fact that it is not my intention that this work should serve as a complete textbook of the theory of descent. The chapters on this subject are intended only, on the one hand, to help the reader to form a clear conception of the meaning of the theory of evolution, the philosophical and scientific principles underlying it, and its limits and causes ; and, on the other hand, to lay before him fresh evidence, derived from my own special department of biology, which tends to prove that the theory of evolution is really better supported than that of permanence. This theory of evolution, which I regard as a well-founded hypothesis, must be polyphyletic and not monophyletic, if it is to correspond with known facts.

With regard to the application of the theory of descent to man, I abide by my previous opinion, and maintain that the mental evolution of man from brutes is impossible, and that his bodily descent from brute ancestors presents, from the scientific standpoint, difficulties that have hitherto not been solved.

In the chapter on the Division of Cells new diagrams have been substituted for those which appeared in the earlier editions, and in other places also fresh diagrams have been added (fourteen in all), which are almost all original. Three extra plates have been added, viz. Nos. II, VI, VII.

Since the appearance of the second edition it has been translated into Italian by Fra Agostino Dott. Gemelli, O.M.[1]

The worthy translator has inserted a long introduction in which he states his own opinions on the theory of evolution,[2] and throughout his translation he has inserted many remarks of his own.[3]

The Italian edition, therefore, for which Gemelli alone is responsible, is in many respects a totally new work, and I trust that it will meet with as friendly a reception in Italy as that accorded to the German edition on this side of the Alps.

I am deeply grateful to all my colleagues who, by supplying information or suggesting additions, have helped me in bringing out this new German edition ; and I am especially indebted to Father Robert de Sinéty for some valuable remarks on the most recent discoveries regarding the problem of reduction in Chapter VI. Father H. Muckermann, S.J., was kind enough

[1] *La biologia moderna e la teoria dell' evoluzione*, Florence, 1906.

[2] Gemelli does not call his theory the theory of evolution, but prefers to speak of polyphyletic evolution (Polifilogenesi). As I also have expressed myself in favour of polyphyletic evolution, there is no actual discrepancy in our opinions, although I have retained the name 'theory of evolution.' The chief difference between us and the Monists on the subject of evolution is not so much whether it is polyphyletic or monophyletic, but it affects rather the fundamental principles underlying it, for we accept the Christian cosmogony, which is in direct opposition to that of Monism.

[3] These remarks are in many cases added to my statements, in such a way as to make it difficult to decide who is answerable for them. This remark, however, does not apply to Chapter X.

to lend me the excellent photographs which are reproduced on Plates VI and VII in this edition.[1]

THE AUTHOR.

LUXEMBURG,
Feast of St. Ignatius, 1906.

[1] These and many other original photographs have been prepared by Dr. Wm. Gray at the U. S. Army Medical Museum in Washington for his new English textbook on physiology, that will shortly be published. (Cf. the list of plates in this edition, p. xxxii.) Any other reproduction of Plates VI and VII is forbidden.

A FEW WORDS TO MY CRITICS

These sketches on biology and the theory of evolution appeared in book form barely two years ago, and I could hardly expect that an edition of 2000 copies would be so soon exhausted. My friends had in fact told me bluntly that the book was too dry to find many readers, and that it made too great demands upon the power of thought possessed by our educated classes.

It is true that the book has not sold so quickly as Haeckel's 'Riddle of the Universe,' but it is not a popular scientific polemic aiming at the overthrow of Christianity, and therefore peculiarly welcome to those lower classes which are especially interested in this overthrow. It is rather an attempt at conciliation, based upon an objectively scientific foundation, and it aims at harmonising the ideas of modern biology with the Christian cosmogony, and thus it was not likely to prove acceptable except to men of culture and intelligence. Nevertheless the comparatively quick sale of the book, and the numerous discussions to which it has given rise, show that it has awakened considerable interest among educated men in Germany.[1]

The kind of interest thus awakened varies according to the personal views of those in whom it exists. They may be divided into three classes, viz. (1) supporters of Christianity, (2) scientific specialists, and (3) opponents of Christianity. The classification is not quite accurate, because there are many scientific men, and especially many zoologists, among the readers of the first class, and among those of the third class zoologists form a considerable majority. Under the second category I include those only who confine themselves

[1] Germany is here used to include Austria and all countries where German is spoken.

to considering the biological contents of my book, without allowing their philosophical pre-suppositions to transpire. Apart from some few expressions of opinion on points of minor importance, the book has been very favourably received by the supporters of Christianity in Germany, both Catholic and Protestant. Some have even described it as a 'rescue from bondage,' because it has shown the right tactics to adopt in the struggle between Christianity and the monistic doctrine of evolution. I will not allude further to the various reviews of it that have appeared in the German Catholic papers. In the *Reformation* of February 26, 1905, there is an article entitled 'Ein Jesuitenpater als Anhänger des Darwinismus?' ('A Jesuit as a supporter of Darwinism?') by E. Dennert, a Protestant reviewer, well known as an opponent of Darwinism, who expresses his complete agreement with my views on the subject of evolution. Of the reviews by Catholic writers in other countries, I will mention only three of the most important. The first appeared in a North American periodical, *The Review*, of November 24, 1904, and the reviewer's opinions coincided on all points with my own. The second, which is very thorough, appeared in the number for April and May 1905 of the Spanish *Razón y Fe*, and although the writer at the close of his article says that he prefers for the present to abide by the theory of permanence, still his verdict as to the author's position with regard to the theory of evolution is favourable. The third review, 'L'Haeckelisme et les idées du Père Wasmann sur l'évolution,' may be found in the Belgian *Revue des Questions scientifiques* for January 1906. The French critic, himself an eminent biologist, in the course of a very careful article, shows that it is not possible to oppose the monistic doctrine of evolution with success, unless we acknowledge the claims of the scientific theory of evolution; on this point he agrees fully with the author's opinions.

Reviews written by critics belonging to what I have called the second class deal with the book from the scientific aspect. On the whole they are appreciative and favourable, although some few objections have been raised. I will mention only the articles contributed by Professor Dr. C. Emery to the *Biologisches Zentralblatt* (February 15, 1905); by Dr. R. Hanstein to the *Naturwissenschaftliche Rundschau* (February

2, 1905); by J. Weise to the *Deutsche Entomologische Zeitschrift* (1905, part I); by Dr. K. Holdhaus to the *Verhandlungen der Zoologisch-botanischen Gesellschaft von Wien* (1905, parts 5 and 6); and by Professor H. J. Kolbe to the *Naturwissenschaftliche Wochenschrift* (July 2, 1905).[1]

The critics of the third class are those who seek to maintain their own monistic theory in opposition to the author, and to prove his position as a Christian untenable. It was easy to foresee that there would be many reviews written from this standpoint, as unfortunately most of the zoologists of the present day have monistic tendencies; and the fact that my book called forth such vigorous opposition may be regarded as far more satisfactory evidence of its success than the most appreciative comments proceeding from the Catholic party. Why have the monists thought it necessary to pay so much attention to my work? The only psychological explanation of their action is that they see in it a certain amount of danger to the supremacy of their anti-Christian views. For this reason they do their best to draw as sharp a distinction as possible between the author as scientist and as theologian. They cannot help recognising the merits of the book, and the only objections they can raise refer to minor points, or are based on misunderstandings and misrepresentations, but naturally they refuse to acknowledge that the author has succeeded in reconciling biology in its recent developments with the principles of Christianity, for such an acknowledgement would at once deprive modern unbelief of one of its chief weapons in the conflict with Christianity.

Of these hostile criticisms I can only refer here to the most important, those, namely, of K. Escherich, H. von Buttel-Reepen, Ernst Haeckel, August Forel, J. P. Lotsy

[1] On pp. 426 and 427, where Kolbe has attempted to give a summary of the 'results' of my opinions, there are some misstatements, that are probably due to some extent to Escherich's review, to which reference will be made later. Kolbe's fourth point, that 'polyphyletic origin of closely allied forms is more likely than monophyletic,' is exactly the opposite of my assertions. The remark on the sixth point regarding 'the great number of primitive types' is, to say the least, inaccurate. The statement on the ninth point that the assumption of a 'creation' of primary types is 'a dualism irreconcilable with the principles of natural science' is devoid of all proof. The reviewer, however, seems to have had in his mind some notion of 'creation out of nothing,' because in discussing the tenth point he says emphatically that 'nevertheless' in another place I have assumed 'that the primary types must originally have been formed out of matter.'

and F. von Wagner. They are not all written in the same spirit, as the following examination of them will show.

'Kirchliche Abstammungslehre'—the Church's teaching on descent—is the title of a long article by Dr. K. Escherich, lecturer on zoology, in the supplement to the *Allgemeine Zeitung* of February 10 and 11, 1905. He speaks very appreciatively of my position with regard to the theory of evolution, and especially of the ninth chapter, in which I have dealt with the inquilines or guests among ants and termites from this point of view. But, on the other hand, he believes that 'theological reasons' have led me to assume a polyphyletic evolution, which distinguishes as many 'natural species' as there are lines of evolution, independent of one another, and he thinks that I have done this in order the better to reconcile the doctrine of evolution with that of creation. My opinions regarding the origin of life and the creation of man seem to him inadmissible, for they contradict the most important postulates of the monistic doctrine of evolution. Escherich sums up the results, which he thinks he can deduce from my opinions, and arranges them under nine chief headings, whence he draws the conclusion 'that any reconciliation of the doctrine of descent with ecclesiastical dogmas is impossible.'

My reply to Escherich's review appeared in the supplement to the *Allgemeine Zeitung* of March 9, 1905. In it I showed that the reviewer's imaginary opposition between an ecclesiastical and a non-ecclesiastical doctrine of descent indicated a biased misrepresentation of facts. He ought to have proved that the doctrine of evolution as a scientific hypothesis and theory was incompatible with the Christian cosmogony, but instead of doing so, he had recourse to the postulates of a monistic philosophy, which are neither based on science nor philosophically correct. I drew attention also to a number of actual misunderstandings with regard to the 'natural species' and the 'inner laws of evolution,' &c. These, I believe, were accidental, but of the nine points which Escherich ascribes to me as summing up my opinions, three at least were wrongly so ascribed, and these were the very three which might have been challenged from the scientific standpoint.

In the 'Closing Word' appended to my reply by Escherich, he acknowledged several of the misunderstandings as such, but he adhered to his assertion that my doctrine of descent ought to be described as 'illogical' in contrast to the 'logical' theory. Unhappily he forgot to add that the logical character of the monistic view, which he maintains, has no scientific basis, but rests upon the unproved postulates of a false philosophy. He concluded by recommending my book to all readers who had had a scientific education, but warned the general public against reading it! I am grateful to him for this recommendation, as I wrote expressly for educated people.

In the *Archiv für Rassen- und Gesellschaftsbiologie* (March–April, 1905) there appeared a very careful criticism of my book, contributed by Dr. H. von Buttel-Reepen, who is a specialist on the subject of social insects. The review is, on the whole, written in a friendly spirit, but it forces into prominence the question of cosmogony. 'Where does science end, and the Jesuit begin?' This is the subject for discussion. The 'science' which the book contains is praised by von Buttel, but he prefers to have nothing to do with 'that web of inconsistency, which, solely in order to save a number of dogmas, draws its illogical and untenable threads over Wasmann's scientific work, obscuring the results of research.' By this 'web of inconsistency' he means my views on the theory of creation, on spontaneous generation, and on the descent of man. That in these points I have not been 'consistent' in the reviewer's monistic sense, may soothe my conscience, not only as a theologian, but also as a scientific man and a philosopher.

By means of his lectures at the Berlin Singakademie (April 1905), Professor Ernst Haeckel, the well-known prophet of Darwinism, undoubtedly did very much to increase the circulation of my 'Biology and the Theory of Evolution.' Special importance may be attached to his criticism, as he states expressly, both in the preface and in the supplement to the printed edition of his lectures on the theory of evolution, that he was induced to deliver them chiefly through the publication of my book. What was the result of this official criticism, which Haeckel as the champion of German monism felt bound to pronounce? On the one hand he welcomes my work as a satisfactory proof that the Catholic Church has ceased to oppose the doctrine of evolution, and on the other hand he calls it a masterpiece of Jesuitical distortion and sophistry. He bestows upon it the highest praise that could proceed from his lips, when he says that the ninth chapter (The Theory of Permanence or the Theory of Descent) might be incorporated as a valuable addition in one of Darwin's works, but at the same time he regards it as one of the achievements of 'the marvellous system of falsification invented by the Jesuits.' I cannot but be grateful to Haeckel for the contradictory eloquence with which he has denounced my book as a dangerous 'snare' for all who are not yet perfectly convinced monists, for I believe that his very denunciation has led no small number of victims into that snare, and has induced them to read the book which he has solemnly placed on the index for Monism.

It would be superfluous for me on this occasion to discuss Haeckel's statements in detail. In an 'Open Letter to Professor Haeckel,' which appeared on May 2, 1905 in the *Germania* and in the *Kölnische Zeitung*, I answered his assertions clearly and decisively.

'Wissenschaft oder Köhlerglaube?' ('Science or charcoal-burner's Faith?') is the title of an article antagonistic to me, that appeared in the *Biologisches Zentralblatt* for 1905, Nos. 14 and 15. It was written by the well-known authority on ants, Professor August Forel. He does not discuss ants in this article, in which in fact he pays a high tribute to my scientific knowledge, but he challenges my 'charcoal-burner's faith,' by which he means my energetic defence of Christianity against the attacks of Monism. Two years previously I had contributed to the same paper (Nos. 16 and 17, 1903) a calm and courteous criticism of Forel's monistic theory of identity,[1] and this was his reply to it, expressed however in by no means the same appropriate terms, but in language that showed irritability, occasionally bordering on fanaticism. In the introduction to his article he states plainly why his reply was so long delayed, and why it displays so much hostility; he says: 'In the meantime Wasmann has worked out and favoured us with a doctrine of descent *sui generis*. . . . Now

[1] See my *Instinkt und Intelligenz im Tierreich*, Freiburg im Breisgau, 1905, 3rd edit., chap. xii.

that Wasmann is beginning to be the apostle of a new doctrine,[1] I regard it as my duty to answer him.'

Forel was therefore annoyed by my attempt to show that the theory of evolution was not irreconcilable with Christianity, and instead of impartially disproving my opinions, he showed a partisan spirit in trying to distort them, and allowed his imagination free scope in ridiculing the 'natural species,' whose primitive forms I assumed to have been created by God. His charges against 'charcoal-burner's faith,' or rather against the Christian standpoint, are based upon a confusion of ideas, such as one would hardly expect in a critic who has been trained in philosophy. Finally, to crown his arguments, he ingeniously makes fun of the letters S.J. (Societatis Jesu) after my name; he says S stands for scientist and J for Jesuit, and advises me to put an end to the unhappy union of the two letters. He goes even further and enlarges upon this distinction in the following words: 'Wasmann S. is a scientific man, whom I respect for his acumen and conscientious work; Wasmann J. is a scholastic Jesuit. But Wasmann S. is a slave under the control of Wasmann J., and can be free and independent only when he deals with matters on which he does not come into conflict with Wasmann J. As soon as any dispute arises, Wasmann S. ceases to think as a man of science and Wasmann J. begins with his syllogisms and scholasticism and all the war of words.'

Such an attack did not really require any answer at all, as it revealed its character plainly enough. Nevertheless, I wrote a short article in reply, entitled 'Wissenschaftliche Beweisführung oder Intoleranz?' ('Scientific Proof or Intolerance?') which appeared in No. 18 of the *Biologisches Zentralblatt* for 1905. I had no difficulty in showing that it would have been better for Forel to have said nothing than to have come forward with such weapons as the champion of Monism.

In their attacks upon my book, both Haeckel and Forel have had many followers in popular scientific circles of the same tendency. There is nothing surprising in this fact, and it does not call for any further comment.

[1] These words allude to my lectures on evolution delivered in Germany and Switzerland.

It is more significant that Forel's joke about Wasmann S. and Wasmann J. has been imitated even in highly learned university lectures.[1]

Lotsy praises the author of 'Biology and the Theory of Evolution' very highly, and says: 'Wasmann is a Jesuit, but at the same time he is one of the best zoologists of the present day, and we must feel the deepest admiration for his investigations into the life of ants. This very eminent man writes on p. 271: "Of two hypotheses in natural science or natural philosophy, put forward as offering an explanation of one and the same series of facts, it behoves us always to choose the one which succeeds in explaining most by natural causes, and on this principle we can hardly hesitate to choose the theory of descent in preference to that of permanence." But as soon as we have to consider man. . . .' Lotsy goes on to refer to p. 283 of my book, where I have limited the scope of zoology with regard to man to his body, declaring it and its attendant sciences incompetent to deal with him on his spiritual side. On this subject Lotsy remarks: 'These words remind me of Lamarck's saying, "Telles seraient les réflexions que l'on pourrait faire, si l'homme n'était distingué des animaux que par les caractères de son organisation, et si son origine n'était pas différente de la leur." Are we to accuse Wasmann of prevarication? Certainly not. I fully agree with what Forel said a few days ago in the *Biologisches Zentralblatt.* Forel sees in Wasmann two distinct personalities, the scientist and the theologian, whom I shall designate by A. and B.' Then follows verbatim Forel's distinction that I have already quoted, the only difference being that for Wasmann S. and Wasmann J., Lotsy writes A. and B.

Lotsy might easily have perceived the weakness of this argument of Forel's, if he had really considered the passage quoted from Lamarck, who agrees with me in declaring zoology alone incompetent to deal with the question of the origin of man. If Lotsy were consistent, he would have to see two personalities, viz. a scientific man and a 'scholastic Jesuit,' in Jean-Baptiste Pierre Antoine de Monet, Chevalier de Lamarck!

[1] J. P. Lotsy, *Vorlesungen über Deszendenztheorien, mit besonderer Berücksichtigung der botanischen Seite der Frage* ('Lectures on theories of descent, with especial reference to the botanical side of the question'), at the Imperial University of Leiden, Part I, Jena, 1906, pp. 328, 329.

Special reference is due to a very detailed criticism of my book that appeared in the *Zoologisches Zentralblatt*, a scientific periodical (1905, No. 22). The review was written by F. von Wagner of Giessen, professor-extraordinary of zoology, yet it is not of a purely scientific character, but shows a partisan spirit, although the author's anti-Christian bias is not so bluntly expressed as is the case in Haeckel's and Forel's articles. It is, however, perceptible throughout the review, which is consequently quite unlike the impartial criticisms that we usually find in the *Zoologisches Zentralblatt*.

In the introduction to the nine pages in which he deals with my book, von Wagner remarks that not a few of his fellow-zoologists have been induced to believe that Wasmann's attitude towards the theory of evolution indicates a 'change of front on the part of the Catholic Church with regard to modern biology.' The reviewer does his best to deliver his colleagues from this 'illusion,' and I am grateful to him for doing so, as, like Haeckel and Forel, von Wagner does not mean by 'modern biology' merely its scientific results, but also the monistic postulates which the opponents of Christianity have insisted upon attaching to these results. I gladly agree with the reviewer, and confess that my views do not coincide with the postulates of a false philosophy, by no means free from hypotheses. This is, however, all that he has really succeeded in proving.

Von Wagner himself acknowledges that within my own field of research I 'apply the principles of evolution in a scientific spirit' (p. 691), and he describes my account of modern cytology, or the study of cells, from the scientific standpoint as 'very successful' (p. 693). He is, moreover, particularly 'grateful' for those parts of the book which contain 'an excellent summary of the important results of Wasmann's investigations from the standpoint of the principle of descent.' The historical account, too, of the development of biology 'describes it accurately in its general outlines.'

We must now consider the reviewer's objections, which can be summed up in one sentence (p. 692): 'The book in question has *one* author, but *two* editors, a scientific man engaged in research work and a theologian. Consequently,

b 2

the whole is a joint production; the theologian takes the lead, and the scientific man may assert himself only so far as the former gives permission.' The conclusion derived by von Wagner from this statement is that the book is written with a bias from beginning to end.

The answer to this is obvious; we need only apply the just quoted words of the reviewer to his own review. 'The review in question has *one* author, but *two* editors, a scientific man engaged in research work and a monistic philosopher. Consequently, the whole is a joint production; the monistic philosopher takes the lead, and the scientific man may assert himself only so far as the former gives permission.' The conclusion that we derive from this statement is that the review is written with a bias from beginning to end.

Let us now examine my book more closely and see how far the 'bias' imputed to it by the reviewers really exists, and how far they are mistaken.

Even in my account of the historical development of biology von Wagner discovers a bias, for he says that I have singled out for praise none but Christian representatives of this science. I do not understand why, if this were the case, I spoke, as he says, with remarkably scant appreciation of Cuvier's achievements in comparative anatomy, and mentioned Bichat's work in more eulogistic terms,[1] whereas if my opinion were really biased, I should have extolled Cuvier rather than Bichat, as being an eminent Christian as well as a scientific man. This fact shows that von Wagner's desire to discover a particular bias in my work is the outcome of his own imagination.

The bias of the book, as von Wagner has discovered (p. 694), is revealed especially 'in what it does not contain.' The author is accused of having purposely withheld from his readers the more general biological evidence in favour of the theory of evolution. I feel inclined to ask whether the reviewer has really read the eighth and ninth chapters of his edition. I am supposed not to have referred to Darwin, Lamarck and Geoffroy St. Hilaire, whereas they are all mentioned on p. 169. He seems not to have noticed the more general relations of the

[1] In speaking thus I relied upon M. Duval's statements in his *Précis d'histologie*, a book with which von Wagner seems not to be acquainted.

theory of evolution to the Copernican theory of the universe, to modern geology and palæontology (pp. 179–85), and the long dissertation following them on the limits and causes of the hypothetical phyletic evolution, but he notices my statements regarding 'natural species' and their connexion with the theory of creation, for these statements give him another opportunity of joining Escherich, Haeckel and Forel in imputing to me a theological bias. On pp. 219, 220, I referred expressly to the mass of indirect evidence supporting the theory of evolution to be derived 'from comparative morphology, comparative history of evolution, comparative biology and especially from palæontology,' but I said that I had no intention on this occasion of writing a textbook of the theory of descent. No one could discover in this any intentional concealment of evidence, who did not wilfully misinterpret my words by imputing to them a bias that is not there. Such a critic is plainly incapable of forming a just and objective opinion.

Let us for a moment regard the matter from the point of view of an extreme supporter of the theory of permanence. He would have quite as much justification for discovering a bias in favour of the theory of evolution from those very statements and omissions, in which a fanatical advocate of the theory discovers a bias hostile to it. He might, for instance, try to account for the fact that I have not discussed in detail the ordinary evidence in favour of the theory of evolution, by declaring that this evidence has lost most of its weight through Fleischmann's criticism, and therefore I have been obliged to establish the scientific justification of the evolution hypothesis upon the new and independent basis of my own research. Moreover, when I have expressed my preference for 'natural species' rather than 'systematic species,' he might discover an intention to set aside the theory of permanence and replace it by that of evolution, under the pretext that the latter is more easily reconciled with the Christian doctrine of creation, &c. I maintain, therefore, that, where it is possible to see in the same statements of any author two totally opposite tendencies, it is plain that both imputations are alike objectively without foundation. I need say no more regarding von Wagner's method of treating my book, as, whilst imputing a biased tendency to me, he shows the same himself.

I must acknowledge that with regard to the doctrine of creation, the hypothesis of spontaneous generation and the application of the theory of descent, I had a bias, and one that is directly opposed to that of my reviewer. I had the intention of proving that a reasonable theory of evolution necessitates our assuming the existence of a personal Creator, and I wished further to show that 'spontaneous generation' was scientifically untenable, and, therefore, could not be a postulate of science. Finally, I desired to prove that to regard man from the purely zoological point of view is a one-sided and mistaken proceeding. I was, however, forced to adopt this threefold bias by the monists, who were exerting themselves with a much greater bias to establish false philosophical postulates in the name of biology, and to force them as 'monistic dogmas' upon all interested in science. I considered it my duty as a Christian and as a scientific man to protest vigorously against these attempts at a fresh subjugation of the human intellect.

It is, moreover, psychologically very interesting to observe how a reviewer, himself an ardent advocate of Monism, seeks to discover throughout my book Christian tendencies, in order to destroy as far as possible its scientific objectiveness. A criticism undertaken on these lines cannot be truly free from prejudice, and the absolutely biased character of von Wagner's review appears most plainly in his closing words (p. 699): 'There is always the same discord, when science is only on a man's lips and not in his heart.' Because I do not accept the unscientific postulates of Monism, all love of science is to be denied me! Is not that plainly monistic intolerance? According to my opinion, science has its abode neither on the lips nor in the heart, but in the intellect or, as von Wagner would say, the brain, which he regards without doubt as the real organ of thought in a human being.

And now I take leave of my critics,[1] and commend the present edition to their kind attention. In it, as far as lay in

[1] A short reply to von Wagner's review has already appeared in *Beispiele rezenter Artenbildung bei Ameisengästen und Termitengästen* (written in honour of J. Rosenthal, Leipzig, 1906, pp. 45–58; *Biologisches Zentralblatt*, 1906, Nos. 17 and 18, pp. 565–580), 55 (577) et seq.

my power, I have taken into account all the really well-founded objections to statements in the previous editions, whether these objections were raised by friends or by opponents. It is in vain, however, to call upon me to conform to the tyrannical requirements of Monism, and such a demand will remain unsatisfied in the future, as it has done in the past.

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CHAPTER I

THE MEANING AND FIRST DEVELOPMENT OF BIOLOGY

'*Knowledge is inexhaustible in its source, unlimited by time or space in its force, immeasurable in its extent, endless in its task, unattainable in its aim.*'—K. E. v. BAER.

AT the close of any considerable epoch it is of peculiar interest to look back upon the historical development of nations and states during that period; to compare their position a century ago with that which they now occupy; to observe the rise and fall of their political power, and the fluctuations in their political and intellectual importance amidst the pressure of contemporary events, and to trace the causes of these fluctuations. In the same way it is most interesting at this juncture to look back at the development of a science. The history of science is a branch of universal history, not indeed accompanied by the thunder of cannon, like the great battles of the world, but, in spite of its silent working, it sometimes has more influence than war upon the destiny of nations and of humanity as a whole.

No one, I think, would deny that during the past century the development of chemistry and physics, and of the technical arts depending upon them, has been of the utmost importance in advancing the growth of civilised nations, and so has played no small part in the history of the world. Modern physics have enabled men to avail themselves of the forces of fire and water, and the discovery of steam power has altered the face of the earth, for now it is covered with a network of railway lines, upon which trains rush to and fro, whilst the sea too is constantly traversed by sea monsters built of steel and driven by steam, which bring the farthest ends of the world into communication, and convey to still uncivilised nations the achievements of modern progress. By means of physics, too, has the human intellect succeeded in subjugating the mysterious waves of ether, both visible and invisible, and now through the electric light we have new suns; electric telegraphs and submarine cables have triumphed over the old limitations of time and space, while Röntgen-rays penetrate even the human body, and fix the outline of its skeleton on photographic plates. The development of physics and chemistry has enabled men to construct innumerable motors and machines, and to devise chemical compounds used in various branches of industry, resulting, on the one hand, in a complete revolution in the economical conditions of the people, and, on the other hand, supplying our armies with terrible guns and deadly explosives, in the invention and perfection of which each nation strives to outstrip its neighbours, in order to annihilate them more speedily, should an opportunity occur.

It is obvious that astronomy and biology owe very much to their kindred science—physics, and especially to optics and mechanics, without which the extraordinary progress made in recent times would have been impossible. Optics and mechanics have supplied the astronomer and the biologist with their instruments, and, in conjunction with chemistry, have given them technical methods, bringing the infinitely distant near to the investigator's eye, enlarging the infinitely small, and even rendering the invisible visible on the astronomer's photographic plate and in the coloured sections of the microscopist, revealing to the one the marvels of the heavens, and to the other the secrets of the most diminutive living beings.

It is not, however, my intention now to dwell upon the development of the physical sciences and their influence in changing the various circumstances of human life; I purpose to deal only with the development of biology, which cannot boast of such wide-reaching triumphs. Nevertheless, the history of biology in the nineteenth century forms part of the history of the human intellect, and is an instructive piece of what may be called internal history, of greater importance to mankind than a merely superficial examination might lead us to suppose.

1. Meaning and Subdivisions of Biology

We must begin by clearly understanding what we mean by *biology*. What is biology? As the name tells us, it is the science of life and of living creatures. This is biology in the widest sense of the word, and it coincides with its oldest historical signification, as it occurs in scholastic philosophy. Biology, or the study of living creatures, is closely connected with cosmology, or the study of the bodies composing the universe, for, strictly speaking, the study of living creatures includes the whole study of plants, animals and men, but this is so vast a territory that we generally apply the name biology to one comparatively small subdivision of it, and speak of the biology of plants and animals in contradistinction to their morphology, physiology, and morphogeny. *Morphology* deals with the forms and component parts (organs, tissues, and cells) of organisms. The history of individual development, or *Morphogeny*, deals with the growth of the organic forms from the egg to maturity. *Physiology* discusses the functions of the various parts of the organism, and establishes their relations to the process of life and also the chemical and physical laws regulating their activity. Finally, *Biology* is concerned with the external activities affecting the organisms as individuals, and consequently governing their relation to all other organic beings as well as to the inorganic world. In this respect biology differs from *Psychology*, the proper subjects of which are the processes of sensitive and intellectual life—essentially internal activities, although these frequently

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come within the scope of biology in virtue of their outward manifestations.

In the narrower sense of the word, therefore, biology may be defined as the science dealing with the mode and relations of life in animals and plants. Human biology forms a distinct branch of knowledge, forming a part of anthropology, and is no longer regarded as belonging to biology in the more restricted sense of the word, now generally accepted by scientific writers.

With regard to the meaning of the word 'biology' and the most convenient definitions to be assigned to it, there are many different opinions, only a few of which can be mentioned here briefly. Almost all scientific men agree in retaining the old name 'biology' (in the wider sense) to denote the whole mass of knowledge regarding life and living creatures.[1] But there is great diversity of opinion as to the designation of the special branch of that science, which we have called biology in the narrower sense. German zoologists used to call it simply biology, until Ernst Haeckel suggested the name *Œcology*. Œcology means 'study of dwelling' or 'science of keeping house,' it approaches the more restricted meaning of biology, but does not cover it. This new name has found favour not only with many zoologists, but also with botanists. Fr. Delpino,[2] F. Ludwig,[3] and J. Wiesner[4] speak of the phenomena of plant life as the biology of plants, whereas other botanists, such as R. v. Wettstein,[5] prefer the name œcology of plants.

Fr. Dahl was the first German zoologist to suggest the adoption of *Ethology*, or science of the habits of life, a word first introduced by French scientific writers to replace biology in the narrower sense.[6]

This new name would certainly be more applicable to animal biology than Haeckel's œcology, but it is not applicable at all to plants, as we can speak of 'habits of life' only with reference to creatures that possess instinct and psychological life. If we are to have a new name, it ought to be applicable both to plants and to animals with regard to their phenomena of life.

An eminent botanist, J. Reinke,[7] is of opinion that we can dispense with the word 'biology' in the narrower sense, and, in order to avoid confusion when it is used in its wider sense, he suggests the simple expression 'Mode of life among animals and

[1] Cf. for instance, O. Hertwig's *Entwicklung der Biologie im* 19 *Jahrhundert*, Jena, 1900.

[2] *Pensieri sulla Biologia vegetale, &c.*, Nuovo Cimento, XXV, Pisa, 1867.

[3] *Lehrbuch der Biologie der Pflanzen*, Stuttgart, 1895.

[4] *Biologie der Pflanzen*, 1902, I.

[5] *Leitfaden der Botanik für die oberen Klassen der Mittelschulen*, 1901, 1.

[6] Cf. Wasmann, 'Biologie oder Ethologie?' (*Biolog. Zentralblatt*, XXI, 1901, No. 12, pp. 391–400).

[7] 'Was heisst Biologie?' (*Natur und Schule*, I, 1902, part 8, p. 449, &c.).

plants' as a substitute for the word in its more restricted signification. This designation is clear and convenient enough, but I scarcely think that it fulfils the requirements of science, for we need some internationally intelligible word for 'mode of life' or 'Lebensweise,' formed from Greek roots on the analogy of 'Morphology,' 'Physiology,' &c.

To supply this deficiency the word *bionomy* or *bionomics* has been introduced in England[1] and North America,[2] and this is perhaps the best word yet suggested to designate the mode of life of animals and plants, for it denotes the laws governing life' (βίος-νόμος), and so means exactly what we defined as biology in the narrower sense, and at the same time it avoids the ambiguity of the word biology. I should have no objection to accept this new name *Bionomics*, to designate the mode of life among animals and plants; but as it is not yet current in Germany, I may be permitted to retain the old name.

The experimental study of the laws of heredity and variation has recently been called *Biometry*.[3] In 1901 a new periodical appeared in Cambridge (England) entitled *Biometrica: A Journal for the Statistical Study of Biological Problems*. Biometry is, therefore, synonymous with Statistical Biology.

The following simile may serve to illustrate more clearly the original meaning of the word *biology*, and the various modifications which it has undergone owing to the progress made by science in the nineteenth century.

Biology, in its widest signification, embraces all that we know about living creatures, and we may compare it with a lofty tree having three main boughs, but many branches, and its stem, boughs, and branches are the biological sciences. The tree is crowned by twigs shooting from the main trunk, and this crown represents the science dealing with man, or anthropology, and the topmost of its twigs, rising up into the domain of the intellectual sciences, is the psychology of man and nations. Below it is human biology in the narrower sense, then human physiology, human morphology and the history of human development, all having many subordinate twigs,

[1] Cf., e.g., G. K. Marshall and E. B. Poulton, 'Five Years' Observations and Experiments on the Bionomics of South African Insects' (*Transactions of the Entomological Society*, London, 1902, part 3).

[2] Cf. Ch. S. Minot, 'The Problem of Consciousness in its Biological Aspects' (*Proceedings of the American Association for the Advancement of Science*, XXXI, p. 272).

[3] Cf. Chr. Schröder, 'Eine Sammlung von Referaten über neuere biometrische Arbeiten' (*Allgemeine Zeitschrift für Entomologie*, IX, 1904, Nos. 11 and 12, p. 228, &c.).

bearing, for the most part, the same names as the corresponding ramifications of the zoological stem. Some few branches belonging to the crown have names of their own, to which zoology supplies analogies only; such are ethnology and archæology, psychopathology, and medicine.

Below the crown a great bough springs from the main trunk of the biological sciences: this is zoology. Its chief offshoots are animal psychology and animal biology (animal bionomics) and the physiology, morphology, and morphogeny of animals. In the course of the nineteenth century a great number of little twigs grew out of each of these branches, of which only a few can be mentioned here. Out of animal biology or bionomics sprang trophology, or the science dealing with the food of animals; œcology, or the science dealing with their habitations; animal geography, dealing with their distribution; and, further, their parasites have been studied, and the tendency of certain animals to live with other animals or near to some particular plants (symbiosis). This has given rise to investigations of a biological nature into the way of life of ants and termites, and one of the most fertile offshoots of modern biology is the study of the inquilines among ants and termites. We cannot do more than name nervous physiology which, with its offshoots, cerebral physiology, physiology of the external organs of sense and of the nerve tracks, threatens to take the place of animal psychology, now said to be out of date.[1]

Modern morphology has even more ramifications, branching out in one direction into systematics, or the science of systematic classification, and in the other into morphology proper, which latter is subdivided into exterior and interior morphology, the interior comprising topographical anatomy, histology or study of the tissues, and cytology or study of the cells—all three well-developed offshoots of morphology. Moreover, all these branches of morphology have their counterparts on the physiological side, in the physiology of the organs, tissues, and cells.

Morphogeny, or the history of the development of animals,

[1] On this subject cf. my article 'Nervenphysiologie und Tierpsychologie' (*Biolog. Zentralblatt*, XXI, 1901, No. 1, pp. 23–32) and also *Instinkt und Intelligenz im Tierreich*, 1905, chap. ii.

has two great branches, viz. ontogeny, or the history of individual growth, and phylogeny, or the history of the race development. Ontogeny is divided into embryology and post-embryonic development, which includes the phenomena of metamorphosis, metagenesis, &c. Finally we must allude to animal pathology as a branch of zoology. Reference has already been made to animal geography as a branch of animal bionomics.

Nearer the root of the tree springs the lowest bough of biology, viz. botany. Nothing is found on it corresponding to the most dignified offshoot of the zoological bough—animal psychology, because plants have no consciousness, and even the most sensitive of them show only a faint resemblance to conscious life.[1]

There are, however, on the botanical bough a good many offshoots corresponding to the other parts of zoology; we have the biology (bionomics) of plants, which includes plant-geography, and we have also plant-physiology and morphology, plant-anatomy and cytology, and finally phytopathology.[2] The botanical branch is further distinguished by possessing one suspiciously luxuriant and poisonous looking offshoot, which boldly rises up to the branch of the crown that we have called 'medicine,' and this is bacteriology. Fortunately it has a less poisonous side in the phenomena of fermentation and assimilation of nitrogen, which are in many respects beneficial to man.

To our astonishment we see that our tree bears one or two apparently dead branches of considerable size; they spring from the same point of the main trunk as the zoological and botanical boughs respectively, and they are called *palæozoology* and *palæophytology*. They are, however, by no means really dead, although they deal with the extinct ancestors of the animal and vegetable kingdoms of the present day.

In the main trunk supporting the crown and the branches

[1] Many modern botanists regard this analogy as constituting real identity (homology), but they are certainly mistaken. Cf. for instance, Haberlandt, *Die Sinnesorgane im Pflanzenreich zur Perzeption mechanischer Reize*, Leipzig, 1900. For a criticism on these views, see J. Reinke, *Philosophie der Botanik*, 1905, 66, &c., 83, &c.

[2] The distinction between anatomy and histology is less marked in the case of plants, as their tissues do not differentiate themselves so sharply into organs as do those of animals.

of the tree of biological knowledge with all their offshoots and twigs rises a stream of sap, representing the comparative and generalising elements belonging to all the biological sciences; these connect all the parts of the tree with one another and enable us to view them intelligently as a whole, and at the same time they enlighten us as to its growth. Comparative psychology effects a close connexion between the zoological branch and the crown of the tree; comparative biology and physiology, comparative morphology, anatomy and histology, comparative cytology and comparative morphogeny send streams of life through all the branches and twigs of the great tree, and show that they are all living parts of one vast whole.

Chemistry and physics, too, and especially mechanics of organic structures, are represented in the roots of the tree, as biochemistry and biophysics, and they connect it with the surrounding domain of the inorganic sciences. But the quintessence of all the sap flowing in the tree of biological knowledge is the scientific conception of life, and the trunk of the tree, which supports and nourishes all these branches and twigs, is the science of life.

2. The Earliest Development of Biology

We have just seen how the tree of biological sciences grew rapidly in the nineteenth century, and produced an indescribable abundance of offshoots, leaves, blossoms and fruit on branches previously bare. Let us now consider the origin of this tree and how it fared whilst still an insignificant seedling.

It was not planted first in the year 1800, nor did it suddenly develop on New Year's Day, 1801, into a trunk sturdy enough to support all the branches and twigs which the new century was destined to add to it. It is far older than this, and we can trace its history for several thousand years. The seed, whence this tree has grown, was planted when God breathed into the first man the breath of life, as we read in the beautiful figurative language of Holy Scripture. The breath of God's spirit, dwelling in man, its all-embracing power of understanding and its never satisfied thirst for knowledge, form the hidden motive power, the inner living force of this tree. Man has always been possessed by a thirst for knowledge, both among civilised nations and among the wild children of nature. The Eskimo of the present day adorns the walrus ivory implements used in shooting his arrows with dogs' heads and outlines of reindeer, birds and human beings, showing that the shapes of the living creatures around him have deeply impressed themselves upon his mind; and, in the same way, the cave-dwellers of Central Europe scratched rough sketches of fish, horses and other animals on reindeer bones. Even if the famous representation of a long-haired mammoth with a long mane, which was found on a piece of a mammoth's tooth, proves not to be genuine, and the much finer engraving, on a reindeer antler from the cavern at Kessler, of a reindeer grazing, is in all probability a modern forgery, still, as J. Ranke says,[1] it is difficult to say exactly when the germ of biological research latent in the mind of man first assumed a scientific form, and appeared as a young plant above the ground. We know, however, one famous gardener, who tended the little tree most skilfully, and that is Aristotle the Stagirite.

Aristotle had predecessors, no doubt; the animal system devised by the followers of Hippocrates of Cos had already prepared the way for him,[2] yet he certainly deserves to be called the Father of Biological Science. His classical works 'Historia animalium,' 'De partibus animalium,' and 'De generatione animalium' are the foundations of our scientific systematic classification and biology, of morphology, anatomy, and morphogeny.[3] In his writings he actually mentions 500 kinds of animals.[4] As he does not allude to many other varieties that are very common and occurred in ancient Greece in his day, we must assume that he did not think it necessary to speak of all the animals with which he was familiar. He divides animals into two chief classes, *ἔναιμα* or with blood (more correctly red-blooded), and *ἄναιμα* or bloodless, and

[1] *Der Mensch*, II, Leipzig and Vienna, 1894, 459, &c.

[2] Cf. R. Burckhardt, 'Das koische Tiersystem, eine Vorstufe der Zoologischen Systematik der Aristoteles' (reprinted from the *Verhandl. der naturf. Gesellschaft in Basel*, XV, 1902, part 3, pp. 377–414).

[3] R. Burckhardt, 'Das erste Buch der aristotelischen Tiergeschichte' (*Zoologische Annalen*, I, Würzburg, 1904, part 1). Also 'Zur Geschichte der biologischen Systematik' (*Verhandlungen der Naturf. Gesellschaft in Basel*, XVI, 1903, 388–440).

[4] We cannot here discuss their division into different classes. Günther remarks that the number of varieties of fish known to Aristotle seems to have been 115 (*Handbuch der Ichthyologie*, 1886, p. 3).

this division practically answers to the modern classification into vertebrates and invertebrates. The eight γένη μέγιστα, or chief classes of the Aristotelian system, agree roughly with our chief classes in the animal kingdom. The conception of the εἶδος or species, introduced by Aristotle, underlies our modern conception of it. But the great philosopher was not only a pioneer in systematic classification, he was equally eminent as a morphologist, an anatomist, a biologist, and an embryologist. He compared animals with regard to their form and structure, and studied their mode of life and the history of their development.

How great a biologist Aristotle was is proved by the fact that some of his discoveries were rediscovered in the nineteenth century, and were regarded as brand-new triumphs of modern science. Aristotle knew that many sharks do not only produce their young alive, but that in their case the young before their birth are nourished by a process closely resembling that of mammals (development of a placenta).. This fact was rediscovered by Johannes Müller, a famous anatomist and zoologist (1801–58). Moreover, Aristotle was aware of the difference between male and female cephalopods, and had observed that young cuttlefish possess a vitelline sac near the mouth. The accuracy of these old observations has been completely proved by modern research. Bretzl has thrown an astonishing light upon the extent and importance of the botanical knowledge possessed by Greeks of Aristotle's time.[1]

When we consider the well-merited prestige enjoyed by Aristotle as founder of biology, when we remember the enormous wealth of knowledge, interspersed though it be with many errors, contained in his works, we cease to wonder that for two thousand years everyone, who studied biology at all, studied Aristotle almost exclusively, quoted Aristotle, made extracts from Aristotle, and wrote commentaries on Aristotle. The work of the Younger Pliny in this department is insignificant in comparison with that of his great predecessor, and even in some respects shows a falling off. Pliny, however, has been the chief source of information for most of the students of nature both of antiquity and of the Middle Ages, who derived

[1] *Die botanischen Forschungen des Alexanderzuges*, Leipzig, 1903. Cf. the review in the *Botanisches Zentralblatt*, XCIII, 1903, p. 97, &c.

from him their biological knowledge, and adopted as genuine all the stories found in Pliny's 'History of Animals,' without in any way testing their truth. A standard work of this description is the famous 'Physiologus' or 'Bestiarium,' in which all the legends connected with zoology are collected, with edifying morals appended to them.

It would be unfair not to acknowledge that, among the great scholastic philosophers of the thirteenth century, there were a number of men who did their best to carry on independent scientific research. Besides St. Thomas Aquinas, the Dominican Order produced in that century three great men, conspicuous not so much for their scholasticism, as for their proficiency in another department of knowledge.

These were Thomas of Chantimpré, Vincent of Beauvais, and Albertus Magnus or Albert the Great (1193–1280),[1] of whose treatise upon animals Victor Carus says, in his 'Geschichte der Zoologie,' p. 226, that, in comparison with the works of the two previously mentioned writers, it is far more thorough and composed with greater self-confidence.

Thomas of Chantimpré was a pupil of Albertus Magnus,[2] and that Vincent of Beauvais used his books is proved by his numerous quotations from them. Although, like all his predecessors, Albert the Great based his work on Aristotle,

[1] Cf. F. A. Pouchet, *Histoire des Sciences naturelles au moyen-âge, ou Albert le Grand et son époque considérés comme point de départ de l'école expérimentale*, Paris, 1853. Cf. also Fr. Ehrle, S.J., 'Der selige Albert der Grosse,' in *Stimmen aus Maria-Laach*, XIX, 1880; G. v. Hertling, *Albertus Magnus, Beiträge zu seiner Würdigung*, written in honour of the 600th anniversary of his death, Cologne, 1880; E. Michael, S.J., *Geschichte des deutschen Volkes vom 13 Jahrhundert bis zum Ausgang des Mittelalters*, III, 1903, pp. 445–460; Arthur Schneider, *Die Psychologie Albert des Grossen: Nach den Quellen dargestellt*, I, 1903, Vorwort VIII.

[2] He describes himself as an *auditor eius per multum tempus*. (Thomas Cantipratanus, *Bonum universale*, Duaci, 1627, l. 2, c. 57, § 50, p. 576. Cf. E. Michael, S.J., 'Albert der Grosse,' in the *Zeitschrift für Katholische Theologie*, 1901, part 1, p. 43.) Borman is therefore probably mistaken in thinking that Thomas of Chantimpré's work was one of Albert the Great's chief sources of information in the compilation of his book on animals. V. Carus falls into the same mistake in his *Geschichte der Zoologie*, p. 227. Cf. also Alex. Kaufmann, *Thomas von Chantimpré*, Cologne, 1899. Thomas was a canon regular in the Augustinian monastery at Chantimpré before he entered the Dominican Order in 1232. His book, entitled *Liber de rerum natura*, was subsequently translated into German by Konrad Megenberg, who belonged to the cathedral chapter at Ratisbon. Its German title is *Buch der Natur* (Book of Nature), and it records the results of much independent research. The same author's work on bees (*Bonum universale de apibus*) is a pious picture of manners rather than a treatise on natural history.

he took more pains than any of them to make independent observations of his own. His treatise on animals consists of twenty-six books, of which nineteen correspond to the writings of Aristotle, whilst seven are of independent origin.[1]

Book XX, the first of those containing his own results, deals with the nature of animals' bodies in general, and Book XXI with the degrees of perfection attained by them (*de gradibus perfectorum et imperfectorum animalium*), a quite modern idea in classification, on the lines of comparative morphology of animals. The remaining five books deal with animals singly, arranged alphabetically within the larger groups. These seven books show conclusively that the author was not content to write a commentary on Aristotle, but aimed at rendering his work more complete by adding the results of his own investigations.

Albert the Great's seven books 'De vegetabilibus et plantis,' which contain his views on botany, have been carefully studied and justly appreciated by E. Meyer, in his 'Geschichte der Botanik,' IV, Königsberg, 1857, but the more important work on zoology has hitherto met with far too slight recognition among scientific men. An attempt to display its merits, made by Karl Jessen in 1867, was frustrated, owing to the defective state of most editions of Albert the Great's works.[2]

E. von Martens subsequently published some observations on several of the mammals mentioned by him, and Victor Carus has devoted a few pages to Albert the Great in his 'Geschichte der Zoologie,' but without discussing his work in detail.[3] Although Carus is by no means a partisan of the Church, he feels bound to confess, on p. 224, that 'Albert, to whom the cognomen "Great" may justly be conceded, is undoubtedly the chief writer of the thirteenth century on the subject of natural science.' If Carus had adhered to the principle which he himself laid down, and had foreborne to judge Albert the Great as a zoologist by the standard of a modern writer on

[1] In the complete edition of Albert the Great's works, published in Paris by Vivès, the treatise on animals is contained in vol. xi (*De animalibus pars prior*) and vol. xii (*De animalibus pars altera*).

[2] 'Alberti magni historia animalium' (*Archiv für Naturgeschichte*, XXXIII, vol. i, 1867, pp. 95–105).

[3] Munich, 1872, pp. 224–237.

science, he would probably have spoken in more favourable terms of his achievements in zoology.

Although Albert the Great could not completely disentangle himself as a zoologist from the prejudices and fancies of his predecessors, his merit lies, not merely in his having gone back from Pliny to Aristotle, but also in his having led the way to independent research, which does not rely blindly upon authority, but looks for itself.[1]

R. Hertwig is perfectly correct in stating in the most recent edition (seventh) of his 'Lehrbuch der Zoologie' (1905, p. 7) that Albert the Great even began to collect his own zoological observations. In many passages of his work on animals he refers to his own investigations, and, when he describes anything, he frequently adds a remark to the effect that he has himself seen the thing in question, and even possesses it in his collection. He devotes several chapters to the habits of falcons, which he seems to have studied with particular interest. In one place he tells us that he took a short sea voyage for zoological purposes, and on the shore of an island he collected ten or eleven kinds of 'bloodless sea-beasts.' After recording the various tales told about the propagation of fish, he adds: 'I believe that none of all this is true, for I have myself made diligent investigations, and have questioned the oldest fishermen engaged in salt and fresh water fishing,' and he proceeds to give the results of his observations and inquiries. He declares that by personal observation he has disproved the popular theory that the left legs of a badger

[1] Men such as Albert the Great are enough to refute the discovery made by certain followers of Darwin, that Christianity has 'stifled the spirit of scientific research' and has 'caused a kind of hostility to the idea of busying the mind with natural objects.' It is unfortunate that such prejudiced statements have found their way into even our modern text-books of zoology. See, for instance, R. Hertwig, *Lehrbuch der Zoologie*, 1900, p. 7. The following words, which I quote from Hertwig, cannot be applicable to Albert the Great: 'The question how many teeth a horse has was discussed in many controversial treatises, in which the authors used all the heavy artillery at their disposal, but it did not occur to one of the learned men to look inside a horse's mouth and see for himself.' It is to the credit of the author of the above-mentioned excellent text-book of zoology, that the words just quoted have been omitted in the two last editions of his book (1903 and 1905). It is satisfactory to observe that the achievements of mediæval scholars in the domain of natural science are gradually receiving fairer treatment, and are being judged by a more unprejudiced standard. Cf. also J. Norrenberg, 'Der naturwissenschaftliche Unterricht in den Klosterschulen' (Scientific Instruction in Monastic Schools), in *Natur und Schule*, III, 1904, part 4, pp. 161–169.

are shorter than the right legs, and he relegates the stories of geese growing on trees, and other zoological marvels, into their proper sphere as fictions of the imagination.[1] It is true that his statements are interspersed with a good many mistakes. He is right in saying that flies have two wings, but wrong in giving them eight legs—and his famous pupil, Thomas Aquinas, is falsely accused of having reckoned ants among the *reptilia quadrupedia*, and thus of having fallen into an opposite error.[2] It is hardly necessary to point out how impossible it was for him to correct the old legends with reference to exotic animals, and so he says that the porcupine shoots its quills at its enemies, that the wild unicorn grows tame when caressed by a maiden, &c. We ought to bear in mind that to a German student of nature in the thirteenth century no other source of information about foreign animals was accessible than the old fabulous stories. What pains Albert the Great took to obtain trustworthy information about animals that he had never seen, is proved by his admirable account of the methods then in use in the whalefishery.

Careful studies in another quarter have recently shown that Albert the Great followed an independent method of investigation. Dr. R. Hertwig, Professor of Zoology at the University of Munich, suggested to Dr. H. Stadler to make a critical examination of Albert's zoology and botany. The full result of this examination has just been published in the *Forschungen zur Geschichte Baierns*, XIV, 1906, first and second parts, pp. 95–114, but Stadler communicated a good deal of it previously, at a lecture delivered on March 20, 1905, to the 'Verein für Naturkunde' in Munich. The title of the lecture was: 'Albert the Great as an independent student'; I subjoin some extracts from it:—

This very prolific writer was a scholastic, but he occupies a position on a level with Aristotle rather than subordinate to him,

[1] The story of the geese growing on trees probably originated in the fact that the barnacle goose (*Lepas anatifera*) often attaches itself to floating tree trunks.

[2] In the *Summa Theologiae*, I, q. 72, ad 2. In Vivès' edition (1871) the passage reads as follows: 'Per reptilia vero (intelleguntur) animalia, quae vel non habent pedes . . . vel habent breves, quibus parum elevantur ut lacertae et tortucae.' There is a note on the word *tortucae*: 'Sic codices, sed nescio qua incuria in Parmensi et in omnibus editionibus *formicae*.' *Tortuca* is *tartaruga, tortue, tortoise*, and is rightly reckoned among the reptiles, only a constantly repeated misprint has turned tortoises into ants!

and did not simply reproduce Aristotle's statements, but, as far as he could, explained, completed and expanded them. He displayed great shrewdness and keen intelligence in carrying on his favourite observations on the animals and plants of Germany, whence he derived the evidence for his scientific statements that he based upon Aristotle. His writings therefore contain all the information on natural history possessed by the people of Germany in his day ; he describes the life of animals as observed by intelligent huntsmen and farmers, fishermen and bird-catchers ; everywhere the biological element and his own personality are prominent, and for this reason his writings form a sharp contrast to the dry book-learning of the periods preceding and following his lifetime. It is true that in dealing with botany he follows the lines of the pseudo-Aristotelian work ' De plantis,' really written by Nicholas Damascenus, but under the form of excursus he gives a far better account of the subject, based upon his own observations. He describes very correctly the vascular bundles of the plantain leaf and the medullary rays of the vine, and divides plants into two classes, cortical and tunical, a division approximately corresponding to that of monocotyledonous and dicotyledonous. He distinguishes parenchyma and bast-fibres in the large stinging nettle, hemp and flax ; he knows the difference between the inner and outer bark, and the importance of each to the life of a plant. He has observed the square stem of the deadnettle, and the diversity in growth between plants in isolation and when cramped for space. He describes very clearly the difference between a thorn and a sting ; he attempts a classification of leaves according to the shape, notices that plants with woody stems have bud-scales, and herbaceous plants have naked buds, and he recognises, as a peculiarity of the grape vine, the fact that fruit and tendrils are opposite to the foliage leaves.

In speaking of blossoms he draws attention to their various forms of insertion, and mentions stamens, pistil and pollen, although he confuses the pollen with wax. He comments upon the deciduous calyx of the poppy, tries in a very primitive fashion to classify the forms of the corolla, insists upon the importance of the seed in preserving the species, and gives a very fair classification of fruits. The position and the significance of the ovules and of the tissues connected with nutrition did not escape his notice. The sixth book, ' De vegetabilibus,' contains many admirable descriptions of single plants, especially of the mistletoe, the hazel, the alder, the ash, the date-palm, the poppy, borage and rose, and in the case of the last-mentioned he gives an excellent account of the æstivation of the calyx and of the alternation of the parts of the flower, and suggests the true explanation of their significance.

We may speak in similar terms of his work on zoology, for which, however, we are unfortunately obliged to use the very unsatisfactory edition published by Auguste Borgnet in Paris, 1891, so that much in it appears open to question. Of animals known in Germany, Albert begins by describing the German marmot and the earless marmot, the two kinds of marten, the garden dormouse and the common dormouse, and he is the first writer who alludes to the chamois, the badger, the rat, the ermine and the polecat.[1]

He gives charming accounts of the mole, the marmot and the squirrel; he knows the *Lepus variabilis* of the North and the polar bear; he describes a whaling expedition and remarks that in his day the elk, the bison, and the aurochs were to be found only in the extreme east of Germany. His description of the cat displays great sympathy with animals and very sharp powers of observation.

In dealing with birds, he discusses the various falcons in the greatest detail, but he is well acquainted with the other birds of prey. He speaks of the peculiar structure and purpose of the woodpecker's claws, and considers the distribution of the hooded crow and the habits of migratory birds.

Blackcock, grouse, and heathcock were familiar to him, and he knew many kinds of singing birds (four varieties of finches, two of sparrows and three of swallows), also the nutcracker and kingfisher; he describes the nest of the magpie and the habits of the cuckoo with great accuracy. The lecturer proposed to speak of Albert the Great's knowledge of fishes on another occasion; he stated that Albert had dissected insects and had perhaps recognised the digestive system and heart. He gives a correct account of the development of cockchafers and wasps, and also of caterpillars and their spinning process, and of the habits of the ant-lion. Of other creatures, the best description given as the result of his own observation is perhaps that of the jelly-fish.

Among the learned Franciscans of the thirteenth century, Roger Bacon, the *doctor mirabilis*, deserves special mention,[2] as he is in many respects the equal of the great Dominican, Albertus Magnus. His chief services to science are in the domain of physics, chemistry and medicine, rather than in that of the descriptive natural sciences. Considering the age in which he lived, he had wonderfully advanced opinions regarding physiology. Much attention has been paid to Bacon by Émile Charles,[3] who declares that the results stated in his

[1] In the printed text of the lecture there is a query after the word *rat*, but having had some correspondence with Stadler, I infer from a letter dated December 4, 1905, that the query ought to be omitted, as Albert the Great was really the first to describe the rat.

[2] See Dr. H. Felder, O. Cap. *Geschichte der wissenschaftlichen Studien im Franziskanerorden bis um die Mitte des* 13 *Jahrhunderts*, Freiburg i. B., 1904, pp. 379-402.

[3] *Roger Bacon, sa vie, ses ouvrages, ses doctrines d'après des textes inédites*, Paris, 1861.

work 'De vegetabilibus' surpass those of Albert the Great. We receive an impression of something quite modern, in fact almost anti-vitalistic, when the mediæval Franciscan speaks thus of the relation in which chemistry (which he calls *alchimia speculativa*) stands to the other natural sciences : [1]

Because students are not acquainted with this science, they also know nothing of its bearing upon natural history, for instance, the origin of living creatures, plants, animals and men. . . . For the constitution of the bodies of men, animals and plants depends upon an intermingling of elements and fluids, and proceeds in accordance with laws similar to those governing inanimate bodies. Consequently whoever is ignorant of chemistry, cannot possibly understand the other natural sciences, nor theoretical and practical medicine. . . .

3. The Development of Systematic Zoology and Biology

As soon as the age of discoveries began in modern times, much more interest was taken in the study of nature, and the tree of biological knowledge put forth one branch after another, all of which were full of vigorous life. In our historical sketch we must follow this process of division, and we will begin by considering the growth of systematic classification, leaving for the present the development of some other branches.[2]

It was natural that external differences in form should be the first things to attract the attention of a student, in the case both of plants and of animals ; later on he tried to learn something about the mysteries of their constituents, of their configuration, and of the vital phenomena of living organisms. It was natural, therefore, for systematic zoology and that *scientia amabilis*, systematic botany, to develop earlier than the other branches of biology. We cannot do more than mention the chief pioneers in systematics. Edward Wotton, an Englishman, wrote in 1552 a book called 'De differentiis

[1] *Opus tertium*, c. 12, ed. Brewer, 39 : Et quia haec scientia ignoratur a vulgo studentium, necesse est ut ignorent omnia quae sequuntur de rebus naturalibus ; scilicet de generatione animatorum, et vegetabilium et animalium et hominum : quia ignoratis prioribus necesse est ignorari quae posteriora sunt. Generatio enim hominum et brutorum et vegetabilium est ex elementis et humoribus et communicat cum generatione rerum inanimatarum. Unde propter ignorantiam istius scientiae non potest sciri naturalis philosophia vulgata nec speculativa medicina nec per consequens practica. . . .

[2] Cf. R. Burckhardt, 'Zur Geschichte der biologischen Systematik,' Bâle, 1903 (*Verhandlungen der Naturf. Gesellschaft in Basel*, XVI).

animalium,' in which he returned to Aristotle's system, which he developed by adding to it the group of zoophytes. Another Englishman, John Ray (1628–1705),[1] defined the Aristotelian idea of species more clearly. His works, 'Methodus plantarum nova' (1682) and 'Historia plantarum' (1686–1704), are very important in systematic botany, whilst his synopses of various classes of animals, especially of quadrupeds and snakes (1693), mark an epoch in systematic zoology. In this way Ray, the son of an English blacksmith, facilitated the work done by the great Swedish knight Karl v. Linné (Linnæus), who was born in 1707, being the son of a Protestant pastor in Råshult. A year after the birth of Linnæus died his chief forerunner in botanical research, the eminent Frenchman, Joseph Pitton de Tournéfort (1656–1708), who in his 'Éléments de botanique ou méthode pour connaître les plantes' laid the foundation of our present classification of plants.

The work of Linnæus (1707–78) marks a fresh stage in the growth of the tree of biological knowledge, and caused it to become a vigorous trunk with many branches. Under his influence it grew strong enough to support the wealth of offshoots which were destined to spring from it during the nineteenth century. He made many journeys to Central Europe in order to study the chief collections of his day, and with unflagging industry he acquired the material for his great work, the 'Systema naturae,' which stands alone of its kind and is of the utmost importance in the history of biology. The first edition appeared in 1735, the fifteenth (which was the last revised by Linnæus himself) in 1766–8. The most complete and best known is the seventeenth edition of the 'Animal Kingdom' brought out by Gmelin, 1788–92.

The chief value of the 'Systema naturae' lies not so much in the fact that Linnæus has in it formed systematic groups of all previously described varieties of animals and plants, adding many fresh ones to those already known, but rather in his having introduced in his binary nomenclature a fixed scientific terminology, so that exact statements of laconic brevity thenceforth took the place of long-winded descriptions. This work of Linnæus had as important a bearing upon the development of descriptive natural science, as the introduction of a

[1] Ray died on January 17, 1705, not, as is generally stated, in 1704.

written language has upon the development of a nation. Until a language possesses a grammar and a vocabulary, it is only a scientific embryo ; its elements lack sharpness and clearness ; it has, so to say, no framework to which they can be attached in orderly fashion.

There is no need for a long explanation of the binary nomenclature. It is enough to say briefly that to every species of animal and plant a scientific double name is assigned, consisting of a generic and a specific name, both latinised in form, and as these names are constant, universally current and unchanging, they are free from arbitrary fluctuations in use, such as are of common occurrence in the case of popular names. To the generic name, which is a noun, the *differentia specifica* is added by connecting with it the specific name, which is an adjective. *Canis familiaris*, *Carabus auratus*, and *Carabus nitens* may be taken as typical examples. Whoever gives a name of this kind adds a concise description of the animal to serve as a means of identifying its species, and a writer using the name appends to it in abbreviated form that of the author who first gave it and described the animal in question, so that, when in future any one reads *Carabus auratus*, L. (Linnæus), he knows exactly once for all what form it is intended to designate. In this way a name such as *Carabus auratus*, L., becomes a generally recognised scientific appellation, leaving nothing to be desired in the way of clearness and simplicity. Through the use of the binary nomenclature, the whole zoological and botanical system has been reduced to a classified catalogue, well arranged and visible at a glance, and in devising it Linnæus conferred an inestimable boon upon biology. The inspiration thus in so simple a manner to arrange logically the vast multiplicity of forms in the animal and vegetable kingdoms is like Columbus' egg—before Linnæus appeared, no one knew how it could be made to stand at all, but after Linnæus had once for all set it upright, no one had anything to do but to follow his example.

On account of his 'Systema naturae' Linnæus is to be reckoned as the founder of modern systematic science. His system of nomenclature is still the standard one, and will probably continue to be so. The laws of zoological nomenclature, as elaborated at the close of the nineteenth century by a committee, specially appointed for the purpose at recent zoological congresses,[1] and universally adopted in scientific circles, are only a logical carrying out and detailed specialisation of the principles laid down by Linnæus. At the annual meeting of the German Zoological Society in 1891, it was decided to appoint a committee to lay down rules securing uniformity in zoological nomenclature.[2] In order to have a firm basis on which to decide disputed points of priority, the German Zoological Society caused a reprint of the tenth edition of Linnæus' 'Systema naturae' to be issued, thus marking the year 1758, in which the tenth edition first appeared, as the date when systematic zoology originated, and fixing as the standard generic names those used at that time by Linnæus.

The International Botanical Association is now dealing with the question of botanical nomenclature at the International Botanical Congresses, of which the first was held in Paris in 1900, and the second at Vienna in 1905.

Linnæus' 'Systema naturae' is a monumental work, such as could be accomplished only at one period, at least by a single individual. By means of the further development of systematic zoology and botany, effected by a closer study of European fauna and flora, as well as by the exploration of foreign countries, which has supplied a boundless and ever-increasing wealth of material, systematic science has now attained such gigantic proportions, that no single human intellect, not even the genius of an Aristotle, would be capable of grasping and assimilating it in all its details. In the year 1901 the total number of species of animals known to science amounted to at least 500,000, of which more than half are insects. In giving the number of species of beetle at 100,000 we are probably rather understating it. In the vegetable kingdom it is estimated that there are about 200,000 species scientifically described, divided into 11,000 genera—there are 50,000 species of cryptogams alone.

[1] *Règles de la Nomenclature des êtres organisés, adoptées par les Congrès Internationaux de Zoologie, Paris,* 1889 *et Moskou,* 1892 (Paris, 1895); *Report on rules of Zoological Nomenclature, to be submitted to the fourth International Congress at Cambridge by the International Commission for Zoological Nomenclature* (Leipzig, 1898); *Règles de la Nomenclature Zoologique adoptées par le cinquième Congrès International de Zoologie* (Berlin, 1901).

[2] *Verhandlungen der Deutschen Zoolog. Gesellschaft,* 1891, p. 47; 1892, p. 13; 1893, p. 89, &c.

In order to collect the enormous mass of information on systematic zoology which is now scattered in numberless articles in numberless scientific periodicals and books, the German Zoological Society determined, at their first general assembly in 1891, to issue a great systematic work entitled 'Species animalium recentium' or 'Das Tierreich' (' The Animal Kingdom '), which should contain systematically arranged descriptions of all the existent kinds of animals as far as they are at present known. This great plan, which in Linnæus' time was not beyond the power of one man, can now only be carried out by a scientific society having at its disposal many workers and abundant means; and even so it is doubtful whether the new ' Animal Kingdom ' will be completed by the year 2000. I have made a careful calculation with regard to entomological literature, the results of which will perhaps be of interest here.[1]

Every number of the work is to be arranged according to the same detailed plan, therefore, from the nineteen numbers that had appeared in 1894, we can form some idea of the probable extent of the whole.[2] Assuming that the same method is followed in subsequent numbers as in those that have already appeared, for the Order of Coleoptera alone, according to a moderate estimate, 111 volumes of 500 pages each will be required, for the whole class of insects at least 300 volumes of 500 pages, and for the whole animal kingdom at least 500 volumes of 500 pages. These 500 volumes would contain approximately 15,625 signatures, so that if the work is to be completed in 100 years, 156 must be issued yearly. But, as a matter of fact, since 1897 on an average less than fifty signatures have appeared each year.

It is not my wish to take a pessimistic view of the matter, but to give the reader some idea of the advance made in biological knowledge. Let us hope, therefore, that the whole enormous task will be completed within a reasonable period, before the ' Twilight of the Gods ' foretold by Wala sets in, for

[1] Cf. my discussion of the first numbers of the 'Tierreich' in *Natur und Offenbarung*, XLIII (1897), 508; XLIV (1898), 635.

[2] Cf. the annual reports submitted to the meetings of the German Zoological Society by Professor F. E. Schulze, the general editor. The publication of the work has now been undertaken by the Berlin Academy of Science. By the summer of 1905 twenty-three numbers had appeared.

this would probably be a twilight of zoologists also; let us hope that the zoology of the future will derive much pleasure and satisfaction from this creation of the German Zoological Society; in any case, the calculation I have made will serve to give my readers some approximate conception of the enormous strides made by systematic zoology in the course of the nineteenth century.

Modern botanists, too, have undertaken the publication of vast systematic works, continuing the enormous task of systematisation on Linnæus' principles. One of these works is 'Die natürlichen Pflanzenfamilien nebst ihren Gattungen und wichtigeren Arten,' von A. Engler und K. Prantl ('The natural families of plants together with their genera and more important species,' by A. Engler and K. Prantl). The Phanerogams were completed before the end of the nineteenth century, in a space of about twenty years, and are contained in eleven stately volumes, but the Cryptogams are not finished yet.

Another huge work on botany, the counterpart of the 'Species animalium recentium,' is being brought out by A. Engler for the Royal Academy of Science in Berlin, under the title 'Regni vegetabilis conspectus.' It has been appearing at intervals since 1900, and numerous collaborators in all parts of the world are engaged on it. We may trust that there are fewer hindrances in the way of its completion than in that of the 'Tierreich,' in the case of which the enormous class of insects presents great difficulties, though it is to be hoped that these will eventually be overcome.

There is one respect, however, in which the systematic advance of modern zoology and botany is not on the lines of Linnæus' 'Systema naturae.' Linnæus was unable to avoid using external differences as the distinctive marks of his systematic groups, and in this way he was led to unite in an artificial system forms that bore no natural relationship to one another. In describing and classifying plants and animals modern systematic science can avail itself of the assistance of other biological sciences, especially of anatomy and of morphogeny, or the history of individual development, and thus it attains to a more or less successful *natural* classification of organic forms. In spite of this difference, however, it is true that modern systematic science is based upon

Linnæus and his 'Systema naturae,' for without this achievement of his powerful intellect we should at the present time have had no natural systems of plants and animals.

The fact that the German Zoological Society regarded it as necessary to issue a fresh edition of Linnæus' 'Systema naturae,' and to undertake the publication of a great work on systematic zoology on the same lines, is testimony enough to the importance of systematics or the science of classification in the development of biological knowledge. It shows at the same time how deeply indebted the representatives of modern science are to Linnæus, and it is to be regretted that in some of the more recent books on zoology Linnæus is mentioned as the founder of the 'unintelligent zoology of species,' and this in more or less plain language.[1]

To a certain class of Haeckelists, systematic science seems like an inconvenient old man, who threatens to check them in their bold intellectual tricks and fantastic speculations, precisely because the actual multitude of forms in the animal world does not coincide with their ideas, and because they are too impatient to be willing to master the subject-matter of

[1] R. Hertwig is however justified in stating in his *Lehrbuch der Zoologie*, 7th edit., 1905, p. 9, that post-Linnæan zoologists, and especially entomologists, have made it their sole aim to describe the greatest possible number of new species, making quantity rather than quality the measure of their achievements. Unfortunately, even at the present day this class of pseudo-systematic biologists is not quite extinct, and there are still some who flood the scientific periodicals with superficial or even 'provisional' descriptions, and thereby put obstacles in the way of studying some groups of animals, for other, more thorough workers, who can make nothing of these superficial descriptions, are hindered by being obliged by the law of priority to take them all into account. An almost incredible story is told of a 'scientific worker' who was employed about fifty years ago at a great museum, and was paid £1 for each new genus and 1*s*. for each new species that he established. In order to work more quickly, he had two bags beside him, one filled with Greek and the other with Latin names. If he wanted a name for a new genus, he put his hand into the Greek bag and pulled out a name haphazard, and bestowed it upon his genus. If, on the other hand, he wanted a name for a new species, he had recourse to the Latin bag, and labelled it with the first adjective that he caught up. It can easily be imagined how applicable the new names thus assigned were to the genera and species, and the descriptions which he appended as 'original' to these names were equally suitable. Such work as this was really 'unintelligent zoology of species,' but it would be unfair to regard zoology of species as responsible for such lack of intelligence. There are excrescences in every branch of knowledge, and they do not occur more frequently in the systematic zoology of the Linnæan school than in the modern doctrine of evolution. Ernst Haeckel's famous book, *The Riddle of the Universe*, affords a striking instance of unintelligent blunders on the part of the Darwinian supporters of this doctrine. See my criticism of the same in *Stimmen aus Maria-Laach*, LX, 1901, p. 428, &c.

systematics before beginning their speculations. They completely forget that but for this stern old father they would have no existence at all.

Mere systematics is certainly by no means the ideal of biological knowledge ; it is not an end in itself, but is only an indispensable aid to biological research. It bears the same relation to the other biological sciences as the dry heart-wood of a tree bears to its tissues permeated by life-giving sap ; it forms the skeleton or scaffolding for other sciences. But just as in the human body the eye has no right to reproach the bones of the foot for not responding to the vibrations of ether, so modern morphology and morphogeny ought not to look down upon systematics for not perceiving many things that these branches of science can discover. In science, as in the living organism, the principle of the subdivision of labour holds good, and the greater the perfection attained by any science, and the more numerous its departments, the more indispensable is it to distinguish clearly the subject-matter with which each single subdivision deals, if any solid progress is to be made.

Let us apply this consideration, the truth of which no modern scientific man will question, to Linnæus' position with regard to biology. Scientific classification or systematics was his speciality, and it was a boon to science that Linnæus with his vast intellect devoted himself to it rather than to anatomy and physiology, for the formation of a strong systematic science was the first and most necessary starting point for all the other branches of biological science, if they were to thrive at all. Without it zoology and botany would have remained a hopeless chaos of forms, through which no one could have found his way.

In order to produce a great systematic work like Linnæus' ' Systema naturae,' even at that time a man was required who should devote his whole ability to this end, for otherwise it would have been unattainable. When his pygmy successors, who have inherited the achievements of his genius, reproach the great Linnæus with being merely a one-sided systematist, they show themselves to be both short-sighted and ungrateful.

CHAPTER II

THE DEVELOPMENT ON MODERN MORPHOLOGY AND ITS BRANCHES INVOLVING MICROSCOPICAL RESEARCH

1. The Development of Anatomy before the Nineteenth Century

We have already shown how Aristotle may justly be regarded as the founder of modern systematics,[1] and he may with equal right be called the first morphologist in the modern sense, because he carried on a comparative study of the varieties of form among animals. Aristotle laid the foundation of the science of morphology in his work 'De partibus animalium,' and Galen (131–201 A.D.) continued what Aristotle had begun, for his famous work on human anatomy is based chiefly upon post-mortem investigations on the higher animals, and so should be called *animal* rather than *human* anatomy. The real originator of human anatomy was Vesalius (1514–64), who dissected human bodies, and thus was able to correct many errors arising out of Galen's studies of animals.

[1] Cf. also on this subject Professor R. Burckhardt, 'Zur Geschichte der biologischen Systematik' (reprinted from the *Verhandlungen der Naturf. Gesellschaft in Basel*, XVI, 1903, pp. 388–440).

Marco Aurelio Severino (1580–1656), a Calabrian, was the author of the first book on general anatomy. It was published in Nüremberg in 1645, and bears the title: 'Zootomia Democritaea, id est anatome generalis totius animalium opificii libris quinque distincta.' Severino treats the 'lower animals' in a very curt fashion; they fare better at the hands of writers towards the close of the seventeenth century. Marcello Malpighi, a Bolognese physician (1628–94), wrote a 'Dissertatio epistolica de bombyce' (1669) on the anatomy of the silkworm, and this work opened the way to the anatomical study of insects, for the discovery of the Malpighian tubes, of the heart, nervous system, tracheae, &c., for the first time revealed insects as organic masterpieces, whose wonderful construction is scarcely inferior in perfection to that of the higher animals, and is more worthy of admiration, because of its diminutive size.

Johann Swammerdam (1637–85), who lived at Amsterdam, in his 'Bijbel der natuure' (*Biblia naturae*), published 1737–8, describes with astonishing accuracy the internal structure of bees, ephemera, snails, &c.; and whoever is acquainted with the excellent anatomical discussion of the larva of the goat-moth, published in 1760 by Pieter Lyonet of Maastricht, cannot fail to recognise its merits even at the present time, when we can avail ourselves of greatly improved instruments and technical methods in dealing with the same subject.

The great scientists mentioned above inaugurated a new era in anatomical knowledge, yet morphology was still not a systematically organised science, but only a collection of interesting monographs. It was raised to the rank of a special science at the beginning of the nineteenth century, by Bichat, a Frenchman, who introduced the idea of systems of organs and systems of tissues. Bichat's 'Traité des membres en général' (1800) and his 'Anatomie générale' (1801) created comparative anatomy, for he divided the constituent parts of the bodies of animals into organs and tissues, and into systems of organs and tissues, thus fixing a firm basis for the comparison of the constituent parts of various animals. It is true that this idea of Bichat's was not altogether new; Aristotle, Galen, and Albert the Great distinguished heterogeneous and homogeneous parts among the constituents of the bodies of animals. The heterogeneous parts are the individual organs, the homogeneous are the tissues, which may be found in various organs, and of which the organs are composed.

A famous Italian anatomist, Gabriele Antonio Fallopius (1523–62), as early as the sixteenth century wrote 'Tractatus quinque de partibus similibus,' in which he distinguished and described a considerable number of tissues. In 1767 Bordeu, a Frenchman, devoted an entire work to one kind of tissue, viz. the mucous connective tissue; his book bears the title 'Recherches sur le tissu muqueux ou organe cellulaire.' Still it was Bichat who first arranged the homogeneous tissues as a scientific whole, distinguishing them from organs and systems of organs. A system of organs is a complex of organs working together to discharge the same vital function and so forming one physiological whole. A system of tissues is a complex of tissues consisting of the same morphological elements, and so forming one logical whole, from the point of view of comparative morphology. Two examples will explain this distinction. The digestive system in man is a system of organs, for it is made up of several organs which unite to produce one and the same physiological result, though they are formed of various kinds of tissue; for, in addition to epithelial tissue, both connective and muscular tissues enter into their structure. But the glandular system in man is a system of tissues, for it consists of essentially similar tissues, viz. modifications of the epithelium, which serve very various physiological purposes; such are the gland of the intestine, the renal gland, the salivary gland, the sweat gland, &c. In other cases the distinction between a system of organs and a system of tissues is not so strongly marked as in those to which I have just referred. For instance, when we speak of the nervous system of man, we are alluding to both a system of organs and a system of tissues. Nevertheless, in theory the two systems are totally distinct even here.[1]

A far greater man, and one who had much more influence on the development of comparative morphology, was Georges Cuvier (1769–1832). He was born at Mömpelgard and educated

[1] Textbooks on zoology treat chiefly of systems of organs, and those on histology chiefly of systems of tissues, therefore a writer on zoology is apt to ignore the histological point of view, and *vice versa*, which is disastrous to perspicuity.

at the Karlsakademie in Stuttgart. Whilst he was professor of comparative anatomy at the Jardin des Plantes in Paris, he published numerous important works. In 1812 he established a new classification of the animal kingdom, which is known as Cuvier's Theory of Types, and is based upon the anatomical comparison of the various groups of animals. According to it animals are divided with reference to their structure into four main classes, which Cuvier called *embranchements,* but Blainville subsequently substituted the name *types.* These are vertebrata, mollusca, articulata, and radiata. Cuvier's Theory of Types was expanded and elaborated by Karl Ernst von Baer (1792–1876), an Esthonian, the founder of comparative embryology, whose theory of germinal layers reduced the embryology of animals to a scientific system.

Cuvier's Theory of Types was not by any means his sole contribution towards the development of modern zoology. His comprehensive work 'Le règne animal' (1816),[1] in the compilation of which he was assisted by many collaborators, is the most important achievement in the domain of systematics since the time of Linnæus. His 'Histoire des sciences naturelles,' published after his death in Paris (1841–5), as R. Burckhardt aptly remarks,[2] presents the history of zoology and the natural sciences in one vast frame, and is a monumental work of wide scope. Cuvier devoted much attention also to fossil animals, and between 1795 and 1812 he brought out several works on the subject, laying down definite morphological principles to be followed in comparing fossils with still existing animals of the zoological system, and he thus became one of the chief founders of modern palæontology. His chief service to comparative biology was that he established the law of correlation, i.e. he was the first to formulate the regular connexion of the organs of any animal with one another, and with its habits and environment. Although Cuvier did not regard as essential the variations of form within his four great types, he was an adherent of the theory of permanence, and in 1798 for the first time he gave a clear concise statement of the meaning of the 'systematic species,' a definition that still holds good. His views on the permanence of species brought him into

[1] The fourth edition in eleven volumes appeared 1836–49.
[2] 'Zur Geschichte der biologischen Systematik,' 390.

conflict with his contemporaries, Jean Lamarck and Etienne and Isidore Geoffroy St. Hilaire, who upheld the transmutation theory. The scientific struggle carried on by the members of the French Academy ended for a time in the victory of Cuvier's opinion, but we shall have to recur in the ninth chapter to the further history of the theory of evolution.

2. The Early History of Cytology

Hitherto, in speaking of the development of anatomy, we have referred chiefly to macroscopic anatomy, which is not dependent upon the microscope ; it is, however, to this instrument that most of the progress made by modern morphology is due.[1]

It was invented some hundreds of years ago, but not until the nineteenth century did the real age of microscopical research begin. As early as the year 1100 the Arab, Alhazen ben Alhazen, described the magnifying power of a convex lens. The English Franciscan, Roger Bacon, who lived 1214–1294, and whom we have already mentioned (p. 16), seems to have constructed complicated optical instruments. He is said to have ground a piece of glass so that people saw wonderful things in it, and ascribed its action to the power of the devil. If this glass deserves to be called a microscope, the honour of inventing this instrument would have to be ascribed to Roger Bacon, but various nations claim to have given birth to the inventor of it. The Italians say that either Galileo or Malpighi invented it, but most people consider two Dutchmen, Hans and Zacharias Janssen (1590), to be more justly entitled to the credit of the invention. The name 'microscope' was first applied to the new instrument by Giovanni Faber in Rome in 1625, and many improvements in it were made about 1646 by the astronomer Francesco Fontana in Naples. Malpighi and Swammerdam certainly used the microscope in their scientific work, and the Dutchman Anton Leeuwenhoek of Delft (1632–1723), the 'Father of the Microscope' as Schlater calls him, used it in examining the ova and stings of bees, and many other things connected with the anatomy of insects.

[1] Cf. Dr. J. Peiser, 'Die Mikroskopie einst und jetzt,' in *Natur und Schule*, IV, 1905, parts 10, 11.

By its aid he discovered infusoria, and drew the attention of scientific men to a new world of diminutive creatures, our knowledge of which was greatly increased by Christian Gottfried Ehrenberg in the middle of the nineteenth century. By means of the microscope Leeuwenhoek was enabled to discover the red-blood corpuscles and the transverse striation of the muscular apparatus, and Hamm to perceive spermatozoa, the key to those mysterious problems of heredity which the greatest biologists of the present day are so eager to solve.

Thus we see that microscopical anatomy made steady progress, and advanced towards the marvellous triumphs of modern histology and cytology. It was, however, a long time before scientific men generally made use of the microscope; it is a surprising fact that even in 1800 it was altogether neglected by Bichat, to whom we have already referred as the founder of comparative anatomy. Consequently he could give no account of cells, the smallest constituents of animal tissues, although they had long before been recognised by other scientific men who used the microscope.

Who discovered cells and the structure of organic tissues out of cells? In plants it is much easier to find the cells, as they possess, as a rule, a more independent existence in plants than in animals. It is therefore only natural that cells were discovered first in botany. An Englishman, Robert Hooke, gave cells their name because of their resemblance to the cells of the honeycomb. In his 'Micrographia,' which appeared in 1667, he gave the first illustration of a plant cell, or rather cell-wall. The figure represents a bit of cork, along which lengthwise run rows of black specks or cells. Hooke's purpose in speaking of cells was not so much to add to the scientific knowledge of botany, as to display the power of his microscope, and so it is usual to ascribe the discovery of cells to two other scholars, the Italian Malpighi (1674), whom we have already mentioned, and the Englishman Nehemiah Grew (1682). Their works on this subject appeared at almost the same time, a few years after Hooke's 'Micrographia.' Ninety years elapsed before another great scientist continued their work. In 1759 Kaspar Friedrich Wolff published his remarkable book 'Theoria generationis,' in which he propounded new ideas on morphogeny, and threw much light on the morphology of organisms. His descriptions and illustrations show plainly that he had studied the cells in both animal and vegetable tissues; he calls those in the former 'globules' or 'spheres' and those in the latter 'utriculi' or 'cells.' With regard to botany, clear evidence that the vascular system of plants consists of cells was adduced by Treviranus in his work 'Vom inwendigen Bau der Gewächse' ('The internal structure of vegetables'), 1808. The honour of having been the first to discover and mention the nucleus of the living cell is generally ascribed to an Italian-Tyrolese, Abbé Felice Fontana, 1781. However, H. Bolsius, S.J.,[1] has recently proved that the discovery was made by Leeuwenhoek, the Dutch scientist already mentioned, in 1686, about a century earlier.

The English botanist, Robert Brown, was the first to discover (1833) the regular significance of the nucleus in its relation to the cell, and for this reason many people regard him as the real discoverer of the nucleus.[2]

It was not until Joseph von Fraunhofer in 1807 constructed the first achromatic lenses, and thus greatly increased the capabilities of the microscope, that modern cytology was able to develop. It is a remarkable fact that just at this time (1809) Mirbel, a Frenchman, began again to apply the name 'cell' to the smallest elements in living organisms; Malpighi's word *utriculus* had long taken its place, but now, at the dawn of modern cytology, the old name was revived, which Hooke had given to these organic elements 150 years before. The word 'cell' is still in use, in spite of various attempts to substitute some more modern name, such as *protoblast* (Kölliker) and *plastid* (Haeckel). The study of the organic tissues composed of cells was first designated *Histology* by Karl Mayer in Bonn in 1819. Germany is therefore the real home of both histology and cytology, and, as even the French scientists acknowledge, both have grown and developed chiefly in Germany.[3]

[1] Antoni von Leeuwenhoek et Félix Fontana, 'Essai historique sur le révélateur du noyau cellulaire,' Rome, 1903 (*Memorie della Pontificia Accademia Romana dei Nuovi Lincei*, XXI).

[2] Cf. O. Hertwig's *Allgemeine Biologie* (1906), pp. 5 and 27. Hertwig's account of the history of the cell theory is very valuable, pp. 4, &c.

[3] Cf. M. Duval, *Précis d'Histologie*, Paris, 1900, p. 12.

Everyone who has ever opened a modern book on zoology or botany must know the names of Schleiden and Schwann.

Matthias Jakob Schleiden, born 1804 in Hamburg, became the founder of modern botanical cytology when, in 1838, he published his 'Beiträge zur Phytogenesis' in Müller's 'Archiv.'[1] The zoologist, Theodor Schwann, born 1810 in Neuss, applied the same principles to animal tissues in 1839, when he published his 'Mikroskopische Untersuchungen über die Übereinstimmung in der Struktur und dem Wachstum der Tiere und Pflanzen,'[2] and he added so much to Schleiden's work that we generally speak of Schwann-Schleiden's theory of cells, or cytology.[3]

In the case of every object of sense perception, human knowledge invariably proceeds from the exterior to the interior, from the shell to the kernel, and this is true of our knowledge of cells. The dry walls of dead plant cells were what Hooke called cells 250 years ago. Malpighi also studied particularly the plant-cell, which is, as a rule, much larger and has thicker and more conspicuous walls than the animal cell, and hence it became the custom to regard the cellular membrane as the essential part of the cell. Malpighi and Wolff represented the cell as being practically an empty tube or bag—and this was equivalent to mistaking a snail shell for a snail. Schleiden and Schwann had a deeper insight into the truth, for they had better aids to research at their disposal; they discovered that each tube or bag is filled with a fluid, and they noticed the nucleus, though this had been discovered long before. Their opinion was that the cell is a little vessel filled with fluid in which a nucleus is suspended. Subsequent examination of young cells has shown that they have no real walls, and the membrane appears to be an accidental part of the cell, and thus the scientific idea of the cell advanced to the third stage, at which it still practically remains. Franz Leydig in

[1] Cf. Jos. Rompel, S.J., 'Der Botaniker Matthias Jakob Schleiden' (1804–81), in *Natur und Offenbarung*, I (1904), parts 4–7; see especially pp. 393–410.

[2] 'Microscopical researches into the accordance in the structure and growth of animals and plants.'

[3] The botanists Treviranus and Meyen ought to be mentioned as having prepared the way for Schleiden. Their works were published in 1808 and 1830 respectively.

1857[1] and Max Schultze in 1861[2] defined a cell as a mass of living protoplasm containing one or more nuclei.

The fluid contents of the cell were called *protoplasm* by Hugo von Mohl in 1846, and the name has been universally adopted, for it conveys an idea fundamental in biological research.[3] Dujardin in 1835 had named the same substance *sarkode,* but no one now uses this word.

Von Mohl drew the attention of scientists to the movements of protoplasm within the cells of plants, but they had been noticed long before by Bonaventura Corti (1774) and C. L. Treviranus (1807), and described as 'rotatory movements of the cellular fluid.'

At this point the question naturally arises: What are the chemical constituents of protoplasm? In the first part of his 'Studien über das Protoplasma' (1881), J. Reinke describes it as 'a mixture of numerous organic compounds.' Von Hanstein, however, in 1879 defined protoplasm as an albuminous compound or a mixture of albuminous compounds, and he proposed to call it *protoplastin.* In his 'Lehrbuch der Zoologie,' R. Hertwig says in a resigned way that we must acknowledge our inability to determine the chemical characteristics of protoplasm. 'It is not known whether protoplasm is a definite chemical body, which from its constitution is capable of infinite variation, or whether it is a varying mixture of different chemical substances. So, also, we are by no means certain whether or not these substances (as one is inclined to believe) belong to those other enigmatical substances, the proteids. We can only say that the constitution of protoplasm must, with

[1] The year 1859 or 1861 is generally given as the date when cytology entered upon its third stage, therefore I will quote here a passage from Leydig's *Lehrbuch der Histologie des Menschen und der Tiere,* published at Frankfurt a. M. in 1857. He writes as follows (p. 9): 'To the morphological conception of a cell belongs a more or less soft substance, originally almost globular in form, containing a central body called the nucleus.' This, therefore, according to Leydig's opinion in 1857 was the essence of the cell—he had already discarded the membrane as non-essential—for he continues: 'The substance of the cell *frequently* hardens so as to form a more or less independent outer layer or membrane, and *when this takes place* the cell is technically said to consist of membrane, substance, and nucleus.'

[2] 'Über Muskelkörperchen und das, was man eine Zelle zu nennen habe' (*Archiv für Anatomie und Physiologie,* 1861).

[3] Cf. O. Hertwig, *Allgemeine Biologie,* p. 7, &c., for the history of the protoplasm theory; p. 12, &c., for investigations regarding the meaning and nature of protoplasm.

a certain degree of homogeneity, have a very extraordinary diversity.'[1]

We may be satisfied to endorse J. Reinke's[2] remark that our conception of protoplasm has always been morphological, i.e. all we know about it is that it forms the primary substance common to every living cell. A detailed account of all the information hitherto acquired on the subject of the chemical composition of protoplasm, as well as on that of the organisation of the cell and nucleus, and their reciprocal chemical relations, will be found in E. B. Wilson's 'The Cell in Development and Inheritance,' New York, 1902, chapter vii; also in O. Hertwig's 'Allgemeine Biologie,' Jena, 1906, chapter ii, pp. 12, &c. On pp. 18 et seq. Hertwig has shown very clearly that the discovery of the substance and process of life is a vital problem, and not merely an affair of chemistry and physics. This subject will be discussed more fully in Chapters VII and VIII.

Our knowledge of tissues and cells has been vastly increased by means of microscopical research since the middle of the nineteenth century. The names of the scientific men distinguished in this branch of research would make a long list; we can mention only the most eminent—Henle, Gerlach, Reichert, Remak, Leydig and Kölliker—some of the more recent zoologists will be noticed later on. Botanists have been no less zealous than zoologists in studying cells under the microscope. We may refer to W. Hofmeister, A. Zimmermann, de Bary and Sachs, as well as to the more recent students—Pfeffer, Wiesner, and Strasburger.

3. Methods of Staining and Cutting Sections for Use under the Microscope

Microscopical research has been greatly facilitated by the discovery of the modern methods of chemical colouring.

As soon as definite colouring matters were applied to animal and vegetable tissues, their structure became more plainly visible, and the structure of the cell itself was revealed, for the nucleus was found to absorb readily certain colouring

[1] English translation, 1903, p. 61.
[2] *Einleitung in die theoretische Biologie*, Berlin, 1901, p. 221.

matters which do not affect the protoplasm of the cell. The nucleus was then seen to contain some darker coloured granules or filaments or nucleoli, which suggested the idea that the nucleus was not a simple but a composite body. In the same way there appeared in the protoplasm darker coloured granules or a network of filaments against a lighter background, and the observation of these led to the discovery of the cell framework. When the colouring process was applied to cells and nuclei in course of division, pictures of wonderful beauty were revealed, from which the laws of the division of the nucleus and of fertilisation were learnt.

Gerlach in 1858 first used carmine as a stain for microscopical purposes, and since his time the number and variety of colouring methods have increased almost indefinitely. Gerlach used carminate of ammonia, others have employed alum-carmine, borax-carmine or carmalum, picro-carmine, &c.

The carmine stains were, however, discarded in favour of haematoxylin, an excellent stain prepared from logwood (*Haematoxylon campechianum*), which is applied in various solutions and combinations, and is still much used in microscopical work. The double stains obtained by using haematoxylin in conjunction with eosin or Congo red or saffranin have lasted admirably, and have produced beautiful and instructive plates, so that haematoxylin has not yet been displaced by its numerous rivals prepared from coal-tar, and known as aniline dyes. The colouring methods just mentioned, and especially the use of haematoxylin and its combinations, are of universal application, and can be employed for almost all histological purposes, but there are also certain special methods of staining particular tissues, especially those of the nerves. Golgi, Ramón y Cajal, and Ranvier used solutions of nitrate of silver, chromate of silver, and formic acid with chloride of gold, in their attempts to overthrow the long-established theory of a central nervous system, and thus extended our knowledge of ganglion cells and their processes.

When Waldeyer formulated his theory of neurones in 1891, and when soon after the theory of fibrils was put forward in opposition to it,[1] the chief arguments adduced in this scientific

[1] At the seventy-second meeting of German naturalists and physicians at Aix-la-Chapelle in 1900, a lively discussion of the two theories took place.

contest were supplied by observations on the nervous system, rendered possible by the use of stains,—methods which Apáthy, Bethe, Nissl, Held, Bielschowsky and others have carried to the utmost perfection. The anatomical and physiological study of nerves owes much to Ehrlich, Retzius and others, who have succeeded in staining the nervous system of a living animal with methyl blue, so that it has become possible to trace the action of the finest fibres and terminations of the nerves.

Quite recently Carnoy and other cytologists at Louvain have used methyl green, and have shown it to be of great service in the development of biology, for it gives a vivid colour to the nucleus of a cell still living, thus rendering visible the most minute details of its structure.

As special stains, used in studying the stages of division of the nucleus in the process of mitosis, we may mention particularly Heidenhain's use of iron alum with haematoxylin and Plattner's metallic nuclear black.

All these colouring methods would avail but little, however, if scientists had not at their disposal a means of cutting organic tissues, as well as entire animals and plants, after artificially hardening them, into layers so thin that light can penetrate them and make their wonderful construction visible under the microscope. The art of cutting sections is as indispensable as the art of staining, and it is by means of both in conjunction that microscopic anatomy has been enabled to make its extraordinary progress in recent times. It owes the one to chemistry, and the other to modern mechanics, which created the microtome and placed it at the service of biology.

The microtome is a mechanical apparatus which passes an extremely sharp knife in a definite direction over an object embedded in paraffin or celloidin or some similar embedding substance, and at the same time a movable plate provided with a scale automatically regulates the thickness of each section.

As at each turn of the plate, about a given angle, the knife is lowered, for instance, $\frac{1}{100}$mm., or (in other microtomes) the object is raised $\frac{1}{100}$mm., a skilful worker is able to obtain an

M. Verworn supported the theory of neurones in his lectures, 'Das Neuron in Anatomie und Physiologie' (reprinted at Leipzig, 1901). See also Fr. Nissl, *Die Neuronentheorie und ihre Anhänger*, Jena, 1903; M. Wolff, 'Neue Beiträge zur Kenntnis des Neurons' (*Biolog. Zentralblatt*, 1905, Nos. 20–22); Wasmann-Gemelli, *La Biologia Moderna*, Florence, 1906, p. 44 note.

unbroken series of sections, each $\frac{1}{100}$mm. in thickness. In the same way he can obtain sections of $\frac{1}{200}$mm., $\frac{1}{300}$mm., $\frac{1}{500}$mm., if he requires them. The microtomes most generally used at the present day are those made by R. Jung in Heidelberg. Microtomes on another system were devised by Professor Hatschek and made by Jensen in Prague; in these the knife does not move up and down along an inclined surface, as it does in Jung's apparatus, but it moves backwards and forwards over a horizontal surface. With the latter I have succeeded better than with the former, and have even prepared very thin and regular sections cut through the hard chitin integument of beetles and other insects. There are also lever microtomes, English microtomes with a pointed spindle, and Minot's new American microtomes intended to cut sections of larger objects. The construction of these ingenious instruments has in the last few years become a special branch of mechanics, and interesting accounts of their great perfection may be found in the illustrated price-lists issued by R. Jung and Walb in Heidelberg, Reichert in Vienna, and others.

4. The Microscopic Study of the Anatomy and Development of a Diminutive Fly

(*Termitoxenia.*) (Plate V)

I should like to illustrate the great advance made in biological research through the adoption of modern methods of staining and cutting sections, and my illustration, derived from my own work, will take my readers out of the gloom of theories into the cheerful atmosphere of practical results.

I am at this moment studying some extremely small insects only 1–2 mm. in length, belonging to the order of Diptera. They have a relatively enormous white abdomen, and in the course of the last few years have been found in the nests of termites in South Africa, the Soudan and India, by G. D. Haviland, Dr. Hans Brauns, J. B. Heim, J. Assmuth, S.J., and Y. Trägårdh.[1]

[1] In subsequent chapters I shall have occasion to refer repeatedly to this remarkable fly, belonging to the family of *Termitoxeniidae*. An account of it is given in Chapter X, 'Theory of Permanence or Theory of Descent,' and illustrations will be found on Plate V.

Diptera of the normal type have two wings, but in their stead this little creature (which I have described under the generic name *Termitoxenia*) [1] has peculiar appendages to the thorax (Plate V, figs. 1, 2, 4, 5) which are morphologically homologous with wings, but have actually so developed as to serve quite other purposes than that of flight, for which their narrow, club-shaped or hooked form and their horny structure render them altogether unsuitable. They are, however, well adapted to perform a number of new functions, closely connected with the insect's habit of living among the termites. The appendages to the thorax of the *Termitoxenia* serve as organs of transport, by which these little inquilines are picked up and carried about by their hosts; they serve to maintain the fly's equilibrium and enable it to balance itself when it walks, as otherwise the enormous size of its body would render walking very difficult; they are sense organs, supplying the creature with a great many percepts by way of touch; they are organs of exudation, through which it emits a volatile element in its blood as a pleasing stimulant to the greed of its hosts; finally they resemble supplementary spiracles, that to some extent are like the tracheal gills of the insect's earliest aquatic ancestors.

These little termitophile Diptera are indeed a store-house of anomalies, whether we consider them from the point of view of morphologists, anatomists, evolutionists, or biologists. They are exceptions to the laws of entomology. They are not merely Diptera without wings, but they are flies without the larval and pupal stages, and are actually insects having neither male nor female!

In order to shorten the lengthy and complete process of metamorphosis undergone by other Diptera, the *Termitoxenia* lays comparatively enormous eggs, from which is hatched not a larva, as is the case with other flies, but a perfect insect,

[1] '*Termitoxenia,* ein neues flügelloses, physogastres Dipterengenus aus Termitennestern,' Part I (*Zeitschrift für wissenschaftliche Zoologie*, LXVII, 1900, pp. 599–618 with plate XXXIII); Part II (*ibid.* LXXX, 1901, pp. 289–98); 'Zur näheren Kenntnis der termitophilen Dipterengattung *Termitoxenia*' (*Verhandl. des V. internationalen Zoologenkongresses zu Berlin*, August 1901, pp. 852–72 with one plate); 'Die Thorakalanhänge der *Termitoxeniidae*, ihr Bau, ihre imaginale Entwicklung und phylogenetische Bedeutung' (*Verhandl. der deutschen Zoolog. Gesellschaft*, 1903, pp. 113–120, with plates II and III).

the imago form, still in a stenogastric or thin-bodied condition. To compensate for the absence of metamorphosis, the *Termitoxenia,* as imago, undergoes a postembryonic development, for its organs of generation, especially the single-tubed ovaries, its fat-body, consisting of large cells joined together end to end, its abdominal muscular system, and even the outer skin of the abdomen, receive their final form only in the course of a long process of growth. Each of these insects is moreover a complete hermaphrodite, there are no distinct males and females at all. The youngest imagines have some quite undeveloped ovaries, such as occur in the larvae of other Diptera, but even in the youngest specimens the male generative glands and the bundles of spermatozoa connected with them are well marked, although they subsequently become atrophied, when the spermatozoa have ripened, whilst the ovaries develop. We have, therefore, here an instance of what is called protandric hermaphroditism, which regularly allows first the male and then the female generative glands to develop in the same individual, so that the *Termitoxenia* is something quite unique in insect biology.

It is most interesting to trace the development of the ovaries. (See Plate V, fig. 6.) Each one consists of a single egg-tube—a phenomenon long sought in vain among insects by the upholders of the theory of evolution, until Grassi discovered it occurring in the very rudimentary ground-flea (*podura*), belonging to the genus *Campodea.*

This single egg-tube on each side of the *Termitoxenia*'s body is, in the case of the youngest specimens, merely one single long terminal chamber, filled with apparently undifferentiated little nuclei.[1]

In course of time the egg-tube contracts in between the eggs, and forms a long series of ovarian chambers, those at the lower end of the ovary being the largest. In each of these chambers the elements of the ovary differentiate themselves into nutritive cells and true egg-cells, so that each chamber eventually contains several large cells, one of which develops

[1] I use the word 'apparently' advisedly, for in one of his recent works ('Untersuchungen über die Histologie des Insektenovariums,' in the *Zoologische Jahrbücher*, Section for Anatomy, 1903, part 1), Gross has proved that the epithelial cells and those that eventually become germ-cells differ from one another even in the terminal chamber.

more rapidly than the rest and becomes the egg. The other cells in the same chamber serve as its food, or, in scientific language, a fusion takes place of the egg-cell with the nutritive cells, the substance of the latter being gradually absorbed into that of the former, and transformed into tiny yolk-capsules collected round the germinal vesicle of the young egg. Thus the egg is nourished and it continues to grow until it occupies about a quarter of the entire abdomen of the full-grown insect. (Plate V, fig. 6 ov.) By this time it has taken up enough yolk-material to serve for the whole embryonic development until it reaches the stage of imago, when it must make its own way in the world. It is fertilised, and, passing along the ovarian duct, it is laid among the eggs of the termites.

The history of the development of a fly belonging to the sub-genus *Termitomyia* is somewhat different, but still more extraordinary. In this case the egg, whilst still within the parent's body, becomes an embryo, which develops until it reaches the form of a stenogastric imago. Therefore this sub-genus lays no eggs at all, but brings forth its young alive. These viviparous insects are a worthy contrast to the oviparous mammals, such as the ornithorhynchus and the Australian ant-eating Echidna.

There is a regular correlation between all the points on which the remarkable anatomy and development of the *Termitoxenia* differ from those usual among insects. The fact that each ovary has only one egg-tube facilitates the formation of eggs few in number, but large and rich in yolk. The large size and richness in yolk of the eggs render the omission of the larval and pupal stages possible, and so the whole process of development is conveniently shortened and simplified, and the imago is produced out of the egg or rather out of the embryo.

Moreover, in the case of the *Termitoxenia,* the complicated process of assigning sex to the individual is simplified in a form that is perfectly ideal for insects, as each individual fulfils both functions. And all these wonderful peculiarities in the morphology, development, and biology of the *Termitoxenia,* its physogastria and its ametabolia, its growth as an imago and its hermaphroditism, the shape of its appendages to the thorax and the formation of the parts of its mouth—

for it has a long proboscis for sucking the tender, juicy young of the termites—all these are closely connected with and dependent upon the affection of these Diptera for the termites!

And how, it may be asked, do we know all this? Have observations been made in India and Africa regarding the habits of these diminutive creatures, and has their development been studied for years in artificial nests of termites? By no means. The discoverers of the six known varieties of *Termitoxenia* merely established the fact that they always are found in the nests of certain kinds of termites and among their eggs and larvae. The inquilines and their hosts were sent to me in alcohol or formol. But the further question arises, how can it be possible, in that case, to make such definite and apparently rash statements as to the habits of these creatures? They are so small, that even a powerful magnifying glass scarcely enables us to distinguish the details of their exterior configuration; even under the microscope it is difficult to make out the halteres or balancers, which are placed behind the thoracic appendages, and prove that the latter morphologically correspond to the wings of Diptera and do not point to a coalescence of wings and halteres.

What scientific evidence is there, then, in support of the account just given of the anatomy, development, and biology of *Termitoxenia*?

The account is based on the results obtained by modern methods of using stains and cutting sections. The series of sections of *Termitoxenia* supply us with material for studying its anatomy, development, and biology.

So far I have obtained by means of the microtome complete series of sections of sixty specimens of five species of *Termitoxeniidae* of various ages, and I have also cut sections of a number of eggs of various species; as a stain I have generally used a double preparation of haematoxylin (Delafield's method) and eosin.[1]

The total number of sections thus prepared amounts to 10,000. Each specimen submitted to microscopical examination furnishes a series of from 80 to 200 sections of $\frac{1}{100}$ mm. in thickness; the number varies according as the sections are

[1] Or a double stain obtained by using haemalum (Meyer's method) and orange eosin, &c.

longitudinal or transverse. Each series of sections therefore forms a book of from 80 to 200 pages, on which are recorded in unbroken sequence the whole exterior and interior morphology of the specimen, and this record is legible under the microscope. If the sections of various kinds of *Termitoxenia* at different ages, and also of their respective eggs, are compared with one another, the morphological volumes come to form a library containing an account of the *Termitoxenia*'s development. As, however, almost every point in the anatomy

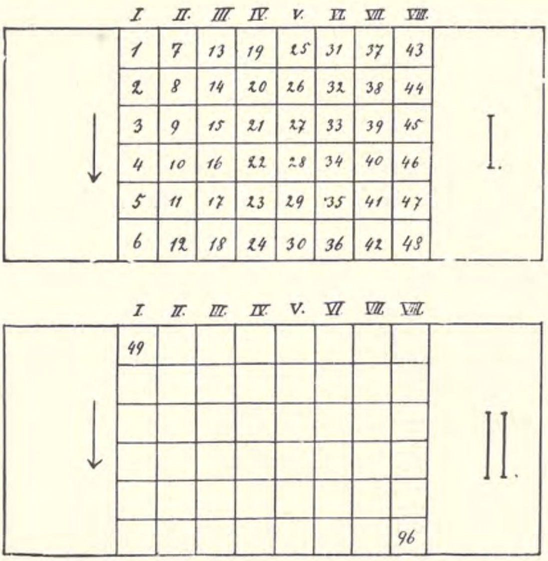

FIG. 1.—Scheme of a series of sections of *Termitoxenia Heimi* Wasm.

and development of these tiny creatures is of significance in their habits, this library supplies also trustworthy information for their whole biology.

The accompanying illustration (fig. 1) represents a series of sagittal sections of *Termitoxenia Assmuthi*. It consists of the longitudinal sections of specimen No. 13 of this variety, arranged upon two slides (i and ii). The Roman numerals on each slide refer to the sequence of the rows of sections, the Arabic numerals to the sequence of the sections in each row. Thus the series begins with No. 1 on the first slide and ends with No. 96 on the second. No. 49, the first on the second slide, is a section cut from the middle of the creature's body—a photograph of it will be found on Plate V, fig. 6, at the end of the book.

I need hardly say that a great expenditure of time and trouble is needed, not merely to make such series of sections, but far more to study them with success. The instances of morphological and biological conformity to law, which a scientist can discover, seem to be written in a mysterious cipher, the key to which is found only by careful study. No one, therefore, will be astonished to hear that I have spent years on my study of the *Termitoxenia*, especially as I had not only to describe my microscopical results in words, but to reproduce them by means of drawings or photographs upon a series of carefully executed plates.[1]

The marvellous beauty of the various sections is no less noticeable than their scientific value in biological research. The material for several series of sections of *Termitoxenia Heimi* and *Assmuthi* was supplied me by J. B. Heim, S.J., Missionary in India, and J. Assmuth, Professor at St. Francis Xavier's College in Bombay. The creatures reached me in very good preservation, having been killed and hardened in a mixture of alcohol and formalin. The sections, stained with haematoxylin and eosin, or some similar double stain, are so beautiful that they cannot fail to arouse admiration in any one who sees them, even in the mind of one who regards all insects alike as 'vermin.' Eosin stains the protoplasm of the tissues various shades of light red, whilst the nuclei, which chiefly serve to differentiate the various kinds of tissue, are coloured light or dark blue by means of haematoxylin or haemalum; the whole picture displays a delicacy of design and a beauty of colouring such as no artist's skill could reproduce in perfection. The most complex and most highly coloured pictures are formed by sections showing the various stages of development in which the mysterious biological processes of cell-division, cell-multiplication, and cell-growth—those elementary functions of life—are most active.

Modern microphotography will, perhaps, succeed in fixing

[1] A fuller account of my work will appear in the *Zeitschrift für wissenschaftliche Zoologie*. A *résumé* of the results obtained hitherto was given in an address delivered at the fifth International Zoological Congress in Berlin, August 1901.

microscopical sections with all their gorgeous colouring directly upon photographic plates. If this is ever done, it will be of the utmost scientific importance, as the precise shades of colour in the nuclei and other parts of the tissues often give a trustworthy clue, of great assistance in histological and cytological research.

A learned professor of theology, on seeing some series of sections of the *Termitoxenia*, remarked very aptly that microscopical research, by means of modern methods of staining and cutting sections, had become a second creation, *creatio secunda*, revealing to us for the first time all the marvels which God at its first creation had concealed within the body of this diminutive fly.

In order to give my readers a wider idea of the application of microscopical study to our investigations into animal biology, the following remarks may be added. Let us suppose that some one asks: '*Why* do ants and termites show such energy and pleasure in licking their "true inquilines"? Upon what does the satisfaction depend which they derive from so doing?'

Before this question can be answered, a reply must be given to another, viz.: 'What tissues underlie the external exudatory organs, which lead to the process of licking the inquilines?' With a view to answering this latter question I have, in the course of the last ten years, prepared about 20,000 sections of various kinds of inquilines among ants and termites (they are chiefly beetles), and studied their tissues under the microscope. In this way I have arrived at the following conclusion:—the exudation of true inquilines, with which they repay their hosts for their hospitality, is partly a direct and partly an indirect product of adipose tissue; when it is indirect, it is partly a glandular secretion and partly an element in the blood plasm of the inquiline.[1]

We are therefore now in a position to divide the genuine inquilines among ants and termites into various classes according to their exudatory tissues, and thus have made a perceptible step towards solving the mystery of true guest-relationship.

[1] Articles on this subject appeared in the *Biologisches Zentralblatt*, 1903, Nos. 2, 5, 6, 7, 8, under the heading: 'Zur näheren Kenntnis des echten Gastverhältnisses (Symphilie) bei den Ameisen- und Termitengästen.'

5. Recent Advance in Microscopical Research

After this little digression let us return to the historical development of modern histology and cytology.

Improvements in the microscope itself, the chief implement in our research work, have kept pace with the adoption of better methods of staining and cutting sections.

As a result of very careful physical studies, Abbe of Jena devised an apochromatic objective, calculated exactly with reference to its refractive and dispersive power. This was worked out by Schott & Co., in Jena, and then further perfected by Karl Zeiss, the able optician in Jena. The apochromatic objective has been imitated with various degrees of success by other German and foreign firms. Its introduction, and that of the corresponding compensating ocular or eye-piece, mark an important stage in the development of the microscope. Speaking from my own personal experience, I can safely assert that the pictures produced by this system of lenses are infinitely clearer than those produced by the achromatic objectives and Huygenian oculars previously in use. It is now possible to see every detail in the structure of tissues even when magnified 1500–2000 times.

This advance in optical appliances has enabled modern cytologists to study the most delicate construction of a resting cell, as well as the processes of division and fertilisation, and to discover the laws governing these most important phenomena of life.

Histology and cytology made great progress during the latter half of the nineteenth century in other countries as well as in Germany, where they had their birth, and where they grew to the rank of independent sciences, in consequence of the research work done by Schleiden, Schwann, Remak, Leydig, and Max Schultze.

I can mention the names of only a few of the more recent workers in this department of science; in Germany, besides Leydig and Max Schultze, we have Strasburger, Weismann, Flemming, Bütschli, Henking, Heidenhain, Boveri, A. Brauer, Reinke, the two Hertwigs, Haecker, Erlanger, O. vom Rath, Schaudinn, Rhumbler, &c.; in Bohemia, Rabl; in Hungary, Apáthy, who has made nerve-cells his special study; in Switzerland, Fol; in France, Ranvier, Balbiani, Giard, Maupas, Kunstler, Guignard, Armand Gautier, and Yves Delage; in Belgium, van Bambeke, E. van Beneden, and the great cytologists of the Catholic University of Louvain, viz. Abbé Carnoy, the author of 'Biologie cellulaire,' and his pupils, of whom G. Gilson, A. van Gehuchten, and Abbé Janssens are well known through their important publications; in Spain, Ramón y Cajal; in Italy, Giardina; in Great Britain and Ireland, A. Sedgwick, Moore, McGregor and Dixon; in Sweden, Retzius and Murbeck; in Russia, Kowalevsky, Tichomirow, Nawaschin and Sabaschnikoff; in North America, Ch. Sedgwick Minot, Chittenden, E. B. Wilson, Th. H. Montgomery and Osborn; lastly, in Japan, Chiyomatsu Ishikawa, director of the zoological institute of the Imperial University of Tokio.

We may therefore well say that all civilised nations of the present time have contributed to the development of modern histology and cytology.[1]

In order that my readers may not regard the Jesuits as 'mediæval obscurantists' trying to stem the advance of science, I may be allowed to add that a Dutch Jesuit, H. Bolsius,[2] has done much to increase our knowledge of the microscopical anatomy of Hirudines or leaches, and has shown himself an authority of the highest rank on this subject. A modern morphological and biological

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[1] This is of course true, not only with regard to the morphology of the cell, with which we are now chiefly concerned, but also with regard to its vital phenomena, especially the processes of cell division and fertilisation, to which we shall have to refer later. I should like to draw particular attention to Carnoy's *Biologie cellulaire*, 1884, which unhappily was never completed; also to Oskar Hertwig's *Allgemeine Anatomie und Physiologie der Zelle*, 1893; and Max Verworn's *Allgemeine Physiologie*, the third edition of which appeared in 1901, and deals mainly with cellular physiology. I regret that Verworn's work is not altogether free from phrases suggestive of Haeckel's influence and wanting in scientific dignity. For instance, on p. 214, in speaking of parthenogenesis among the lower animals, he refers to 'the ancient legend of the Immaculate Conception.' The author seems to be as far as Haeckel from a comprehension of the dogma of the Immaculate Conception.

[2] 'Nouvelles recherches sur la structure des organes segmentaires des Hirudinées,' 1890; 'Les organes ciliés des Hirudinées,' 1891; 'Le sphincter de la Nephridie des Gnathobdellides,' 1894; 'La glande impaire de l'Haementaria officinalis,' 1896; 'Recherches sur l'organe cilié de l'Haementaria officinalis,' 1900 (this article appeared in *La Cellule*). I might also mention a number of other articles which the same author contributed to the *Annales de la Société scientifique de Bruxelles*, to the *Memorie della Pontificia Accademia dei Nuovi Lincei*, to the *Zoologischer Anzeiger* (Leipzig), and the *Anatomischer Anzeiger* (Jena), &c.

work, universally regarded as a masterpiece, has been written by J. Pantel, a French Jesuit, on the larva of *Thrixion halidayanum*; [1] and no less excellent are an anatomical and histological study of the anal glands of beetles by a Belgian Jesuit, Fr. Dierckx,[2] and a biological and anatomical study of walking-stick insects by a French Jesuit, R. de Sinéty.[3]

These publications, as well as most of the works of Carnoy, Gilson, van Gehuchten and Bolsius, appeared in *La Cellule*, a periodical published by the Cytological Institute of the Catholic University of Louvain, a society founded by Abbé Carnoy. This periodical is highly esteemed by German scientists, and forms a complete refutation of the old fiction that Catholics, and especially those of Romance nations, must needs be bad men of science. In the sixth chapter I shall have to refer to some articles on the chromosomes in the eggs of Selachii and Teleostei by J. Maréchal, a Belgian Jesuit, and among Italian scientists, a Franciscan, Dr. Fra Agostino Gemelli, has written some excellent works on anatomy and histology during the last few years.

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[1] 'Le *Thrixion halidayanum*, Rond.: Essai monographique sur les caractères extérieurs, la biologie et l'anatomie d'une larve parasite du groupe des Tachinaires,' 1898 (*La Cellule*, XV).

[2] 'Étude comparée des glandes pygidiennes chez les Carabides et les Dytiscides,' 1899 (*La Cellule*, XVI); 'Les glandes pygidiennes des Coléoptères,' 2nd mémoire, 1900 (*ibid.* XVIII).

[3] *Recherches sur la biologie et l'anatomie des Phasmes*, Lierre, 1901. This work contains splendid illustrations; in the eighth chapter the author discusses the karyokinetic processes in the spermatogenesis of Orthoptera, a subject of peculiar interest as throwing light on the accessory chromosomes.

CHAPTER III

MODERN DEVELOPMENT OF CYTOLOGY

1. The Cell, a Mass of Protoplasm with one or more Nuclei

On p. 33 we have seen that Franz Leydig in 1857 and Max Schultze in 1861 defined the cell as a small mass of protoplasm containing one or more nuclei. This has remained to the present day the fundamental idea of the cell, as we may see on referring to the definitions of it given by Richard Hertwig in the seventh edition of his 'Lehrbuch der Zoologie,' [1] Matthias Duval in the second edition of his handbook of histology,[2] and Oskar Hertwig in his 'Allgemeine Biologie.' [3] With regard to this definition there is almost unanimous agreement on the part of the chief cytologists of various nations, and this is a very significant fact, especially as modern cytology is a much debated subject. If it is possible in any branch of knowledge to speak of a *sententia communis doctorum*, we may regard

[1] Jena, 1905, p. 50: 'The cell is a little mass of protoplasm containing one or more nuclei.'

[2] *Précis d'Histologie*, Paris, 1900, p. 26: 'La cellule est essentiellement une petite masse de protoplasma avec un noyau.'

[3] 1906, p. 27: 'The nucleus is just as essential to the existence of a cell as is the protoplasm.' Cf. also the more detailed account given by O. Hertwig in the third chapter of the same work.

the definition of a cell as such in a very conspicuous degree.

I must acknowledge, however, that this unanimity exists among zoologists and histologists more than among botanists.[1]

In many of the smallest forms of plant life, especially in many bacteria, the presence of a true, clearly differentiated nucleus has not yet been established.[2] I use the words 'true, clearly differentiated nucleus' advisedly, for cytologists are more and more adopting the opinion that even in those micro-organisms previously regarded as devoid of nucleus the nuclear substance is present, though divided into smaller particles, which R. Hertwig has designated *chromidia*.[3] This opinion gains support from the discovery of a true nucleus existing at a definite stage in the formation of the spores of the *Bacillus Bütschlii*.[4]

We shall have to return later on (Chapter VII) to the most recent investigations made by biologists on the subject of the absence of nucleus in these extremely small forms of life. For the present it is enough to say that the idea of a living cell involves that of a nucleus, either as a whole or in parts, but the chromatophores that exist in most plant cells besides the cytoplasm and the nucleus are certainly not essential to the existence of the cell, for they are absent in Bacteria and fungi, and in all animal cells.[5]

Let us now proceed to study the structure of a cell more in detail.

In shape and size cells vary greatly. The normal shape of a free cell, not united with others of the same kind to form a tissue, is spherical, but even the unicellular plants and animals are seldom quite round, and cells united to form tissues still less often approach a spherical shape; they are rounded, or oval, or cylindrical, or cubical, or pentagonal, or hexagonal;

[1] Cf. *Lehrbuch der Botanik für Hochschulen* by Strasburger, Noll, Schenk and Karsten, 6th edit., Jena, 1904, pp. 46–7, 270, 274, where it is stated that the presence of a nucleus in the lowest plants (Cyanophyceae and Bacteria) is still uncertain. (English translation, 3rd edit. 1908, pp. 53 and 332.)

[2] Cf. J. Reinke, *Einleitung in die theoretische Biologie*, 1901, pp. 256, &c.

[3] R. Hertwig, 'Die Protozoen und die Zellentheorie' (*Archiv für Protistenkunde*, I, 1902, pp. 1–40).

[4] Fr. Schaudinn, 'Beiträge zur Kenntnis der Bakterien und verwandter Organismen,' I. *Bacillus Bütschlii*, n. sp. (*Archiv für Protistenkunde*, I. pp. 306, &c.).

[5] Cf. Strasburger, &c., pp. 46, 47 (Eng. trans. p. 53).

sometimes they are of almost the same thickness in all three dimensions, at other times they are flattened out like those of the pavement epithelium (fig. 2d), or extraordinarily long, like

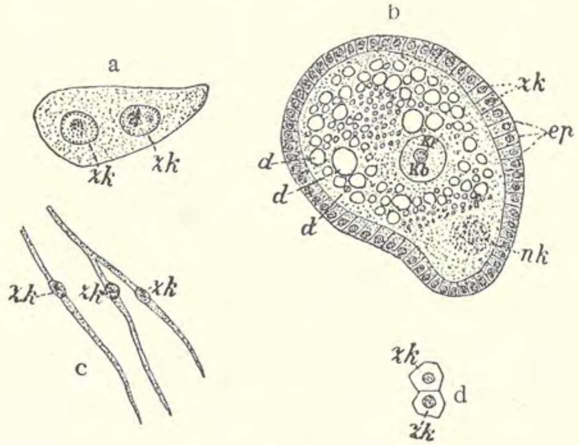


Fig. 2.

Magnified 230 times [Zeiss D, Ocul. 2].

All the figures have been prepared with the camera lucida from series of sections.

Key to Fig. 2.

a = Giant cell containing two nuclei from the abdominal fat-body of a physogastric specimen of *Termitoxenia Heimi* Wasm.
zk, *zk* = nuclei.
b = young egg of *Termitoxenia Heimi* Wasm. The egg-cell is still enclosed within the follicular epithelium of the ovary. (From a sagittal section of a physogastric specimen of *Termitoxenia Heimi*.)
ep = epithelial cells of the one-layered follicle.
zk = nuclei of the epithelial cells.
kb = germinal vesicle of the egg.
kf = nucleolus of the germinal vesicle.
dd = vitelline spherules.
nk = remains of the nucleus of a nutritive cell, the material of which has served to form the yolk.
c = three unicellular muscular fibres from the cutaneous muscular apparatus of the abdomen of a stenogastric specimen of *Termitoxenia* (*Termitomyia*) *mirabilis* Wasm.
zk = nucleus.
d = two epithelial cells from the hypodermis of the abdomen of a stenogastric specimen of *Termitoxenia Heimi*.
zk = nucleus.

the spindle-shaped cells of the smooth muscular fibres, and the still more slender cells that form the transversely striated muscular fibres (fig. 2c).

As a rule, the cells that make up tissues have no prolongations, but in making this statement I am not challenging Heitzmann's discovery (1873) of protoplasmic cell-bridges.[1] Many cells, however, possess long offshoots, which give them a ramified appearance; this is particularly the case with nerve-cells, and is closely connected with their telegraphic functions.

The shape of the nucleus varies less than that of the cell,[2] it is mostly round or oval, although other shapes not infrequently occur. Very remarkable are the branching nuclei of the Malpighian tubes in certain caterpillars, and the nuclei resembling a string of beads in some unicellular Stentors.

In speaking of the size of a cell, we must have a standard by which to measure it. In this respect little cells resemble so-called tall men; we cannot measure either by any usual method, an old-fashioned foot-rule and a modern metre measure are equally out of place. Cells have to be measured under the microscope, and the following method is the simplest. The number of times that the object is magnified is carefully noted, and a sketch of the cell is made on paper by means of a camera lucida. This sketch is then measured with a very exact millimetre measure, and the number thus obtained is divided by that of the magnifying power. For instance, if a cell, magnified 230 times, measures 23 mm., its real magnitude is 0·1 mm. This would be a giant cell if it belonged to animal tissue. Such giant cells as this (cf. fig. 2a) compose the abdominal fat-body of the *Termitoxenia*, a variety of Diptera living among termites, as we have already seen (pp. 37, &c.). Most cells in animal tissues are dwarfs in comparison, and dwarfs among dwarfs are the average blood corpuscles, especially of insects, and the spermatozoa of most animals. Therefore, as a constant unit for microscopical measurement of cells, the thousandth part of a millimetre has been adopted, which is known as a micromillimetre or micro, and is designated by the letter μ. The giant cells of the *Termitoxenia*'s fat-body have a diameter of 100μ. Cells of 10μ (e.g. figs. 2d

[1] A further account of these protoplasmic cell-bridges will be found in Wilson, *The Cell*, pp. 56, 60, where there is a careful discussion of the evidence for their existence among very various kinds of plant and animal cells. See also O. Hertwig's *Allgemeine Biologie*, pp. 400, &c.

[2] For the shape, size, and number of nuclei, see O. Hertwig, *Allgemeine Biologie*, pp. 28, &c.

and 2b, &c.) are of medium size, so the former may well be called gigantic.

But there are some animal cells far larger than these, viz. the egg-cells. These are the largest in the animal kingdom.[1]

The ripe egg-cell of a diminutive insect such as the *Termitoxenia*, barely 2 mm. in length, measures almost 1 mm., i.e. it is half as long as the creature's whole body. The eggs of this fly are reckoned, therefore, among the relatively largest in the entire animal kingdom; the absolutely largest occur among birds; it is in fact possible to use a yard measure to ascertain the size of the eggs of the ostrich or moa. A bird's egg before fecundation consists of one huge cell, but to the egg-cell belong in this case not only the germinal vesicle, which represents the nucleus of the protoplasmic part or formative yolk of the egg-cell, but also a quantity of nutritive yolk or deuteroplasm,[2] which is really the yolk of the bird's egg. The white of the egg and the shell appear only after fecundation, and are outer coverings, and not parts at all of the egg-cell. Animal egg-cells owe their conspicuous size to the presence of deuteroplasm or nutritive yolk, which is found in the eggs of all creatures that are oviparous and not viviparous. In the case of the former a considerable quantity of nutritious matter must be stored up in the egg itself, in order that the embryo may develop. My readers must not, however, fancy that, when they see a new-laid hen's egg, they have only one huge egg-cell before them; for, quite apart from the above-mentioned exterior coverings, which grow before the egg is laid, the egg itself is already fertilised, its germinal vesicle has become a germinal disc, i.e. a still very diminutive embryo chick, consisting of numerous segmentation cells, and the huge egg serves as its lodging and store-room during its further development.

In order to illustrate the various shapes and sizes of the cell by examples, I have reproduced some cells of *Termitoxenia* on p. 50. To the explanations already given I may add that,

[1] Very large cells constitute the plasmodia of the Mycetozoa, which are also reckoned among the lower orders of plants and called Myxomycetes, whilst by others again they are classed with the Protozoa. Cf. R. Hertwig, *Lehrbuch der Zoologie*, 7th edit., 1905, pp. 49 and 168 (Eng. trans. pp. 60, 61, 198).

[2] E. van Beneden called the nutritive yolk 'deutoplasm,' to contrast it with protoplasm; 'deuteroplasm' is a more correct form of the word.

with a view to economising space, I chose for Fig. 2b not a ripe and fully developed egg-cell, but a young cell, still surrounded by a thick follicle of epithelial tissue, and having at its lower end the remains of an incompletely consumed nutritive cell. As the latter is already incorporated with the substance of the egg, the young cell (without the epithelium) measures 135μ in length and 95μ in breadth. A ripe egg-cell of the same kind of *Termitoxenia* would, if drawn on the same scale (magnified 230 diameters), occupy a space of 2 dm., and cover a whole page of this book.

Some plant cells are also very large; for instance, there are bast-cells 2 dm. in length and of considerable breadth. Among the lower plants too, such as the *Caulerpa* (one of the Algae), there are cells several decimetres in length; in fact, according to J. Reinke and other botanists, the whole plant with its root, stem, and leaves consists of one cell with many nuclei.[1]

The dwarfs among plant cells are many of the Bacteria, which have a longitudinal diameter of not quite 1μ ($\frac{1}{1000}$mm.). The petal of a violet consists of about 50,000 cells which are comparatively large.

By far the greater number of cells have but one nucleus, and if they are found to contain more than one, it is generally because the process of cell-multiplication by division is just beginning. There are, however, some cells that always contain several nuclei; such are, for instance, those in the marrow of vertebrates, and partly also those known as *syncytia* in the adipose tissue of insects and other Arthropods.[2]

In his classical and suggestive work on cell-division among the Arthropods,[3] Carnoy expresses the opinion that these are all multinuclear giant cells, not masses of cells formed by the fusion of others. This view cannot be adopted without reservation, as there are undoubtedly cases in which syncytia arise from a gradual breaking down of the cell-walls. This takes place, for instance, in *Termitomyia*, a sub-genus of *Termitoxenia*. In the sub-genus *Termitoxenia* (in the narrower sense)

[1] See Reinke, *Einleitung in die theoretische Biologie*, p. 213, and his *Monographie der Gattung* Caulerpa. See also Frank, *Synopsis der Pflanzenkunde*, III, Hanover, 1886, § 890; van Tieghem, *Traité de Botanique* (1891), pp. 9, 10.

[2] On the subject of *syncytia* or cell-fusions see also O. Hertwig, *Allgemeine Biologie* (1906), pp. 378–381.

[3] 'La Cytodiérèse chez les Arthropodes' (*La Cellule*, I, 1885, n. 2, p. 235, &c.).

these adipose cells are very large, but they are distinct one from the other, though in full-grown physogastric specimens, in which no further cell-division occurs, there are frequently two nuclei (cf. fig. 2a) instead of one. According to Weismann[1] multinuclear cells occur also in the festooned columns of cells found in the larvae of flies. I have myself found cells with two or more nuclei in the halteres of *Termitoxenia*, and Bolles Lee discovered them before me in those of common Diptera.[2] In many of the lower orders of plants, such as the Thallophyta, cells containing several or even many nuclei are of frequent occurrence, and among the Siphonaceae, a subdivision of the Algae, there are plants (*Caulerpa*, *Vaucheria*, &c.), which consist of one huge multinuclear cell, as has been already stated.

Just as in the tissues of living organisms there may be, and actually are, cells which contain several nuclei, but still do not divide into more cells, so, in the lowest forms of animal life, the Protozoa, there are unicellular organisms containing two or more nuclei, but not forced on that account to split up into several individuals.

The reader must, however, carefully distinguish the multinuclear cells just mentioned, from others which contain beside or in the true nucleus one or more little round bodies known as *nucleoli*. The founders of cytology, Schleiden and Schwann, noticed these bodies and regarded them as having some essential importance in the structure of the cell. This opinion has proved to be erroneous, and most nucleoli seem to be merely differentiations of the ordinary substance of the nucleus. For this reason I have purposely refrained from referring to them until now, when we are concerned with the more detailed morphology of the cell.

2. The Structure of the Cell examined more closely

In an account of the origin of modern cytology, Gustav Schlater writes as follows:[3] ' The cell is a little mass of protoplasm, endowed with all the properties of life. This was the

[1] *Die Entwicklung der Dipteren*, Leipzig, 1864, p. 132 and Plate 8, fig. 10.

[2] ' Les balanciers des Diptères ' (*Recueil Zoolog. Suisse*, II (1885), 389 et pl. XII, fig. 18).

[3] G. Schlater, ' Der gegenwärtige Stand der Zellenlehre ' (*Biolog. Zentralblatt*, XIX, 1899, Nos. 20–24, p. 667).

definition given by Max Schultze, and at the time our idea of a cell seemed to have reached its full development. Thenceforth, we had only to submit cells to examination from many points of view, and the representatives of every branch of biology did in fact turn their attention to the cell. The word "Protoplasm" was ever on their lips, and the number of works devoted to the examination of the structure and life of this elementary unit in living substance is so great that it would be quite impossible for anyone to read them all. This examination has proved very fertile in results; every step has supplied fresh evidence supporting the general biological importance of the cell-theory; every book written has proved that we must start from the cell in order to extend our knowledge of nature. The reputation of the cell increased; it revealed itself as more and more complex in its formation. Within it, in this little mass or drop of living substance, modern research has discovered a complicated structure, and more and more details of this structure, and each day adds to the interest taken by men of science in the whole complicated vital processes that go on in the small compass of the cell.'

The interesting question arises here: Are we to consider the cell simple or complex? Is it the ultimate biological unit in the structure of organisms, or is it itself a diminutive organism made up of subordinate units? This is a weighty question, having an important bearing on the problem of life, and students are apt to overlook its twofold character. In order to emphasise it, let us divide the question into two, and ask: (1) Is the cell morphologically simple? (2) Is it the ultimate biological unit of organic life, or is it an aggregation of lower elementary units? It is possible to deny the simplicity of the cell and at the same time to affirm its unity, for, according to the unchanging laws of thought which are still binding upon the *Homo sapiens* of the twentieth century, simplicity and unity are two quite different ideas. Modern research will never attain to assured philosophical results regarding the nature of life, if it confuses unity and simplicity. Let us try to give to both questions an answer based upon facts.[1]

[1] Cf. O. Hertwig, *Allgemeine Biologie*, 1906, chapters ii and iii; Wilson, *The Cell*, 1902; Yves Delage, *La structure du protoplasma et les théories sur l'hérédité*, Paris, 1895.

Is the cell simple? No, it is not simple, but extremely complex in many cases, a true microcosm. It consists of a number of parts that differ morphologically, chemically,[1] and physiologically, and yet on their harmonious connexion depends the biological unity of the vital process of the cell. Although all parts of the cell participate more or less in its vital activities, still the nucleus is of chief importance in the principal processes.[2]

Such are briefly the results of the most recent investigations of cytology, and we have now to consider them more in detail.[3]

The two chief morphological constituents of the cell are the cell-body and the nucleus, and this has been universally acknowledged ever since Leeuwenhoek discovered the nucleus (see p. 31). At the present time everyone regards them as essential to the cell, whilst the membranous covering of the cell and the nucleoli within the nucleus are not essential.[4] In 1882 Strasburger suggested the name *cytoplasm* to designate the protoplasm of the cell-body, and his suggestion has generally been adopted.[5]

It was originally regarded as absolutely homogeneous, but after Dujardin's study of it (1835) little granules were noticed in it, and further examination revealed a structure variously described as filar, reticular, or alveolar. There are many modern theories regarding the structure of cytoplasm. All students, with the exception of those mentioned first, agree in recognising in the protoplasm of the cell-body two distinct substances, one being transparent and forming the foundation of

[1] The chemical constituents of protoplasm and the morphological variety of the parts of the cell are not discussed here in detail, because very little is as yet known with certainty about them. (Cf. Chapter II, p. 33.) How complicated the chemical composition of the nucleus is may be seen on reference to Dr. Hans Malfatti's work, 'Zur Chemie des Zellkerns' (*Berichte des naturwissenschaftlich-medizinischen Vereins*, Innsbruck, XX, 1891-2).

[2] This fact is acknowledged even by those who, like J. Reinke, regard it as not essential to differentiate the nucleus as a distinct morphological formation. (See Reinke's *Einleitung in die theoretische Biologie*, 1901, p. 256.)

[3] An excellent account of the morphology of cells and of the various theories regarding the structure of the cell-body and the nucleus will be found in Wilson's *The Cell*, pp. 19–62.

[4] The subject of the centrosomes will be reserved for discussion in Chapter V. See O. Hertwig, *Allgemeine Biologie*, pp. 45–49.

[5] O. Hertwig prefers to retain the older meaning of the word protoplasm, in which it was originally used by von Mohl, Max Schultze and Leydig, to designate the substance of the cell-body as distinct from the nucleus. Strasburger's cytoplasm is thus identical with the protoplasm of these earlier writers.

the cell (*hyaloplasm*, as Leydig calls it), and the other granular, consisting of microsomes, which form the framework of the filar, reticular, or alveolar structure (*spongioplasm*, as Leydig calls it). The former is also very suitably called *cytoplasm*, and the latter *cytomitom*, but a great number of names have been given to both,[1] names calculated to astound any ancient Hellene who heard the modern derivatives coined from the wealth of old Greek words.

Those who believe cytoplasm to be homogeneous do not recognise the presence in the living cell of two morphologically distinct substances, but they regard the granules and threads and meshes of the so-called cell-framework as merely artificial products, resulting from the chemical reactions and the use of stains for microscopical purposes.

There are, however, good reasons why this theory does not find many supporters at the present day,[2] for recent microscopical research has revealed in the living cell a structure, which is not produced by the processes of fixing and staining, but is only rendered visible by means of them. This is especially true of the filar structure of spongioplasm, which is practically identical with the reticular structure or framework. It was discovered first by Karl Frommann in 1875, but Flemming recognised it as filar,[3] and his observations have been confirmed by those of many other scientists, such as Klein, Leydig, E. van Beneden, Carnoy, Heidenhain, Zimmermann, &c., and are now regarded as of unquestioned accuracy. It is of secondary importance to decide whether, as Flemming thinks, the protoplasmic threads are of greater significance, or, in agreement with Klein, Carnoy, &c., we should lay stress particularly on the network formed by these threads.

Bütschli's alveolar theory represents another view of the structure of the cell. According to it the protoplasm of the

[1] See Bütschli, 'Über die Struktur des Protoplasmas,' 19 (*Verhandl. der deutschen Zoolog. Gesellsch.*, 1891, pp. 14–29).

[2] A. Fischer, whose theory regarding the polymorphic character of protoplasm will be discussed later on, must not be reckoned among those who uphold the homogeneity of protoplasm.

[3] See W. Flemming, 'Über den gegenwärtigen Stand unserer Kenntnisse und Anschauungen von den Zellstrukturen,' a paper read at the opening of the thirteenth meeting of the Anatomical Society at Tübingen on May 22, 1899 (*Naturwissenschaftliche Rundschau*, XIV, 1899, Nos. 35 and 36).

cell has a structure resembling honeycomb or foam, due to the mechanical mixture of the various fluid constituents of protoplasm. That suspended in the fluid hyaloplasm there are often vacuoles, filled with another kind of fluid, is a fact not questioned even by the opponents of this theory, but they deny that the minute structure of the protoplasm depends merely upon the presence of these vacuoles; for, whereas spongioplasm, treated according to Bütschli's methods, appeared to reveal an alveolar structure, closer examination has shown that a reticular structure really underlies it. The chief evidence brought forward by Bütschli in support of his alveolar theory is derived from artificial mixtures of various fluids, which bear a superficial resemblance to cell-structures, but cannot of themselves prove anything about the real structure of the cell.

I have no wish, however, to condemn Bütschli's alveolar theory, for we ought, in speaking of it, to distinguish between his view of the honeycomb structure of the cell, and his explanation of that structure by assuming a mechanical mixture of various fluids. The latter hypothesis is extremely doubtful, and has been thoroughly discussed by Oskar Hertwig in his 'Allgemeine Biologie' (p. 23). On the other hand, Bütschli's theory of the alveolar structure of many cells has been strengthened by recent research. In very thin microscopical sections very highly magnified, what appears as a network seems in fact often to be only a section of a framework consisting not of meshes but of closed chambers; and, if this is true, in these particular cells the protoplasm has really not a reticular but an alveolar structure. In my series of sections of the large gland-cells in the wing-covers of a termitophile beetle (*Chaetopisthes Heimi*) I have occasionally perceived a distinctly alveolar structure of the spongioplasm.[1] It seems, therefore, that the alveolar theory may stand beside the reticular theory, although latterly it has been attacked by those who are inclined to regard the alveoli seen under the microscope as an artificial product, or as a pathological vacuolisation of the protoplasm.[2]

[1] Cf. 'Zur näheren Kenntnis des echten Gastverhältnisses bei den Ameisen- und Termitengästen' (*Biolog. Zentralblatt*, XXIII, 1903, Nos. 2–8, p. 269).

[2] Cf. A. Degen, 'Untersuchungen über die kontraktile Vakuole und Wabenstruktur des Protoplasmas' (*Botanische Zeitung*, 1905, Part I, pp. 163–225).

Less satisfactory than Bütschli's alveolar theory is Altmann's granular theory,[1] which is based upon the granular structure of protoplasm. If Altmann merely asserted that numerous granules, now generally termed microsomes, are embedded in the transparent hyaloplasm of the cell, there would be no objection to his theory, for it would rest on actual observations. But he goes on to deny the fibrillar or reticular structure of the spongioplasm, and thinks that it may be explained as a close series of granules. Flemming, on the other hand, rightly points out that the microsomes are often arranged like beads on the reticular framework, but do not actually form that framework. Moreover, a large proportion of Altmann's famous granules have been proved not to be microsomes at all, but merely artificial products accidentally resulting from chemical reaction ; in fact, they are metaplasmic bodies and consist of protoplasm and foreign substances embedded in it, and were mistaken by Altmann for his granules, and the scientific value of his theory is greatly diminished in consequence. Its chief defect, however, is that it regards the granules contained in protoplasm as alone forming its essential active basis, and that it boldly accepts them as elementary organisms out of which the cell, as a secondary formation, is composed. This view is devoid of all real foundation in facts, and has been rejected by most scientists. We shall have to refer to it again later, in discussing the unity of the cell.

There is great diversity of opinion as to the relative importance of the two morphologically distinct constituents of the cell-body, viz. hyaloplasm (cytoplasm) and spongioplasm (cytomitom). Heitzmann, van Beneden, Reinke, Carnoy, Ballowitz and others agree in thinking the latter, which forms the framework of the cell, its really living, moving and contractile element, whereas others, and especially Leyden, ascribe these qualities to the former, and regard the hyaloplasm as the living substance. As Flemming saw, these two opinions ought probably to be united, for, as no living cell contains hyaloplasm exclusively or spongioplasm exclusively, both must be considered essential constituents of protoplasm, although most scientists agree with Flemming in assigning

[1] Cf. Richard Altmann, *Die Elementarorganismen und ihre Beziehungen zu den Zellen*, 1894.

greater importance to spongioplasm than to hyaloplasm. It is obvious that for the present we must be content to accept hypotheses of various degrees of probability, and these various theories regarding the more minute structure of the cell are all more or less of a hypothetical character.

Quite recently, in 1895–6, another theory as to the structure of the cell has been brought forward by Friedrich Reinke and elaborated by Wilhelm Waldeyer, and Gustav Schlater calls it the newest achievement of modern research into the morphology of the cell.[1] This theory attempts to reconcile the various views as to the structure of protoplasm. According to it, in the homogeneous ground-substance of the cell (i.e. in the *cytoplasm*, as other writers call it) there is embedded a reticular framework (*cytomitom*); the formation of the latter varies, but in the main it is alveolar and in its walls lie very small granules (*microsomes*), which in certain cases are aggregated, so as to form filaments and network. The chief framework of the cell owes its alveolar structure to the larger vacuoles and granules which it contains. Reinke-Waldeyer's theory thus harmonises the views of other scientists, and we may regard it as summing up all that was known of the structure of the cell in the year 1900; there is, however, one drawback to it theoretically, for it lays too little stress upon an essential element, viz. the meshwork or alveolar structure of the cell-framework, with the rows of microsomes arranged along it, and it lays comparatively too much stress upon an unessential element, viz. the vacuoles and larger granules which the cell contains.

3. The Minute Structure of the Nucleus

Hitherto we have discussed only the details of the cell-body, now we must consider the structure of the nucleus. Here again we find two chief substances, which, however, differ morphologically, physiologically, and chemically far more from one another than do the spongioplasm and the hyaloplasm of the cell-body. It is often possible to discover in the nucleus not only two, but three or four protein substances differing under chemical and microscopical examination. The nucleus is

[1] *Biolog. Zentralblatt*, XIX, 1899, No. 20, p. 676.

therefore, as O. Hertwig rightly remarks, a very complex [1] formation, so far as its constituents are concerned. According to their behaviour when stains are applied to them to facilitate their microscopical examination, the two chief substances in the nucleus have been called *chromatin* and *achromatin*; according to their chemical properties they are called *nuclein* and *linin* respectively. Chromatin or nuclein takes a brilliant colour when treated with carmine, haematoxylin, &c., whereas achromatin or linin is either not stained at all or takes a colour only under special circumstances. Achromatin resembles in structure the protoplasm of the cell-body, for it contains a fluid known as *karyoplasm*, and a fibrillar or reticular or alveolar framework known as *karyomitom*. These are analogous to the cytoplasm and cytomitom of the cell-body. Large nuclei are bounded on the outside by a peculiar nuclear membrane.

Chromatin has been mentioned as one of the chief substances in the nucleus; the parts that are readily stained are formed of it, and it is composed of nuclein.[2]

Closely connected with it, though differing chemically both from chromatin and from achromatin or linin, is another substance, less readily stained, known as *plastin* or *paranuclein*. Nuclein and plastin together form the chromatin nucleoli, the chromatin nuclear framework, or the chromatin skein-like nuclear filaments; these are only different names for the different forms assumed by the nuclein-plastin elements in the nucleus.

With regard to the relation in which they stand to the achromatic nuclear framework, many theories have been propounded by Flemming, Carnoy and others, but we cannot discuss them in detail now. For the present let it suffice to say that two distinct kinds of nucleoli have been discovered, the one kind very readily stained, the other less so, but both consisting of combinations in different proportions of nuclein and paranuclein, whilst on the other hand the *true nucleoli* or *plasmosomes* are not susceptible to any stain, consist only of paranuclein (pyrenin), and form more or less transparent vacuoles.

[1] *Allgemeine Biologie*, p. 29. For further details as to the constituents of the nucleus, see pp. 29–44.

[2] Cf. J. Reinke, *Philosophie der Botanik*, 1903, pp. 69 and 72.

It may be asked why different parts of the cell behave in such different fashions, when the same stain is applied to them, and so render it possible for us to penetrate into the mysteries of its structure. Two theories have been put forward to account for this behaviour. According to one, which is known as the chemical theory of stains, it is assumed that the degree of readiness with which the various parts of the cell take a stain depends upon the amount of chemical affinity existing between the various albuminous compounds and the stain applied. According to the other and newer theory, certain parts of the cell are susceptible to stain, only because of the changing physical qualities of the thing stained, and, as a result, its powers of absorption vary. Alfred Fischer is the chief supporter of this physical theory.[1] It seems probable that both theories are more or less true, and that the staining capacity of the various morphological elements of the cell may be ascribed partly to chemical and partly to physical causes.

In close connexion with his examination of the effects of fixing and staining upon the substance of a living cell, A. Fischer has propounded a new theory, which he designates that of the polymorphism or pleomorphism of protoplasm.[2] He believes protoplasm to be in general viscous, containing structures of various shapes, granular or reticular, some of which remain permanently, whilst others are of a transitory nature. All these varieties in the cell-framework are due to definite albuminous compounds fluctuating between a fluid and a solid condition. Moreover, Fischer is of opinion that protoplasm is often homogeneous on the surface, but in the interior occur granules, filaments, reticular framework, and occasionally also Bütschli's alveolar structures. Fischer is not a supporter of the absolute homogeneity of protoplasm, for in the face of ascertained facts this can no longer be defended, but he admits that the various cellular structures observed by modern scientists are, at least to a great extent, not artificial products, i.e. the results of staining and fixing, but occur also in the living cell. He does not, however, believe that

[1] *Fixierung, Färbung und Bau des Protoplasmas*, Jena, 1899.

[2] We find similar ideas in Yves Delage's *La structure du protoplasma et les théories sur l'hérédité*, pp. 30 and 31.

these structures point to any chemical difference in the parts of the cell, but are the outcome of the physical conditions affecting the protoplasm at any given moment. Fischer obviously does not intend to deny the complex chemical composition of living substance, but he doubts whether there is any necessary connexion between the chemical constitution of the parts of the cell and their staining capacity—such a connexion as would justify our assuming that a chemical difference exists between parts that show a different staining capacity.

Although Fischer's theory of the polymorphism of protoplasm has a good deal that is hypothetical about it, there is far more actual foundation for it than for Altmann's granular theory ; in fact, the latter bears the character of a phylogenetic speculation rather than that of a scientific theory. The theory of the polymorphism of protoplasm has one great advantage, viz. that it reconciles the conflicting opinions regarding the morphological structure of the cell with one another, and supplies one uniform explanation of the actual variety of phenomena.

4. Survey of the Historical Development of the Morphology of the Cell

What, then, is the morphology of the cell in the light of modern research ? This question can be answered best, if we glance back at the views regarding the structure of the cell that have been current at various stages of cytological research. They may be represented by the diagram on p. 64 (figs. 3–6).[1]

Fig. 3 is a cell as Malpighi (1678) and Wolff (1759) conceived it ; it consists simply of the enclosing membrane, and so is nothing but an empty sac.

Fig. 4 is a cell such as Schleiden and Schwann described (1838–9). The membrane is still an essential part, but it is now partly filled with fluid, in which is suspended another essential part, viz. the nucleus, with one nucleolus.

Fig. 5 is the cell according to Leydig (1857) and Max Schultze (1861). The viscous fluid fills the whole sac, and

[1] Cf. M. Duval, *Précis d'Histologie*, 1900, pp. 25, 31. Also G. Schlater, 'Der gegenwärtige Stand der Zellenlehre' (*Biolog. Zentralblatt*, XIX, 1899, p. 756).

surrounds the nucleus and its nucleolus, but the membrane has disappeared as not essential to the existence of the cell. Subsequently the finer structure of the cell was more closely examined, and the mass of apparently homogeneous protoplasm was seen to be a compound formation, consisting of framework and fluid, whilst the nucleus, too, was found to contain, besides the nucleolus, an achromatic framework embedded in nuclear fluid, and also a chromatin framework that assumes various forms. We may connect the names of

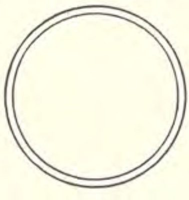


FIG. 3.

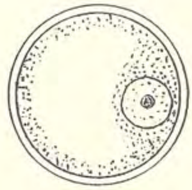


FIG. 4.

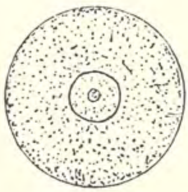


FIG. 5.

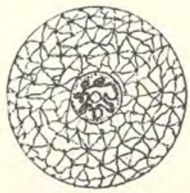


FIG. 6.

Schlater, Reinke, and Waldeyer with this stage of cellular morphology (1894–5).

Fig. 6 represents it according to Carnoy,[1] who regards the cellular framework as reticular, and the chromatin nuclear framework as consisting of a coil of nuclein-plastin thread.[2] This conception of the cell harmonises best with my own cytological examination of the huge pericardial [3] cells of the *Termitoxenia* (*Termitomyia*) *mirabilis*.

[1] Carnoy's valuable work in the development of cytology has been already mentioned. See p. 46.

[2] Cf. also E. B. Wilson, *The Cell*, p. 35. Fig. 13A is an admirable representation of a permanent spireme nucleus, showing chromatin in a single thread (*Balbiani*).

[3] This is the name given to some peculiar cells, allied to the adipose cells, and connected with the 'heart' of the insect, i.e. with its vas dorsale.

Within the chromatin thread of the nuclear framework it is possible in many cases to perceive a still finer morphological differentiation. In the American salamander *Batrachoseps* the threads are plainly divided and each *pronucleus* contains, according to Gustav Eisen, twelve chief parts or *chromosomes*.[1] Each chromosome as a rule is subdivided into six *chromomeres*, in each of which on an average six of the most diminutive bodies or *chromioles* can be traced. There are therefore about 400 distinguishable parts in the chromatin thread of the nucleus!

There are also other animal and vegetable cells, which, before division, show only a coil of chromatin thread, or a chromatin framework, but, in the course of indirect or mitotic division, this develops into definite groups of chromatin knots or chromosomes; whilst within the achromatic framework, that was previously scarcely visible, there now appear as organs of cell-division tiny round *centrosomes*, in the midst of which rises an achromatic spindle. All these phenomena will be discussed more fully in Chapters V and VI, for they do not properly belong to the morphology of the resting cell, or cell not in process of division.

The cell is therefore far from being a simple formation; it is, on the contrary, composed of parts differing widely from one another, and having different functions in its life. We have now to consider the chief kinds of activity in the cell, and the parts taken in this activity by the morphologically different elements of it, and then we shall be in a position to discuss the question whether the cell is the ultimate unit in organic life, or whether it is equivalent to an aggregate of still more simple and elementary units. A result of this discussion will be to show us what ought to be our attitude, as students of natural science, towards the famous theory of the spontaneous generation of organic beings.

[1] *Pronucleus* is the name given to the nucleus of both the egg- and sperm-cells immediately after their union in the process of fertilisation. See Chapter VI.

CHAPTER IV

CELLULAR LIFE

1. The Living Organism as a Cell or an Aggregation of Cells

Cells are the bricks composing the whole building of the organic world. Therefore to them also is the Creator's command addressed : ' Increase and multiply,' for without growth and multiplication of cells no organic life is conceivable. All living creatures consist of one or more cells ; if they are unicellular, increase is possible only if from one cell several cells are formed ; if they are multicellular, growth and increase are possible only by way of growth and increase of the cells composing their organs and tissues.

In the previous chapter we discussed the structure of the resting cell, as revealed to us by modern microscopical research ; we have now to turn our attention to the cell as active and alive. In the case of unicellular animals and plants, the diminutive mass of protoplasm with its one nucleus is the one organ that has to discharge all the functions of life ; it is, to compare small with great, a Jack-of-all trades in the economy of life. Nutrition and multiplication, as well as independent movement and sensation (as far as these latter manifest themselves in unicellular creatures), all depend upon one and the same atom of living substance. It is true that here, in spite of the diminutive size of the creature under consideration, we have something analogous to what is called ' organisation ' in higher animals, for, as we shall show later on, the morphologically different parts of the cell have various functions. Still, strictly speaking, the parts of the cell ought not to be called *organs*, although, perhaps, we may follow some recent writers and call them *organellae*, at least when speaking of the multicellular animals known as metazoa. In their case, whenever we use the word organ, we mean some part consisting of definite tissues and serving as an instrument in the vital activity of an individual. As the tissues are made up of cells, which are therefore the ultimate constituents of the organs, it would be logically wrong to apply the same word ' organs ' to the smallest parts of the cells themselves. It has lately become too much the custom to disregard the connecting membrane which unites cells together to form tissues, and tissues to form organs. The result of this has been that, in both the higher animals and plants, the cell has come to be regarded as having an independent existence, as being an individual of a lower order. This view is, however, altogether mistaken, and it is no less wrong to apply the name ' organs ' to the minute constituents of the cell, which differ morphologically and physiologically. If they are organs at all, they are so only in a loose, metaphorical sense.

It is only in the case of unicellular organisms that this theoretical opinion corresponds with facts, for in them the constituent parts of the cell really discharge the vital functions of the individual, and so are equivalent to the organs of multicellular organisms. For this reason the unicellular organisms form the lowest rung of the ladder of organic perfection. The higher we ascend, the more are the various parts differentiated to perform distinct functions, and the greater is the perfection of the organisation. A vertebrate animal, or even a tiny insect, is a well-ordered and regulated state, whose inhabitants and officials are thousands and tens of thousands of cells.[1]

[1] The reader must notice that this expression is figurative. In reality, as has been already pointed out, the cells of a multicellular organism are not individuals, because they are not physiological units complete in themselves, as are unicellular organisms. On this subject see Chapter VII, § 1 : ' The cell as the ultimate unit in organic life.' Cf. also O. Hertwig, *Allgemeine Biologie*, 1906, chapters 14–17.

All are democrats, for none is of higher origin than the others; the nerve-cell of the brain, which exercises control, like the ruler of the state, is a cell in exactly the same way as the glandular cell of the stomach, or the epithelial cell of the skin. But in spite of their genuinely democratic disposition, the cells are by no means anarchists; there prevails among them a most perfect harmony, based upon a regular division of labour between the various organs, tissues, and cells.[1]

Just as in every well-ordered state different duties are assigned to different officials, so to various organs are assigned the functions of nutrition, digestion, circulation of the blood, respiration, propagation, movement and all the work done by the nerves and senses. But these organs, which resemble the heads of departments in the state, are themselves made up of different kinds of subordinate tissues, and each tissue consists of a more or less varied combination of cells, differing in the case of the different tissues. All these millions of cells compose what we call an organism, and in spite of their vast number and endless variety they all have the same origin, for they all proceed from an egg-cell fertilised by means of a spermatozoon; such at least is the ordinary process of development of any higher organism.[2]

The continuation of the process of cleavage, begun in the first cleavage or segmentation nucleus, leads eventually to a differentiation of the living creature into various cells, tissues and organs, until it attains its full development, and then the work of propagation renews the cycle of life. But even the egg-cells and the spermatozoa, although they carry on the task of propagation, differ in no respect from other cells, as far as their origin is concerned; in the course of embryonic development they are differentiated from common cells, into which the fertilised egg split up at the formation of the periphery of the embryo.[3]

[1] On the subject of the division of labour in an aggregation of cells, see O. Hertwig, chapter 17, pp. 417, &c.

[2] I say 'ordinary,' because of the phenomena of parthenogenesis among insects, &c., where the egg-cell develops without fertilisation. (See Chapter VI, § 6.)

[3] See Chapter VI, § 3, for the most recent results of investigations regarding the distinction between somatic and germ cells, which is either very early or even original.

All the cells, therefore, in the organism enjoy absolute 'equality before the law,' but it is an equality, not of death but of active life, inasmuch as from cells, at first similar, the mysterious laws of organic development produce the living being in all its wonderful, complete, and complex structure.

Such is in outline the cellular life of the multicellular organism, which we cannot now discuss in greater detail. What has been said will suffice to show that the cell must be called the lowest unit of organic life in multicellular animals and plants. Let us now study more closely the vital processes affecting cells as such, whether they are united to form tissues of a higher order, or lead an independent existence as unicellular beings. This study will give us a deeper insight into the real nature of the cell, this marvel of creation.

Life is, in its physiological aspect,[1] an uninterrupted process of movement, every phase of which tends to the preservation of the individual and of the species. The interior movements, which form the really essential processes of vegetative life, tend to the assimilation of fresh material, and so to the growth of the individual. These processes of assimilation, depending as they do upon nutrition and respiration, are necessarily closely connected with analogous phenomena of dissimilation,[2] for the building up of what is new requires a tearing down of what is old, and the reception of fresh nutritive matter and its transformation into living substance necessitate a removal of what is worn out. Growth is based upon assimilation and leads naturally to numerical increase. As soon as a cell has reached a definite maximum size, it divides and forms new cells; if these remain united in one aggregate of tissues, the division of the cell promotes the growth of the individual; if, however, the new cells separate from the parent organism, so as to form new independent individuals, then the division of the cell is a process of propagation, and furthers the preservation of the species. To these interior processes of movement in the living substance correspond other exterior

[1] For further details regarding the physiology of the vital processes, the nutrition and transmutation of energy of cells, and the processes of assimilation and dissimilation, see Bunge, *Physiologische Chemie*, and J. Reinke, *Einleitung in die theoretische Biologie*, chapters 26–29.

[2] The word *dissimilation* was introduced by Hering as an euphonious abbreviation of *des-assimilation*, which, being a clumsy word, is now but little used.

movements, due to the susceptibility of protoplasm to definite external stimuli; these latter movements tend to procure the material necessary to support the interior vital processes, whether it be by the assimilation of food to promote individual growth, or by the union of individuals to promote the preservation of the species; finally, the exterior movements protect the organism from its enemies. Thus all the exterior movements are subservient to the interior, even when, as voluntary, they belong to conscious existence, and therefore are on a higher level than the vegetative processes, for the whole conscious life of an animal aims at the preservation of the individual and of the species; it stands to living matter in the position of a slave; its sole aim is material, and it has no power to rise above the material, as the intellectual life of man enables him to do.

2. Activity of Living Protoplasm

The foregoing general observations will enable us to understand the phenomena that we are now about to consider.

Oskar Hertwig in his 'Allgemeine Biologie,' pp. 108, &c., recognises several distinct kinds of movement in protoplasm, and we may safely follow him on this point. Real protoplasmic movement either belongs to a complete protoplasmic body, such as an amœba, or it takes place in the interior of a cellular membrane. This latter form of movement occurs chiefly in plants, and is divided into rotatory and circulatory movements. The rotatory movement was discovered by Bonaventura Corti as early as 1774. We must distinguish these genuine movements of protoplasm from those due to exterior appendages on the cells, such as cilia and flagella, with which we shall deal in the next section of this chapter. We must refer also to the movements of pulsating vacuoles in unicellular animals, and to the manifold passive alterations in shape and position undergone by the cells of an organism in consequence of the vital process going on within it as a whole. At present, however, we are concerned only with a few instances of true protoplasmic movement.

The protoplasm of a living cell is in a state of constant activity, and moves on definite lines inside the cell, its course being apparently determined by the framework of spongioplasm. At the end of the eighteenth and at the beginning of the nineteenth century Corti and Treviranus noticed (see p. 33) that the chlorophyll granules, which give plants their green colour, are frequently in vigorous movement within the cells; later on, in 1848, von Mohl discovered this granular movement not to be active, but passive, and due to the power of contraction possessed by protoplasm. In many of the lower animals protoplasm appears capable of active movement, but we must be careful to distinguish two forms of activity—the active movement of the protoplasm framework, that manifests itself especially in external changes of shape, and a more passive flow of the granules in the cell-sap, which is a result of the contraction and expansion of the protoplasmic framework. It is obvious that these processes of movement cannot always and everywhere be traced with the same clearness in living cells. They can be seen very well in various little unicellular creatures possessing no enclosing membrane, such as the *Amœba proteus*,[1] and still better in other animals belonging to the same class of Rhizopods, but having a thin shell, through the openings of which the so-called pseudopodia protrude, as, for instance, in the case of the *Gromia oviformis*.[2]

The body of the Amœba is subject to constant changes of shape, whence the creature has received its name. It can protrude protoplasmic continuations of its substance in all directions and again withdraw them. The pseudopodia are outstretched to catch food and to effect a change of place; they are withdrawn when any danger threatens. If the pseudopodia of an Amœba are fed with very small grains of carmine, these grains are at once surrounded by the protoplasm of the pseudopodia and absorbed by it, and then they share in the interior flow of the protoplasm and render it visible under the microscope. In Amœbae there is no sharp distinction between interior and exterior movements, for both are nothing but the same flow of the same protoplasm. When the pseudopodia discover anything edible they close round it, and it at once becomes the centre of a vortex of

[1] The changes of shape undergone by this little Amœba were described as early as 1755 by Roesel von Rosenhof.

[2] Within the pseudopodia of true Amœbae no movements can be discerned, although they occur in the other Rhizopods.

protoplasm, for the creature's whole body contracts round its prey. The same protoplasm, which sought and captured its food, now proceeds to assimilate it, and digests as much of it as is digestible, and then rejects the rest by uncoiling the enclosing ring of protoplasm.

More vigorous movements than those of the Amœba can be observed, as already stated, in the pseudopodia of many other Rhizopods, especially the Foraminifera and Radiolaria, which possess a solid skeleton of chalk or silica, and through its openings protrude the long pseudopodia in quest of food or to effect change of place.

Amœboid movements as well as the granular flow of protoplasm may be produced, checked, and altered by mechanical, chemical and thermal stimuli, and this constitutes the chief proof of the irritability of living protoplasm.

Analogous to the action of the Amœbae and their relations in the water is that of some cells in the organism of multicellular animals, especially of the white blood-corpuscles or *leucocytes*. They too possess amœboid prolongations, enabling them to move and traverse all the tissues of the body. In order to pass through a narrow crevice, they put out a pseudopodium first, and gradually the whole body of the cell follows it. Cohnheim, who discovered the power of the leucocytes to wander through the tissues of the body, bestowed upon it the very suitable name of *Diapedesis*. These wandering cells have an almost insatiable appetite; they are like tramps, always hungry and thirsty, and they attack other cells, as well as any extraneous substances that have penetrated into the body, and encounter them on their way. The leucocytes surround these on all sides and devour them, hence their other name of *Phagocytes*. Their voracity gives them a high degree of importance in the life of the organism. The white blood-corpuscles discover the red blood-corpuscles that are old and incapable of taking up oxygen, and seize them and carry them off, and thus, by consuming the useless members of the community of cells, the leucocytes are able to impart the nourishment so obtained to other active formative elements of the body. They are the police, appointed to keep order in the cell-republic that we call an organism. They go to and fro through all the tissues and purify them from hostile bacilli and other wrongdoers. Whenever they light upon anything harmful, they simply close round it and devour it; or, if it is altogether inedible, e.g. a speck of coal dust, they arrest it and drive it over the frontier. The leucocytes are therefore real sanitary inspectors in the organisms of man and the higher animals. Many authors ascribe to their agency the assimilation of the nutritive matter absorbed in the intestinal glands, as well as the diffusion of nourishing lymph throughout the whole body,[1] and from this point of view the wandering leucocytes appear as nurses, supplying food to the other cells and tissues. On the other hand, however, under certain morbid conditions, leucocytes increase with such overpowering rapidity as to become dangerous. They then attack cells that ought to be left in peace, and so excite a kind of revolution resulting in inflammation and suppuration of the tissues, and tending to the eventual destruction of the whole organism. In spite, therefore, of their physiological merits, leucocytes have acquired a bad reputation in cellular pathology. Moreover, the most recent investigations carried on by Ehrlich, Metchnikoff and others have deprived leucocytes of many of the police functions generally ascribed to them. According to the most modern views, the struggle between health and disease is fought out chiefly by toxins and antitoxins, the former being chemical substances injurious to the organism, and given off by harmful bacteria, &c., whilst the latter are the chemical antidotes, produced by the organism itself as a protection against toxins. Modern processes of inoculation aim at causing immunity from certain diseases by producing specific antitoxins.

A harmless counterpart to the pathological action of leucocytes in the bodies of men and the higher animals occurs in the phagocytes of those insects which undergo a complete metamorphosis. To these cells is assigned the pleasing task of devouring the old tissues of the larval body during the pupal stage, in order to impart the stored-up nutritive matter to other cells concerned in the formation of the new tissues of the imago.

A flow of protoplasm occurs also in cells where it has deposited an exterior membrane and cannot therefore protrude

[1] Cf. M. Duval, *Précis d'Histologie* (1900), p. 42.

pseudopodia, but in this case the movements are limited to the interior of the cell. This movement of protoplasm in plant cells has long been known to botanists and often described, for instance, in the leaf cells of the *Elodea canadensis* and in the stamens of the *Tradescantia*, &c.

3. Exterior and Interior Products of the Cell [1]

Just as the activity of the protoplasm inside a cell enables it to form a solid membrane as its envelope, so it can produce movable processes on the surface of the cell, such as cilia and flagella, which facilitate the locomotion of the cell. In this way ciliated and flagelliform cells arise. The latter have either one or a few long, thick processes, whilst the former have rows of delicate hair-like threads. Among the Infusoria there is a class of unicellular creatures called Flagellata, from their having these flagelliform processes, and another class of Protozoa is known as Ciliata, because their cell-walls are provided with cilia, which enable them to move about in the water. Cilia are important in the ingestion of food, for these creatures, though unicellular and of diminutive size, have voracious appetites. The ring of cilia surrounding the oral aperture of an infusorian by its rhythmical motion produces a vortex in the water, at the centre of which is the mouth of the little animal. If a tiny diatom or another of the Algae is caught in this vortex, it has no chance of escape; it is sucked down and vanishes in this Scylla, and only its indigestible remains are eventually thrown up.

Flagelliform and ciliated cells occur also in multicellular animals. Spermatozoa are simple flagelliform cells, of which the nucleus forms the head, and a long thread of protoplasm the body and tail. Ciliated cells occur chiefly in the respiratory and digestive apparatus, and in this case the cilia do not assist in the movement of the cell to which they are attached, but in that of the substance passing over them. The cilia of the trachea serve to expel small foreign bodies that have entered the respiratory orifices, and those of the œsophagus help to carry down the nutritive fluids taken in through the mouth, and to keep them in steady movement towards the digestive

[1] See O. Hertwig, *Allgemeine Biologie*, 1906, pp. 79, &c., pp. 100, &c.

organs. In many of the higher and lower animals ciliated cells occur in the real digestive canal. I have seen very beautiful ones, magnified 1500 times, in the transverse sections of the mesenteron of the *Termitoxenia* (*Termitomyia*) *Braunsi.*

The outward or exoplasmic products of the cell are the external results of the internal activity of the protoplasm. They may take the form of a cellular membrane, whether it is homogeneous with the protoplasm (as is the case with most animal cellular membranes), or whether it is a chemical product of protoplasm, as is the case with the cellulose cell-walls of plants,[1] or the shells of many of the lower animals (e.g. the Foraminifera) or the coverings of plants (e.g. the Diatomaceae) which have been hardened by taking up silicic acid or carbonate of lime. Further exoplasmic products of the cell are the elastic intercellular bridges uniting cells with one another, and the cilia and flagella which protrude from the cellular membrane.

The internal or endoplasmic products of the cell are contained in its interior. They are of most frequent occurrence in the vegetable kingdom. In the chemical laboratory of the living plant cell grains of starch are being prepared which supply the world with sugar, either directly, or indirectly through the activity of the plant. Starch is the form in which the plant stores up the carbo-hydrates that produce sugar. The protoplasm of plants was believed to form chlorophyll under the influence of light, thus giving its colour to the foliage;[2] but recently many scientists have inclined to the opinion that chlorophyll is not a cellular product, and that its presence, not only in many lower animals, such as the *Hydra viridis,* but also in plants, is due to a symbiosis of special chlorophyll cells with other vegetable or animal cells.[3]

[1] The young membrane of a plant cell consists always of cellulose, but in many instances the cell-walls harden later on into cork or wood.

[2] The granules which convey the colouring matter originate in the plant cell even without the influence of light, although the green colour, which can be extracted from them, only develops as a rule when light is admitted. Young fir trees are green, however, and full of chlorophyll, even when grown in the dark, and several cryptogams become green in spite of complete exclusion of light.

[3] Cf. C. Mereschkowsky, ' Über Natur und Ursprung der Chromatophoren im Pflanzenreiche ' (*Biolog. Zentralblatt,* XXV (1905), No. 18, pp. 593–604). He believes the Cyanophyceae to be independent chromatophores, and tries to account for the origin of the vegetable kingdom, and its difference from the animal kingdom, by assuming that they have penetrated into animal cells. In fact a lion, sleeping under a palm tree, would change places with it,

Animal and vegetable fat is a product of the interior activity of the cell, and is stored up in its empty spaces. In the animal kingdom this biochemical branch of industry is of great importance, and a special class of fat-forming cells, called adipose cells, often make up large quantities of tissue. In their vacuoles little drops of fat collect and grow, until finally the whole cell resembles a ball of fat surrounded by a membrane. The neighbouring cells that are not of this class can feed upon this stored-up fat by way of endosmosis. The protoplasmic product that we call fat is of great importance in the nutrition of the animal organism. It used to be regarded as the material for supplying heat in the process of combustion connected with respiration. In insects fat is closely connected with the formation of blood, for which reason, in speaking of them, we often call the adipose tissue simply the blood-forming tissue. I found many instances of this connexion between fat and blood in the course of my microscopical study of the inquilines among ants and termites, and especially in the physogastric guests of the termites, which rejoice in an extraordinary abundance of fat. In the larvae of the termitophile beetle of Ceylon, known as *Orthogonius Schaumi*, the outer edge of the huge adipose tissue may be seen just at the spot where it touches the hypodermal masses of blood, and it is frequently in a state of disintegration, and being absorbed almost imperceptibly by the diminutive corpuscles of the insect's blood. I observed similar phenomena in other genuine inquilines among the termites, which become physogastric through their abundance of adipose tissue ; the same transition from adipose to blood tissue appeared on a series of sections of a termitophile insect, *Xenogaster inflata* of Brazil. The ants and termites seem to appreciate the advantages of their guests' adipose tissue, and hold to the dictum *Omne pingue bonum* ; for all their true inquilines, belonging to the class of beetles, possess a great deal of fat, and it is this tissue which directly or indirectly emits the volatile exudation that attracts them so greatly and induces them to lick their guests.[1]

provided the cells in his body were filled with chromatophores (p. 604). This is certainly a very bold theory.

[1] Cf. on this subject 'Zur näheren Kenntnis des echten Gastverhältnisses bei den Ameisengästen und Termitengästen' (*Biolog. Zentralblatt*, XXIII, 1903, Nos. 2, 5, 6, 7 and 8, p. 68).

There are a number of other products of the interior of the cell which might be mentioned; some of them occur in animal cells and some in vegetable, and take the form of essential oils, colouring matters, nectar, caoutchouc and india-rubber, resin, tannic acid, poisons of various kinds, digestive ferments, &c., thus serving the most manifold and interesting biological purposes.

In vertebrate animals the haemoglobin of the red blood-corpuscles is one of the products of the interior of the cell. This haemoglobin, to which blood owes its colour, carries the life-giving oxygen which we breathe in; the molecules of oxygen are brought through the lungs into the blood, and accompany the red blood-corpuscles over the whole extent of the arterial circulation, making their way through the finest capillary vessels to the single cells of the tissues, where they give out their oxygen and so oxydise the existing organic connexions. The free carbonic acid, which is the chief combustion product of the vital process, has now to be expelled from the body by the same means; so the red blood-corpuscles are accompanied by carbonic acid molecules on their way back from the capillary vessels, through the whole extent of the venous circulation, until they reach the lungs, where the carbonic acid is breathed out into the air, and at the next inspiration fresh oxygen is taken up, to join the red blood-corpuscles on their next journey through the body. The arterial and the venous blood differ in colour because the haemoglobin of the red blood-corpuscles forms a soluble chemical combination with the oxygen, producing bright red oxyhaemoglobin, whilst the same blood-corpuscles, after giving off their oxygen to the cells of the body, resume their previous dark bluish-red tint.

4. The Predominance of the Nucleus in the Vital Activities of the Cell

We have now considered some characteristic instances of the processes of cell-nutrition, cell-growth, and cell-motion. Before passing on to a new and important class of phenomena of cellular life, viz. the process of multiplication by cell-division, we must examine more closely the part played by the nucleus in the manifestations of cell life already described.[1] We have to answer this question: Are the nutrition and growth of the cell and the formation of its interior and exterior protoplasmic products to be ascribed to the cell-body, or does the nucleus participate in them as an essential element?

R. Hertwig says, in his 'Lehrbuch der Zoologie,' 7th ed. p. 55 (Eng. trans. p. 67), that 'for a long time the functional significance of the nucleus in the cell was shrouded in complete darkness, so that it began to be regarded, in comparison with the protoplasm, as a thing of little importance.' In fact, a merely superficial consideration of the phenomena already described might easily lead us to doubt any participation in them on the part of the nucleus. If, for instance, a little Amœba grasps its still smaller prey with its pseudopodia and devours it, we can observe a series of movements about and in the viscous protoplasm of the creature's body, but we can perceive no change in its nucleus. If, on the other hand, a plant cell is trying to thicken a definite portion of its enclosing membrane by depositing layers of cellulose, the nucleus may be seen to quit its former position in the centre of the cell, and to approach that part of the periphery where the depositing action of the protoplasm is at its height, and, when the task is accomplished, the nucleus comes back to the middle of the cell. In the same way the nuclei of certain unicellular plant-hairs approach the offshoot as long as it is in process of formation, but when its growth is complete they return to their original place. The eggs of the threadworm (*Rhabdonema nigrovenosum*) have been observed during the process of cleavage, and the nuclei of the newly formed cells moved towards the surface of the cell, where the fresh membrane was forming, and after remaining there for some time, on the completion of its formation, they withdrew into the centre of the cells.[2]

[1] Cf. on this subject especially O. Hertwig, *Allgemeine Biologie* (1906), chap. 10, pp. 249, &c.

[2] Cf. L. Rhumbler, 'Über ein eigentümliches periodisches Aufsteigen des Kerns an die Zelloberfläche innerhalb der Blastomeren gewisser Nematoden' (*Anatomischer Anzeiger*, XIX, 1901, pp. 60–88). See also the address delivered by the same scientist at the seventy-sixth assembly of German naturalists at Breslau, on September 23, 1904, and printed under the title 'Zellenmechanik und Zellenleben' in the *Naturwissenschaftliche Rundschau*, 1904, Nos. 42 and 43. See especially pp. 546 and 548.

Numerous similar phenomena, pointing to a participation of the nucleus in the processes of nutrition and formation, were described in 1887 by Haberlandt, an eminent botanist,[1] and in 1889 by Korschelt, a zoologist.[2] These two scientists deduced the following conclusions from their observations :—

1. The fact that the nucleus occupies a definite position only, as a rule, in a young cell in course of development suggests that its functions are connected primarily with the processes of cell-development.
2. From its position we may assume that the nucleus is especially concerned, during the growth of the cell, with the thickening and spreading of the cellular membrane ; but it is quite possible that in a fully grown cell the nucleus has other functions to discharge.
3. The nucleus is concerned not only with the cell's power of secretion, but also with its nutrition. We can infer this both from its position and also from the fact that it sends out numerous branches, thus increasing its surface on the side nearest to the place where secretion or nutrition is going on.[3]

We must refer here also to the correlation between the size of the protoplasmic body and that of its nucleus, which R. Hertwig calls the *Kernplasmarelation*.[4] It can be explained by the interior reciprocal action of the cell-body and cell-nucleus. What actual observation pronounced probable has been confirmed by experiments. Gruber, Nussbaum, B. Hofer, Verworn, Balbiani, Lillie, Klebs and others had recourse to

[1] 'Über die Beziehungen zwischen Funktion und Lage des Zellkerns bei den Pflanzen,' Jena, 1887.

[2] 'Beiträge zur Morphologie und Physiologie des Zellkerns' (*Zoolog. Jahrbücher*, Section for Anatomy, IV, 1889).

[3] This accounts for the occurrence of nuclei with corners or even branches in the gland-cells of certain insects when in a state of active secretion. I noticed such nuclei on my series of sections of the ant-inquiline *Paussus cucullatus*, which has a strongly marked layer of gland-cells in its antennae. Similar nuclei occur in the large frontal glands which open through an exudatory pore of the forehead. Cf. 'Zur Kenntnis des echten Gastverhältnisses bei den Ameisengästen und Termitengästen' (*Biolog. Zentralblatt*, 1903, pp. 240, 241, 244, 245).

[4] Cf. R. Hertwig, 'Über Korrelation von Zell- und Kerngrösse für die geschlechtliche Differenzierung und die Teilung der Zelle' (*Biolog. Zentralblatt*, 1903, Nos. 1 and 2). See also O. Hertwig, *Allgemeine Biologie*, p. 257.

merotomy, and cut unicellular creatures into several parts,[1] and the results of these investigations are extremely instructive.[2]

If an Amœba be cut into several pieces, the part that is fortunate enough to contain the nucleus continues its previous way of life ; it moves about and feeds, and so it replaces what it lost in living substance and recovers its normal size. The other parts, however, which contain no nucleus, soon cease to move, and in course of time the network of protoplasm that forms their body begins to disintegrate, until nothing is left of them. A non-nucleated fragment of an Amœba is as incapable of feeding as it is of moving. It can no longer contract so as to enclose any particle of nourishment and absorb it into its own body. If a portion of an Amœba had already begun such a nutritive movement before its separation from the main body, its action is soon arrested and the inactivity of death sets in. In the case of unicellular Rhizopods, which deposit a chalky shell, this process of secretion, being analogous to the formation of membrane, becomes impossible as soon as the nucleus is removed, but the nucleated fragments are able to secrete a shell wherever a wound has been inflicted.

With regard to plants, too, Klebs has shown[3] that only the nucleated portions of a plant cell are able to form a new cellulose membrane, and so to close an opening cut in the cell-body.

Balbiani has succeeded in establishing,[4] by means of merotomical experiments on Infusoria, the precise part taken by the chromatin of the nucleus in the nutrition and growth of unicellular creatures. In a previous chapter (pp. 60, &c.) we discussed the morphological importance of chromatin or nuclein in the finer structure of the nucleus ; its physiological importance is now to be revealed.

In many Infusoria the chromatin is arranged in numerous

[1] Merotomy must not be confused with merogony, which is a name given to attempts to fertilise or develop ova that have been cut up or otherwise artificially mutilated. We shall refer to this subject again in Chapter VI, § 8.

[2] Cf. Wilson, *The Cell*, pp. 342, &c. Also O. Hertwig, pp. 254, &c.

[3] *Untersuchungen aus dem botanischen Institut zu Tübingen*, 1888, II, p. 552.

[4] 'Recherches expérimentales sur la mérotomie des Infusoires ciliés' (*Revue Zoologique Suisse*, V, 1889) ; 'Nouvelles recherches expérimentales sur la mérotomie des Infusoires ciliés' (*Annales d. Micrographie*, IV, 1892 and V, 1893).

somewhat coarse granules in the interior of the nucleus. Balbiani succeeded in cutting a ciliated Infusorian (Stentor) into three pieces in such a way that the nucleus was also cut, each segment containing a part of it (fig. 7).

The upper division containing the mouth received four granules of chromatin, the middle portion received one, and the lowest three. All three parts of the Stentor continued to live, and in twenty-four hours each had become a fresh individual. The one formed from the middle piece of the

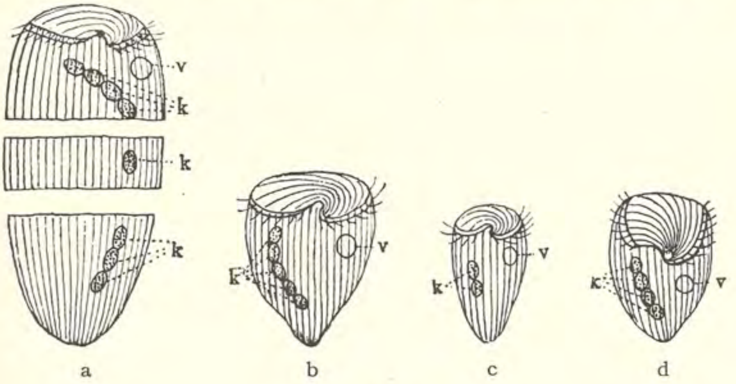


Fig. 7.—Stentor.

On the left (a) is the specimen cut into three parts; on the right (b, c, d) the new specimens formed by regeneration.

k = nucleus ; v = vacuole.

original specimen was, however, considerably smaller than the other two, because its nucleus had possessed only one chromatin granule.

In 1896 Lillie succeeded in dividing a Stentor into as many pieces as he wished, by simply shaking the glass vessel containing it.[1] In this way he was able to show that fragments consisting of only $\frac{1}{27}$ of the creature's volume were capable of regeneration, provided they contained a particle of the nucleus ; all non-nucleated portions perished.

In other merotomical experiments made by Balbiani, the Infusorian was only partially severed, so that the two parts remained connected by the protoplasm of the cell-body. If the

[1] 'On the smallest parts of Stentor capable of regeneration' (*Journal of Morphology*, XII, Part 1).

nucleus was not cut, the wound healed quickly and the creature recovered its previous appearance; it never happened that two individuals were formed in consequence of a division of this kind. If, however, the nucleus also was severed, each part of the Infusorian grew into a new animal, and, as they were connected by a piece of the protoplasm, the result of this division was the production of a monstrous double creature that reminds one of the famous Siamese twins. In course of time, however, the two individuals began to approach one another, their nuclei came together and coalesced, and the monstrosity became one normal specimen.

Other experiments, carried on by Verworn in 1891,[1] and Balbiani in 1892 and 1893, have led to a modification of views based on the experiments just described, inasmuch as they have thrown additional light on the participation of the protoplasm in the life of the cell, and so put us on our guard against overrating the importance of the nucleus. Verworn chose as the subject of his experiments a spherical Protozoon, *Thalassicola,* which measures half a centimetre across, a gigantic size for a unicellular creature. He succeeded in isolating the nucleus from the protoplasm of this huge cell-body, and demonstrated unequivocally that the nucleus cannot live alone without a particle of protoplasm; it died and did not form a new cell-body. On the other hand the non-nucleated cell-bodies continued alive for a considerable time and went on feeding, but they were unable to multiply by means of division, and so they too eventually died. In his more recent experiments Balbiani compared very exactly the varying behaviour of nucleated and non-nucleated portions of Infusoria. He came to the conclusion that nucleus and cytoplasm are each the complement of the other in discharging the most important functions of life, although the nucleus plays the chief part. Cytoplasm alone was able for some time to produce the movements of the body and of its ciliated envelope, the ingestion of food and the contraction of the pulsating vacuoles of the body. The nucleus was, however, indispensable to secretion, regeneration, and the processes of division, without which the cell-plasm must inevitably die.

[1] 'Die physiologische Bedeutung des Zellkerns' (*Pflüger's Archiv für die gesamte Physiologie*, LI).

Not only zoologists, but also botanists, have recently been making careful experiments with a view to determining the part taken by the nucleus and the cell-body respectively in the vital processes of the cell. The results show that in plants too the value of the cell-body must not be underestimated, although the nucleus actually controls the vital activity of the cell.[1]

I have already (p. 80) quoted Klebs' assertion that fragments of vegetable protoplasm containing no nucleus are incapable of forming a cellulose membrane. This statement has been challenged by Palla and others, who think that they have traced the formation of a new cell-wall in non-nucleated fragments, although other botanists regard this as very doubtful.[2]

Klebs himself mentions the fact that non-nucleated fragments of Algae remained alive for weeks, but eventually died. I may therefore on this point agree with J. Reinke, the botanist, when he says:[3] 'The nucleus is unquestionably the most important organ in the cell-body.'

The total results of these merotomical experiments may be summed up shortly as follows:—Nucleus and cytoplasm are both essential to the life of a cell. A cell-body without a nucleus has no more practical value than a nucleus without a body of protoplasm. In a normal cell the nucleus is to a certain extent the central point, the organising principle of the living matter, or, as Wilson aptly expresses it, 'the controlling centre of cell-activity.'[4] Nevertheless, after the nucleus has been removed, the cytoplasm alone is in many cases able for a time to continue the vital processes already begun, but it is incapable of producing any notable new formations, and is absolutely unable to divide and to perpetuate the species. The nucleus is, as will be shown more clearly in other chapters, the real bearer of heredity, and within the nucleus in its turn the chromatin is chiefly concerned with heredity.

The division of an Infusorian into a definite number of nucleated pieces results in the formation of the same number

[1] Further information on this subject will be found in Chapters V and VI, where I shall deal with cell-division and fertilisation.

[2] Cf. Pfeffer, *Pflanzenphysiologie*, I (1897), pp. 45, &c.

[3] *Einleitung in die theoretische Biologie*, 1901, p. 256.

[4] *The Cell*, p. 30.

of fresh animals, therefore we are justified in calling the nucleus the principle of individuation of living matter ; and here again, within the nucleus, it is to the chromatin that this property must especially be ascribed, for just as many new individuals are formed as there are fragments of nucleus containing chromosomes. If an Infusorian is partially severed, a double animal is formed only if the nucleus be cut in half.

That the protoplasm of the cell-body is not, however, without importance in the formation of a living unit seems to be proved by Balbiani's experiment with the double Stentor. The nuclei of the two creatures gradually approached one another, and one normal animal resulted from their coalescence. If there had been no living bond to unite them, they would not have grown together again into one animal.

Later on I shall have to discuss the important part played by the nucleus and its chromatin in the processes of cell-division and fertilisation. In this place I may, however, quote a passage bearing on our subject from R. Hertwig's 'Lehrbuch der Zoologie,' 1905, p. 55 (English translation, p. 67). He is insisting upon the significance of the nucleus, and says : ' The evidence that the nucleus plays the most prominent rôle in fertilisation has altered this conception (of its secondary importance). Then arose the view that the nucleus determines the character of the cell ; that the potentiality of the protoplasm is influenced by the nucleus. If from the egg a definite kind of animal develop, if a cell in the animal's body assume a definite histological character, we are, at the present time, inclined to ascribe this to the nucleus. From this, then, it follows further that *the nucleus is also the bearer of heredity* ; for the transmission of the parental characteristics to the children (a fact shown to us by our daily experience) can only be accomplished through the sexual cells of the parents, the egg- and sperm-cells. Again, since the character of the sexual cells is determined by the nucleus, the transmission in its ultimate analysis is carried on by the nucleus.' [1]

[1] For the biological and physiological importance of the nucleus, see also Wilson, *The Cell*, pp. 358, 359.

CHAPTER V

THE LAWS OF CELL-DIVISION

In a previous section (p. 66) we spoke of the cells as the bricks composing the building of the organic world. But they are at the same time the architects, always rebuilding the organic world in an unbroken series of generations. They are *living* constituents, growing and multiplying in virtue of the laws of development imposed upon them, and they unite to form tissues, organs, and living creatures of various kinds. The fundamental process upon which the architecture of the cell depends in all multicellular organisms is that of cell-division. What the delicate scalpel of the scientist effects violently, when he vivisects unicellular organisms (see p. 80), is done automatically under certain circumstances, in accordance with the interior laws of organic growth ; and one cell, by dividing, forms two or more.

Let us now study this natural cell-division and the interesting processes that attend it.

1. Various Kinds of Division of the Cell and Nucleus

Whenever the development of an individual requires an increase in the number of cells, whether to make new tissues, or to enlarge those already existing, or to form new creatures and carry on the process of propagating the species,—in every case the cells concerned have to divide. In cells containing one nucleus, the first step is the division of the nucleus. Then the protoplasm of the cell-body either divides too, or remains undivided; [1] in the latter case a uninuclear cell becomes multinuclear; in the former, which is much more common, one cell becomes several. If the cellular membrane is divided and fresh cell-walls are formed, we have *exogenous* cell-division; but if the daughter-cells remain within the membranous covering of the mother-cell, we have what is called *endogenous* cell-division.[2] When exogenous cell-division takes place, the new cells either remain side by side, so that a cellular tissue is formed, or they leave their homes and migrate. Again, when a cell divides, it may form two or more cells of equal size, and this is simple cell-division; or the new cells cut off from the mother-cell may be much smaller than it is; this kind of division is called *gemmation*—it occurs in the growth and multiplication of many of the lower animals, for instance, in the *Podophrya*, the *Hydra*, &c., and in some plants, such as the yeast fungus. Whatever be the form of cell-division, its chief feature is invariably the division of the nucleus, and we must therefore devote attention particularly to it. We here touch upon a subject with regard to which modern microscopical research has been most successful; in fact, it would be difficult to name any other subject in dealing with which microscopical research has produced more brilliant results, so great have been the delicacy and intelligence with which the investigations have been conducted, and so bold and shrewd the conclusions deduced from their results, although these conclusions are to a large extent still hypothetical. Modern cytology has succeeded in some degree in solving the mysteries of heredity, by means of microscopical research. If we are careful to distinguish the actual results from the conclusions deduced from them, we shall be able

[1] The process of division which affects only the nucleus and does not result in a cell-division is sometimes called 'free nuclear division.' (Cf. Strasburger, *Lehrbuch der Botanik*, 1895, pp. 55, &c. Eng. trans. 1893, pp. 89, 90.) This free nuclear division must not be confused with 'free formation of the nucleus,' to which I shall refer later.

[2] On the subject of endogenous increase of nuclei, resulting in the presence of several nuclei in one cell, see O. Hertwig, *Allgemeine Biologie*, 1906, pp. 213, &c.

subsequently to form a true opinion of the modern theories of heredity.

Nuclear division is either direct or indirect. In the former, the division of the nucleus takes place without causing any essential change in its structure; but in the latter it is accompanied by a complicated mechanism, involving great changes in the structure of the nucleus, and partially also in the protoplasm of the cell. These changes are chiefly in the position and arrangement of the chromatin constituents of the nucleus, viz. the nuclear thread and its chromosomes; but there are also no less regular formations of fibres and asters out of the achromatic nuclear substance.

On account of the characteristic movements of the chromatin in the nucleus, the indirect nuclear division is sometimes called *karyokinesis* (nuclear movement), while the transformation

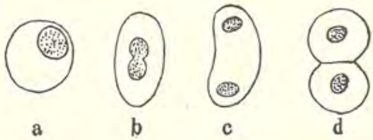


Fig. 8.—Direct division of the nucleus in red blood-corpuscles.

and breaking up of the chromatin thread and the simultaneous appearance of achromatic spindle fibrils have given rise to the name *mitosis* (μίτος = thread) or mitotic division, whereas the direct division is called amitotic. Let us begin by considering the latter, as it is the simpler form, and will help us to understand the more complex process of indirect division.

Direct division of the nucleus was observed by Remak in red blood-corpuscles as early as 1841. Young corpuscles contain one nucleus, the division of which leads to their multiplication. The process is very simple, as the accompanying figure will show.

The nucleus in the cell is at first spherical, then it elongates, gradually contracting in the middle. At the same time the cell itself assumes an oval shape, having previously been round. The nucleus next splits in half, and the two halves retire from one another; then the protoplasm of the cell-body contracts in the middle, the indentation deepening until finally two spherical blood-cells are formed, each with a round nucleus in its centre. Therefore, in the course of direct cell-division, the nucleus by simply contracting breaks into two, and then the protoplasm of the cell-body and the cellular membrane divide likewise. This form of division of the nucleus and cell occurs frequently among Protozoa, especially among those possessing a nucleus that is rich in chromatin.

There is some uncertainty as to the discoverer of indirect division. Wilson (' The Cell,' p. 64) ascribes the discovery of mitosis to Anton Schneider, a zoologist, in 1873. Sachs thinks J. Tschistiakoff,[1] a botanist, has a better claim to the honour, as his work, published in 1874, gave the first impulse to modern research on this subject. Others again mention E. Strasburger, the botanist, as the discoverer of this complicated form of cell-division. There is no doubt that the German anatomist, Walter Flemming, was the first to formulate and expound the process of mitosis in his ' Beiträge zur Kenntnis der Zelle und ihre Lebenserscheinungen ' (1878–82).[2] Abbé Carnoy, a Belgian, has thrown much light upon the subject in his ' Biologie cellulaire ' (1884), and by means of his admirable study of cell-division in Arthropods.[3]

It would be superfluous to mention more names, for the study of mitosis has now become a favourite branch of cytological research, and we know that, in the case of very different kinds of tissue, indirect division of the nucleus occurs far more generally than direct. The two great forms of division of nucleus and cell are, however, connected by various intermediate forms.

A very thorough discussion of all the phenomena observed in mitosis may be found in Wilson's ' The Cell,' pp. 65–121, a book that I have frequently had occasion to mention. My own account of the process must be limited to the barest outlines.

2. Various Stages of Indirect Division of the Nucleus

We have seen that in direct division of the nucleus, or amitosis, the division of the chromatin elements of the nucleus

[1] Sachs, *Vorlesungen über Pflanzenphysiologie,* 1887, p. 115, note 4. Tschistiakoff's work to which Sachs refers is his ' Matériaux pour servir à l'histoire de la cellule végétale ' (*Nuovo Giornale Botan. Ital.* VI). See particularly Plate VII, figs. 11–13.

[2] *Archiv für mikroskopische Anatomie,* XVI–XIX.

[3] ' La Cytodiérèse chez les Arthropodes ' (*La Cellule,* I, 1885, No. 2).

in the mother-cell, so as to form the nuclei of the two daughter-cells, is effected by means of a rough partition of the mother-nucleus, which first contracts in the centre and then splits in half. In indirect cell-division, or mitosis, there is a complicated series of phenomena, all aiming at dividing the chromatin of the mother-nucleus in a most exact and regular fashion between the two daughter-nuclei. This may be called the fundamental idea underlying the whole process of karyokinesis or mitosis, and all the other incidents are subordinate to it.

It is, however, as E. B. Wilson rightly remarks, difficult to give a connected general account of mitosis, because the details vary in many respects in different cases, and especially because great uncertainty still hangs over the nature and functions of the so-called centrosome. In German textbooks of zoology we generally find the process of karyokinesis exemplified by the nuclear divisions of the epithelial cells of the spotted salamander (*Salamandra maculosa*), and my own experience shows that these supply us with an excellent means of tracing the process of karyokinesis conveniently. It is only necessary to cut off a piece of the epidermis from the tail of a salamander or triton larva, to treat it in the usual way with carmine or haematoxylin, so as to prepare it for the microscope, and then it is possible to see a series of karyokinetic figures in the cells of the epithelium. In order to be able to distinguish the single chromosomes, we generally have recourse to some special staining methods, and Heidenhain's stain with iron-haematoxylin can still be recommended. In discussing the subject, however, I shall refrain from alluding to differences in single instances and in staining methods, and shall follow Wilson's admirable account of karyokinesis in 'The Cell,' pp. 65–72.

We may distinguish four groups of phenomena as four successive stages in karyokinesis. There are :—(1) the *Prophase* or preparatory changes; (2) the *Mesophase* or *Metaphase*, in which the chromatin substance of the nucleus is actually divided; (3) the *Anaphase*, in which the divided nuclear elements are rearranged so as to form the daughter-nuclei; (4) the *Telophase*, in which the cell finally divides and the daughter-nuclei return to the state of rest.

These four stages are, of course, not sharply marked off from one another, but one gradually passes into another.

In all four we see a double series of changes going on simultaneously in the cell. The first involves the chromatin figures of the nucleus, formed by the change in position and the halving of the chromatin substance of the nucleus; the second series involves the achromatic nuclear figures, resulting from changes in the achromatic nuclear framework, and to some extent also from changes in the achromatic cell-framework. The first series of changes effects the actual division of the nucleus; the second series is subsidiary, and consists of a radiating arrangement of the protoplasm, rendering possible the movements that occur in the first series.

Let us now examine some diagrams (figs. 9–16) which will give us a better idea of the marvellous mechanism of karyokinesis.

1. *Prophase.*—The first step towards indirect division of the nucleus is a change in the chromatin substance. When the cell was resting, this appeared as a coil of thread or as a reticular or alveolar framework, but now it thickens into a skein. Fig. 9 represents a cell at rest, with its reticular chromatin framework of the nucleus. The dark spot *n* within the network is a nucleolus (see pp. 54 and 61), but its presence is not essential; *c* is the centrosome already in process of division—it is a spherical body, only slightly susceptible to stains, which is also called the polar body, from its position. Boveri terms it the organ of cell-division, and he is probably right in so doing, as we shall see later.[1]

In Fig. 10 the prophase of karyokinesis has begun, and the chromatin thread of the nucleus has thickened and contracted, so as to form one unbroken skein. The nucleolus *n* is still visible, the centrosome has divided, so that there are now two, which are moving apart and beginning to send out delicate rays of protoplasm to form the attraction-sphere *a*. This is sometimes called the chromatin skein or spireme stage of cell-division, from the arrangement of the chromatin substance of the nucleus. As it often forms a kind of rosette, it has also been described as the chromatin monaster (single star) stage.

[1] This polar body must not be confused with the directing or polar globule of the egg-cell. See Chapter VI, § 2.

Lastly, as the achromatic centrosome figure (*a* in fig. 10) resembles a double star, it is sometimes called the achromatic amphiaster stage. The farther apart the two centrosomes move in order to take up their position at the opposite poles

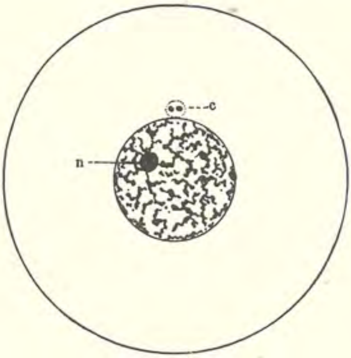


Fig. 9.

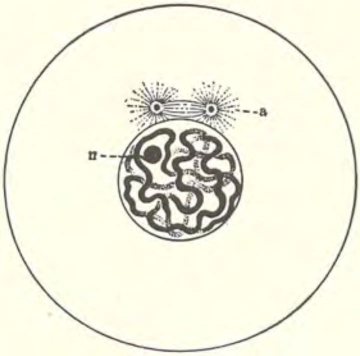


Fig. 10.

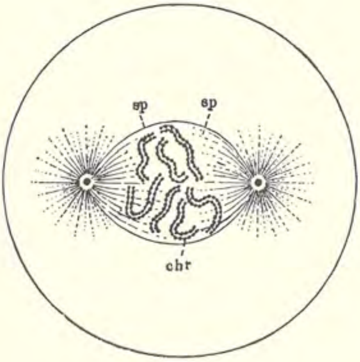


Fig. 11.

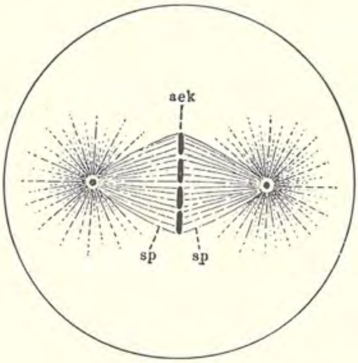


Fig. 12.

Fig. 9.—Cell with resting nucleus.

Figs. 10–12.—Prophases of mitosis (Wilson).

c = centrosome; n = nucleolus; a = amphiaster; sp = spindle; chr = chromosomes; aek = equatorial plate.

of the nucleus, the more applicable becomes the name *amphiaster* to this achromatic figure.

Fig. 11 represents the second stage of prophase. The double star or amphiaster now forms an achromatic spindle, and the chromatin figure shows remarkable changes. The chromatin spireme thread has broken up into a number of regular segments, which form the chromosomes. They originally composed the chromatin network of the nucleus, and at each cell-division they appear in the same shape and number.[1]

The chromosomes of the same nucleus are generally all of the same size and shape, but occasionally they form a series of pairs, and in some very rare cases superfluous or accessory chromosomes appear. They have, as a rule, the shape of a fairly regular U or V, sometimes however they are rod-like or even spherical. In certain cases the lengthwise division of the chromosomes, which takes place in the metaphase, is suggested previously, as each splits lengthwise into two parallel parts, which remain connected by delicate transverse fibres. (See the chromosomes in fig. 11.)

As we shall see in the next chapter, the chromosomes are of very great importance in the propagation of the race and in the transmission of hereditary characteristics, and therefore we must devote a little more attention to them. In all plants and animals propagated by the union of two sexes, the number of chromosomes in every cell is invariably *even*, one half being derived from each of the parents. Further, with very few exceptions, every species of plant and animal has always the same fixed number of chromosomes in every cell.[2]

Only the germ-cells are an important class of exceptions, as we shall see in the next chapter, for they contain only half as many chromosomes as the other cells of the body.

The number of chromosomes in each cell varies very greatly in different species of animals and plants. It ranges from 2 to 168. Sometimes there is a considerable difference in the number of chromosomes of closely related species, whilst on the other hand those of unconnected species are often identical in number. Any one who is interested in the subject may find the chromosome numbers of sixty-two species of

[1] Boveri has based his theory of the individuality of chromosomes upon this fact. See Chapter VI, § 9.

[2] The threadworm, *Ascaris megalocephala*, has two varieties, one of which contains four, and the other two, chromosomes in the cells of its body. For other instances see Korschelt and Heider, 'Lehrbuch der vergleichenden Entwicklungsgeschichte der wirbellosen Tiere' (*Allgem. Teil*, part 2, p. 612).

plants and animals tabulated on p. 206 of Wilson's 'The Cell.'[1]

I quote from it a few numbers by way of example; they are those of the chromosomes in the somatic cells of each species; in the ripe germ-cells, as has been said before, only half the number of chromosomes occurs.

In many worms there are 2 or 4 chromosomes; in others 8; in some *Medusae*, grasshoppers and Phanerogams, 12; in one *Hydrophilus*, a snail, the ox and man, 16; in the sea-urchin and a sea-worm (*Sagitta*), 18; in an ant (*Lasius*), 20; in the lily, the salmon, the frog and the mouse, 24; in the torpedo, 36; in a worm (*Ascaris lumbricoides*), 48; and in a little fresh-water crab (*Artemia*), 168.

Let us now turn to fig. 11, and follow the movements of the chromosomes during karyokinesis. We see that the chromatin within the nucleus now appears as an independent formation. The nuclear membrane enclosing the nucleus has meantime disappeared, and so has the nucleolus (*n* in figs. 9 and 10).[2]

The two centrosomes, which in fig. 10 are still above the nucleus, have now taken up their position at its two poles. The protoplasmic rays proceeding from them have grown longer, and now meet in the centre of the nucleus forming the nuclear spindle (*sp*). This is also called the direction spindle, because it serves to direct the chromosomes in their movement both before and after the actual division. The chromosomes now lie apparently free in the middle of the cell, but in reality they are connected with the fibres of the achromatic spindle, which are, as a rule, formed out of what was previously the achromatic nuclear framework, but in some cases out of the cell framework, or out of both together.[3]

This stage (fig. 11) is called, from the chromatin nuclear figure, the stage of chromatin loops, or, from the achromatic figure, the stage of the direction spindle.

[1] Cf. also O. Hertwig's *Allgemeine Biologie*, 1906, p. 203, where the same table is given with some additions.

[2] On the behaviour of nucleoli in different cases, see Wilson, *The Cell*, pp. 67, 68.

[3] There was for a long time great divergency of opinion regarding the origin of the protoplasmic spindle-fibres. Modern research seems to show that we ought to distinguish three kinds of spindle: (*a*) those that are formed of the nucleus alone; (*b*) those that are formed of the cell cytoplasm; and (*c*) those that are of mixed origin. Cf. O. Hertwig, *Allgemeine Biologie*, 1906, pp. 193–195.

Fig. 12 depicts the third part of the prophase, which leads on to the metaphase. The chromosomes are moving along the spindle-fibres towards the centre, and finally group themselves in the form of a ring in a plane passing through the equator of the spindle, which is known as the equatorial plate.[1]

From the chromatin nuclear figure, this stage is called that of the equatorial plate, or rather crown (*aek* in fig. 12), because the chromosomes remain distinct from one another, and only group themselves in the shape of a ring. The achromatic nuclear figure, the spindle (*sp*), is best seen in this stage.

2. *Metaphase.*—The middle stage, or metaphase, now begins, and is the culminating point of the whole karyokinesis, because in it the actual division of the nucleus takes place (fig. 13). In 1880 W. Flemming discovered that this division consists of the splitting of the chromosomes lengthwise into two exactly similar halves. If each chromosome had originally the shape of a V, it now becomes a W; if it was a simple rod, it is now a double one. This division of the chromatin nuclear substance takes place with such extraordinary exactitude, that it is impossible to avoid regarding it as of great importance to the processes affecting heredity. As W. Roux showed in 1883, the entire chromatin of the nucleus in the mother-cell is divided according to the strictest rules of distributive justice, so that the nuclei of the daughter-cells receive precisely equivalent portions, and each portion is arranged in exactly the same number of chromosomes as there were in the mother-cell. It is a matter of indifference whether the lengthwise splitting of the chromosomes in the metaphase was anticipated by a longitudinal division of each single chromosome (fig. 11), or whether the whole process takes place at once. The nucleolus *n* may remain visible during the metaphase (as in fig. 13) or it may disappear. Its behaviour is of minor importance.

This central stage of indirect cell-division, which we have just described, is known as the stage of doubling the equatorial crown.

3. *Anaphase.*—In this stage the daughter-nuclei of the

[1] For the sake of simplicity, the chromosomes on the diagram are represented as rod-like rather than curved, although the latter is the more usual form. Each loop points to the centre of the equatorial plate.

new cells are built up. After splitting lengthwise in the metaphase (fig. 13), the two halves of each chromosome begin to draw apart. Those on the right group themselves about the right pole of the spindle, and those on the left about the left pole, the spindle-fibres serving as guides. Fig. 14

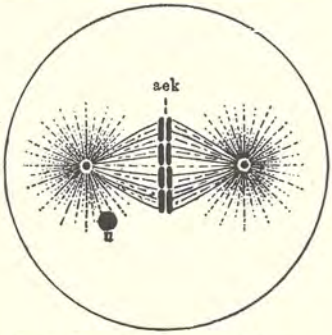


FIG. 13.—Stage of metaphase.

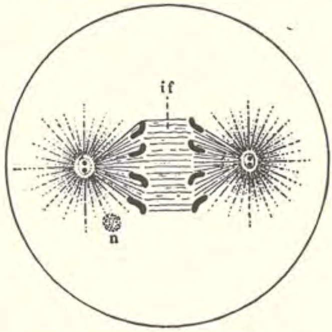
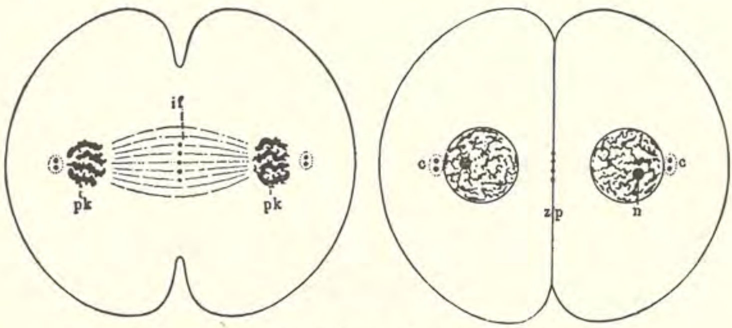


FIG. 14.—Stage of anaphase.



FIGS. 15 AND 16.—Stages of telophase (Wilson).

c = centrosome; n = nucleolus; if = interzonal fibres; ep = equatorial plate; pk = polar caps; zp = cell-plate.

represents this stage of the anaphase. It is known as that of dicentric orientation of the daughter-chromosomes.

4. *Telophase.*—The process of karyokinesis now advances rapidly through its final stages or telophase. Fig. 15 represents the transition from the anaphase to the telophase. The chromosomes of the daughter-nuclei have now reached the two opposite poles of the spindle, have grouped themselves together and sent out delicate fibres, which bind them together

and will eventually enable them to unite and form the chromatin framework of the daughter-nuclei. In some cases the chromosomes do not directly coalesce to form the new nuclear framework, but it is produced by the fusion of vesicles to which the chromosomes have given rise (vacuolisation).[1] From the chromatin nuclear figure, which forms a dark coloured ring round the two poles of the cell in course of division (fig. 15), this stage has been called that of the two polar caps or crowns. If these crowns assume a stellate shape, it is called the stage of the *chromatin diaster* or double star. When, as in the epithelial cells of Amphibia, the egg-cells of *Ascaris* and many plant cells, the chromatin framework of the new daughter-cells is not produced by vacuolisation of the chromosomes, but by their thickening and growing together, the chromatin diaster stage is followed immediately by that of the *chromatin dispireme*. We can form some idea of this, if we imagine the ends of the chromosomes within the future daughter-cells in fig. 15 to be united. This would produce two skeins similar to that which we noticed in the prophase (fig. 10) as the beginning of the division of the chromosomes.

The fibres of the spindle, which appear in fig. 15 uniting the two chromatin asters, have now another name. They are called interzonal or connecting fibres (*if*). In almost all plant cells, and occasionally in animal cells, they are thickened in the middle, and these thickened portions subsequently make up the cell-plate (*zp*) or mid-body of the dividing cells.

At the end of the telophase we reach the last stage of indirect division of the nucleus (fig. 16). The two chromatin skeins of the daughter-nuclei have surrounded themselves with a membrane, within which the new framework has been formed. We can again perceive the nucleolus (*n*) in the nucleus. Each daughter-nucleus has brought with it a centrosome into the new cell, where it will divide, and the two fresh centrosomes will move from the poles to the two sides of the equator of the original karyokinetic figure and take up their position there. This is, however, not always the case. Sometimes they vanish altogether, and reappear only when the process of division is to begin again. The fate

[1] For further information regarding the growth of the nucleus, see Wilson, *The Cell*, p. 71.

of the interzonal fibres (*if*), which remind us of the spindle of the former achromatic karyokinetic figure, varies greatly. In plant cells they remain, and by thickening they help to build up the new cell-walls formed by the secretion of cellulose.[1] Fig. 16 gives us an instance of this. The perpendicular line in the middle represents the cell-plate (*zp*) or mid-body of the cell in course of division. In animal cells, on the contrary, the interzonal fibres generally disappear early and no trace of them remains, as they are not in this case needed to form a cell-plate. Fig. 15 shows the mother-cell with deep indentations above and below; these increase until it finally splits in half, and the two daughter-cells are formed, and thus the process of indirect division of the nucleus and cell is completed.

3. General Survey of the Process of Karyokinesis

Let us review once more the phenomena of karyokinesis. The first two stages of the prophase, those, namely, of the chromatin spireme and the chromatin monaster, correspond exactly to the last two stages of the telophase, those of the chromatin diaster and the chromatin dispireme. The stages lying between these two extremes belong to the doubling of the equatorial plate or crown. This culminating point is connected on the one hand with the prophase, by the breaking up of the chromatin monaster into V-shaped segments, and by their grouping to form a simple equatorial plate; it is connected on the other hand with the anaphase, by the dicentric orientation of the daughter-segments in the double equatorial plate, and with the telophase by their withdrawal to the poles and formation of the two polar caps or crowns. Indirect karyokinesis is therefore a process that is at once marvellously complex in its conformity to law, and wonderfully simple in design. Its object is to divide the chromatin of the nucleus in the mother-cell into two absolutely equal parts, in such a way that the nucleus of each of the two daughter-cells shall receive the half of every chromosome in the mother-cell, and that the number of chromosomes in each daughter-nucleus shall be the same as that of the chromosomes in the mother-nucleus.

[1] Cf. Strasburger, *Lehrbuch der Botanik*, 1895, p. 52.

The account just given of indirect karyokinesis and the diagrams illustrating it must be regarded as in some degree theoretical, for many modifications occur in various kinds of animals and plants.[1]

Reinke says very truly in his 'Einleitung in die theoretische Biologie,' p. 260: 'To variations in the structure of the nucleus in different organisms correspond variations in the course of mitosis, as will be seen by comparing them. But we find everywhere four fundamental phenomena, viz. the formation of the chromatin and achromatic figures out of the resting nucleus; the splitting of the chromosomes; the movement of the divided chromosomes to the poles of the mitotic figure; and the rearrangement of the parts so as to reproduce the configuration of the resting nucleus. The persistence of the number of chromosomes from generation to generation in nuclei of the same species may be added as a fifth point.'

The polar bodies called centrosomes were discovered by Flemming in 1875,[2] and I have designated them and the spindle radiating from them a biomechanical contrivance for securing a regular division of the chromatin. This view is confirmed by the account of karyokinesis given by the best authors. We may therefore follow Boveri, Weismann, and others in calling the centrosomes the especial organs of cell-division.[3]

R. Bergh is inclined to ascribe even greater importance in the process of cell-division to the achromatic than to the chromatin nuclear figure.[4] E. van Beneden, Flemming, Guignard and others are also, perhaps, disposed to overrate the importance of the centrosomes.[5]

[1] This is true of the normal processes concerned in karyokinesis, but there are other modifications which are matters of pathology, and which we cannot discuss here. See O. Hertwig, *Allgemeine Biologie*, pp. 214, &c.

[2] On the subject of centrosomes see O. Hertwig, *Allgemeine Biologie*, pp. 45–49, 195, &c., and E. B. Wilson, *The Cell*, pp. 50, &c., 74, &c., 101, &c., 208, &c., 354, &c.

[3] In the next chapter we shall have to examine Boveri's opinion regarding the importance of the centrosomes as fertilising elements. Cf. also Boveri, *Zellenstudien*, Part 4. 'Über die Natur der Centrosomen' (*Jenaische Zeitschrift für Naturwissenschaft*, 1901).

[4] 'Kritik einer modernen Hypothese von der Übertragung erblicher Eigenschaften' (*Zoologischer Anzeiger*, XV, 1892, No. 383).

[5] See also V. Haecker, 'Über den heutigen Stand der Centrosomenfrage' (*Verhandl. der Deutschen Zoologischen Gesellschaft*, 1894, pp. 11–32). This work is a standard one, but only for the state of knowledge on the subject when it was written.

Fol's famous 'Quadrille of Centres,' which the two halves of the male and female centrosomes were supposed to dance round the segmentation nucleus of the fertilised egg-cell, has proved to be erroneous. Strasburger and his followers[1] think that centrosomes are wanting in the higher kinds of plants, and in the division of Protozoa they are either altogether absent or of rare occurrence. They are present in the segmentations of the nucleus which lead to the formation of spindle-poles before fertilisation in the sun-animalculae (*Actinosphaerium*).[2]

If centrosomes were absolutely essential to the action of heredity, they would inevitably be present whenever cells divide, or at least whenever those cells divide which are connected with the preservation of the species, and this is not the case.

The whole question of the function of centrosomes is still involved in much obscurity, and Strasburger sums up the difficulties admirably in the following words:[3] 'At the present moment and at the present state of our investigations, I must content myself with the thought that individualised centrosomes disappear in the more highly organised plants. Why otherwise should we fail to trace them in any of the Pteridophyta and Phanerogams, whilst we succeed in the Bryophyta, (Mosses)? I am quite willing to agree with Flemming, who thinks it possible that in the future centrosomes will be found also in the higher plants. . . . No one as yet has been able to form a conclusive opinion regarding the origin, structure, function, persistence or disappearance of the centrosomes whilst the cell is at rest, nor is much known as to their distribution, although the reasons brought forward by Flemming for believing them to occur everywhere seem very weighty, when considered separately. Carnoy, however, takes a decidedly opposite view.'

We must refer our readers to Wilson and O. Hertwig for further information on the subject of centrosomes. These two writers have collected a quantity of material involving

[1] *Histologische Studien aus dem Bonner Botanischen Institut*, Berlin, 1897.
[2] O. Hertwig, *Allgemeine Biologie*, 1906, p. 189.
[3] 'Über Reduktionsteilung, Spindelbildung, Centrosomen und Cilienbildner im Pflanzenreich' (*Histolog. Beiträge*, 1900, Part 6, pp. 170, 171).

much research. Strasburger concludes with a reference to a theory based on recent research, according to which the centrosome is a mass of kinoplasm, not only serving the purpose of cell-division, but also concerned in the movement of the flagella and cilia of many cells and especially of the spermatozoa. O. Hertwig has adopted this view in his 'Allgemeine Biologie,' 1906, p. 122, &c.[1]

As Strasburger says in the above quotation, we still know very little as to the origin of the centrosomes. Some regard them as composed of the protoplasm of the cell; others, with more probability, think that they are a product of the nucleus. A new theory is that the centrosomes are not permanent constituents of the cell,[2] but are merely microsomes, representing a part of the achromatic framework of the cell or nucleus, which have a temporary importance during the processes involved in karyokinesis, inasmuch as such a microsome, by taking up its position at the pole of the nucleus in course of division, becomes the focus of the protoplasmic rays from which the spindle proceeds. If this theory is true, the centrosomes, and the attraction sphere which they form, are perhaps not the causes of nuclear division, but a result of the beginning of the process. Mitrophanow tried to prove this theory as early as 1894, in his 'Contribution à la division cellulaire indirecte chez les Sélaciens' (*Journal international d'anatomie et de physiologie*, XI).

Wasilieff thinks that the centrosome is only a temporary product of the joint action of nucleus and protoplasm;[3] and this theory is supported by experiments (to which reference will be made in the next chapter) by Morgan, Loeb and Wilson, who succeeded in artificially producing centrosomes in the unfertilised eggs of sea-urchins by means of salt solutions.

The astral rays of the nuclear spindle may all be formed of

[1] See also Ikeno, 'Blepharoplasten im Pflanzenreich' (*Biolog. Zentralblatt*, XXIV, 1904, No. 6, pp. 211-221). Recent investigations made by Russo and di Mauro in 1905, and by Gemelli in 1906, seem however to show that the flagella and cilia are not connected with the centrosomes, but with special basal bodies formed by a thickening of the cell-wall.

[2] Cf. the views expressed by Brandes and Flemming in the *Verhandlungen der Deutschen Zoolog. Gesellschaft*, 1897, pp. 157–162.

[3] 'Über künstliche Parthenogenesis des Seeigeleis' (*Biolog. Zentralblatt*, XXII, 1902, No. 24, pp. 758, &c.).

the achromatic nuclear framework, or of the spongioplasm of the cell-body, or they may have a mixed origin.[1]

We really know nothing of the cause producing this radiation, nor do we know what makes the V-shaped loops of chromatin split in half lengthwise.[2]

The only certain facts are that karyokinesis depends upon the partition of the chromosomes, and that the protoplasmic rays of the nuclear spindle determine the direction in which the chromosomes move. We are also convinced that great importance in the processes of evolution must be assigned to the persistence in the number of chromosomes contained in the somatic cells of individuals belonging to one and the same species, which number is most accurately preserved during karyokinesis by the longitudinal division of the chromatin loops. If we compare this normal form of mitosis with the method of dividing the chromatin in the germ-cells (cf. the next chapter) we shall lay still greater stress upon the importance of this point. We must, however, remember that the science of the present day is quite unable to tell us anything about the inner causes that produce the wonderfully complicated phenomena observed in indirect karyokinesis.

'We must acknowledge that we are not in a position to form any plausible theory at all as to the kind of reciprocal

[1] Cf. Henking, 'Über plasmatische Strahlungen' (*Verhandl. der Deutschen Zoolog. Gesellschaft*, 1891, pp. 29–36); also Yves Delage, *La structure du protoplasma*, 1895, p. 75; O. Hertwig, *Allgemeine Biologie*, pp. 192, etc.

[2] Cf. also H. E. Ziegler, 'Untersuchungen über die Zellteilung' (*Verhandl. der Deutschen Zoolog. Gesellschaft*, 1895, pp. 62–83.) A great number of theories have been advanced to account for the nuclear figures in karyokinesis, but none of them can claim a high degree of probability. This remark applies to Ziegler's own comparison of these figures with the lines of force in a magnetic field. Yves Delage (pp. 310–314) gives a good summary and criticism of the various theories regarding the causes of cell-division and of the formation of karyokinetic figures. He says with much truth of the comparatively best of these theories—that, viz., advanced by Henking—that it would be just as reasonable to see in the lion, the scales, and the fish of the zodiac a real lion, real scales and real fish, as to act like the propounders of these theories, and pretend that their mechanical representations of cell-structures and karyokinetic figures are real cell-structures and real figures. Another attempt, no more satisfactory than its predecessors, at explaining the mechanism of cell-division has been made quite recently by V. Schläpfer in his article 'Eine physikalische Erklärung der achromatischen Spindelfigur und der Wanderung der Chromatinschleifen bei der indirekten Zellteilung' (*Archiv für Entwicklungsmechanik*, XIX, 1905, pp. 107–128). It is an undoubted fact that many physical and chemical influences are at work in the process of karyokinesis, but we possess as yet very little real knowledge of their power to direct and further the biological aim of the division of cell and nucleus.

action existing between the cell-body and the nucleus. We have no foundations of facts upon which to construct a theory.' [1]

Whoever cares to see a summary and criticism of the various hypotheses regarding the mechanism of mitosis propounded by E. van Beneden, Heidenhain, R. Hertwig, Fol, &c., may refer to Wilson, 'The Cell,' pp. 100–111. His *résumé* of the whole discussion is as follows: 'A review of the foregoing facts and theories shows how far we still are from any real understanding of the process involved either in the origin or in the mode of action of the mitotic figure' (p. 111).[2]

The secret physiological causes that motive cell-division are unknown to the scientist, whose microscope reveals to him only their morphological action. They are a problem of cellular physiology, a problem containing in itself the whole mystery of life. We have now to trace this mystery in the phenomena of fertilisation and heredity, and we shall be able to approach its solution in Chapter VIII, where we shall deal with the processes of organic development.

[1] Korschelt and Heider, *Lehrbuch der vergleichenden Entwicklungsgeschichte* (Allgem. Teil, Part I, pp. 153, 154).

[2] See also Wilson's chapter on 'Some problems of cell-organisation.'

CHAPTER VI

CELL-DIVISION IN ITS RELATION TO FERTILISATION AND HEREDITY

(See Plates I and II)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