

# THE VARIOUS ASPECTS OF BIOLOGY

ESSAYS BY A BOTANIST ON THE CLASSIFICATION AND MAIN  
CONTENTS OF THE PRINCIPAL BRANCHES OF BIOLOGY

BY

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VERHANDELINGEN DER KONINKLIJKE NEDERLANDSE  
AKADEMIE VAN WETENSCHAPPEN, AFD. NATUURKUNDE

TWEEDE REEKS, DEEL LIV, No. 2

1962

N.V. NOORD-HOLLANDSCHE UITGEVERS MAATSCHAPPIJ  
AMSTERDAM

AANGEBODEN SEPTEMBER 1961  
GEFUBLICEERD MAART 1962

## PREFACE

This book is an attempt to render justice to the various points of view from where the organism may be envisaged. It is hoped that the exposition will lead to a critical insight in these points of view, and that this will ultimately find its expression in a better-balanced co-ordination of the different parts of the biological curriculum. The biology courses offered by our universities pay, as a rule, insufficient attention to the fundamental differences between the major aspects of the subject, and this is one of the principal reasons why the exposition so often impresses the students as irritatingly rambling. This applies to botany as well as to zoology, and although this book is written by a botanist and is intended in the first place for botanists, a zoologist too may perhaps find some inspiration in it. The author, however, does not lay claim to a more than superficial knowledge of this branch of biology, and begs to be excused for the shortcomings that his exposition on this account will possess. He does not pretend to omniscience in the field of botany either, and does not offer these essays as a handbook, but merely as a collection of classified remarks that may prove useful to those who set themselves to the compilation of such a work; he hopes that they may also be sufficiently inspiring to interest the ordinary student.

Biological research has doubtless made considerable progress in the last decennia, but the teaching of botany and zoology at our universities and agricultural colleges has merely marked time. We may safely say that the teaching of botany has undergone no important changes since the appearance, now more than seventy-five years ago, of Sachs' "*Lehrbuch der Botanik*". The well-founded criticism with which Tschulok in 1910 in his "*System der Biologie in Forschung und Lehre*" approached his fellow-biologists in order to open their eyes to the unsatisfactory state of the biological training at our universities, has apparently made but little impression. From an educational point of view some of the latest handbooks are, at any rate, even less adequate than their predecessors.

The unsatisfactory nature of these books is partly due to the fact that they are not in the first place intended for prospective biologists but for the propaedeutic instruction of medical, veterinary and pharmaceutical students: aspects that with more or less right are considered immaterial to the latter, are therefore neglected. This is wrong: a work that pretends to be a handbook of botany or zoology—several of them present themselves even as handbooks of "general" botany or zoology<sup>1)</sup>—should take

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<sup>1)</sup> The term "general" is in biological literature often used in opposition to "special". What we find in this case under the heading "special" botany or "special" zoology, appears to be a mixture of taxonomy and the kind of information on specific plants and animals that is better relegated to an encyclopedia. The

every aspect of the subject into consideration. The author, of course, does not deny that it may be desirable to have special guides for those students to whom botany or zoology are but auxiliary subjects, but such guides should lay no claim to the title of handbooks of (general) botany or zoology.

The teaching of these subjects at our universities suffers from the same inconvenience as the handbooks. It is customary that students to whom botany and zoology are major subjects, hear in their first year the same lectures as their medical, veterinary and pharmaceutical associates. That the agricultural students attend the same lectures, is, at least in so far as botany is concerned, an arrangement to which no objection can be raised, for these students doubtless need a very comprehensive knowledge of this subject. The requirements of the medical, veterinary and pharmaceutical students, on the other hand, are more restricted, and some of the aspects of biology are to them of little or no importance. When all these students are herded together in the same lecture room, this is a compromise which evidently must have drawbacks for all of them. Some of the aspects of biology, e.g. the morphological one, are in these courses nowadays almost completely neglected, with the result that the biological student is apt to develop a most regrettable bias. Even fully qualified biologists are at present often unaware of the wide gap which separates morphology from mere description of form and structure!

Our universities have in the long run lost a good deal of their efficiency. They are institutions of medieval origin, which in the time of the renaissance obtained a fresh impulse from the study of the classics, and reached their zenith towards the end of the eighteenth century. In most countries, however, they failed to realize the importance of the change brought about in the nineteenth century by the rapid development of the science of nature, and perhaps somewhat dazzled by the ever increasing number of their students, they did very little to stem the tendency to withdraw important parts of their task, like the higher technical training and the scientific study of agriculture, from the sphere of their influence. The faculty of science kept up, at least in theory, its connection with the exponents of subjects like theology, letters and law, with whom it has hardly any interests in common, and with medicine, from which it benefits but little, but lost its contact with technology and agriculture, i.e. with the application of its deductions. The easiest way to re-establish this contact would be a dissolution of the faculty and the severance of the ties by which it is bound to the university. In fact, it might on good grounds be argued that the university in its conventional form has had its time, and could better be dissolved in a number of special schools. The latter would probably offer more scope for a free development of the various branches of learning.

"general" part of such books pays no attention at all to taxonomy, and in this case therefore, the term "general" is obviously misapplied.



That the highest form of education should be provided by an institution in which all kinds of subjects are taught, is perhaps not more than a pleasant fiction. At the time the venerable old universities were young and vigorous, they were indeed places in which the student was instructed in everything that was considered worth knowing. In those days it was not uncommon that boys of fourteen or even younger, not rarely chaperoned by their private tutor, entered the university, and this entailed not the slightest inconvenience on them, for a sufficient familiarity with latin, the language in which the lectures were delivered, was practically all that was required. The real "universities" of to-day are not the institutions to which the name still clings, but the secondary schools, for it are the latter in which the pupils are equipped with a more or less encyclopedic knowledge. It is true that their standard is not always fully satisfying, but this might easily be remedied by extending their course with another year and, in some countries, by a better training of the teachers.

The special schools of the future would not be able to content themselves with the training of professional men and women, but like the universities of to-day they would also have to turn out research workers. The schools of technology should not merely train technologists of various description but also physicists, chemists, mineralogists and geologists, and in the same way the schools of agriculture should be equipped for the training of biologists. In my opinion these schools would suffice for this purpose. This does not mean that the existing departments of botany and zoology should be abolished, but merely that they should be removed to the more congenial environment of the agricultural school.

The old and time-honoured connection between biology and medicine is now almost completely obsolete. This judgement may perhaps raise protests, for although it will readily be conceded that decoctions, Spanish flies and leeches have had their time, it is on the other hand hardly disputable that medicine, at least in so far as it deals with physical diseases and injuries, is a form of applied biology. However, when we take into consideration that medicine, except when it occupies itself with parasites, which, after all, is but a minor part of its task, restricts its attention to a single species, we will have to admit that most aspects of biology, viz. taxonomy, ecology, biogeography and paleontology, are of little or no importance to the medical student. Therefore, we may safely say that he is not greatly interested in pure biology. It can, on the other hand, not be denied that the schools of medicine will always need biologists as teachers and research workers, but this demand would easily be satisfied by the remodelled schools of agriculture.

Agriculture is interested in a large number of living beings. It is true that Algae, Mosses and Ferns and several groups of animals, like Sponges, Coelenterata, Echinodermata and Brachiopoda, play but a subordinate part in its pursuits, and that the plants and animals in which it is inter-

ested, form in each group but a small fraction of the total number, but they are, at any rate, far more numerous than the animals and plants with which other occupations are concerned, and for this reason agriculture is more or less interested in all aspects of biology, paleontology perhaps excepted.

Biological products play a part in several branches of technology, but it is, as a rule, only a subordinate one. Biological technology, however, occupies in this respect a different position, but it seems to me that it would be more at home in the school of agriculture than in that of technology. It is true that the preparation of the biological products requires a good deal of machinery, but as agriculture itself is becoming more and more industrialized, the schools of agriculture will have to pay more and more attention to technological problems, and although the initiative in the construction of new machinery will have to be left at least partly to specialists who have received their training at the schools of technology, the schools of agriculture will have to provide sufficient instruction in these subjects to enable the student to understand the technical difficulties.

The removal of the biological training to a remodelled school of agriculture would also prove advantageous for another reason. It would enable the student to postpone the choice between the practical and the theoretical side of the subject, i.e. between agriculture and pure biology, until he is somewhat better acquainted with it, and has found out in what direction his inclination goes.

However, how desirable a reform of our universities and schools of agriculture may be, more urgently needed is a reform of the training of the future biologists. As stated above, it must be based on a critical insight in the various aspects of biology.

The form of these essays is perhaps somewhat unusual, and a few words of explanation may therefore be welcome.

In the introductory essay the reader may wonder why no recent classifications have been considered, the latest one being that of Tschulok, which dates from 1910. To this the author replies that it was not his intention to give a full account of the subject but that he confined himself to what in his opinion is of real importance. The more recent attempts have been neglected because they are not, like that of Tschulok, the outcome of a critical study of the problem, but were in a large measure inspired by a predilection of the proposers for their own speciality, genetics, sociology or whatever this happened to be.

Another peculiarity that may cause wonder and perhaps even some offence, is that but few prominent biologists have been mentioned by name. This is partly due to the fact that the author does not attach much value to the historical method of treatment, with regard to which he agrees with Karl Pearson, who qualifies it in his "Grammar of Science"

as "the death to all clear exposition", and partly to the circumstance that he originally intended to add three more essays to his book, viz. one on biogeography, one on paleontology, and one on the history of biology; in the last-named one he hoped to render justice to the merits of these men. In order to keep the size of the book within reasonable limits, this plan was abandoned.

The facts that are discussed, have almost all become common property, and as they are to be found in all the larger handbooks, it was not deemed necessary to give references to the literature. Their interpretation, however, may differ from the commonly accepted one, but in this respect too the author lays no claim to originality. Even though the views expressed in this book may sometimes, e.g. in the essay on morphology, look rather revolutionary, most of them have already been expressed by others.

It is perhaps not superfluous to add that the length of the various essays should not be taken as a measure of the importance that is to be attached to the subject with which they are dealing. Some of them enter more into details. This applies e.g. to the essay on heredity, and in this case it is due to the author's predilection for an exposition that could be based on a scientific theory.

I may conclude this introduction perhaps with a few remarks on the origin of this work.

What I have tried to express here, may be regarded for a large part as the outcome of reflections that arose in my mind during the years I lectured on general botany at the University of Pretoria, and, apart from some minor additions and emendations, it was written during the last year of the second world war and the months immediately following it, i.e. in a period when lack of material compelled me to interrupt the taxonomic studies in which I was engaged at that time.

After the war I tried to find a publisher, but as I did not succeed, I put the manuscript away, and decided to deal in a series of separate papers with some of the subjects on which my opinion differed more or less markedly from the generally accepted one. This led to the following publications.

1. "Is it necessary to assume that part of the hereditary factors have their seat outside the nucleus?" in *Proc. Kon. Ned. Akad. v. Wetensch., Amsterdam, Ser. C.* 54: 433-439 (1951).
2. "A re-examination of Cesalpino's classification" in *Acta Bot. Neerl.* 1: 580-593 (1953).
3. "Linné's views on the hierarchy of the taxonomic groups" in *Acta Bot. Neerl.* 2: 242-253 (1953).
4. "Over morfologie, taxonomie en ontwikkelingsfysiologie" in *Vakblad voor Biologen.* 33: 101-108 (1953).

5. "The concepts on which a morphology of the Vascular Plants should be based" in *Acta Bot. Neerl.* 5: 122-134 (1956).

6. "Specific and infraspecific delimitation" in *Proc. Kon. Ned. Akad. v. Wetensch., Amsterdam, Ser. C.* 62: 91-110 (1959).

My views on the restricted value of phylogenetic speculations had already been expressed in some previously published papers, but they were expounded in a more comprehensive way in:

7. "Some comments on the doctrine of evolution" in *Proc. Kon. Ned. Akad. v. Wetensch., Amsterdam, Ser. C.* 62: 460-471 (1959).

However, as these papers deal only with subordinate points, and as the aim I had in view when I wrote this book, is not reflected in them, it seems to me that the publication of the whole work may still serve a useful purpose, even although it is perhaps no longer in every detail entirely up to date. Since the appearance in 1910 of "Das System der Biologie in Forschung und Lehre" by Tschulok, no work of this kind seems to have been published, and as on account of the ever proceeding specialization of the biologists, it will become increasingly difficult to find an author who is not only sufficiently interested in the aspects of biology that are of no direct importance to himself, but who is also willing to undertake the writing of such a book, it seems to me that the publication of this work is fully justified.

## RECONNAISSANCE

A well-known Dutch botanist, who in the beginning of this century occupied a chair at one of the larger universities in his country, used to open his yearly course for the younger students with a pronouncement in this vein: "To explain to you in a few words what the name botany really stands for, is impossible to me, but when you attend this course regularly, you will by the end of the year have obtained some idea of the problems in which this science nowadays is interested." As the lectures of this professor were carefully prepared, the material critically sifted, and all new discoveries scrupulously taken into account, it is not improbable that the intended result really was obtained. However, that a course with such a modest aim should have given insight in the points of view from where the isolated facts are to be considered, and in the way in which they must be put together to form a logically justified whole, i.e. in the science of botany, seems doubtful, and I am afraid that the more critical students must have felt disappointed.

The attitude, or should I say the restraint, which finds its expression in the pronouncement quoted above, was at that time by no means unusual, and proves that the aversion for scientific abstraction provoked by the superficial speculations of the nature philosophers who flourished in the first half of the preceding century, had not yet fully subsided. The successful investigations of the group of gifted and critical investigators who towards the middle of the nineteenth century were preparing the way for a new and more truly scientific study of the natural phenomena, had engendered in the rising generation of those days a mighty outburst of enthusiasm, and the respect with which these elders were regarded, is doubtless responsible for the fact that their disciples followed them not only in their methods of investigation but also in their dislike for the prevailing schools of philosophy, which was often extended to philosophy as a whole and even to the most modest attempts at generalization. The accumulation of new facts seemed to many of them the only achievement worth considering, and even attempts to elucidate the real aim of the study of nature were regarded askance. However, this exaggerated worship of the concrete fact was bound to create distress, for it led to an accumulation of knowledge in which it became more and more difficult to find a way.

To create order in such a chaotic accumulation of knowledge it is necessary to investigate from what points of view the material may be considered, and what aims the botanist in various instances has in view. The importance of a study of this nature should not be underestimated, and in my opinion the students should already at the commencement of their study be acquainted with its results. This first reconnaissance, it



is true, will of necessity be superficial, but it will lay the foundation on which by and by, as the student obtains the mastery of a more extensive collection of facts, a more satisfactory structure may be erected. Such a preliminary orientation is the more desirable as biology, on account of the fundamental differences between the points of view from where the facts are considered, should not be regarded as a single discipline<sup>1)</sup> but as a group of disciplines, and as it is a matter of common experience that the various points of view do not appeal to everyone in the same measure, the student should already at the beginning of his academical study be enabled to make a choice in accordance with his natural inclination. However, before entering into a discussion of the various standpoints from where the biological facts may be viewed, we will first of all have to find out whether a satisfactory definition can be given of biology itself. As the latter owes its origin to a fusion between botany and zoology, this is perhaps also the best place to explain why this book is said to deal with biology whereas its contents are mainly of a botanical nature.

It is not possible to give a logically justified delimitation either of botany or of zoology. The subdivision of biology, the science of the living beings, into botany and zoology rests on the distinction of the living beings in plants and animals, which for a long time was accepted as perfectly legitimate. The objections against the naturalness of these groups, however, have continually increased in number and in weight, and it is now no longer possible to ignore them. We will have to admit that it is mostly out of conservatism or, when this is realised, out of utilitarian considerations, that the division of biology in botany and zoology is maintained. By accepting a larger number of groups we could doubtless arrive at a more satisfactory subdivision, but as this would cause practical difficulties, it is not to be expected that the time-honoured but in fact since long antiquated division in botany and zoology will soon be given up.

Botany and zoology are both sciences with a long history, and as they originally confined their attention to the larger and more conspicuous plants and animals, their spheres of interest possessed hardly any points of contact, and they could accordingly for a long time develop in nearly complete independence. Even in our own time this particularism has not yet fully disappeared. This finds its explanation partly in the enormous number of organisms: the impossibility to survey this, explains how even now in botany as well as in zoology often limitations are accepted that go much further than the use of the names botany and zoology would suggest. In the field of morphology botanists appear to confine themselves almost entirely to the Vascular Plants, and zoologists to the Vertebrates, and for easily comprehensible reasons in the fields of physiology and ecology

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<sup>1)</sup> The somewhat archaic term "discipline" for an independent part of the curriculum would seem to deserve preference above the commonly used "subject" because it emphasizes the academic character of the subdivision.

too these two groups have long played the principal part; it must, however, be admitted that in the last decennia other groups of living beings have obtained a share in the attention. At any rate, where such arbitrary restrictions were for a long time accepted without protest, it is certainly not surprising that but little attention has been paid to the difficulties by which the delimitation of botany and zoology is beset. As my argumentation will be applicable to both, it is at this juncture unnecessary to enter into these difficulties. From now on I will therefore deal with biology as a whole. However, before entering into our main problem, the subdivision of biology according to the points of view that so far have played a part in the study of living nature, we will have to find out whether the group of living beings itself can be delimited in a satisfactory way. It is by no means inconceivable that the delimitation of this group too might offer difficulties, and for those who believe in the existence of gradual transitions between plants and animals, it is perhaps not unnatural to assume the presence of similar transitions between living and non-living nature.

The belief that no sharp line can be drawn between the living and the non-living products of nature, is wide-spread in biological circles. It rests on the conviction that each group of natural products is connected by transitions with one or more of the other groups. This conviction is already of very ancient date, and found in more recent times its expression in Leibniz' well-known aphorism "*natura non facit saltus*" (nature makes no jumps). In the field of biology it formed the foundation of the older theories of evolution, but here it lost a good deal of its former significance when a better insight into the nature of the differences between the lower taxonomic units was obtained. The study of the phenomena of heredity has convincingly demonstrated that the so-called gradual transitions by which, according to the earlier evolutionists, allied species and varieties would be connected with each other, are in reality non-existent, and as therefore the absence of transitions in the groups of lower rank can no longer be doubted, there is obviously no longer any reason to assume their presence in the case of the groups of higher rank, where, in fact, their presence has always been problematical. It has already been stated that the difficulties with which we are confronted in the delimitation of plants and animals, are not due to the presence of transitions, but to the entirely unjustified wish to restrict the number of main groups to two, and that these difficulties can be overcome by accepting a larger number of groups. Whether it would be desirable to distinguish also more than two groups among the products of nature as a whole, is a problem into which we need not enter. Although in passing we may draw attention to the fact that it is impossible to formulate a definition for what we are accustomed to call the non-living products of nature, we will confine ourselves here to the question whether the group of living beings can be defined in a satisfactory way.

From the considerations of the preceding paragraph the conclusion may

be drawn that there are no a-priori arguments by which we would be compelled to accept the existence of transitions between the living beings and the other products of nature, and that it is therefore more plausible to accept the evidence at its face value and to regard the absence of such transitional forms as the expression of a fundamental difference. It is perhaps worth recording that most taxonomists are convinced that the demarcation lines, which in nearly related forms are not always easily observable, become gradually more marked when we pass on to groups of a higher order. However, this argument is less valuable than one might perhaps be inclined to assume, for no logical grounds can as yet be adduced for this rule, which after all might prove to be an unjustified generalization. The counter-argument that several of the Angiospermous orders are less easily distinguishable than the majority of the families that belong to them, has, on the other hand, but little value, as the naturalness of these orders is often questionable. However, it is time to leave these a-prioristic considerations and to turn our attention to what has been advanced in the guise of proof.

The existence of transitions between the living beings and the other products of nature might be regarded as sufficiently established when it could be shown that living beings might develop out of the latter. In ancient times most people were firmly convinced that all kind of living beings with a more or less hidden mode of life, like worms and insects, and even more easily observable ones, like mice and toads, might develop in this way, but by and by it was recognized that none of the organisms with which we are sufficiently familiar, arise out of non-living substance, and when Pasteur had shown that the Bacteria too, the smallest and most elusive of all living beings, develop only in such places where one may suppose that their germs are already present, it looked as if the possibility of this so-called "spontaneous generation" or "heterogenesis" need no longer be taken seriously. This conclusion is not fully justified, for the experiments of Pasteur merely prove that "spontaneous generation" does not occur under the circumstances under which the experiments were taken, not that it is excluded under all circumstances. It has accordingly in later years not lacked in attempts to obtain "spontaneous generation" by changing the conditions of the experiments, and some of the investigators even claimed success, but so far they have not been able to overcome the scepticism of their critics.

The existence of transitions would also be proved when attributes that are considered characteristic for the living being, could be found in some of the non-living products of nature. Apart from the living being's peculiar intricacy of structure, which is difficult to define, the following attributes must be considered to be of paramount importance: 1°. the faculty to grow and develop by the aid of substances built up by the organism itself out of constituents derived from the medium in which it lives; 2°, the faculty to carry out movements or, more generally, of doing



work by the aid of energy obtained by the decomposition of substances which, as a rule, have been prepared either by themselves or by other organisms, the decomposition taking place at temperatures varying, roughly estimated, between  $0^{\circ}$  and  $55^{\circ}$  C; and 3°. the faculty to multiply.

When under the influence of the doctrine of evolution biologists became more and more inclined to doubt the fundamental nature of the differences between living beings and the other products of nature, the conviction that it ought to be possible to trace these transitions somewhere, began to gain ground. For some time it looked as if this opinion received support from the phenomena of movement and growth observed in the so-called fluid crystals and in the plant-like structures that owe their origin to a precipitation membrane formed between two salt solutions of different composition and strength, and which continue to expand because the semi-permeable membrane after a while bursts and allows part of the stronger solution to escape and form a new membrane at its surface. In later years the viruses have often been regarded as such transitions. In the first mentioned instances the way in which growth and movement are brought about, is obviously so entirely different from the way in which these phenomena are engendered in the living organism, that it seems superfluous to dwell on these rather far-fetched analogies. The viruses, however, deserve a closer inspection.

Viruses are products that in certain diseases can be isolated from the affected organism, and of which a small amount proves to be sufficient to induce the same disease in a healthy one: from the living beings by which diseases are brought about, they differ in the submicroscopical size of the particles of which they consist, and also because they can not be cultivated outside the body of the host. From the fact that a minute amount of virus suffices for an infection, whereas afterwards a much larger quantum can be isolated from the infected organism, the conclusion has been drawn that the virus is able to multiply inside the latter. It would therefore possess two of the three attributes that were recognized above as characteristic for the living organism, viz. the faculty of growth and that of multiplication. This conclusion, however, is overhasty, for it is by no means sure that the increase in the amount of virus is due to growth and multiplication of the original units. It is not at all unthinkable that the new virus units are produced by the diseased organism, and that the virus therefore forms a part of the latter. Some viruses have been obtained in the crystalline state, and of these it is even exceedingly improbable that they would be able to increase in the same way as living beings. The increase of the living being is based on the assimilation, i.e. the absorption and transformation, of food, a process that demands a more complex substrate than we may expect in a crystal, which is to be regarded either as a combination of identical molecules or of ions arranged in a regular pattern. As there seems to be no reason to assume a fundamental difference between those viruses than can be obtained in the crystalline state

and the other ones that as yet have not been obtained in this form, we may safely state that the viruses also are too far removed from the living beings to be accepted as transitions between the latter and the other products of nature. When we abide by the attributes enumerated above, the delimitation of the living beings appears to offer no difficulties.

It is not necessary to enter into the subdivision of biology in subjects that occupy themselves with groups of a more limited extent than those of the plants and animals, i.e. in subjects like ornithology, herpetology, entomology, bryology, mycology and bacteriology; and the regional and chronological study of the flora and fauna too may be left out of consideration. As we can restrict our attention to any of the groups that have been recognized by the taxonomists, to the living beings of any region wheresoever it may be found, and to the fossil remains of whatever geological period, the subjects of this kind correspond in number to the groups that the taxonomists consider of sufficient importance to be provided with a name, to the number of regions in which, for one reason or another, geographers or sociologists are interested, and the number of fossiliferous strata accepted by the geologists. As the points of view from where the material is considered, do not differ in these cases from those that play a part in general biology, these subdivisions are not of fundamental importance. The practical value of this kind of specialization, on the other hand, should not be underestimated, for restriction of the field of our activities is both in research and in education often urgently needed.

As the living beings show in structure and habit an extraordinary range of diversity, the number of terms required to account for this diversity must obviously be very large. The elaboration of this terminology is a necessary preamble, its continual extension and perfection an important accessory to the proper work of the biologist. In this respect we are especially indebted to the phytographers and zoographers, i.e. to those biologists who have made it their task to enlarge our knowledge by describing hitherto unknown plants and animals and by correcting and extending the descriptions of organisms with which we are already more or less acquainted.

Some of the descriptive biologists restrict their attention to those structures for whose study the use of the microscope and eventually a special sectioning and staining technique are required. This field of study is called micrography, and comprises histology, i.e. the study of those parts that consist of similar cells or aggregates of cells, cytology, which occupies itself with the structure of the various kinds of cells, and caryology, whose study object is the cell nucleus and the changes the latter undergoes in the course of its development. The description of the early stages in the development of the organism is often set apart as a special subject called embryology, and that of the monstrosities, the teratology is also given a place of its own.

In dealing with the subjects enumerated in the preceding paragraph

our first and foremost task is to draw up suitable descriptions, and for this reason they may all be included under descriptive biology. We will not discuss them, because when no more is wanted than a serviceable description, it is obviously not necessary to place oneself on a special standpoint. This does not mean that in these descriptions exclusively neutral terms are used. The introduction of some of the more general morphological and ecological terms means in many instances a marked simplification. They are, however, not indispensable, and as they introduce a hypothetical element in the descriptions, their use requires more circumspection than that of the neutral terms.

Before definitely turning away from descriptive biology it is perhaps not superfluous to add that in dealing with the subjects enumerated above it is not necessary to confine our activity to mere description, but that we may also try to analyse and classify the material from a definite point of view. In that case these subjects are merged in one or another of the main disciplines to be dealt with below. The discipline that in this connection occupies the most prominent place, is morphology, and in dealing with the latter we will therefore have to revert to them. In order to be quite clear with regard to their dual nature, it might be advisable to make a distinction between histography and histology, cytography and cytology, caryography and caryology, embryography and embryology, teratography and teratology, using the suffix-"graphy" when mere description is meant, and the suffix-"logy" for the more scientific treatment. In most of these subjects the latter plays as yet but a subordinate part.

The subdivisions with which we have occupied ourselves so far, merely aimed at a restriction of the field of study, and accordingly their most characteristic feature is that each subject is either entirely included in another one, as caryology in cytology, and the latter in histology, or entirely free from the others and in juxtaposition with them, as the study of the New Zealand flora stands beside that of the flora of Australia and of South America, and as micrography stands beside macrography. In the subdivisions with which we are now going to deal, this is quite different, for here the distinction rests on differences between the points of view from where the facts are judged, and here it is therefore by no means uncommon that the same fact, although in a different setting, turns up in two or more of the subdivisions.

As every time the facts are envisaged from a new point of view, a new biological discipline is born, it is obviously of the utmost importance to obtain a clear insight into the nature and the number of these points of view. It is, however, not my intention to give a historical survey of the gradual increase of their number and of the various classifications that have been evolved in the course of time. Those who are interested in this development, may find the necessary data in a book published in 1910 by Tschulok under the title "*das System der Biologie in Forschung und Lehre*" (Fischer, Jena). I will confine myself to the main points.

The classifications I have in view, appear to be of two kinds: some of them are a-prioristic, others empiric. The first group goes out from the hypothesis that it must be possible to construct a general scheme for the subdivision of science as a whole and of each science separately, in which, because it is based on a general principle, each subject finds its proper place. Schleiden and Haeckel appear to have been the first biologists to apply such a scheme to biology; in later years some more of these classifications have been proposed. They start nearly all from the supposition that the attributes of the living beings can be reduced to two categories, viz. form and function. Schleiden as well as Haeckel identified these two categories by the aid of rather superficial arguments with the categories matter and force on which their main classification of the natural sciences was based. It does not seem necessary to discuss either these arguments or the classification proposed by these authors, as form and function are obviously not the only attributes of the living beings which deserve our attention. Moreover, form plays only a very subordinate part in morphology<sup>1</sup>), but a very important one in ecology, which by these authors was included in physiology, and it is also an object of study for the physiologist *sensu stricto*, viz. when he directs his attention to the causal relations in the organism's development.

To a certain extent the a-prioristic classifications are comparable to the artificial systems that played for a long time an important part in the classification of plants, for these systems too were based on attributes, or characters as they are usually called by biologists, to which on account of a far too superficial study a preponderating value was assigned. Just as these systems had to be given up when it became clear that the choice of these characters had been wrong, and that the attempts to justify their choice by means of arguments derived from the supposed significance of the characters to the life of the organisms are of no value whatever, the a-prioristic classifications of the sciences will, for the time being, have to withdraw in favour of the empiric ones. When in the long run one of the latter will prove to be more serviceable than all the others, it will perhaps be worth while to attempt a thorough analysis of the differences between the points of view on which it has been based, and then the elements for a fully logical system may perhaps be found. It is possible, although by no means certain, that the points of view whose diversity led to the subdivision of biology, will prove to play a part in the whole realm of natural science, but the study of this problem lies outside the scope of this essay.

As examples of empiric systems I will discuss the second of the two classifications drawn up by A. P. de Candolle and that of Tschulok. The

<sup>1</sup> Form is, as I will point out further on, not in the first place an object of study for the morphologist, but for the ecologist. The morphologist occupies himself with the "plan" on which the organism and its parts are built, i.e. with the position the various parts occupy with regard to each other.



system of de Candolle dates from 1832, and has with slight modifications maintained itself up to the present day. That of Tschulok was published in 1910, and takes into account some points of view that were new at that time or to which previously insufficient attention had been paid. However, as this system too is not fully satisfactory, I will end my discussion with the exposition of a new one.

The system of de Candolle was intended for the subdivision of botany, but can be applied, as the author remarks, to zoology too, and is therefore suited to biology in general. It distinguishes three kinds of subjects: main subjects, accessory ones, and applications. The first group comprises: 1°. organography, which in his delimitation consist of the terminology destined for the description of the outward form, morphology, and part of what is now called ecology, 2°. physiology, which is here not sharply differentiated from ecology, and 3°. methodology or taxonomy. The accessory subjects are also three in number, viz. bio-geography, paleontology, and the history of biology. The applications comprise agronomic biology, pharmaceutical biology, and biological technology.

The applied branches of biology confine their attention to data pertaining to those living beings that are either directly or indirectly of importance to man, and are therefore mere abstracts from the main subdivisions. As they do not differ fundamentally from the latter, they need not be discussed.

In the accessory subjects the characters of the living beings play no part of any importance. To the bio-geographer and the paleontologist the living beings and their remains are not fundamentally different from other products of nature. They are but the means to arrive at a certain end, which in the case of the bio-geographer is to round off our knowledge of the surface of the earth, and in that of the paleontologist the recognition of the successive strata by means of the organic remains that are found in them. The history of biology too is not interested in the living beings themselves, but merely in the considerations to which their study has led. These three subjects therefore can not be regarded as parts of biology proper. They are only in so far connected with the latter as this provides those who occupy themselves with these disciplines with the material they require for their study. The points of view from which they classify their material belong to other sciences, viz. to geography, geology, and history. That the votaries of these disciplines are often at the same time and even in the first place biologists, will be no matter of surprise, but is for the classification of these subjects of no importance.

The system of de Candolle had for a time to give way to that of Schleiden, in which only two subjects are distinguished, namely 1°. a subject which he calls morphology, but which is in reality a mixture of descriptive biology and ecology, and 2°. physiology. This system owed its success mainly to the great authority of its propounder, but as it was based on a wrong a-prioristic standpoint, and proved to be unserviceable,

it was in the long run unable to maintain itself against that of de Candolle. The circumstance that the latter underwent but slight changes, proves that it satisfied the needs of the time. The most serious objection which in my opinion can be raised against it, is that it puts the terminology dealing with the outward form under morphology, but as it was left in that position by almost all subsequent authors, which means that the unsatisfactory nature of this decision was almost generally overlooked, there is no reason to censure de Candolle too severely for this mistake. As a further excuse it may be mentioned that part of the terms used by him indubitably belong to the field of morphology. In his first system de Candolle had inserted this list of terms in the section dealing with taxonomy, and as the greater part of the terms is used only by taxonomists, this was doubtless a better place. However, it is clear that every branch of science must have its own terminology, and that similar lists of terms might therefore be given in each section of the system.

Tschulok's system allows no special place to applied biology, and neglects de Candolle's distinction of the remaining subjects in main and accessory ones. The first decision will hardly raise protests, but the second is, in view of the fundamental difference between these two groups, a step in the wrong direction. Tschulok recognizes seven subjects: 1°. taxonomy, which he defines as the classification of the organisms according to the degree of similarity; 2°. morphology, of which he says that it studies the laws regulating the form, which is, as I will show presently, a wrong definition; 3°. physiology, or the science of the processes taking place in the living organism; 4°. ecology, which he describes somewhat lamely as the science of the adaptations; 5°. bio-geography; 6°. paleontology; and 7°. a subject to which he applies the name "genetica", but which is usually called phylogeny. The term "genetica" or "genetics" is by biologists generally reserved for the study of the phenomena of heredity: in this sense it was, I believe, used for the first time in 1906 by Bateson. It is possible that this had escaped Tschulok's attention, but as he once more employed the term in his own way in an article that appeared in 1933 in the second edition of the "Handwörterbuch der Naturwissenschaften", it looks more probable that he disagreed with Bateson's use of the term, possibly because it had already been employed in a more general sense. This objection, however, may also be raised against Tschulok's own use of it, for this too is a restriction of the original meaning. The study of what at present is called "genetics", i.e. of the phenomena of heredity, was not recognized by Tschulok as a separate discipline, but this should not surprise us too much, as it was at that time still in its infancy. However, that it is also entirely neglected in Tschulok's article of 1933, strikes us as rather anomalous.

Tschulok's seventh subject, which I will indicate in the usual way as phylogeny, is in my opinion better omitted. It aims at the construction of a general genealogical tree, i.e. a genealogical tree in which at least a

large part of the organisms, living and extinct, would find a place. However, as it is impossible to construct a genealogical tree if we lack the means to detect the ancestors, it is highly improbable that we will ever make the slightest advance towards this end. The supposition that the ancestors of the recent animals and plants should be represented among those fossil remains of which we have cognizance, already betrays an unpardonable optimism. Most of the ancestors will doubtless have disappeared without leaving a trace. However, even if this were not so, it would be of little avail, for it would be impossible to recognize them. The phylogeneticists assume that there exists a certain family resemblance between the ancestors and their descendants, but this assumption does not take into account that genetic or blood relationship is not necessarily expressed in the degree of similarity. Our experience in the field of genetic relationship is based on the outcome of hybridization experiments, and is therefore restricted to nearly related individuals. It is, of course, by no means certain that the results obtained in this way are generally applicable, but as they are our only hold, we are obliged to take them into account. They teach us that similar individuals may arise out of crosses between different pairs of parents ( $AaBb$  may arise as well out of a cross between  $AABB$  and  $aabb$  as out of a cross between  $AAbb$  and  $aaBB$ ), whereas on the contrary dissimilar individuals may be the result of the union of parents showing the same type:  $Aa \times Aa$  gives  $AA$ ,  $Aa$  and  $aa$ . In all these cases we look in vain for the expected parallelism between genetic relationship and the degree of similarity, i.e. taxonomic relationship, and as in the only instances where a study is possible, no definite connection appears to be present, there is obviously no reason to assume its presence elsewhere. In types that are more fundamentally different than those that are used in hybridization experiments, it is, moreover, impossible to find out in which way the common characters have been brought about. That they should always be inherited from common ancestors, is evidently a mere hypothesis. A direct way to find the ancestors is therefore obviously non-existent.

Efforts to reconstruct the genealogical tree by the aid of indications obtained in an indirect way are also doomed to failure. In this case an appeal is made to rules like Haeckel's "fundamental law of biogenetics", Dollo's "principle of the irreversibility of the evolution process", and the connection that according to Willis should exist between the age of the taxonomic unit on the one hand and either the size of the area occupied by it or the number of its representatives on the other. None of these so-called rules, however, is based on experience, and as none of them can ever be tested, they possess no real scientific value. The genealogical trees of the phylogeneticists are, in fact, mere products of phantasy. It can, of course, not be denied that they give an easily surveyable illustration of the taxonomic relationships, but we should always bear in mind that the chronological sequence expressed by them represents but a single

possibility out of a very large number, and that they are therefore always more or less misleading. On account of this arbitrariness it does not seem right to regard phylogeny as a branch of scientific biology.

In comparing the remaining six subjects of Tschulok's classification with the main and accessory subjects of de Candolle, it appears that one of them, ecology, is new, whereas one of the latter's subjects, the history of biology, has been omitted.

The history of biology is excluded because it does not deal with the organisms themselves, but with the results to which their study has led, and with the investigators who played the more important parts in its development. This is right, but in this respect de Candolle's other accessory subjects, viz. bio-geography and paleontology, are in a similar position, for in these disciplines too the organisms themselves play but a subordinate part. The bio-geographer must know that the names he uses in his exposition, indicate organisms or groups of organisms that in one way or another differ, but in what way they differ, is of no importance to him. In discussing de Candolle's classification I expressed this by saying that the bio-geographer has to receive his material from the biologist. The historian who studies the history of biology, is in the same position, for he too has to rely for his material upon the biologist. In tracing the development of a biological conception he is, moreover, not interested in the biological value of the successive stages, but in the influence they have exercised. The history of biology therefore belongs to those subjects that on account of the way in which the facts are considered, pertain to another circle of scientific interest, but which possess a strong biological flavour because their material is of biological origin and because most of their devotees are biologists; the exclusion of this one discipline therefore goes either too far or not far enough.

The data on which at a later date ecology was to be based, were dealt with by de Candolle partly under organography and partly under physiology. At a slightly later period, e.g. in the work of Alph. de Candolle, they are included mostly under the heading plant-geography. Since then, however, the conviction that they deserve a place of their own, has gradually grown in strength, and when Tschulok developed his classification, it seemed time to raise ecology to the rank of a major subject. Tschulok defines it as the science of the adaptations. With adaptation he does in this case not mean the process of adjustment, but merely the fact that the organisms fit into their environment, i.e. that they develop and multiply in the latter in a normal way. The use of the term "adapted" for this condition deserves no recommendation, as it is bound to suggest an actual process of "adaptation", and as there seems to be no reason to assume that the actual "adaptations" of the individual organisms are ever inherited, the fact that the organism as a whole fits into its environment, can obviously not be ascribed to actual "adaptation".

As development and multiplication, the main processes with which the



ecologist is concerned, depend upon an adequate food supply, and are therefore in their general aspect physiological problems, ecology is evidently based on physiology. In contradistinction with the latter it deals only with organisms living in their natural environment: to the physiologist the naturalness or unnaturalness of the environment is entirely irrelevant. Ecology is, moreover, not interested in the general aspect of the life phenomena, but only in the special character the latter assume in the various kinds of organisms. The analysis of the phenomena of life therefore recedes into the background in order to make place for a study of their width of variation, for it is the latter that decides the choice of the environment in which the species will be able to maintain itself. When the interest shifts from the organisms to the character of the environment, we leave the field of ecology and enter that of ecological bio-geography. The latter divides the surface of the globe on account of differences in climate and soil in a number of regions, and uses the communities that develop in these regions, as a means to recognize them.

Ecology does not confine its attention to the relations between the organisms and their non-living environment, but extends it to the relations between the living beings themselves, no matter whether the latter are of the same or of a different kind. The basis on which these relations rest, is in many instances not fundamentally different from that on which the relations between the living beings and their non-living environment are founded. The phenomena of competition and symbiosis e.g. may for the greater part be reduced to reactions on the favourable or unfavourable changes that are brought about in the environment by the activity of the organisms themselves. However, not all relations between the organisms seem to fit into this scheme.

An ecological problem that can not be reduced to a question of food supply, is that of the transport of spores, gametes, fruits and seeds. It is worth noting that the individual organisms by which these organs of dissemination are produced, experience, as a rule, neither advantage nor disadvantage from their transport, and that there seems to exist in this case therefore no direct connection between the survival of the individual and that of the species. However, if we realize that these organs of dissemination are necessary links in the chain of individuals that together form the surviving species, it seems allowed to regard them as a special kind of individuals alternating in this chain with the ordinary ones. In the ecological sense spores, gametes, fruits and seeds are individuals whose survival up to the time they give rise to new individuals of the ordinary type, is just as necessary for the maintenance of the species as the survival of the ordinary individuals up to the time at which they produce their organs of dissemination. The life of this particular kind of individuals is, however, as a rule but short and very often more or less latent, and for this reason the question of the food supply recedes here into the background.

As an example of such a transport problem we will deal in some detail with the transport of pollen by animals. With regard to the transport of their pollen some plants, as is well known, are in a large measure dependent upon the presence of particular pollinators, mostly insects. Their dependence upon these animals is entirely different from the dependence of a parasitic plant upon its animal host. The relation between the latter is once more a question of food supply, and belongs therefore in the same compartment as that between a phytophagous animal and its food plants. As we are well acquainted with relations of this kind, they do not impress us so strongly as the fact that a particular kind of insect is enticed to enter a particular kind of flower, and that the latter is in this way pollinated. This relation strikes us as rather mysterious, for the pollination is to the insects themselves of no direct importance, and indirectly only in so far as it enables the plant species to maintain themselves so that in future too they will continue to provide the insects with pollen or nectar. Sprengel, to whom we owe the first comprehensive treatment of the devices by which pollination is ensured, called his book "Das entdeckte Geheimniss der Natur im Bau und in der Befruchtung der Blumen", by which he must have meant that it dealt with this mysterious interaction between insects and flowers, to which Koelreuter had drawn his attention<sup>1)</sup>. Sprengel himself gave a teleological interpretation of this interaction, and he was doubtless firmly convinced that the latter provided a satisfactory explanation of this mystery. Darwin, who also showed a keen interest in these phenomena, tried to remove the mysteriousness by describing the situation as the result of the selection of deviations that accidentally went in a suitable direction. The supposition that the deviations between which a choice is made, should be accidental, is arbitrary and neither better nor worse than the opinion that they are directed towards a definite end; the last-mentioned standpoint is that of the vitalists, and does not materially differ from the one occupied by Sprengel, who ascribed the origin of the various devices to single acts of creation. In considering Darwin's interpretation we should bear in mind that terms like accidental and purposeful have a well-defined meaning only when they are applied to our own conscious actions. With regard to the aims that "nature" may have had in view, we are completely in the dark, and we possess therefore no means to make out whether the observed phenomena are purposeful or accidental.

After what I have said in the preceding paragraph, it needs no special

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<sup>1)</sup> Koelreuter says with regard to this interaction: "Gewiss ein jeder anderer, der vor mir diese Betrachtungen angestellt hätte, würde sie längst entdeckt, und sich und allen Naturforschern von diesem Geheimnisse der Natur den Vorhang weggezogen haben". As Verne Grant recently has shown (in *Torrey* 76: 217-222, 1949) Koelreuter was indeed not the first to note the importance of insects for the process of pollination. More than ten years previously Arthur Dobbs had already published observations leading to a similar conclusion.

emphasis that I do not attach much value to Tschulok's opinion according to which ecology studies a teleological or final relation, and physiology a causal one. Moreover, if we define ecology as the discipline that occupies itself with the phenomena aiming at the maintenance of the species, we might define physiology as the discipline that deals with the phenomena aiming at the maintenance of the individual. However, as no individuals are known to have outlived a short span, and as countless species already have disappeared, it certainly does not mean much when we say that the physiological phenomena aim at the maintenance of the individual, and the ecological ones at the maintenance of the species! For this reason it seems more appropriate to avoid these teleological formulations, and to stick to non-teleological ones. We may say e.g. that physiology studies the actions of which the individual is capable, ecology the phenomena that are shown by species living in their natural environment.

Above I have already dealt with some branches of biology to which in a classification that is based on the fundamentally different points of view from where the material may be considered, no independent position can be allocated. They were partly sections dealing with particular groups of organisms or with the flora or fauna of particular regions, and partly preliminary stages in the development of science confining themselves to mere description, viz. of the external or internal structure, of the latter's development, and of deviations from the normal condition. There are, however, some other branches to which neither de Candolle nor Tschulok have given an independent position. The principal ones are pathology, parasitology, bio-sociology (bio-coenology) and the study of heredity. The first two are subjects of old standing whose position has already long ago been settled. The last two, which in later years have come to the fore, deserve a more ample discussion. Finally we will have to pay some attention to psychology, which is usually and rightly referred to the spiritual sciences, but for which in recent years a position has been claimed in biology.

Pathology may be defined as the study of the phenomena of life in the diseased organism, and as the latter is not separated by a sharp line from the healthy one, there is, of course, no well-marked difference between pathology on the one hand and physiology and ecology on the other. As the pathologist, as a rule, restricts his interest to diseases that are either directly or indirectly of importance to the welfare of mankind, pathology is in the main applied biology: the diseases of man himself belong to the field of medical biology, those of the domestic animals to veterinary biology, and those of the cultivated plants to agronomic biology.

In the study of parasites the attention is usually centred on their mode of life, and in that case the subject is to be regarded as part of ecology. However, when emphasis is laid on the nature of the diseases caused

by them, we enter the field of pathology. These two standpoints are not always kept apart, but when we wish to elevate the treatment to a really scientific level, this ambiguity should be avoided. For our present purpose it is enough to realize that the study of the parasites does not open up new vistas.

Bio-sociology, or bio-coenology as it is called by those who take exception to the barbaric sound of the name bio-sociology, studies the way in which organisms, according to the circumstances under which they live, are united in communities of definite composition. Sometimes the attention is centred on the circumstances under which these communities develop, and than the latter are used as a means to recognize the nature of these circumstances: in this case we are dealing with questions pertaining to ecological bio-geography. The way in which the communities come into being, i.e. the way in which the organisms influence each other, is, on the other hand, an ecological problem. So far the last-mentioned point of view has not made much headway in the field of bio-sociology, so that for the time being the latter may be regarded as a branch of ecological bio-geography.

The study of heredity, or of genetics as this discipline is now often called, occupies a far more independent position than any of the subjects mentioned above. It deals with the connection existing between the characters of the parents and those of their descendants, a problem for which there seems to be no place in any of the branches of biology recognized either by de Candolle or by Tschulok.

As in the study of genetics no fundamental importance can be attached to the causal explanation of the differences in the vital functions that are found in the various members of a family, it is clear that this discipline, notwithstanding the fact that it has often been included in physiology, has but little affinity with the latter. This conclusion may perhaps cause some wonder, as it is nowadays customary to regard the study of heredity as an experimental subject, and as such more readily comparable to physiology than to any other biological discipline. However, there are serious objections against this view, to which, in my opinion, not enough attention has been paid.

What the geneticist calls experimenting, viz. the arbitrary combination of parents and the raising of their offspring as separate families, is doubtless an important procedure in this study, but it is by no means an essential part of it, for when the geneticist occupies himself with the phenomena of heredity in man, this kind of experimenting is, of course, excluded; the way in which in that case conclusions are drawn from data which the investigator obtains by the study of a number of families, is nevertheless fully comparable to that by which elsewhere conclusions are drawn from material obtained by intentional crossings. Moreover, in the way in which these "experiments" are carried out, there is certainly more similarity with taxonomy than with physiology, for occasionally the



taxonomist too enters into methodical cultures, namely when he wants to make sure that the differences observed between two or more individuals are due to inequality of their genetic constitution and not merely to inequality of the circumstances under which they grew up. Hybridization too is practiced by the taxonomist, although it must be admitted that the crossings of the latter have a different aim. The taxonomist makes use of this device when he wants to find out whether individuals that seem to be more or less intermediate between the representatives of different species, owe their origin to a cross between the latter. The geneticist, on the other hand, enters into hybridization experiments in order to find out whether the characters by which the parents differ, are exchangeable, and whether these characters are simple or compound ones. Hybridization, therefore, is to the taxonomist a means to test the correctness of a supposition, whereas it is to the geneticist in the first place a device by the aid of which he obtains in an easy way a sufficient amount of material for analysis.

Another argument that might be advanced in favour of the view that the study of genetics is nearly related to physiology, is found in the circumstance that the successive generations owe their existence to acts of fertilization. However, if we realize that the physiological analysis of the phenomena of fertilization is to the geneticist of no importance, this argument too falls flat.

That the opinion according to which there would be a near affinity between genetics and physiology, has maintained itself so long, is the more astonishing as the study of genetics has of late obtained an unmistakable morphological bias, for the view that the hereditary characters are localized in the chromosomes, and that they occupy in the latter a quite definite position or, in other words, that they are arranged according to a definite "plan", is a purely morphological conception. It is, however, desirable to bear in mind that the view according to which the hereditary characters should be recognizable in the chromosomes as separate particles, rests on observations made on the strongly enlarged chromosomes found in the salivary glands of the fruit fly, and as experience gained in the field of colloid chemistry makes it somewhat dubious that the so much smaller chromosomes found elsewhere in the body should possess the same arrangement of particles, this opinion still remains a disputable hypothesis. Therefore, although this assumption may, for the present, seem to be a serviceable base for the exposition of the rules according to which the hereditary characters are transmitted from the parents to the offspring, its hypothetical character should not be forgotten.

Far more obvious than its relation to morphology is that to taxonomy, as both disciplines centre their attention on the hereditary characters of the organisms. Genetics, however, centres its attention on the characters the parents have in common with their offspring, taxonomy on those that are met with in less closely related organisms. Moreover, the char-

acters that are taxonomically important, appear to differ from those that are studied by the geneticist. The latter impress us as occurring in pairs, and it is assumed that they are based on the presence or absence of units that are distributed more or less at random over the sexual cells to be reunited according to the laws of chance in the zygotes that form the starting-point of the next generation, but the characters in which the taxonomist is especially interested, are apparently always transmitted as an indivisible whole. The method of investigation, however, is the same in both disciplines: its essential feature is the comparison of as many characters as possible, and apart from the question whether the characters are exchangeable or not, it does not matter of what kind they are.

The preceding paragraph showed that there are not only weighty points of agreement between the study of genetics and taxonomy, but also noteworthy differences. However, the most important one among the latter has not yet been mentioned. It lies in their entirely different aim. The main purpose of taxonomy is to arrange the organisms in such a way that those units to which a place in the same group is given, show among each other more points of agreement than with any unit outside this group. In this way the position allocated to such a unit becomes the key to a more or less extensive collection of data, namely to all those pertaining to the group to which that unit belongs. The main purpose of the study of heredity is to find out what combinations of characters are to be expected among the descendants of parents differing in certain respects, and what kind of individuals must be mated in order to obtain definite combinations of characters among the offspring. This demands an analysis of the characters that are involved in the difference; the geneticist must, in other words, try to find out what hereditary factors or genes are responsible for the transmission of these characters. In general, therefore, it is desirable that he obtains a survey of the genes that are present in his study objects, and then, of course, he must know the rules according to which these genes are transmitted from the parents to their progeny. As the character analysis can only be carried out when a cross between the differing individuals leads to the production of a fertile progeny, the field of genetics is rather narrowly restricted. An enormous number of characters, and among them all those that are of importance for the distinction of the groups of higher rank, are excluded. It is perhaps not superfluous to draw once more attention to the fundamental difference between the characters that are of importance to the taxonomist and those that form the object of study of the geneticist: the first are transmitted in an indivisible whole, whereas the latter are more or less independent of those belonging to the first group, and may be exchanged against other ones or disappear.

The study of genetics is often combined with that of variability. Although it can not be denied that a well-founded knowledge of the latter

is of the utmost importance to the geneticist, it would be wrong to assume an essential relation between the two. Variability is due to inequality of the circumstances under which a process takes place, and plays therefore a part in all natural phenomena. The study of variability must accordingly be regarded as an independent discipline of whose results biology and all other natural sciences partake in the same way. To the biologist it is therefore, like chemistry and physics, an auxiliary discipline. That variability plays in biology a more important part than it does in those natural sciences that study the behaviour of non-living objects under severely controlled conditions, finds its explanation in the fact that the circumstances under which the organism lives, vary, as a rule, very considerably, and can even in artificial media not be kept fully constant. The study of variability is to the biologist, and especially to the taxonomist and geneticist, also of importance because a distinction must be made between differences due to constitutional inequality and those caused by inequality of the circumstances under which the study object lives, i.e. between hereditary differences and true variability. Certainty with regard to the nature of a difference can only be obtained by cultivating the differing individuals, and eventually their offspring, under identical circumstances. However, as such cultures claim a good deal of space and time, the taxonomist, who, as a rule, has to deal with an enormous number of organisms, is but rarely in a position to carry them out, and therefore he will often have to content himself with a certain degree of probability. He will, moreover, not always be able to detect the hereditary differences, for when the latter are of a quantitative character, they may easily remain hidden under differences due to the inequality of the medium, and in such cases there is, of course, no reason for him to enter into culture experiments. However, when there are indications that an organism assumes under different circumstances or in successive generations a different aspect, he has no other choice than to study its behaviour under controlled conditions. Examples of alternating generations of different aspect are very frequent among plants as well as among animals; in the latter they are found e.g. in aphids and gall wasps, where generations consisting of parthenogenetic females alternate with generations composed of normal females and males. As an example of an organism that changes its habit in accordance with the circumstances under which it lives, we may cite the case of *Polygonum amphibium*, which is found sometimes in the guise of a glabrous waterplant with long-petiolate floating leaves and flaccid hollow shoots and sometimes as a hairy landplant with erect shoots and shortly petiolate leaves.

The last problem we have to discuss, is the position of psychology, whose inclusion in biology has in the last decennia found many advocates. The claim that it should be reckoned to the sphere of biology, was the natural outcome of the rise of a new subject that has been designated with the name animal psychology. The latter studies the way in which

the animal's reactions to various stimuli undergo a change when the stimuli are repeated. This is no doubt a biological problem, but it is not so sure that it is rightly referred to psychology. It is true that this kind of problems are also discussed in works on human psychology, but they are in that case considered from another point of view, viz. in connection with our consciousness. This is not denied by the devotees of this subject, but they have another reason to refer these changing reactions to psychology. They are of opinion that the changes in the reactions are purposeful, and that their study therefore falls outside the field of physiology and ecology, which in their opinion should confine themselves to causal relations. However, here as in all similar instances falling outside the domain of our own conscious actions, the use of the term purposeful seems open to objection. Moreover, so long as the possibility to explain these phenomena as causal events is not fully excluded, there seems to be no reason to refer this study elsewhere. That so far no satisfactory explanation has been found, can not be regarded as a sufficient reason, for this applies also to numerous other phenomena to whose inclusion in physiology or ecology never any objection has been raised. The study object of psychology is our consciousness, and this, it seems to me, has too little affinity to the study objects of the biologist to be included in the same science.

The preceding considerations have led to the distinction of five main biological disciplines, viz. taxonomy, heredity, morphology, physiology, and ecology, and three accessory ones, viz. bio-geography, paleontology, and the history of biology. In the following paragraphs we will once more try to characterize these disciplines.

Taxonomy studies the degree of similarity between the organisms, living as well as extinct, in order to arrange them in accordance with this degree of similarity in groups that in their turn according to their degree of similarity are combined into groups of higher rank. As there appears to exist a correlation between these groups and definite areas and geological strata, their distribution in space and time is also drawn into the sphere of its interest.

Taxonomy goes out from the supposition that the various groups of organisms, no matter of what rank they are, are separated from each other by sharp demarcation lines. The assumption of the phylogeneticists that such lines do not exist, finds no support in our experience, and as a serviceable classification, i.e. a classification that tells us something definite of the participants of a group, can not be based on this fiction, it should definitely be abandoned.

The study of heredity centres its attention on the characters in which parents and descendants differ from each other, and tries to discover the relations existing between the characters of the descendants and those of the parents; when the descendants appear to be provided with characters



that were not found in the parents, these characters are supposed to be due to a combination of hereditary factors that were separated in the latter. These factors, for which the name "gene" has been coined, are thought to be unalterable. The main object of the study of heredity is to find the rules according to which the genes are distributed over the progeny. The redistribution of the parental genes which at the moment of fertilization are brought together, takes place during the so-called reduction division by which the original number is restored.

The expositions of the geneticists are based on the supposition that the genes are unalterable, and further on the assumption that some of them are completely independent of each other, whereas between other ones a certain degree of correlation is present which ranges from nearly complete dependence to nearly complete independence, but which is constant for any two of them.

When the observed phenomena can not be explained in this way, it is assumed that one or more of the genes have been lost or have undergone a change; such a loss or change is called a mutation.

Morphology divides the life cycle of the organism in phases and their body in parts whose position with regard to each other in time and space is bound by definite rules. It does not base its conclusions exclusively on the condition found in the normal adult individual, but makes use also of data obtained by the study of the preceding stages of development and of accidental deviations from the normal condition, i.e. of embryology and teratology. Whether the organisms are living or extinct is as immaterial to the morphologist as it is to the taxonomist.

The word morphology can be translated by science of the form, but the name was wrongly chosen. That form plays no part in this discipline, appears at once when we consider the contents of the concepts with which it works. As an example we may choose the concept leaf. A leaf in the morphological sense may be simple or compound, entire or provided with incisions of varying depth, radially symmetrical, dorsiventral, laterally flattened or asymmetrical, straight, curved or spirally twisted, in short it may possess nearly every imaginable form, and it must therefore be clear that the latter is of no importance whatever for its delimitation. With the other morphological conceptions it is just so. The diversity of form is no morphological problem: because of the close relation existing between form and function, the study of the form must be regarded as part of the task of the ecologist.

Morphology is based on the supposition that the successive phases of the life cycle and the various parts of the body do not only follow each other in a definite sequence, but that they are also sharply defined. When their limits are indistinct or when they seem to occupy an anomalous position, it maintains its faith in their existence and in the position the theory assigns to them: in these cases some special assumptions have to be made.

Physiology studies the processes of life, and tries to analyse them. This analysis consists in an attempt to resolve these processes in elements that can be described in the same terms as the phenomena observed in non-living objects. It differs from ecology because it concentrates on the analysis of the vital processes; the ecologist, on the other hand, studies their width of variation, because it is the latter that decides in what kinds of environment a species will be able to maintain itself.

Apart from the true vital processes, i.e. the processes depending on the presence of living protoplasm and on the activity of the latter, physiology occupies itself with processes like the imbibition and cohesion movements of fruit valves and sporangium walls, the evaporation on the surface of the plants and the transport of watery solutions inside the latter, i.e. with processes which are not directly dependent on the presence and activity of living protoplasm, but which nevertheless play an important part in the life of the organism.

Physiology is based on the supposition that the phenomena of life are capable of a causal explanation, and that they are, moreover, reduceable to processes which, at least in a large measure, are identical with those that play a part in the world of the non-living.

Ecology investigates the relations existing between the various species and their dead and living environment, and tries to classify them according to the nature of these relations. However, as the latter are of various kinds, the organisms can be classified in various ways, and as there seems to be no good reason to prefer one of these classifications above the other ones, it seems best to treat them all in the same way.

As there exists a close relation between mode of life and bodily structure, the study of the latter belongs also to the task of the ecologist.

Ecology further occupies itself with such problems as the transport of spores, gametes, fruits and seeds, because this transport, although not belonging to the life processes, is of great importance for the maintenance of the species. In this respect ecology behaves in the same way as physiology, by which, as I have already pointed out, also a number of phenomena that can not be regarded as vital processes, are drawn into the sphere of its attention.

Ecology is based on the realization of the fact that the various species are not only structurally different, but that they differ in their physiological requirements too. Differences of this kind explain why they are bound to a special environment. Some difficulty is caused in this respect by organisms that are able to maintain themselves in fundamentally different environments. *Polygonum amphibium* is a striking example of such a species. From an ecological point of view they must be regarded as possessing a twin nature: they are to some extent an ecological counterpart to the twisted and non-twisted individuals occurring in a culture of *Dipsacus silvestris torsus*; in the latter, however, the structural inequality is not accompanied by a well-marked physiological differentia-

tion, and shows therefore no correlation with the particular constitution of the environment.

Bio-geography studies the distribution of the organisms over the surface of the earth and in the seas. Its aims are two-fold. It may concentrate its attention on the correlation existing between the special character of the environment and the composition of the communities of living beings adapted to the latter: this is the field of ecological bio-geography; but it may also try to find out how taxonomically related organisms are distributed over definite parts of the world, in order to draw conclusions with regard to the changes the surface of the earth must have undergone in preceding epochs: the presence of identical or closely related forms in regions that are now completely separated from each other, makes it probable that these regions were at one time united; the absence of certain organisms in regions that are now open to them, may be interpreted as due to the presence of obstacles that were not long ago removed: the study of these relations is called historical bio-geography. When we do not restrict our attention to identical or very closely related organisms, but are turning it to taxonomically less closely related ones, we should bear in mind that taxonomic relationship is not, as I have pointed out, necessarily identical with genetic relationship, and that conclusions based on this kind of material will therefore always bear a hypothetical character.

Paleontology studies the distribution of the organisms in the successive strata, and tries to classify the latter by the aid of the remains or of other indications of organic life that are contained in them. Taxonomy and morphology of the extinct forms, however, do not belong to this field of study but to that of general taxonomy and general morphology. It is true that paleontology has often been defined as biology of the extinct organisms, but such a delimitation has no sense, for the extinct organisms can only be reconstructed by comparison with living ones, and this applies a fortiori to their mode of life.

The history of biology occupies itself with the way in which our knowledge of the organic world has gradually developed, with the considerations to which the study of the biological phenomena has led, and with the part which biology and its various branches have played in the successive periods of the history of civilization in the social as well as in the spiritual sphere.

The applications are best classified in connection with the fields of interest in which they play their part. In this way we come to the distinction of agronomic, technological, pharmaceutical and medical biology. A special characterisation of these subjects would be out of place in a work dealing with biology in general.

At our universities and colleges the subjects are not rarely delimited in a different way. Ecological problems, for instance, are often dealt with in connection with physiological ones, and sometimes the whole subject

is merged in this way in physiology. As ecology and physiology have much in common, there are no grave objections against such a course. Far more questionable is the adequacy of the mixture of ecology and morphology that is often offered under the name of the latter, for these two branches of biology are of an entirely different stamp. No objection can, of course, be raised against excursions in the field of other branches of biology or even of other sciences so long as the true nature of such excursions is clearly understood. The taxonomist, for instance, will not rarely venture into the field of morphology and in that of genetics, sometimes also in that of ecology, and very often in that of bio-geography. As ecology demands of its devotees a thorough acquaintance with a large number of organisms, it is no wonder that ecology and taxonomy often go hand in hand. With regard to the history of biology I may point out that it is obviously in many instances desirable when we enter into a new subject, to give a short exposition of its history. We should, however, not forget that in order to obtain a clear insight into the nature of the biological problems, it is desirable to keep the various points of view severely apart. In this field too we should be guided by Bacon's well-known aphorism "Truth comes out of error much more rapidly than out of confusion".

In the following essays I will confine myself to the main disciplines. The accessory ones are better discussed in relation to the sphere of scientific interest to which they belong.

## THE PRINCIPLES OF TAXONOMY

The branch of biology that forms the subject of this essay, has for a long time been known by names that were more or less misleading because they were also used in a wider sense. When an entirely unprepared reader in perusing a biological work is confronted for the first time with one of the terms systematics or classification, he will probably be inclined to assume that an arrangement of the whole of our knowledge of the living beings is meant, and it will doubtless be a surprise to him when he learns that Linné and A. P. de Candolle used for the classification of the living beings such a vague term as methodology. So long as this kind of classification remained the principal concern of the biologists, no serious objection could be raised against the use of these designations, but when other points of view began to come to the fore, and botany and zoology grew out to sciences of a more universal character, it was felt that these terms could no longer be regarded as fully adequate.

The ambiguity in the meaning of the words systematics, classification and methodology may, of course, be obviated by the addition of some qualifying term. "Classification of the organisms" and expressions like "zoo-systematics" and "phyto-systematics" can certainly not be misunderstood, but they are rather clumsy. It is therefore no wonder that an attempt has been made to replace the earlier designations by new ones that are not encumbered by these drawbacks. It led to the introduction of the terms "taxology" and "taxonomy", two compounds expressly made for this purpose from Greek roots. It is true that these terms when literally translated prove to be as vague as their predecessors, but as they had not yet been used in a more general sense, their meaning could be limited by definition. "Taxology" may be defined as acquaintance with the momentarily prevalent classification of the organisms, whereas "taxonomy" is supposed to occupy itself especially with the laws ("nomoi") according to which a more or less ideal classification is to be developed. Taxonomy accordingly confines its attention to the natural system, i.e. to a classification of the organisms that is based on the largest possible number of attributes. Artificial classifications, which are developed by the aid of a limited number of more or less arbitrarily chosen properties, are now only used for the construction of identification keys, where, in fact, they found their starting point, and where they will continue to serve a useful purpose, but although the construction of such keys is doubtless a praise-worthy occupation, it can not be regarded as an essential part of the task of the taxonomist: from the latter's point of view the artificial systems are of no importance.

Taxonomy has been defined as the discipline that aims at a classi-



fication of the organisms according to the degree of similarity. This means that it does not restrict its attention to the distinction of the basal units, viz. those that comprise individuals between which, apart from the varietal differences of which we will speak hereafter, only such diversity seems to be present as may be ascribed to the influence of the environment, but that it occupies itself also with groups of a more comprehensive character; it aims, in fact, at the development of a complete hierarchy of such groups. Some of the groups of a more comprehensive kind, e.g. mammals, birds, insects, flowering plants, toadstools, were already generally acknowledged at a very early time, and are indeed more easily recognizable than many of the less comprehensive ones, but this is no general rule, for some other groups of a high order have been based on characters whose discovery required a good deal of acumen and of scientific training. In fact, several of the most important groups, like the Chordata and the Embryophyta, have been recognized only at a comparatively recent date. Other groups, which at one time were accepted as perfectly natural, had, on the other hand, to be abandoned, e.g. Invertebrata, Cryptogamae; and several were lifted out of positions into which originally they seemed to fit quite well, e.g. sea-anemones and corals out of the vegetable kingdom, Brachiopoda out of the Mollusca, Coniferae out of the Angiosperms. Of less fundamental importance are the changes brought about by the splitting up of large but at first sight rather uniform groups. Operations of this kind are usually carried out for practical reasons, viz. to obtain a more easily surveyable arrangement.

The definition of taxonomy given in the preceding paragraph makes use of two conceptions that require a closer examination. In the first place we will have to come to an agreement with regard to the nature of the units on which the classification is to be based, and in the second place we should know what is meant by the expression "degree of similarity".

The units on which the present classifications are based, are the species, and the latter are supposed to comprise all individuals whose differences the taxonomist is unable to distinguish from the fluctuations that are brought about in organisms of the same hereditary constitution by the inequality of the conditions under which they live, and further also those individuals who differ from the other ones in a small number of peculiarities that, although hereditary, are regarded as non-essential. This means that the varieties and the so-called pure lines are excluded from the field of study of the taxonomist. The differences between related pure lines are entirely or almost entirely of a quantitative character, and as they fall, as a rule, for a more or less considerable part within the limits of the variability caused by the inequalities of the medium, they are apt to escape the attention of the taxonomist. In fact, they are, as a rule, recognized only when in such groups of common descent the mean values of the properties are determined. To this end we require of each pure line a fairly considerable number of representatives that are to be chosen at

random. As the taxonomist will but rarely find himself in a position to carry out such determinations, he will have to leave the study of the pure lines to the geneticist. Differences that are confined to a small number of properties fall also, as already has been stated, outside his field of study. They rest, as the genetic analysis has shown, upon the presence or absence of a single gene or of a small number of genes. Groups of individuals differing in this way are called varieties. The botanical taxonomist, who, as a rule, has to base his conclusions on herbarium material, is often unable to recognize these varietal characters, as many of them, e.g. differences in flower colour, tend to disappear in dried plants. For this reason the study of the varieties has never appealed to him, and he is well content to leave it to the geneticist<sup>1</sup>).

The groups of individuals that are indicated by the names elementary species, Jordanons, sub- or micro-species, occupy a somewhat different position. They differ from the pure lines in the nature of their distinctive characters, which, although on account of their minuteness apt to escape our attention, are of a qualitative nature and therefore for a careful observer recognizable in every individual. In order to determine the differential characters of a group of Jordanons, it is often desirable to compare a larger number of individuals, and to this end the investigator may have to turn to methodical cultures, but once the differences have been ascertained, this detour becomes superfluous.

On account of the long-windedness of the method by which the differences inside the groups of pure lines are to be studied, the genetic analysis of the latter has made but little progress, but it seems safe to assume that these differences are of the same kind as those found between varieties, i.e. that they are due to the presence or absence of a limited number of genes. The genetic analysis of the Jordanons is beset with even greater difficulties, and will often prove impossible, viz. in the many instances in which they can not be crossed. This may be due to the same incompatibility that is observed in so many of the more widely diverging species, but it may also be caused by the circumstance that they are apomicts, which means that their sexual reproduction has been replaced by apogamy, i.e. by a kind of vegetative propagation in which use is made of egg-cells with a diploid nucleus or, eventually, of nucellus cells that develop without fertilization into new plants. This has been noted in several of the Jordanons of which it is known that they are of hybrid origin (species of *Hieracium*, *Taraxacum*, *Alchemilla*). Other Jordanons of hybrid origin remain true to type because their genes are not readily exchangeable but remain united in a more or less stable whole, and because among the

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<sup>1</sup>) That the monographers nevertheless complete, as a rule, the description of the species by a more or less detailed account of their varieties, is only natural, because they have to draw attention to these aberrant forms in order to prevent that taxonomists who are not acquainted with the range of variability in a particular group, mistake them for distinct species.

combinations formed by their sexual cells those only that repeat the parental type, prove viable. In such cases a genetic analysis is not entirely excluded, but its success is by no means assured, and as the genes can not all be separated from each other, the analysis will never proceed very far.

The definition of the Jordanon remains a difficult problem. Although it can, at least in theory, be separated from the variety and the pure line, it is not to be expected that we will ever be able to draw a sharp line towards the Linneon, as the more readily recognizable species is called. Whether a difference is to be regarded as easily recognizable or not, will obviously remain to some extent a matter of subjective appreciation. The decision will depend largely upon the degree of technical training and of freedom from preconceived notions reached by the investigator. Differences that are easily overlooked by inexperienced or biased observers, are often detected without difficulty by a more experienced or a more open-minded one, and characters that may seem unimportant to the novice, are often recognized by the trained student as more reliable and therefore more serviceable than the more striking ones. As an example we may quote the often very important differential characters that have been revealed by the use of the microscope, e.g. the presence or absence of definite types of crystals and of incrustations of the cellwall (cystoliths), the structure of the vascular strands and of the elements of which the latter are composed, etc. However, as the differences inside a group of Jordanons are in the same way as those between Linneons, of a qualitative kind, their valuation will always remain more or less arbitrary, and it is not to be expected that even equally trained and equally open-minded investigators will appreciate them in exactly the same way. Theoretically there are therefore no grounds to regard the Jordanons as different from those Linneons that can not be split. Linneons that can be split, on the other hand, are apparently units of a higher order that have wrongly been classified as species. However, even when a taxonomist is convinced that a splitting ought to be carried out, he will often refrain from it for practical reasons, for instance when the number of Jordanons is very considerable or when they are mixed with a continually changing swarm of hybrids. In such cases he will, as a rule, be unable to obtain enough material to arrive at a fully justified arrangement of the different forms, and under these circumstances he will acquiesce in the maintenance of the status quo ante.

Whether a difference in aspect between various individuals is due to hereditary inequality or to inequality of the circumstances under which they grew up, and whether a hereditary difference is of varietal or of higher order, are questions that the taxonomist, as a rule, will decide on grounds of analogy, i.e. on account of what he has learned from examples that have been worked out by geneticists. It is clear, however, that such decisions can never be regarded as final, and when they are challenged, or when the taxonomist is unable to reach a decision in this way, he will



be compelled to set up methodical cultures, and eventually he will even have to resort to hybridization experiments. When he has no living material at his disposition, this is of course impossible.

It was stated above that our "present" classifications are based on the species. The qualification "present" had to be added because originally there was a tendency to base the classification on the genera. Linné's binomials, which have maintained themselves up to this day because of the practical advantage found in a reduction of the number of names required for the distinction of the species<sup>1)</sup>, doubtless owe their origin to this tendency. In conformity with the earlier taxonomists Linné regarded the species as of subsidiary importance only, i.e. in the same way as the varieties and pure lines are regarded by his modern colleagues. However, it is now generally recognized that the genus is even more difficult to define than the species, and that it is for this reason much less suitable to be used as the basal unit of the classification. To the difficulties with which the definition of the genus is beset, we will come back further on.

When agreement has been reached with regard to the definition of the species, we will have to turn our attention towards the question of the degree of similarity, and we will have to find out in what way the latter is to be estimated.

A fully objective estimation of the degree of similarity is obviously but seldom possible, namely in those cases only where the differences are of a quantitative nature and confined to a single property. This means that it can only be carried out in the case of varieties and pure lines, groups that we have excluded, although admittedly in a somewhat arbitrary way, from the domain of taxonomy. However, as they allow us to study the problem in its simplest form, we will for the moment ignore this decision in order to find out what we can learn from them. The differences in the degree of similarity that we observe in varieties and pure lines, are undoubtedly of little importance, but their estimation has the advantage that it allows a comparison with the results of genetic analysis, and in the case of the more important differences this is, of course, but rarely possible, for the latter are found between forms that, as a rule, can not be crossed.

The comparison meant in the preceding paragraph leads to the conclusion that the magnitude of the differences found in the quality that we have chosen for study, is not necessarily proportional to that of the differences in hereditary constitution, and that it can therefore not be regarded as a reliable measure of the latter. A single example will suffice

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<sup>1)</sup> It is usually overlooked that a ternary nomenclature which would combine the name of the family, eventually in an abbreviated form with that of the genus and that of the species, would be even more economical, as it would enable us to use the same generic names in different families.

to make this clear. To this end we will consider a number of varieties differing in a single quality, e.g. in flower colour. We will suppose that the latter varies from white through various shades of pink to red, and we will assume furthermore that the different shades are due to the presence or absence of a number of genes, of which one is a hypostatic factor without whose presence no colour is produced. When this factor is absent, the flowers therefore are always white, no matter how many of the other genes may be present. The hereditary constitution of the white-flowered plants is therefore, notwithstanding the uniformity of their aspect, not necessarily everywhere the same, and may even differ considerably. The genetic analysis reveals moreover that some of the genes exercise a much stronger influence on the intensity of the colour than other ones, and it seems even possible that one or more genes may be present that tend to decrease the intensity. Neither the absence of colour nor its intensity can therefore be regarded as a reliable indication of the number of genes that are involved.

Although the differences between a number of varieties or pure lines that vary in a single quality, may be expressed in figures, the latter therefore do not necessarily give a reliable picture of the differences in genetic constitution. To obtain an idea of the magnitude of these differences we would have to estimate the number of genes that are involved. However, figures obtained in this way, would not be fully trustworthy either, for it is by no means certain, and not even probable, that the genes themselves are all of the same value; their entirely different outward manifestation certainly stands in the way of such an assumption. When we assume that the genes are localized in the chromomeres, i.e. in the easily staining parts of the chromosomes, and when the chromomeres are regarded as representing the lateral chains of the long catenary molecules that are supposed to constitute the axis of the chromosomes, it would be plausible to regard their value as dependent upon the number and the specific nature of the atoms that are present in these side-chains, and it needs no special emphasis that both the number and the specific nature of these atoms will vary. It appears therefore that the estimation of the genetic relationship between these nearly allied forms is beset with similar difficulties as the estimation of the taxonomic affinity between the more distantly related ones. However, it has one redeeming feature. When the number of genes that are involved in a difference between two forms, becomes very large, the individual contrasts in their value will lose a good deal of their significance, for in that case the influence of genes with a supra-normal value will be counterbalanced by that of genes with an infra-normal value. Therefore, the larger the number of genes that are involved, with the more confidence we may use their number as a measure of the degree of relationship.

When the differences can not be reduced to the presence or absence of an accurately determinable number of genes, i.e. when we have to deal

with other than varietal differences, we will obviously be compelled to base our conclusions on the differences themselves. In that case we will have to compare the number of points in which the members of the group agree with the number of those in which they differ, in which procedure the points that are common to all the members of the group must, of course, be left out of consideration. Here too we will have to bear in mind that not all points of agreement or disagreement are necessarily equivalent. That, on the contrary, very considerable differences in value may be involved, can not be doubted, for some of the characters prove to be common to a large part of the members of the group, namely to all those that in other respects too are very similar, whereas other ones appear to be confined to a single member or to return in members that otherwise have but little in common. To obtain some insight in the value of a character we will have to estimate the number of characters with which it is constantly associated. How far disregard of this principle may lead us astray, is well exemplified by Linné's mistake with regard to the systematic position of the peloric form of *Linaria vulgaris*, which, as is well-known, was referred by him to a genus of its own, whereas we now know that it is a mere variety differing from the type in a single gene.

As some knowledge of the relative value of the various characters is, of course, indispensable, the taxonomists have always done their best to find attributes by the aid of which this value might be ascertained. The earlier taxonomists were apparently of opinion that this offered no difficulty, and among their more modern colleagues too there were many who seem to have had no doubts on this point. It is noteworthy, however, that the way in which this value according to the latter is to be determined, is diametrically opposite to that in which the earlier taxonomists thought they were able to find it.

The earlier taxonomists were of opinion that the value of the characters on which they based their classifications, depended upon the importance of the part played by these characters in the life of the organisms. In later times it has often been assumed that their groups were exclusively based on such a-prioristically chosen characters, and that the older systems are for this reason to be regarded as "artificial" ones, but this is a mistake. As this is a rather important point, it seems worth while to enter here into some detail.

It can in my opinion not be doubted that the earlier taxonomists derived the characters on which they based their classifications, from groups that were recognized more or less intuitively but at any rate on account of a certain similarity in aspect as natural ones. Their approach of the subject was therefore in the main the same as that of the taxonomists of a later date. Their method, however, differed from that of the latter in so far that they did not classify all the organisms that were known to them at once, but began with those whose affinity could not be doubted. Those characters of the latter that seemed to have diagnostic value, as e.g. the

number of stamens, were subsequently used to classify the remaining organisms, and in this part of their procedure, which was a kind of extrapolation, the taxonomists of a more recent epoch have apparently seen a confirmation of their belief that the earlier classifications were based on a-prioristic grounds. This, however, is doubtless an undue generalization.

To justify their view that the characters whose significance had been revealed by the preliminary analysis, might be used for the separation of other groups, the earlier taxonomists assumed that these characters were for some reason or other of general importance to the organism, and the idea that they would derive this importance from the part they play in the life of the organism, must have seemed plausible enough in a time in which teleology reigned supreme. It certainly took a long time before this idea was given up, and before it was generally recognized that characters of diagnostic value are by no means always of great importance in the life of the organisms.

The tendency to base the subdivision of groups of the same rank on variations in the same set of characters is indeed a prominent feature of the earlier attempts at classification, but it should not be assumed that it was always strictly followed. Already in the earliest attempts difficulties were experienced which prevented a consequent application of this principle, and forced the taxonomist to turn his attention to other characters. The fact that even in recent systems not rarely reminiscences of this procedure are met with, may be taken as an indication that the taxonomists have but gradually and apparently in a large measure subconsciously, freed themselves from this tendency.

The erroneous view that the earlier taxonomists based their classifications on a-prioristically chosen characters, finds its explanation in the circumstance that these taxonomists gave no account of their method. As the latter was in a large measure intuitive, it did not dawn upon them that this might be desirable. Instead they tried to render the results of their endeavours acceptable by an explanation a posteriori, which, in accordance with the custom of those days, was placed in front. In this way the impression was created that this explanation formed their starting-point. As has already been stated, it pretended that the subdivisions had been based on characters that are correlated to important differences in the mode of life. The custom to place "logical" explanations of this kind in front, has unfortunately even now not yet entirely subsided. The "phylogenetic" classifications are a warning example of this logical flaw, for the "phylogenetic" interpretations that are put in front, are in reality explanations "a posteriori". Against this uncritical way of presenting one's results, no protest can be emphatical enough.

To illustrate in what way the earlier classifications in reality must have been evolved, I will give an analysis of that proposed by Cesalpino (*De Plantis Libri XVI*, 1583). I choose this one not only because it is the earliest botanical system of any importance that has come down to us,



but also because it is the model on which all the earlier systems were formed. For comparison the classifications subsequently evolved by Ray and by Linné will also be subjected to a somewhat closer inspection.

The first book of Cesalpino's „*De Plantis Libri XVI*” gives an idea of the picture the author made himself of the life and the other essential features of the plant, and in the last three chapters of this book an attempt is made to justify the classification of the plants that is expounded in the fifteen following books. This classification is the result of a number of successive divisions, and in the three last chapters of the first book he tries to justify the choice of the characters on which these divisions were based, by pointing out that the characters were taken from those parts in which the two most important functions of the plant are vested. These two functions are “nutrition” and “reproduction”. The first term is applied in the same way as it is used now, but the use of the term “reproduction” is restricted to reproduction by means of seeds, and as there are plants in which no seeds are found, this function is obviously less general and therefore less important than the other one, which, of course, is always present.

For the purpose of “nutrition” the plant is said to be provided with root and shoot: the root which absorbs the food from the soil, and the shoot in which it is further elaborated and distributed for use. These two parts are said to show a parallel differentiation: they may consist of a stronger and harder substance (*substantia habitior et durior*), and then we have to deal with representatives of the first main group, viz. that of the woody plants, or they may be thinner and softer, and then the plants belong to the second one, viz. that of the herbs. In view of the gradual transition from the herbaceous to the woody type of growth, it is difficult to see how a critical observer like Cesalpino could have felt satisfied with this division. The unfortunate choice of this main character shows how strong the influence of a purely conventional notion may be: Cesalpino apparently accepted these time-hallowed groups because nobody had as yet dared to question their real significance. However, we should not censure him too severely for this flaw, for it would take another century and a half before the idea to use this almost entirely illusory difference for classificatory purposes was given up. Oddly enough it has been revived in recent times.

Cesalpino's next division is said to be based on the parts to which the second important function of the plant is entrusted, viz. on the fruits and seeds. The plants in which these parts are lacking, are dealt with in the last book, i.e. at the end of the herbaceous plants: woody plants without fruits and seeds were unknown in those days. The seedless plants are divided in a number of smaller groups, the first one containing the plants that in the structure of their vegetative parts agree with those provided with seeds, viz. the ferns, the horse-tail and the genera *Ophioglossum* and *Botrychium*. Then follow the *Hepaticae*, the *Musci*, the

Lichenes, the Algae, with which some Coelenterata (Corallium, Alcyonium) and the genus Lemna are mixed, and the Fungi. The arrangement is on the whole quite natural.

The differences in the reproductive parts on account of which the seed-plants are divided in groups, are found in the number, the position and the general aspect of these parts (numerus, situs, figura).

In the first main division, that of the woody plants, those provided with "solitary seeds" (with this expression are meant the one-seeded fruits in which the pericarp is not readily separable from the seed-coat) or with "solitary one-seeded fruits" (viz. fruits in which the seed lies in a cavity) are dealt with in book II, and those with several seeds per fruit (or with several one-seeded fruits in a receptacle, e.g. Ficus) are brought together in book III. In the plants dealt with in book II the rootlet of the embryo is, as Cesalpino points out, usually turned away from the place where the seed is attached to the pericarp, whereas in the plants of book III, it faces the latter. This is doubtless a rule with many exceptions, but it nevertheless deserves our attention because it shows what a marvellously keen investigator Cesalpino must have been. In the group of plants with which book II begins, and which is said to have the "blossom" ("flos", by which here the male flowers are meant) above the fruit, the rootlet indeed points outwards, and this group is doubtless a natural one: it is that of the Amentiflorae. It is divided into two smaller groups according to the structure of the pericarp, which is either thin and tough (Quercus, Castanea), or provided with a bony inner layer (Juglans). In the next group the "blossom", by which here the perianth is meant, is at the base of the pistil. This is a rather heterogeneous mixture (Prunus, various trees from which balsam is obtained, Palmae, Musa). In book III also two subgroups are distinguished. In the first one, the perianth is either inconspicuous or it is found on top of the fruit (Ficus, Opuntia, Morus, Sambucus, Hedera, Viscum), whereas in the second subgroup the ovary is superior. Among the latter a division is made between plants in which the seeds are attached to the base of the pericarp and those in which they spring from the latter's lateral walls or from the inner angle of the fruit cells. A further division is made according to the number of fruit cells, and the still comparatively large group with pluri-locular ovary is once more divided in "Conifera" and "Mali". That the structure of the cone was misunderstood, is no wonder, but that apples and pears with their distinctly inferior ovary were placed in this group, is rather strange.

Among the herbaceous plants first of all four main groups are distinguished: 1° those with "solitary seeds" or with uni-locular fruits, 2° those with two "seeds" or with a bi-locular fruit, 3° those with three "seeds" or with a tri-locular fruit, and 4° those with four or more "seeds" or with four or more cells in the fruit.

Group one is dealt with in the books IV-VI. The enumeration begins

with those that are provided with "naked seeds", i.e. with one-seeded fruits in which the seedcoat is not readily distinguishable from the pericarp: *Valeriana*, *Thymelaea*. Then follows a group with inferior ovary and an embryo whose rootlet points outward, and after that a more important group in which the flower is said to be surrounded by a "conceptacle": this group is once more divided according to the position of the embryo in the seed; in the first subdivision the rootlet points outward (*Urticaceae* and *Chenopodiaceae*), and in the second downward (*Gramineae*). This group is followed by the "Junci", plants with a flowering shoot consisting of a single internode (*Cyperus*, *Typha*, *Juncus*). The next group consists of plants whose fruits contain several seeds: among these there is first (book V) a subgroup consisting of plants provided with berries (*Cucurbitaceae*, *Solanaceae*, various *Liliaceae*, *Arum*), and then (book VI) follows a group provided with dry fruits. This is split in a section in which the ovules are arranged in a longitudinal row (*Leguminosae*, subdivided according to the presence or absence of tendrils) and a section in which the ovules spring from a central placenta (*Caryophyllaceae*, *Primulaceae*).

The second main group of the herbaceous plants, that with the bicoccous and bilocular fruits is dealt with in the books VII and VIII. Book VII deals with those plants in which the seedcoat and the pericarp are not easily distinguishable (*Umbelliferae*), book VIII with those with a distinctly bilocular ovary. The latter group comprises 1° plants with an inferior ovary and a single seed per fruit cell (*Agrimonia*, *Poterium*, *Rubia*, *Galium*), and 2° those with several seeds in the fruit cells. The latter form a large group, which accordingly is once more subdivided, the division being based on the position of the sept, which is either perpendicular to the symmetry plane of the flower (*Scrophulariaceae*, *Acanthaceae*, *Solanaceae* with dry fruits, *Pirola*, etc.) or parallel to the latter (*Cruciferae*).

The plants with 3-coccous and 3-locular fruits are dealt with in the books IX and X. This group is divided in three subgroups: 1° those in which the seedcoat is not readily distinguishable from the pericarp, 2° those in which each of the three fruit cells contain a single free seed (*Euphorbiaceae*), and 3° those with several seeds in each of the fruit cells. The latter are once more divided in plants without bulbs (*Hypericum*) and plants with bulbs (*Liliiflorae*); the bulbaceous plants are dealt with in book X. They are once more divided according to the position of the ovary with regard to the perianth. In this book also a number of *Monocotyledons* are mentioned that are not provided with bulbs but whose affinity with the bulbaceous *Liliiflorae* had apparently been recognized by *Cesalpino*; this had led him to deal with them at this place.

Book XI deals with the plants provided with 4-coccous and 4-locular fruits. They are divided in two subgroups: 1° those with the rootlet of the embryo pointing upwards (*Boraginaceae*), and 2° those with the rootlet pointing downwards (*Labiatae*).

The plants whose fruits according to Cesalpino are provided with more than four seeds are dealt with in the books XII–XV. The books XII and XIII occupy themselves with the Compositae, i.e. with those plants in which each of the “seeds” (in reality, of course, the one-seeded fruits) bears at its top a “blossom”, whereas the books XIV and XV deal with those plants in which a number of fruits is surrounded by a common “blossom” (Ranunculaceae, Rosaceae, Malvaceae, etc.). The Compositae are divided into a group corresponding with the Liguliflorae and a group agreeing with the Tubuliflorae, and between these a small group is intercalated which comprises the Artemisias. Book XIV deals with those plants whose separate fruits contain but a single seed (several Ranunculaceae, Rosaceae, Geraniaceae and Malvaceae, but also some Monocotyledons like *Alisma* and *Sagittaria*), and book XV with those whose separate fruits contain more than one seed (the rest of the Ranunculaceae, Oxalidaceae, Crassulaceae, Rutaceae, etc.). The fruits are considered to be free when they develop from carpels that are each provided with its own style.

I have entered rather deeply into the details of Cesalpino's classification, but I had to do this, because the summary given by Linné is incomplete and on some points even incorrect, which is the more deplorable as most of the subsequent authors, e.g. Sachs in his “Geschichte der Botanik”, have based their opinion on this summary. It is, for instance, not true that each of the fifteen books in which Cesalpino gave his exposition, corresponds to a main group, and that Cesalpino therefore distinguished fifteen classes. In reality the number of main groups which he distinguished in these fifteen books is much larger. Nor is it true that the subdivision of the two principal divisions, the woody and the herbaceous plants, has been based on the position of the embryo in the seed which Linné described with the not very suitable terms “*cor ex apice seminis*” and “*cor a basi seminis*” (“the rootneck from the top of the seed” and “the rootneck from the base of the seed”), expressions that are not used by Cesalpino, whose description of the position of the embryo is more accurate. The main division of the woody and the herbaceous plants is based by Cesalpino on the production of one or more seeds per flower, and in the case of the presence of more than one seed, on the number of locules in the fruit. “*Situs*”, i.e. the position of the embryo in the seed, and the position of the ovary with regard to the perianth or, in the Amentiflorae and similar plants, of the female flower with regard to the male ones, and “*flos*”, i.e. those parts of the flower, or eventually of the inflorescence if the latter functions as a single flower, that are not directly concerned in the development of the fruit, come in the second place only, whereas features like the nature of the pericarp, the presence or absence of tendrils (in the Leguminosae), the equality or inequality of the florets in the Compositae, the fibrous or fleshy character of the underground parts in the Liliiflorae are used only when the resulting groups are considered too large; these



are the characters which fall under the heading "figura", which we may translate by "habit". That Cesalpino should have shown a marked preference for the position of the rootneck, as Sachs in his "Geschichte der Botanik" pretends, is therefore erroneous, and Sachs' opinion that Cesalpino was guided in the elaboration of his classification by the preconceived notion that the rootneck should be regarded as the seat of the vegetable soul, is therefore unfounded. That Cesalpino turned his attention towards the structure of the seed and the seedling when the groups based either on the number of seeds per fruit or on the number of locules proved to be too large, is after all not so very strange. A century later Ray was brought by a similar trend of thought to a renewed study of the seedling, which led to the discovery that the number of cotyledons is to be regarded as an important taxonomic character. By the taxonomists of the nineteenth century, moreover, it was generally agreed that Cesalpino had been right in attributing a fairly high value to the position which the embryo occupies in the seed.

The main points of difference used by Cesalpino for subdividing the woody as well as the herbaceous plants are, as we have seen, 1° the presence or absence of seeds, 2° the production of one or more fruits per flower, 3° the presence of one, two, three, four or more than four cells in the fruit, and 4° the presence of one or more seeds per cell. The difference mentioned sub 1° seems to be the only one to which an important part in the life of the plant can be ascribed; of the other ones it is difficult to see what effect they might have. It seems excluded that Cesalpino really did choose the characters on which he based his groups because of the part played by them in the life of the plant. The only admissible conclusion that can be drawn from the nature of the diagnostic characters of which he made use, seems to be that he had a predilection for differences in the structure of the fruit. However, his subdivision of the Leguminosae on account of the presence or absence of tendrils, that of the plants with a 3-celled ovary on account of the structure of the subterranean parts, and that of the Compositae on account of the structure of the "compound flowers" prove that he did not feel himself bound to an exclusive use of the fruit characters. As a matter of fact Cesalpino was in this respect less dogmatic than several of his successors, e.g. than de Jussieu, whose system is nevertheless, in contrast with that of Cesalpino, accepted as a "natural" one. For the reasons expounded above it seems improbable that Cesalpino choose his characters on a-prioristic grounds.

A closer examination of the data given above leads to the conclusion that Cesalpino will probably have proceeded as follows. First of all he will have studied one or more groups of plants that struck him as natural assemblages. He may, for instance, have started with the Liliiflorae, i.e. with the group dealt with in book X. In that case he will have noted that these plants are all provided with a 3-celled fruit, and that their underground parts are swollen. As a division of the herbaceous plants on

account of the nature of the underground parts could not appeal to him, he will have discarded this character and turned his attention to the number of ovary cells. Therefore his next step will have been the creation of another group for the remaining herbs with 3-celled fruits; these are the plants brought together in book IX. After that he will have created groups for the herbs with 1-, 2- and 4-celled fruits. The groups with 2-celled and with 4-celled fruits will have struck him as quite natural ones, for the first consists mainly of the plants that are now known as the Umbelliferae (book VII), and the second comprises the rather similar Labiatae and Boraginaceae (book XI). The herbs with 1-celled fruits, on the other hand, did not form a natural group. This, he will have noted, was due to the circumstance that their fruits are sometimes produced singly and sometimes in clusters. The first are dealt with in book IV, the latter in the books XII–XIV. That they are so widely separated from each other, evidently means that Cesalpino must have come to the conclusion that the antithesis fruits singly and fruits in clusters is of greater importance than the differences that are found in the number of cells in the fruit. That the plants brought together in book XIV showed but little affinity to those dealt with in the books XII and XIII is no wonder, as the real nature of the capitula of the Compositae had not yet been recognized.

Instead of the Liliiflorae Cesalpino may also have chosen as starting-point the Umbelliferae, the plants with 4-celled fruits or the Compositae, but this is a question of minor importance, as the result would have been the same. It might be argued that he may also have started by comparing two of his natural groups, e.g. the plants dealt with in the books VII and XI. In that case his method would have led to the discovery of only two really natural groups, viz. those dealt with in the books IX and X and in XII and XIII. When he had recognized already from the start three of the really natural groups, then the result would have been rather disappointing, for in that case only one other natural group would have come to light. For this reason I presume that he started with a single natural group, and that at least some of the other natural groups will have been brought to light in this way: this would have encouraged him to proceed. However, the application of this method could not everywhere lead to satisfactory results.

The other systems that have been classified as artificial ones, are all very similar to that of Cesalpino. A careful examination leads to the conclusion that they must all have been evolved in the same way.

Ray's system was published about a century after that of Cesalpino, and is doubtless more satisfactory, but in principle it is much the same. Sticking to the old view that the works of Creation show various grades of perfection, and as unaware as Cesalpino and the modern phylogeneticists of the possibility that his appreciation of the latter might be wrong, Ray too arranged his groups in a definite sequence, which differs from that

of Cesalpino in so far only that it begins with the "lower" plants. In the same way as in Cesalpino's system the whole vegetable kingdom is divided in herbaceous and woody plants, and the herbaceous ones are split by him too in a group that do not produce seeds (*Imperfectae*) and a group in which seeds are present (*Perfectae*). In Ray's time too this division could not be extended to the woody plants, as woody "*Imperfectae*" were not yet known.

The herbaceous seedplants and the woody plants were both divided in mono- and di-cotyledonous ones. At this point therefore a character was introduced that had escaped Cesalpino's attention, and for which an important part was reserved in the classifications of a later period. The further subdivision of the four groups that were obtained in this way, is based on the nature of the fruits, but in the way in which it is carried out, there is a rather important difference between Ray's system and that of Cesalpino. Ray did not even try to base the subdivision of these groups everywhere on the same characters, and this greater freedom allowed him to find a more natural delimitation of his groups.

The well-known "sexual" system of Linné deserves our attention not only because of the important part it has played as a means to arrive at a preliminary catalogue of the numerous new species that were discovered in the next century, but also because it was expressly qualified by its author as "artificial" and contrasted with another system that was put forward by him as an approach to a "natural" classification. Linné himself published the latter only in the form of a list of generic names arranged under a comparatively large number of "natural orders", of which, at first, no descriptions were given. In Giseke's edition of Linné's "*Praelectiones in Ordines Plantarum*" (1792), however, the majority of the orders have been provided with diagnoses, and their interrelations are sometimes discussed in considerable detail.

A comparison of these two classifications of Linné is the more desirable as the distinction between artificial and natural systems, which has maintained itself to this day, is based on the exposition given by Linné.

Linné's sexual system surpasses those of his predecessors in serviceableness, because it distinguishes a larger number of groups, and because the latter are, on the whole, more sharply defined. If we leave out of consideration that the characters on which Linné based his classification, were derived from the structure and composition of the androeceum and the gynoecium, and not from the structure of the fruit and of the embryo, and if we confine our attention to the way in which the characters are used, we will have to admit that there is but little difference between the sexual system of Linné and the systems of Cesalpino and Ray.

It is generally assumed that the artificiality of Linné's sexual system is premeditated, but this seems to me very improbable. In this respect it is noteworthy that the qualification "artificial" is used by Linné in two different ways, viz. sometimes with evident appreciation in order to

denote a classification carried through with the "art" of the accomplished taxonomist, and sometimes as opposed to "natural". A careful study of his works has convinced me that Linné was originally of opinion that the characters on which his sexual system was based, would prove to be an adequate foundation for a truly natural classification. The way in which he pleads for the naturalness of the base on which his sexual system had been erected, leaves in my opinion no room for another conclusion.

It is difficult to see why the differences in the structure of the androeceum and of the gynoeceum should have been considered by Linné to be of greater importance to the life of the plants than the differences in the structure of the fruit and the characters of the embryo in which Cesalpino and Ray had put their faith. It would seem that neither the one nor the other kind of differences could in this respect carry any weight. This can not have escaped Linné's attention, and it is therefore clear that he must have had another reason for his preference. I suppose that the study of some of the really natural groups created by his predecessors will have led him to the conclusion that the latter could be more easily characterized by the aid of the special features of the androeceum, eventually supplemented by those of the gynoeceum, than by those of the fruit. Once arrived at this conclusion he will have tried to find out whether plants with another structure of the androeceum, eventually in combination with a special type of gynoeceum, would not form natural groups too. The success by which these attempts were crowned, will have encouraged him to proceed in this way. His attempt to explain the serviceableness of his principles on the ground of the important part played by the stamens and carpels in the life of the seedplants, will have to be seen as a concession to the Aristotelian trend of thought by which the scientific world of those days was so strongly imbued that hardly any one could free himself of it. His contemporaries would certainly have regarded his classification as scientifically unjustified if it had been offered to them without this embellishment.

In the years in which Linné published his epoch-making words, he handled an enormous number of plants, and the insertion of the latter in the classes of his sexual system will continually have reminded him of the artificiality of his classification. This will doubtless have been an exhortation to look for a solution of the problem in another direction. As a preliminary measure he began by arranging the plants that were available to him, in more or less natural groups. However, with the analysis of the latter he made but little headway, and their delimitation accordingly remained very vague. This "natural" system was first published in 1738, i.e. shortly after the appearance of his "sexual" system, in the form of a list of "orders" each containing a number of genera but without any further definition. This list was reprinted with slight alterations in his "*Philosophia Botanica*". It is known, however, that he has at a later date twice given a course of lectures on this subject, viz. in



1764, when notes were made by Fabritius, and in 1771. The last course was attended by Giseke, who gave a very interesting summary of these lectures in a work published in 1792 under the title "*Linnaei Praelectiones in Ordines Plantarum*", in which the notes taken by Fabritius during the earlier course were also considered.

Linné's ideas with regard to the real character of the natural system were not very clear <sup>1)</sup>. Two points, however, are worth noticing: 1°. that he repeatedly emphasized his conviction that it would be impossible to find a sharp delimitation for the natural orders, and 2°. that he was apparently unable to free himself from the notion that the arrangement ought to rest upon some general principle. That he himself went in search of this philosopher's stone, appears from his remark that this principle might perhaps be found in the position of the embryo in the seed. At a much later time this idea, which Linné, as he himself admits, had derived from Cesalpino, was revived by van Tieghem. When the latter published his classification, it was, however, already generally recognized that in this way, i.e. by the use of the variations in a single character, no satisfactory system can be evolved, and van Tieghem's effort strikes us therefore as an anachronism.

Linné's opinion that the natural groups are never clearly defined and that on the contrary everywhere transitions are to be found, has not been confirmed. However, on account of Linné's great authority it has exercised a very strong and most regrettable influence on the development of taxonomy. This badly founded notion of the man who is often regarded as one of the most headstrong supporters of the idea of the immutability of the species, was in fact the base on which a great deal of the speculations of the evolutionists were founded, and in this notion afterwards the phylogeneticists too thought to find an excuse for their inability to define their groups.

That the sexual system occupied a much larger place in Linné's scientific activities than his natural system, need not surprise us. It is well-known that the description and preliminary classification of new plant species was one of Linné's chief concerns, and as it often proves difficult or even impossible to find a place for a new species in a natural system, whereas its insertion in the sexual system does not offer any difficulty whatever, it is not to be wondered that his work on the natural system, which meant a strenuous effort and often led to disillusion, receded somewhat into the background.

Linné's sexual system comprises, as he himself admitted, a comparatively large number of artificial groups, whereas his natural system contained in his own opinion no groups of this kind. His modern col-

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<sup>1)</sup> A better insight is displayed by Adanson in his "*Familles des Plantes*", issued in 1763, but as the influence of this work was apparently not very great, I will leave it out of consideration.

leagues are, of course, unable to agree with him in this appreciation, for most of his orders will strike them as rather heterogeneous. Moreover, Linné's natural system is, according to his own words, but a fragment. If he had succeeded to his own satisfaction in his search for the general principle that he supposed to be present at the back of his classification, he would doubtless have completed the list of his orders by adding a number of new ones of which the greater part would have been entirely artificial. It is certainly very fortunate that he escaped this snare, but if he had completed it in this way, his system would have offered a place to every new plant, and this is more than a really natural system will ever achieve.

The preceding considerations will have made clear that the difference between the earlier classifications and those of a later period does not lie in the supposed a-prioristic base of the first. We will, on the contrary, have to admit that the earlier systems too were based on empiric data. In one respect there is nevertheless, as we have seen, a rather important difference. The earlier systems were based on characters that were brought to light by the analysis of a single natural group or, sometimes, by the comparison of a few groups of this kind. The more recent classifications are not based on such a preliminary investigation of a single or of a few natural groups, for the taxonomists no longer believe that the characters that are recognized as serviceable for the subdivision of one group, will necessarily be suitable for the subdivision of another one. For this reason the larger groups are independently of each other divided in smaller ones, and in doing this the taxonomist relies entirely on the degree of similarity. As it is not to be expected that the representatives of the groups will all be known to us, it remains always possible that a plant will turn up for whom there appears to be no place in any of the subdivisions that previously have been recognized; in that case a new subdivision will have to be created for its reception. The earlier systems were all built on the dichotomous principle, one group being provided with a certain property and its antagonist lacking it, and these systems were therefore always open to receive a new-comer, no matter what its peculiarities might be. A plant is either woody or it is not woody, it reproduces by means of seeds or in another way, it develops a single fruit per flower or more than one, it has one stamen per flower or more than one, in the latter case it has either two stamens per flower or more than two stamens, etc. As we have already stated at an earlier occasion, these systems are in the main identification keys. For this reason they may, of course, be regarded as artificial, but if we place ourselves on this standpoint, we will have to include in this group also some of the later ones, e.g. that of de Jussieu, whose main groups have doubtless been built, as I have already indicated, on the dichotomous principle. It is apparently impossible to draw a sharp line between the artificial systems and the natural ones, and it would therefore be better to drop this distinction.

After this expatiation on the gradual emancipation of taxonomy out of the bounds of Aristotelean dogma, a development during which the idea that the taxonomic value of a character runs parallel with the importance of the part it plays in the life of the organism, receded further and further into the background, we will turn our attention to the entirely opposite view held by the taxonomists of the Darwinian period.

The taxonomists of the Darwinian period maintained that the highest taxonomic value was not to be assigned to those characters that play an important part in the life of the organism, but on the contrary to those of which it is impossible to assume that they are of any use to the organism. Sachs found this so self-evident that he lost in his "Geschichte der Botanik" no word on the question of the origin and the development of this view. This may partly be due to the fact that the latter fell in the years after 1860, i.e. in a period that is not covered by his history, but it is nevertheless rather striking. After he had pointed out (l.c. p. 88) that Linné's sexual system would have possessed exactly the same value when the view that the stamens play an important part in the reproduction process, had proved erroneous, because the classification is in reality based on characters of the stamens that from this point of view are certainly of no importance whatever, viz. their number, relative length and mutual independence or concrescence, he proceeds as follows: "so ist zugleich hervorzuheben, dass überhaupt der Verfolg der Wissenschaft gezeigt hat, wie Linné's Sexualsystem gerade deshalb, weil die von ihm benutzten Eigenschaften der Staubgefässe von ihrer Function ganz unabhängig sind, vielfach zur Aufstellung natürlicher Gruppen führen musste, denn wir dürfen es als ein wichtiges Ergebnis betrachten, dass den grössten classificatorischen Wert diejenige Eigenshafte der Organismen darbieten, welche von der Function der Organe ganz oder zum grössten Teile unabhängig sind".

The view that in this quotation is brought to the fore, was, I believe, first expressed by Darwin in his "Origin of Species". About 1875, when Sachs published his "Geschichte", it was apparently already wide-spread, and even at present it still enjoys a remarkable popularity. It rests upon the idea that differences in characters that are of no importance in the life of the organisms, must be immune against the influence of natural selection. As they are therefore neither favoured nor repressed, there is, of course, no reason why they should change.

The view that a property might undergo a change in a definite direction when subjected to the influence of natural selection, rests, as we now know, upon observations made on material that was not genetically homogeneous, but consisted of a mixture of various pure lines and, eventually, of hybrids between the latter. In such "populations" the mean value of a property may indeed be shifted in a definite direction, but this is due to the elimination of part of the genetically differing types, and as soon as the number of these types has been reduced in this way to a single

one or to a few that do not differ in the property which is affected by the selection, no further effect is to be expected. When the material is genetically homogeneous, selection is unable to produce a lasting effect.

It might be argued that natural selection, although unable to effect a lasting shift in the characters of a species whose variability is entirely of the fluctuating type, might well be able to produce such a change when the variability is partly due to the splitting off of mutations. The latter may have a better chance to survive when they differ from the parental type in characters that are of no importance in the struggle for life. When genes which are responsible for ecologically important characters are affected, there is, of course, a chance that the new forms will all be defeated in the competition with the ancestral type, but it is also possible that one of them proves to be provided with better qualities, and then it may, at least under otherwise favourable circumstances, take the place of the parents. Such an event, however, will doubtless be very rare. It should, on the other hand, not be forgotten that the production of mutations may to some extent depend upon external circumstances, and that genes which are responsible for ecologically important characters might therefore, because of their interaction with the environment, be more apt to mutate than genes which are responsible for characters that are of no importance in the struggle for life. If this would be so, the greater frequency of mutations of this kind would raise their chance to survive. However, as we can hardly expect to solve the problem by means of speculations of this kind, it seems advisable to see what we can learn by direct observation.

Actual experience appears to be at variance with the view that the taxonomically important characters must necessarily belong to those that are of no ecological value. Although we will have to concede that there are numerous taxonomically important characters of which it is difficult to see how they might be of any worth in the struggle for life, it can, on the other hand, not be denied that this does not apply to all of them, and that there are doubtless taxonomically important characters that are at the same time of considerable ecological value. A few examples will suffice to make this clear.

Some of the main groups of the Algae differ in the colour of the chromatophores, and this colour is therefore in these groups a character of the highest taxonomic value. However, it can not be denied that it is also of great ecological importance, for it determines the depth at which these plants find their optimum environment. In the *Convolvulaceae* the faculty to wind round a support is doubtless a property of great ecological importance, but as it helps to distinguish this family from its nearest allies, it is also an important taxonomic character. The parasitism of the *Rafflesiaceae* too is doubtless from an ecological as well as from a taxonomic point of view an important feature. In comparison with the colour of the Algal chromatophores and with the faculty of the *Convolvulaceae*



to wind round a support, which are both to some extent variable characters, the parasitism of the Rafflesiaceae appears to be an entirely constant property. The saprophytism of the Pirolaceae is, like the parasitism of the Rafflesiaceae, from a taxonomic as well as from an ecological point of view an important character, but it is not always equally conspicuous, for in some of the representatives of this family the leaves are green and of a fairly normal size, and in these plants saprophytism by means of the endotrophic mycorrhiza goes therefore hand in hand with autotrophism. In *Angiopteris* the swollen base of the "petiole" continues to increase in bulk after the rest of the "leaf" has been thrown off, and during this time it accumulates a food reserve; when this part too is finally thrown off, it develops adventitious buds that may grow out to new plants. This particular behaviour is doubtless both ecologically and taxonomically an important feature.

That taxonomically very important characters prove to have little or no ecological value, is, of course, a phenomenon of very frequent occurrence. In the Angiosperms this category comprises such well-known characters as the structure and position, and to some extent also the number, of the ovules, the surface relief of the pollen grains, which is on the whole a very constant and reliable character, the position of the cells surrounding the stomata, the structure of the vessels in the secondary wood and the position and perforation of their transverse septa, etc.

That ecologically important characters are from a taxonomic point of view of little value, is not rare either. The power of resistance to drought, which is found in plants that are taxonomically far removed from each other, and the accessibility to the attacks of definite groups of parasites like the Uredinales and the Orobanchaceae, may be quoted as examples. Ecological adaptations of this kind are nevertheless from a taxonomic point of view not entirely devoid of interest. Some hosts may, on account of their very marked susceptibility to the attacks of a definite parasite, prove to be almost always infected, and then they are sometimes more easily distinguishable from their nearest allies by the presence of the parasite than by the ordinary diagnostic characters, and this applies also to the presence of some kinds of symbionts. However, the presence of a definite parasite or symbiont would only be of really important taxonomic interest when it was found in all the representatives of a taxonomic group of supraspecific rank, and this is apparently an exception. The Bacteria that form the root nodules of the Papilionatae and the Cyanophyceae found in the rhizomes of the *Gunnera* species or in the coral roots of the Cycads may be quoted as such exceptions.

The examples given in the preceding paragraphs show that there is neither a positive nor a negative correlation between the taxonomic value of a character and its ecological importance, and no conclusions can be drawn therefore from our knowledge of one of these aspects with regard to the other.

As the two hypotheses that have been proposed for the determination of the taxonomic value of a character in an a-priori way, appear to be in contradiction with the actual facts, and as there seems for the present to be no chance to find another a-priori method, we will have to content ourselves with the empiric way.

That the various characters differ in their taxonomic value, follows from the fact that some of them are the common property of groups of primary importance, whereas others are confined to groups of a subordinate rank. This does not mean that the taxonomic value of a character depends upon the frequency with which it occurs. White flowers are doubtless a very common feature in the whole group of the Angiosperms, but the taxonomic value of this character is nevertheless but small. It is, as I will show hereafter, not in all subdivisions of this large group equally unimportant, but that its value may, at any rate, be very small, follows from the fact that numerous Angiosperms differ from their nearest allies merely in the presence or absence of colour in their flowers, and in all these instances the white colour is therefore a varietal character, i.e. a character of the lowest taxonomic rank. Varietal characters differ from those of higher rank in their more or less complete independence of the rest of the characters, and in their complete independence of the more important ones; the last-mentioned point is apparently decisive. The taxonomic value of a character therefore does not depend on the frequency with which it occurs, but on its association with other characters: it is, as has already been stated, the greater the more numerous the characters are with which it is constantly associated. When this criterion is applied e.g. to a character like the cohering anthers in the flowers of the Compositae, its importance is at once recognized, for there appears to be a complete correlation between this feature and the other family characters.

The estimation of the taxonomic value of the various characters occurring in a group can only be carried out after the latter has been split in subdivisions of successive rank. The characters of the highest value are those by which the primary subdivisions are distinguished, whereas those of lower value serve as a means of recognition for the subdivisions of subsequent rank. Once these values have been established, the characters can be used for the identification of the various subdivisions, e.g. inside a family for the identification of the subfamilies, tribes, subtribes, genera, subgenera, series, species and varieties.

The empiric determination of the taxonomic value of the various characters is doubtless of great importance, but it is nevertheless in a certain sense rather disappointing, for there is good reason to doubt whether these values are constant and whether they may be applied therefore in all groups of the same rank in a similar way. The earlier taxonomists had, as we have seen, no doubt whatever on this point, for they always tried to base the subdivision of their groups on the same characters, but to us the unsatisfactory nature of their classifications

seems, on the contrary, to indicate that this assumption was wrong. Whether this conclusion is fully justified, is difficult to decide, but it is certainly not difficult to prove that there are characters with a varying taxonomic value.

White flowers are, as has already been stated, in many instances a varietal character. The number of species in which individuals with coloured flowers occur side by side with white-flowered ones, is doubtless very considerable. In other species, however, the flowers are never coloured, and in these cases the absence of colour is therefore a species character. We are also acquainted with genera and even with families in which the flowers are always white, and the white colour of the flowers may therefore also be a generic or a family character. The taxonomic value of entire leaves varies in a similar way. In *Urtica pilulifera* the entire leaf is a varietal character, in several other cases it is a specific or a generic one, in the Caryophyllaceae and Rubiaceae it is a common feature of the whole family, and in the Liliiflorae even of a whole order.

When we say that the taxonomic value of a character varies, we seem to imply that this character is in the various groups the expression of an identical hereditary quality, and that the differences in its value are due to causes of secondary importance. This, however, is by no means sure. The parts by the aid of which bats, birds and insects fly, are all called wings, but we know quite well that they are from a morphological, and therefore also from a taxonomic, point of view of entirely different value. For such parts, which resemble each other in function and in general aspect, but prove to be built on a different plan, the morphologist uses the term "analogous". The question with which we are confronted in the case of the white flower and in that of the entire leaf, might therefore be formulated in this way: Are characters that return in taxonomic groups of different rank, perhaps to be regarded as analogies? In the next paragraph we will adduce some arguments in favour of this view.

A study of the leaf structure leads to the conclusion that there exists a distinct relation between the nature of the margin and that of the nervation. In most of the families in which the leaf margin is always entire, the leaves are either parallel-veined or else provided with a marginal vein, and it is certainly not easy to believe that such a leaf could develop incisions. In *Urtica pilulifera* we find, on the other hand, a kind of nervation that is ordinarily met with in leaves with a dentate margin. The supposition that the absence of teeth rests in these cases on entirely different causes, therefore appears plausible. In the white flower the absence of colour may be due to a defect in the mechanism by which the colour is produced, e.g. to the absence of an oxydase, and in that case it would probably be a character of varietal rank, but it is also possible that the whole mechanism is absent, and then the white colour of the flower might indicate a group of higher rank.

As there proves to be good reason to believe that the differences in the

taxonomic value of the white colour of the flower and of the entire leaf are correlated with differences in the mechanism by which the colour of the flower and the character of the leaf margin are determined, it seems possible that similar differences may be involved everywhere where the taxonomic value of a character is found to vary. However, so long as no such differences have been revealed, we will in actual practice have to take the presence of these differences in taxonomic value for granted, and in discussing questions of taxonomic rank, we will have to be careful not to base our valuation on the presence of a single or of a very few characters, which after all may belong to the group of those whose value varies. There are, of course, also fully constant characters, which are confined to a single group, and are therefore absolutely reliable indications with regard to the position of the organism, e.g. the faculty of the microspore to grow out into a pollen tube, which proves that our plant belongs to the Phanerogams, or the presence of a pericarp, which shows it to be an Angiosperm, but the number of characters that, taken separately, fail to give us reliable information with regard to an organism's position, is doubtless far greater.

When we wish to determine the degree of affinity between two organisms, we have to ascertain what the smallest group is of which they form part. The affinity is, of course, the more remote, the more comprehensive this group proves to be. *Lamium album* and *Fucus serratus* show but very little affinity, namely in so far only as they are both plants; *Lamium album* and *Polytrichum commune* are both Embryophytes, and although their affinity is very remote, it is already somewhat more pronounced than that between *Lamium album* and *Fucus serratus*; the affinity between *Lamium album* and *Lycopodium clavatum* is still more obvious, because they both belong to the same subdivision of the Embryophytes, viz. the group of the Vascular Plants; *Lamium album* and *Pinus sylvestris* are both Phanerogams, which means that they have still more features in common; this applies to an even higher degree to the couple *Lamium album* and *Lolium perenne*, both of them Angiosperms; *Lamium album* and *Papaver rhoeas* belong both to the Dicotyledones, and they are therefore even nearer to each other than the preceding couple; *Lamium album* and *Linaria vulgaris* are both Tubiflorae, which means that they show already a remarkable degree of similarity, and the latter is still more pronounced between *Lamium album* and *Stachys palustris*, both of them Labiatae, whereas it is very large indeed between *Lamium album* and *Lamium purpureum*, two species belonging to the same genus. The rank that we assign to the various groups, is therefore an indication of the degree of similarity found between their representatives.

That the groups should be arranged in a series of which each subsequent term is more specialized and therefore less comprehensive than the preceding one, is easily understandable, but it is not so obvious that this series should consist of a definite number of terms. Such a schema



doubtless appeals to our sense of order, but this should not blind us for its drawbacks. Especially by the use of definite suffixes, -ales for orders, -ineae for suborders, -aceae for families, -eae for tribes, -inae for subtribes, we are apt to create the impression that the rank of these groups is everywhere the same, and this is certainly not true. That this cause for misunderstanding is no mere phantom born in the mind of the critic, appears e.g. from the redaction of article 10 in the 3rd edition of the "International Rules of Botanical Nomenclature, 1935", which reads: "Every individual plant, interspecific hybrids and chimaeras excepted, belongs to a species (species), every species to a genus (genus), every genus to a family (familia), every family to an order (ordo), every order to a class (classis), every class to a division (divisio)" <sup>1)</sup>. When we consider the case of one of the isolated taxonomic units, e.g. that of *Ginkgo biloba*, we will see at once that this is not only meaningless but even misleading.

According to art. 10 of the "International Rules" *Ginkgo biloba* would belong to a genus *Ginkgo*, a family *Ginkgoaceae*, an order *Ginkgoineae*, a class *Ginkgoales*, and by the intermediary of the latter it would moreover form part of the *Gymnospermae* or, if this group is, as I have proposed elsewhere, rejected as unnatural, of the *Phanerogamae*. What, however, is the meaning of all these names?

*Ginkgo biloba* is the only living representative of a well-marked and quite isolated group whose extinct members, so far as they are known to us, differ apparently from the surviving one in subordinate points only, and this group might therefore be regarded as a genus. Usually, however, part of the differences are valued somewhat higher, and then two genera are accepted. If this arrangement is preferred, there is indeed reason to recognize a family *Ginkgoaceae*, but if we refer them all to the same genus, there is apparently no justification at all for the recognition of such a family. In order to define a family we must be acquainted either with the common features of the genera of which it consists, or else with the traits by which it is separated from the other families with which it is united into a group of higher order, and as there would be in this case no genera with which it could be united, and as there are no families from which it ought to be separated, it would be impossible to define the family *Ginkgoaceae*. Moreover, as we are unable to tell whether a character is of generic or of family rank, in cases like this genus and family run into one. With regard to the suborder *Ginkgoineae* and the order *Ginkgoales* similar objections may be raised, for there is no reason to assume that the *Ginkgoineae* might comprise more than one family and the *Ginkgoales* more than one suborder. Family, suborder and order are in this case therefore fully identical. The recognition of an order *Ginkgoales* may, however, be justified by the reflection that it forms

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<sup>1)</sup> In the new "International Code of Botanical Nomenclature" (Utrecht, 1952) for the corresponding article 12 a more cautious formulation has been used.

together with the Cycadales, Bennettitales, Cordaitales, Coniferales, Gnetales, Welwitschiales and Angiospermae the group of the Phanerogamae, so that the group to which Ginkgo belongs, must be more or less of the same standing as the other subdivisions of the latter. If we assume that the extinct allies of Ginkgo biloba belong to the genus Ginkgo, we arrive at the series Phanerogamae—Ginkgoales—Ginkgo, if they are partly referred to another genus, the sequence becomes Phanerogamae—Ginkgoales—Ginkgoaceae—Ginkgo. In the first series the intermediate term has been given the rank of an order, in the second one the two intermediate terms are regarded as occupying the rank of an order and of a family, but it will be clear that in the absence of one or more of the intermediate terms, the rank of the others becomes indeterminable.

The application of the otherwise rightly praised binary nomenclature to species of which no near allies are known, is also and for the same reason both meaningless and misleading. To concentrate our thoughts we will consider here the case of Welwitschia, the gymnospermous desert plant of South West Africa, so remarkable for the presence of a rudimentary ovule in the male "flower" and for its two enormous leaves that at the top are torn in several slowly decaying slips, while they are at the same rate regenerated at their base.

The nearest allies of Welwitschia are the Gnetum and Ephedra species, and then the various Conifers, Cycads, Ginkgo, etc. with which it forms the group of the Phanerogamae. It is still a point of debate whether it is better to place the Welwitschiales as an order alongside the Gnetales or to distinguish a suborder Welwitschiineae, which would form with a suborder Gnetineae an order "Gnetales", but it can, at any rate, not be denied that Welwitschia is a very isolated form. What meaning is in this case to be attached to the binary name? The orthodox supporters of the present system of nomenclature will answer that the addition of a specific epithet makes the name Welwitschia to a generic one, but this is precisely what I object to. In my opinion there can be no question of a genus Welwitschia so long as no second plant species has been discovered that belongs to the suborder Welwitschiineae (or to the order Welwitschiales), and even then it would remain debatable whether we would have to regard the higher unit as a genus or as a group of higher rank, for in order to consider it a genus, it must be possible to contrast it with other genera. That the binary nomenclature is in such cases apt to lead us astray, appears from the custom to make a distinction between characters that are brought together in a "generic" diagnosis and characters that are relegated to a description of the "species". When related genera are known, a few points may, of course, be set apart to distinguish the plant from these genera, but as the description of a genus must be based on the common features of its species, we require at least two species before we can begin with such a description. When more species are discovered, the original generic description will almost certainly prove too narrow,

because characters will have been included that are confined to these first-studied species. The chance that a generic description will stand the test, increases, of course, with the number of species on which it is based.

With regard to the choice of the characters on which the genera are to be founded, we are always apt to make mistakes, but to avoid the latter as much as possible, we should free ourselves from preconceived notions with regard to the value of the characters. Even differences in the size and shape of the leaves, of which it is commonly assumed that they are of importance only for the distinction of species and varieties, may occasionally prove to be of a higher value. The microphyllous *Ericas*, *Casuarinas* and *Cupressineae* may be quoted as examples.

In the earlier formulation of the article of the "International Rules" we recognize a reminiscence of Linné's standpoint according to which the groups of subsequent rank are not to be regarded as the more or less accidental results of our attempts to arrive at a suitable classification, but as the expression of a differentiation brought about by successively operative factors, and therefore of essential significance. In the quaint form in which he used to present the results of his speculations, and in which probably the influence of the well-known mystic Svedenborg is reflected, it reads (*Genera Plantarum*, ed. 6, 1774):

"1. Creator T.O. in primordio vestitit Vegetabile medullare principiis constitutivis diversi corticalis, unde tot difformia individua, quot ordines plantarum prognata." (The Thrice Best Creator has in the beginning covered the Vegetable medulla with the substances out of which the various kinds of cortex are formed, and in this way as many different individuals were produced as there are now natural orders.)

"2. Classicas has plantas Omnipotens miscuit inter se, unde tot genera ordinum, quot inde plantae." (These vegetable prototypes the Almighty mingled with each other, and of the plants formed in this way there were as many as there are now genera in the orders.)

"3. Genericas has miscuit natura, unde tot species congeneres, quot hodie existunt." (These primary representatives of the genera were mingled with each other by nature, and this led to as many species in the genera as there are now found.)

"4. Species has miscuit casus, unde totidem quot passim occurrunt varietates." (These species were mingled by accident, and this has led to the varieties that are everywhere met with.)

The successive use of the terms "Creator T.O.", "Omnipotens", "natura" and "casus" indicates that the difference between the orders, genera, species and varieties was in Linné's opinion not merely gradual, but that there existed important genetic differences between them. The prototypes of the orders were the first plants and owed their origin therefore to an "act of creation", the mingling of these prototypes, which according to Linné led to the origin of the genera, could not be expected to take place under ordinary circumstances, and required therefore the hand of "the

Allmighty". The crossing of the genera, however, offered in Linné's opinion no difficulty. He himself interpreted a species of *Veronica* whose leaves resembled those of a *Verbena*, as the result of a cross with a species of that genus, which was referred by him to the same order (*Personatae*).

In the preceding paragraph we presumed that the mingling of the prototypes of which Linné spoke, was a kind of hybridization. That this really was Linné's meaning, is revealed in the notes made by Fabritius of Linné's lectures on the natural system. These notes are to be found in the already quoted "*Praelectiones in Ordines Plantarum*" edited by Giseke.

That Linné did not realize that crossing between the prototypes would have been more apt to obscure the boundary lines between them than to differentiate new types within the original groups, is not so strange as it seems. This too is explained in the notes made by Fabritius of Linné's lectures. From these notes we learn that Linné, whose knowledge of hybrids was almost entirely confined to the metroclinous hybrids between horse and donkey, assumed that all hybrids would be metroclinous. The hybrid was supposed to inherit its most important characters from the mother, whose sexual cells were assumed to be derived from the medulla, whereas the male parent, whose sexual cells were of cortical, i.e. more vulgar origin, contributed the less important differentiating characters.

When we indicate the primordial medulla, which was covered by the "Thrice Best Creator" with the different kinds of cortex, by the letter *A*, and the different kinds of cortex, of which there must have been more than fifty, for that was the number of orders recognized by Linné, by the letters *a*, *b*, *c*, *d*, etc., the prototypes of the orders may be designated by the formulae *Aa*, *Ab*, *Ac*, *Ad*, etc. If the medulla and the cortex did not influence each other, the crossing of these prototypes would not have produced anything new, for the female sexual cells would in this case all have been of the type *A*, and the male cells all of the types *a*, *b*, *c*, *d*, etc. Linné must have assumed therefore that the medulla underwent in each of the prototypes a change. That of *Aa* will have become *A<sub>a</sub>*, that of *Ab* *A<sub>b</sub>*, etc. As the cortex must have remained unchanged, the crossing of the prototype *Aa* with the prototypes *Ab*, *Ac*, etc. would have resulted in the production of individuals with the constitution *A<sub>a</sub>b*, *A<sub>a</sub>c*, etc., and together with *A<sub>a</sub>a* the latter would have formed the prototypes of the genera belonging to the order *Aa*. In the same way the crossing of the prototype *Ab* with the other ones would have given individuals of the constitution *A<sub>b</sub>a*, *A<sub>b</sub>c*, etc., which together with *A<sub>b</sub>b* would have formed the prototypes of the genera belonging to the order *Ab*, etc. The 50 orders would in this way have developed  $50 \times 50 = 2500$  genera. If we assume that in the prototypes of the genera the medulla was once more modified by the influence of the cortex, it becomes comprehensible that an enormous number of species may have been evolved. Moreover, in the prototypes



of the genera the cortex too might have undergone a change, for the medulla is now no longer everywhere the same, but we will leave this possibility out of consideration. We assume therefore that the prototype of the genus  $A_aa$  will have formed female sexual cells of the type  $A_{aa}$ , that of the genus  $A_ab$  female sexual cells of the type  $A_{ab}$ , etc., and crossing of these prototypes would therefore have led to the production of the prototypes of the species  $A_{aaa}$ ,  $A_{aab}$ ,  $A_{aac}$ , etc. belonging to the genus  $A_{aa}$ , of the prototypes of the species  $A_{aba}$ ,  $A_{abb}$ ,  $A_{abc}$ , etc. belonging to the genus  $A_{ab}$ , etc. In the order  $Ab$  crossing of the prototypes of the genera  $A_{ba}$ ,  $A_{bb}$ ,  $A_{bc}$ , etc. would have led to the production of the prototypes of the species  $A_{baa}$ ,  $A_{bab}$ ,  $A_{bac}$ , belonging to the genus  $A_{ba}$ , of the prototypes of the species  $A_{bba}$ ,  $A_{bbb}$ ,  $A_{bbc}$ , etc. belonging to the genus  $A_{bb}$ , etc. This would account all in all for  $2500 \times 50 = 125000$  species.

We now know that Linné based his theory on an erroneous view of the results that are to be expected of crosses, which means that it has no foundation in actual fact, and we realize, moreover, that he made entirely arbitrary assumptions with regard to the intervention of a supranatural power where natural means were known to be ineffective, which places his theory outside the bounds of natural science, but we will have to admit that there is a kind of formal logic in it, and that it gives us at any rate a good idea of what was at the back of Linné's mind, viz. the essential difference between the various taxonomic ranks. Although there is, as we have seen, good reason to assume that a difference of this kind is present between the variety and the species, there seems to be no reason to assume the presence of such sharply defined differences between the other ranks. In nearly all the groups, no matter of what order they are, a varying number of intermediate ranks can be distinguished, and there is certainly no reason to assume that the occasional absence of some of the intermediate ranks must be due to extinction, which would be the only plausible explanation if the ranks represented, as Linné assumed, necessary stages in the development of the hierarchy.

As it appears impossible to allow a definite value to the successive taxonomic ranks, our assertion that the groups themselves are always well defined, might be regarded as unconvincing. We will therefore have to come forward with the grounds that have led to this conclusion. This is the more necessary as there are numerous taxonomists who profess themselves adherents of the opposite view, and who maintain that definite boundary lines are either absent or due to special circumstances, viz. to the extinction of the intermediate forms. Especially when Darwinism stood in the zenith of its career, this standpoint had many followers. When the origin of new species should be due to the action of natural selection, no sharp demarcation lines could be expected between them and the ancestral forms. The adherents of this view thought to find support for it in the so-called geographic races, between which no sharp lines can be drawn. However, it could be made probable that the presence

of transitions is in these cases due to the fact that the "species" to which the races belong, are in reality "populations" consisting of a more or less considerable number of genetically differing forms, and the composition of such a population may, of course, easily be modified under the influence of the environment. This would explain why such a "species" may appear in the guise of different "geographic races" <sup>1)</sup>. When the analysis of such a population is carried far enough, the continuity appears to be spurious. As a matter of fact the "geographic race" is not even a taxonomic concept, for the individuals of which such "races" consist, are not brought together on account of similarity but on account of the circumstance that they are found in the same area. In reality they are therefore ecological groups.

The adherents of the view that all taxonomic groups are discontinuous, point to the presence of a more or less easily demonstrable discontinuity between the groups of the lower ranks, the varieties and pure lines, and argue that the discontinuity between the groups of higher rank is, as a rule, so obvious that there is every reason to believe that the few exceptions are due to misinterpretations. The absence of sharp demarcation lines between several of the orders of the Angiospermae is, for instance, almost certainly due to the artificialness of these groups. The biogenetic theories of the future will have to accept this ubiquitous discontinuity as a fact, but how the wide gaps that are observed between most of the larger groups, are to be explained, will probably for a long time to come remain an unsolved enigma.

With regard to the units of lower rank, the varieties and pure lines, the question of the origin of the discontinuity was answered by the genetic analysis, which brought to light that the variation must be discontinuous because it is due to the presence or absence of one or more genes. For those units of higher rank between which crossing is possible, the discontinuity could be shown to rest on the same base, and it is therefore plausible to assume that this applies to all groups of this rank, no matter whether they can be crossed or not. The only difference between these forms and the varieties and pure lines seems to be that the genes that are responsible for the more important differences, are so firmly united that they are difficult to separate. As representatives of the more widely differing groups can never be crossed, we possess at present no means to penetrate into the nature of their differences.

There is one more point to which we will have to pay some attention. This is the choice of the characters on which we are to base our classification. As we will never be able to take all characters into consideration, some kind of choice will have to be made, but as such a choice may easily lead us astray, it should be made with the utmost care. For the sake of

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<sup>1)</sup> The term "geographic race" has also been used for micro-species with a limited area of distribution, but this deserves no recommendation.

brevity we will confine our attention here mainly to the Angiosperms. However, at the end of our discussion of the latter we will also cast a glance on the group of the Vascular Plants as a whole.

The characters on account of which the various groups of the Angiosperms are distinguished, are derived from the flower and, more rarely, from the leaves or the underground parts. This means that they all belong to the sporophyte, and not even to all parts of the sporophyte, for the features displayed by the sporangium, viz. the anthers and the ovules, and by the spores, viz. the pollen grains and the embryosac-cell, are either not considered at all or only in a half-hearted way. We will have to find out therefore whether the study of these parts and also that of the gametophyte will lead to the same classification as the study of the flower parts. Those who place themselves on the standpoint that the natural classification is the expression of a genetic affinity between the classified units, will have no doubt with regard to this point, but it seems to me that their confidence is ill-founded, and that in reality so far no sufficient attention has been paid to this problem.

The differences in the structure of the anthers are certainly not negligible, but they are as yet imperfectly known, and from the little that has come to light, no general conclusions can be drawn. A detailed investigation of these structures might lead to interesting results. With regard to the structure of the ovules we are somewhat better informed, but the features to which attention so far has been confined, viz. the number of the integuments and the development of the nucellus, show too little diversity to allow far-reaching conclusions. The "megaspore" of the Angiosperms, which does not seem to have much right to this name as it is hardly larger than the pollen grain, shows but little differentiation, and can therefore not be regarded as a promising study object. Among the pollen grains, however, there is a wide range of variability, and the differences between the various types are, moreover, well-defined and remarkably constant. For this reason their particularities have since long attracted attention, and they are at present studied on a larger scale than ever before. Further on we will deal with them in some detail. When we come to the gametophyte, we note that the study of the pollen tube does not look promising, but that the embryosac displays a good deal of diversity, and for this reason it has been studied in several families with great care.

As starting point for a discussion of the taxonomic value of the pollen structure, I will choose the Acanthaceae, not only because I am well-acquainted with this family, but also because its pollen shows a greater diversity in structure than that of most other families.

First of all we note that the families Mendonciaceae and Thunbergiaceae which were formerly included in the Acanthaceae, but which differ from the latter i.a. in the structure of the fruit, possess each a type of pollen which is entirely different from that found in the Acanthaceae themselves. The pollen grains of the Mendonciaceae are subglobose,

smooth and provided with a thick exine differentiated into two quite distinct layers, and they possess in the way of pores a fairly large number of narrow and short vertical slits, all situated in the equatorial zone; this is a type which, so far as I know, is not met anywhere else. The Thunbergiaceae possess pollen grains without pores. When the wall of the grain is of sufficient thickness it shows, as a rule, a curious relief caused by twisted depressions along which the grain bursts in the period of swelling that precedes the development of the tube. The pollen grains of the monotypic genus *Meyenia* are of a somewhat different kind, viz. depressed globose and provided with a number of blunt ribs; they burst along lines that are situated at the top of the blunt ribs. Neither this type nor that of the other Thunbergiaceae is met with in any of the families that are regarded as their nearest allies, but the more common type returns, strangely enough, in the Eriocaulaceae, i.e. in a family belonging to the Monocotyledones.

The Acanthaceae themselves show a great diversity in the structure of their pollen grains. The latter can be divided into two main groups. In the Acanthoideae, the subfamily which is characterized i.a. by the absence of cystoliths, they are "colpate", i.e. provided with longitudinal grooves but without pores, whereas in the other subfamily, the Ruellioideae, where cystoliths are always present, the pollen grains are always provided with pores.

In the Ruellioideae a great diversity of pollen forms is found, and most of them appear to be confined to special tribes or subtribes. Lenticular pollen grains with a pore in the centre of each of the two convex sides are found in the Trichanthereae, the Whitfieldiae and the Rhytiglossinae (syn. Isoglossinae), a subtribe of the Justicieae, and nowhere else. In the Rhytiglossinae they are much smaller than in the two other groups, and provided with a marginal zone that differs in its relief from the parts surrounding the pores, a differentiation that is also met with in the pollen grains of almost all other Justicieae. In the Whitfieldiae the grains are nearly smooth, and in the Trichanthereae they are provided with a system of parallel bands, and each pore is surrounded by two protruding lips; the directions of the bands and lips on the opposite sides prove to be perpendicular to each other. The Lepidagathideae and the Andrographideae possess comparatively small ellipsoidal grains provided with three equatorial pores, which in the latter are surrounded by a thickened rhomboidal frame; in this tribe the grains are moreover, as in the majority of the Justicieae, slightly flattened at the poles. The pollen grains of the Herpetacanthae are globose and areolate, and each areola is ornamented with a small spinule. The grains of the Ruelliae are either globose or ellipsoidal and much larger than those of the Lepidagathideae. In the subtribe Hygrophilinae they are provided with four equatorial pores and numerous equidistant bands; in the Blechinae they possess three grooves each provided with a pore, but otherwise without



a well-marked relief; in the Petalidiinae and in most of the Strobilanthininae they are also, as a rule, 3-porous, but ornamented with equidistant bands; the first have the pores in the middle of a band, the second between the bands; in the Ruelliinae and the Barleriinae the surface is usually reticulated, but in the first the grains are globose, whereas in the second they are more or less distinctly prolate and triangular. In the large tribe of the Justicieae, which in my delimitation comprises all Ruellioideae provided with an imbricate corolla and two ovules in each of the ovary cells, there are usually either two or three pores, and the neighbourhood of the pores shows, as a rule, a different structure and is more or less distinctly flattened. In the Rhytiglossinae they are, as stated above, lenticular, but in the other subtribes the polar axis is, as a rule, lengthened, and the poles are usually flattened.

The exposition given above indicates that there is in the Acanthaceae on the whole a striking agreement between the structure of the pollen grains and the characters upon which the subdivision of the family in subfamilies, tribes and subtribes originally was based. There are, however, a few exceptions. In the Aphelandreae (*Stenandrium* sect. *Sphaerostenandrium*), the Ruelliinae, the Strobilanthininae and the Justicieae (species of *Asystasiella* and of *Pseuderanthemum*) sometimes globose grains are met with that are covered with knobs or spinules, and this kind of pollen is known to occur also in other families.

The irregular distribution of the globose grains provided with an echinulate exine, whose pores, moreover, are often evenly spread over the whole surface instead of being confined to the equator, might perhaps be explained by assuming that this relief is due either to the absence of a factor required for the production of the normal one, or else to the presence of a factor by which the latter is suppressed. The suppression of the expected relief might lead to the appearance of an underlying more general type or to the development of an entirely new one. In the genus *Blechnum* the appearance of the wide-spread type characterized by the presence of three meridional grooves each provided with a pore, suggests a similar cause, but the extreme simplicity and the common occurrence of this type make it improbable that it should be a new one.

The similarity between the pollen type of *Thunbergia* and that of the Monocotyledonous genera *Eriocaulon* and *Aphyllanthes* is also a difficult problem, for which I am unable to suggest a solution. A more detailed investigation, however, might reveal differences by which the problem would be placed in another light. The aberrant pollen structure of the Thunbergiaceae is in itself also a riddle, for in none of the related families pollen of this kind is met with, nor does it seem readily reducible to any of the types found in their nearest allies.

Resuming we may say that the agreement between the results obtained by the study of the pollen structure and those arrived at by the study of the other characters, is on the whole quite good in the Acanthaceae.

There are, however, a number of discrepancies. With regard to the latter it should certainly not be overlooked that the suppositions by means of which we have tried to eliminate them, can not be verified. Similarity between the aberrant pollen types of the Thunbergiaceae and of the Acanthaceae and pollen types met with outside these families presents another problem for which as yet no satisfactory solution could be found.

For comparison we will consider the various pollen forms occurring in the Monocotyledones.

The pollen grains of the Monocotyledones appear to belong for the greater part to two types, viz. grains provided with a single, more or less distinct pore, and grains without pore but provided with a single, usually rather wide groove. The type with the pore is by far the most common, but it is perhaps no fully natural group, for the pore shows rather marked differences in aspect. In some cases it is but ill-defined, in other ones rather wide and perhaps not really distinct from the groove found in the grains of the other type, but there are also pores surrounded by a thickened ring, which show therefore a superficial resemblance to the bordered pits in the tracheids of the Coniferae. All these types seem to be bound to definite circles of affinity, and to be mutually exclusive.

Pores and grooves may also be absent in the pollen of the Monocotyledones, but in those cases the wall is usually thin, and such grains may therefore be regarded as modifications of the more common types. More fundamentally different are the pollen grains of Eriocaulon and Aphyllanthes, of which mention has already been made when we discussed the pollen structure of Thunbergia. In the pollen grains of the Cyperaceae the pore is situated at the distal end and is, as a rule, accompanied by three more or less slit-like, often ill-defined lateral ones. The Alismataceae also possess a pollen type of their own; their pollen grains are globose and provided with a fairly large number of ill-defined pores that are evenly spread over the whole surface; it is noteworthy, however, that in the genus Sagittaria sometimes but a single pore seems to be present.

Pollen grains provided with a single pore are outside the Monocotyledones rather rare; they have been found in some Coniferae and in Drimys, a Magnoliaceous genus that already once before had attracted the attention of the taxonomists, viz. when it was discovered that its wood contains no vessels. The pollen of the Coniferae shows in other respects but little resemblance to that of the Monocotyledones, and as there seems to be no reason to accept a nearer affinity between these two groups, the presence of a single pore in the pollen grains of some of them is best regarded as an analogy, i.e. as from the morphological point of view more or less accidental. Of more importance is the presence of this pollen type in the genus Drimys, because the pollen grains of the other Magnoliaceae are also of a Monocotyledonous type: they prove to be provided with a single large groove. The Magnoliaceae and Nymphaeaceae appear to be the only Dicotyledonous families in which this type occurs, and this

coincidence is the more noteworthy as both these families are included in the Polycarpiceae or Ranales, an order that on account of the floral structure has been regarded as allied to the Monocotyledonous families Alismataceae, Butomaceae and Hydrocharitaceae. The position of the Nymphaeaceae as a Dicotyledonous family is perhaps not so well assured as is, on the authority of A. P. de Candolle, usually assumed, but that of the Magnoliaceae with their secondary wood which is, except in the somewhat aberrant genus *Drimys*, of the normal Dicotyledonous kind, can certainly not be doubted. In the other families included in this order, e.g. in the Ranunculaceae, the pollen grains are of a different type, usually of that provided with three grooves, which makes the interpretation of the aberrant type found in the Magnoliaceae even more difficult. There seem to be two possibilities. It is either a case of convergence comparable to that observed in the pollen of *Eriocaulon* and *Thunbergia* and as incomprehensible as that, or it is an indication of real affinity, and then it would lead to the conclusion that the Monocotyledones and the Dicotyledones are no natural groups, for it is, of course, impossible that units belonging to two different groups are more nearly related to each other than to the units of the group in which they have been included. However, although I do not believe that the division of the Angiosperms in Mono- and Dicotyledones is the last word in the taxonomy of this group, I am not convinced that the resemblance between the so-called Polycarpiceae or Ranales and the Alismataceae and their Monocotyledonous allies is to be ascribed to a near affinity: this too might just as well be a case of convergence. As we know that the pollen grains of such widely separated genera as *Eriocaulon* and *Thunbergia* show the same type, the reappearance of the grains provided with a single groove in a family like the Magnoliaceae would in itself not be sufficient to prove a nearer affinity between the latter and the Monocotyledonous families for which this kind of pollen is typical.

Our survey of the pollen types met with in the Monocotyledones confirms the conclusion we have reached by that of the more extensively studied pollen of the Acanthaceae, viz. that the differentiation of the pollen types runs in the main parallel to the differentiation of the parts upon which the classification of the group so far has been based. There are, however, in both cases exceptions, and the meaning of the latter remains as yet obscure.

In the Angiosperms the gametophyte is not sufficiently differentiated to offer a suitable base for a classification. The pollen tube shows hardly any variability that would be worth considering, and the differences between the embryosacs are mainly confined to the number of nuclei, which are the result of the two, three or four successive divisions of the megaspore nucleus, and to the moment of the reduction division; it is known that the megaspore-mothercell does not always produce a megaspore but may develop itself into an embryosac, in which case the reduction

division is shifted to the latter. As the factors by which the number of these successive divisions and the moment of the reduction division are determined, need not everywhere be the same, there is apparently no good reason to expect that the number of the nuclei in the embryosac and the moment of the reduction division will prove reliable guides to the degree of affinity.

The differences between the types of gametophyte found in the main groups of the Vascular Plants are of far greater importance than those observed between the gametophytes of the Angiosperms, and it is therefore to be expected that a comparison between a classification of the Vascular plants based on the characters of the gametophyte, and the ordinary one that was based on the characters of the sporophyte, will be more instructive.

There can be little doubt that in a classification of the Vascular Plants on account of differences in the gametophyte the main division will have to be based on the presence of one or two kinds of gametophytes. One kind of gametophyte is found in *Lycopodium*, in the Ophioglossales and in the Filicales, in all of which it is bisexual. The gametophytes of *Equisetum* are unisexual and differ somewhat in size, and for this reason this genus might be kept apart. In *Selaginella*, *Isoetes*, the *Salvinia*ceae, the *Marsilia*ceae and the seed-bearing Vascular Plants there is a far more conspicuous difference between the male and female gametophytes. This group is to be subdivided in one in which the megaspores are set free, and another one in which the megaspore, here always a single one, remains enclosed in the megasporangium; the latter is the group of the seed-bearing plants.

The classification outlined in the preceding paragraph differs widely from that based on the characters of the sporophyte. This is well exemplified by the homosporous *Lycopodium* species, the heterosporous *Selaginellas* and the seed-bearing *Lepidocarpon*, which in the latter classification are referred to the same group, and which in a classification based on the structure of the gametophyte would have to be placed in three totally different groups. The situation can, of course, be saved by assuming that in all the main groups of the system that is based on the sporophyte characters, the gametophyte has undergone a similar differentiation, but this is a somewhat gratuitous hypothesis, for the similarity in the sporophyte characters might also, and more or less with the same right, be ascribed to convergence.

So long as problems like that with which we were confronted in the preceding paragraph, remain unsolved, we will not be able to answer the question whether the natural classification really is to be regarded as the expression of genetic relationship. When the classification based on the structure of the gametophyte should prove irreconcilable with that based on the sporophyte characters, we will have to admit that at least one of them can not be based on genetic affinity, and as the way in which



these classifications were arrived at, is the same, there would apparently be no reason to regard either of them as genetically determined, which means that the idea would have to be abandoned.

That a natural classification need not be the expression of genetic relations, is obvious, for non-living objects can just as well as the living ones be arranged according to the degree of similarity, and that a natural classification of living beings need not be of this kind, can, as I have indicated already in the introductory essay, easily be shown. Two different varieties, *AA* and *aa*, may both be descended from a hybrid *Aa*, whereas on the other hand an organism with the genetic formula *AaBb* may owe its origin as well to a cross between individuals of the genetic constitution *AAbb* and *aaBB* as to a cross between *AABB* and *aabb*. Genetically identical individuals may therefore possess different parents, whereas genetically different individuals may be descended from genetically identical parents. With regard to the origin of the taxonomically more important groups we are still completely in the dark, and it is therefore impossible to say whether the latter too may not have been evolved in different ways. The frequent occurrence of convergences even in the characters on which the classifications usually are based, might certainly be interpreted in this way.

Whatever the explanation of the natural system may be, there can be no doubt that the latter has to be based on the degree of similarity, and that in order to determine this degree as many characters as possible should be taken into consideration. However, what we have learned from our comparison between a classification of the Vascular Plants based on the characters of the gametophyte and one based on the sporophyte characters, will make it clear that our classifications are apt to remain to some extent arbitrary. Their value is therefore to be estimated according to their serviceability, which means that preference should be given to that one in which the various groups are characterized by the greatest number of common properties that are of importance to us, so that the place assigned to a group proves to be the key to the largest possible collection of information.

## HEREDITY

### AN ESSAY DEVOTED TO THE STUDY OF A BIOLOGICAL THEORY

Heredity owes its rather unique position among the biological disciplines to the circumstance that its expositions are based on a single, all-embracing theory. For this reason it impresses us as more sharply defined and better co-ordinated than the other biological disciplines, which in comparison strike us as somewhat rambling structures.

The advantage found in the conciseness and logical co-ordination of the expositions based on such general theories should not blind us for a drawback that is also inherent in them, viz. the tendency to divert the attention from phenomena that do not readily fit into the general scheme. We are, as a rule, only too apt to overlook the possibility that the theory may after all prove less universal than it pretends to be. In physics and in chemistry, where by the aid of a few comparatively simple hypotheses a strikingly efficient structure has been evolved in which each substance has its place and in which each change the energy content of an object may undergo, is accounted for, it is not always sufficiently realized that there are still several aspects of matter on which the theory does not shed sufficient light: it offers no explanation for the fact that every substance congeals and boils at a definite temperature, breaks and absorbs the various rays in a definite way, that it has in the solid state a definite specific gravity, a definite conductivity for heat and electricity, a definite resistance to stress, etc. In the domain of heredity it seems at first sight that the observed phenomena fit very well into our schema, but we should not forget that here too the domain had to be drastically restricted in order to ensure this result. We will have to enquire therefore first of all in what way the term heredity nowadays is used, and how its domain has been fenced in.

Heredity is the discipline that occupies itself with the hereditary features, i.e. with the features whose importance lies in the fact that they return in successive generations. These features may be immutable and common to all the members of the group in which they occur, but it is also possible that they are confined to part of the latter or that they are developed in the individual members to a different degree. Characters of the first kind are recognized when the group in which they occur, is compared with other ones in which they are absent; they belong for the greater part to those that form the study object of the taxonomist. The characters of the other kind are usually also at once recognizable, but to obtain a good idea of their value, we must find out how they behave in successive generations, i.e. we must study the fluctuations in the percentage of individuals in which they appear, and the changes in their average value. Such studies can be carried out irrespective of the nature of the

group, and it is therefore not surprising that the term heredity is not always used in the same way.

To obtain a clear insight in the nature of the phenomena of heredity, we should make a distinction between groups of individuals that belong together because of their occurrence in the same area or under similar circumstances, and groups of individuals united by family ties, i.e. that belong together on account of their common ancestry. As this must be regarded as a difference of fundamental importance, it is not to be expected that generalizations arrived at in one of these fields will always be applicable in the other one. To avoid confusion it is therefore advisable to restrict the use of the term heredity to one of them: among biologists it is now generally confined to groups of the second kind. This is more or less arbitrary, for it is by no means sure that the term is in this way used in its original meaning. The primitive man may have inherited his cattle, tools and weapons from his parents, but it is also possible that the young men of the tribe inherited these valuables from the former possessors irrespective of the degree of relationship existing between them, i.e. a heritage may originally have been passed on according to the degree of family relationship, but it is also thinkable that the private possessions of the individual were at his death declared common property, and distributed according to the rules prevailing in the community.

Failure to appreciate the fundamental importance of the difference between the two kinds of groups in which the transmission of habits and characters may be studied, has led in the past to a good deal of misunderstanding. Galton and afterwards Pearson and his school, the "biometricians", who studied the transmission of properties in groups of individuals that belonged together because of their presence in the same area or in similar localities, and who should therefore be classed as sociologists, failed to recognize the importance of the work done by the so-called "Mendelians", who studied the transmission of similar properties in groups of individuals of common descent. The latter, in their turn, were but rarely interested in the sociological side of the problem, and had not always sufficient appreciation for the more critical treatment of the numerical data that was practised by the biometricians. They certainly made a mistake when they regarded the work of the latter somewhat contemptuously as mere statistics, for the important share the biometricians took in the development of the statistical methods, in itself already a praiseworthy achievement, is not the only accomplishment for which they deserve our recognition, nor was it the main object of their endeavours. As soon as we acknowledge that the biometricians focussed their attention on the fate of the community, whereas the Mendelians were from the beginning interested in the individual as a link between its parents and its progeny, i.e. that there existed between biometricians and Mendelians originally a similar difference as between ecologists with their interest in the species and physiologists, who concentrate their attention

on the life of the individual, we will be in a position to give them both their due. The work of the biometricians, however, does not interest us here: we will confine ourselves to the conception of heredity which is usually called the "Mendelian" one, though in reality we owe it to Hugo de Vries.

When the study of heredity is restricted to groups of individuals connected by family relationship, its main problem lies in the fact that the offspring of some individuals appears to be uniform and true to type, i.e. similar to these individuals themselves, whereas the descendants of other ones are at least partly of another kind. It appears that this difference in the nature of the offspring finds, as a rule, its origin in the hybrid or non-hybrid character of the parents.

The statement made in the preceding paragraph draws attention to the important part that sexual reproduction plays in the domain of Mendelian heredity. Some authors even are inclined to restrict their interest entirely to groups of individuals that are propagated in this way. However, before we acquiesce in this new restriction of our field of study, it is worth while to see whether dissimilarity among the offspring is confined to hybrids. If it should prove to be present in non-hybrid organisms too, this fact should certainly be taken into consideration when we are going to interpret the results obtained with the hybrid ones.

In colonies of bacteria, a group of organisms in which sexual reproduction is unknown <sup>1)</sup>, it is sometimes found that part of the individuals differ in one or more of their characters from the rest. This applies even to colonies of which we are quite sure that they have been raised from a single cell and in which contamination with stray germs was entirely excluded. In order to observe this phenomenon two conditions are essential; in the first place the bacteria must be grown on a solid medium for otherwise the descendants of the aberrant individuals are lost among the normal ones, and in the second place the aberrant individuals must differ from the others in easily observable characters, e.g. in colour. When these conditions are fulfilled, the aberrant individuals form groups that are recognizable as narrow isosceles triangles with their apex at some distance from the centre and their base on the periphery of the circular

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<sup>1)</sup> Sexual reproduction has repeatedly been reported in bacteria, but so far none of these reports can be regarded as convincing. The argument that sexual reproduction must be present because in mixed cultures of bacteria sometimes new combinations of characters are observed, does not prove that sexual reproduction must have taken place. In a mixture of chemical compounds too new combinations may arise! That in colonies of unicellular or filamentous organisms genes may be exchanged in another way than in a multicellular organism where the sexual cells are the only ones with a different hereditary constitution that come in contact with each other, is certainly not excluded, but as the way in which this exchange in the unicellular organisms takes place, is as yet unknown, these organisms will in this essay be left out of consideration.



colony. How these changes are brought about, is unknown. The fact that they can artificially be provoked by the same means by which in sexually reproducing organisms mutations are induced, does not solve the problem, for although it suggests that here too in the course of the reproduction process irregularities in the distribution of the hereditary factors and eventually changes in the structure of these factors may play a part, it throws no light on the nature of the changes the internal organization of the cell has to undergo in order that such irregularities may take place. The phenomenon finds perhaps a counterpart in the differentiation of the various tissues in the body of the more bulky organisms, but as the way in which this kind of differentiation is brought about, is also completely unknown, this comparison does not bring us any further.

Apart from the differentiation in tissues referred to in the preceding paragraph the body of the more bulky organisms sometimes shows an entirely different kind of differentiation; the latter leads to local changes of a varietal character. Illuminative examples of this phenomenon are observed in some Angiosperms, where parts exhibiting a varietal deviation are sometimes found in the form of longitudinal strips beginning somewhere in the shoot and ending in the growing-point: individuals showing this abnormal character are known as "sectorial chimeras". Bamboos and other grasses with yellow-striped shoots may serve as an illustration. The strips with the aberrant character apparently owe their origin to a change in a cell of the growing-point, and they arise therefore in a similar way as the aberrant sectors in the bacterial colonies discussed in the preceding paragraph. Because of this it is rather strange that the faculty to produce sectorial chimeras is usually regarded as dependent on a hybrid constitution. According to this view the differentiation among the cells of the growing-point would be similar to that which we observe among the sexual cells of a hybrid, i.e. to the kind of differentiation that is, as we will see hereafter, the cause of the dissimilarity among the latter's offspring. That the paternal and maternal components of a hybrid nucleus may show a certain degree of incompatibility, and that this antagonism may lead to irregularities in the nuclear division, is certainly not unthinkable, and it is doubtless quite plausible to assume that under these circumstances the cells of the growing-point may undergo the kind of differentiation that is required for the development of a sectorial chimera, but the circumstance that a similar differentiation takes place in colonies of bacteria, where sexual reproduction is unknown, and where a hybrid origin of the individual cells therefore seems unlikely, should warn us against a too absolute faith in this hypothesis.

Not all sectorial chimeras owe their origin to a differentiation among the cells of the growing-point; they may also come into being when a bud is formed at a place where the tissues of two different organisms meet. This condition is fulfilled in grafts, but in order to obtain buds from the zone where the tissues of scion and stock are in contact with each other,

a somewhat devious technique has to be applied. To this end we must wait until scion and stock are firmly fused, and then the greater part of the scion must be removed by a cut passing under an acute angle through the zone of contact; by this act a surface is exposed in which cells of the scion and of the stock lay side by side, and when on this surface adventitious buds are formed, there is a chance that their cells are derived partly from the scion and partly from the stock.

The character of the buds whose origin was described in the preceding paragraph, is determined by the way in which the two kinds of cells are disposed. When they form groups separated from each other by more or less radial planes, the result will be a sectorial chimera, but it is also possible that one of the groups is completely overgrown by a single or double layer of cells belonging to the other partner. The growing-point of the shoot that develops from this bud, retains the latter's original structure; its interior part therefore consists of cells of one type, whereas one or two of the outermost layers consist of cells of the other kind. The characters of these so-called "periclinal chimeras" prove to be more or less intermediate between those of the plants to whom they owe their origin, and for this reason they were originally known as "graft-hybrids". That their nature is entirely different from that of the true hybrids, is revealed when they are self-fertilized, for in that case the whole offspring is found to revert to the type of one of the parents. This is easily comprehensible. Here as elsewhere the sexual cells are derived from the subepidermal layer of the growing-point, and their character is therefore determined by the genetic constitution of this layer. The identity of the offspring with the parent out of whose cells the subepidermal layer was formed, proves that the genetic constitution of these cells remained unchanged.

Organisms provided with a body consisting of parts that differ in genetic constitution, may also be met with outside the plant kingdom. Herbst describes the fertilization of Echinid eggs whose nucleus has undergone its first division. This leads to the development of a larva that may be regarded as a sectorial chimera, for its body consists partly of cells provided with nuclei descended from the fertilized one, and partly of cells provided with haploid nuclei derived from the unfertilized one. When the fertilization is effected by means of a sperm obtained from another species or variety, the component with the diploid nuclei will in addition possess a hybrid constitution.

There are also composite organisms whose components are far more fundamentally different than those of the chimeras discussed above. Striking examples are the perpetual symbioses, e.g. those between a number of Angiosperms (Rubiaceae belonging to the genera *Pavetta*, *Psychotria* and *Heterophyllaea*, Myrsinaceae belonging to the genus *Ardisia* and some of its nearest allies, two species of *Dioscorea*) and Bacteria. The latter form a kind of galls on the leaves of these Angiosperms

and a layer of slime round their growing points. The perpetuation of the symbiosis rests in these cases on the presence of the bacterial slime round the growing points, for this slime spreads from the latter over the primordia of the carpels to the young ovules and penetrates in a subsequent stage into the micropyle. The pollen tube has to pass through this slime on its way to the embryosac, and its top will almost certainly carry some of the germs into the vicinity of the egg-cell. It is therefore practically certain that the embryo will be infected. As the Bacteria are in this way transmitted from generation to generation, their presence apparently answers the definition given above of a hereditary character, and the name "spurious heredity" that is sometimes applied to this manner of transmission, is therefore open to objection. It may, of course, be argued that the presence of the Bacteria can not be regarded as a feature of the Angiosperm but only as one of the composite organism formed by the latter and the symbiont, and that the term heredity is better restricted to simple organisms. This would do no harm, for we will have to discuss the perpetual symbioses at any rate under the heading ecology, where the relations existing between organisms that live in each other's vicinity, are dealt with.

If the term hereditary is deemed to be inapplicable to the perpetual symbioses dealt with in the preceding paragraph, it should not be applied either to the special features by which the various kinds of Lichens are characterized, for the Lichens too are composite organisms, and their special features are at least partly due to the interaction between the two components, one of them either a Cyanophyceae or a Green Alga, the other one a Fungus. The difficulty with which we are confronted in this case, lies in the circumstance that the special features of the Fungus as well as those of the Cyanophyceae or the Green Alga which with good right may be regarded as hereditary ones, are of a similar kind as those that are exhibited by the composite organism, which we would have no right to regard as hereditary. Still, if we wish to remain logically consistent, we will have to leave them out. The question is especially of interest to the taxonomist, for if the distinguishing characters of the various kinds of Lichens can not be regarded as hereditary, it is impossible to accept the latter as species, and in that case they can, of course, not be brought together in groups of higher order either. The most important argument in favour of the view that the Lichens should form a taxonomic unit, has, moreover, lost its value, for the lichenic acids that for a long time were regarded as their most characteristic feature, are now known to occur also outside this group.

After this excursion into the field of vegetative mutation and into the domain of the chimeras and other composite organisms, we must return to the problem presented by the difference between individuals producing an offspring that is not only uniform but also true to type, and individuals of hybrid origin whose offspring is not uniform and there-

fore in its entirety never true to type. The key to this problem must, of course, be found in the character of the hybrid.

How completely for a long time the importance of the hybrid for the elucidation of some of the main problems in the field of heredity was overlooked, is perhaps best illustrated by the fact that as late as the seventeenth century a controversy could exist between two groups of scientists with regard to the way in which the hereditary characters are transmitted, one group, the animalculists, maintaining that the spermatozoids should be regarded as the carriers of these characters, the other group, that of the ovists, insisting that this function should be credited to the female sexual cells. If they had been aware of the fact that in the hybrid the characters of both parents are combined, and that it is often entirely irrelevant which of the two forms is used as the male parent and which as the female one, this controversy could, of course, never have arisen.

The equality that so often is found between the products of the reciprocal crosses, is the first point we will consider. It is thought to throw some light on the localization of the hereditary characters in the first place in the sexual cells themselves, but by extension also in the other cells of the body. It is a well known fact that the amount of cytoplasm present in the male cell is, as a rule, smaller than that in the female one, and may sometimes be reduced to an almost negligible rest; it is even possible, although difficult to prove, that this rest is at the moment of fertilization entirely suppressed. The circumstance that in crosses between varieties the influence of the male cell on the character of the hybrid is nevertheless as great as that of the female one, is therefore a strong argument in favour of the assumption that the hereditary characters are localized in the nuclei. It might be objected that the nuclei of the male and female sexual cells themselves may also differ in size, but this difference, which is but rarely of considerable value, may probably be ascribed to the presence of substances that are not directly involved in the transmission of the hereditary characters. The much larger difference between the amounts of cytoplasm in the male and female sexual cells might, however, also be due to the presence of such substances, and as the argument based on the difference in the amount of cytoplasm can therefore not be regarded as conclusive, we will have to look for other ones.

Boveri at one time claimed to have proved the superfluity of the cytoplasm by means of experiments in which enucleated fragments of Echinid eggs were fertilized by sperms belonging to another species; the larvae should have shown the character of the male parent. Afterwards he had to admit that not all sources of error had been excluded, and as a repetition of the experiments apparently remained unsuccessful, their results can not be regarded as convincing.

The parallelism between the way in which the chromosomes and the hereditary characters are transmitted, has led to the view that the



chromosomes are the carriers of the hypothetical elements in which the hereditary characters are vested. If it could be shown that the chromosomes are the only parts in which these elements could find a place, the question would, of course, be decided, for as the whole set of chromosomes is confined within the nucleus, the latter would carry the complete set of elements that are responsible for the transmission of the hereditary characters. This so-called chromosome theory of heredity will be discussed further on, but a single objection must here already be brought forward. The parallelism between the tetrad or reduction division and the differentiation of the sexual cells of different genetic constitution, the argument on which the theory originally was founded, is doubtless-very striking, but it has apparently always been overlooked that there is good reason to assume that the reduction of the chromosome number is accompanied by a reduction of the amount of cytoplasm, and it may therefore be argued that there might also exist a parallelism between the latter and the distribution of the hereditary characters over the products of the tetrad division. It might after all be more or less accidental that the reduction division of the nucleus may be studied in considerable detail, but that the changes going on in the cytoplasm remain hidden to us. It can hardly be denied that at times changes of considerable extent must take place in the latter, although we see nothing of them, for the differentiation of the various parts of the body is doubtless carried out through the intermediary of the cytoplasm, and this must involve important changes in the latter. That during the reduction division no changes in the quality of the cytoplasm are observed, can therefore not be taken as proof of their absence.

So far we have placed ourselves on the standpoint that the whole set of hereditary characters must be contained in the nucleus, and we have tried to show that the observed phenomenon, the identity of the results of reciprocal crosses, is in good agreement with this supposition, but we may also attack the problem from the other side, and it is by no means sure that this will lead to the same conclusion. The question may be formulated also in this way: are there any indications for an active participation of the cytoplasm in the transmission of hereditary characters?

Arguments in favour of the view that the cytoplasm too plays a part in the transmission of hereditary characters, have been derived from exceptions to the rule that the results of reciprocal crosses are identical. These exceptions therefore deserve a critical examination.

Inequality between the results of reciprocal crosses may be due to the hybrid nature of at least one of the parents, which produces therefore, as we will see hereafter, sexual cells of different genetic constitution. Before entering into the question how this may lead to differences between the results of the reciprocal crosses, we will first of all have to find out under what circumstances the hybrid nature of a parent may remain concealed.

The hybrid nature of an organism may remain concealed because its

sexual cells lack a factor that is required in order that the difference in their genetic constitution may reveal itself. The hybrid or heterozygotic nature of such organisms is brought to light when they are crossed with individuals in which this additional factor is present. In this case it makes no difference whether the individual with the hidden heterozygotic nature is used as the male or as the female parent.

The hybrid character, however, may also remain concealed because there is a selective mating between the sexual cells or because the zygotes that are obtained by the union of the various kinds of sexual cells, are not all viable. If the sexual cells are of two kinds, which we will indicate for the sake of convenience by the letters *a* and *b*, the fusion between two cells *a* and that between two cells *b* may be impossible because the cells of the type *a* are all male and those of the type *b* all female, or it may prove ineffective because *aa* and *bb* are not viable. In both cases but one combination is possible, viz. that between *a* and *b*. This zygote develops into an individual whose sexual cells are, as we will see hereafter, also of the two types *a* and *b*. So long as hybrid individuals of this kind are self-fertilized or mated with each other, the strain therefore remains true to type, and its heterozygotic condition passes unobserved. However, when the sexual cells of such a hybrid come together with sexual cells of another genetic constitution, the combination with *a* as well as with *b* may prove viable, and then, of course, the heterozygotic condition is unmasked.

In the case considered in the preceding paragraph the result of the reciprocal crosses will be unequal when the difference in genetic constitution is correlated with a difference in sexual function, the eggs being all of the type *a* and the male cells of the type *b*. This applies e.g. to the sexual cells of *Oenothera muricata* and of *O. biennis*. If we indicate the genetic constitution of the egg of *O. muricata* by *a* and that of its male cell by *b*, that of the egg of *O. biennis* by *c* and that of the latter's male cell by *d*, we will recognize at once that the results of the reciprocal crosses must be different, for seeds harvested from plants of *O. muricata* fertilized by *O. biennis* owe their origin to the fusion of cells with the constitution *a* and *d*, whereas those obtained from plants of *O. biennis* pollinated by *O. muricata* will have been formed as the result of a fusion between cells of the types *b* and *c*.

The inequality between the results of reciprocal crosses that finds its origin in the heterozygotic condition of the parents, does not shed any light on the question of the cytoplasmatic influences, and in the following exposition we will confine ourselves therefore to those cases where the parents may be regarded as truly homozygotic, and where the sexual cells of each of them therefore are of one kind.

In the case of truly homozygotic individuals inequality between the products of the reciprocal crosses seems to occur mostly when the parents are but distantly related. The interspecific crosses between Musci carried out by F. Wettstein and those between various *Epilobium* species studied

by Lehmann and Michaelis are of special importance. The fact that in all these cases the hybrids proved to be "metroclinous", i.e. that they resembled the female parent, makes it plausible that the difference is due to an influence exercised by the cytoplasm of the motherplant.

Wettstein observed in the genus *Funaria* that reciprocal crosses between varieties gave identical results, but that reciprocal crosses between species led to unequal products.

In the crosses between *F. mediterranea* and *F. hygrometrica* the difference already showed itself in the structure of the sporogonia. Hybrid ones developing on plants of *F. mediterranea* were on the whole similar to the latter's non-hybrid sporogonia, whereas hybrid sporogonia developing on plants of *F. hygrometrica* resembled in most respects the latter's homozygotic ones; the hybrid sporogonia therefore were distinctly "metroclinous". The differences between the reciprocal hybrids stood out more clearly when, by the aid of a method devised by Ed. and Em. Marchal, the sporogonia were induced to form diploid moss plants, i.e. gametophytes with the same number of chromosomes in their nuclei as the sporogonia. Haploid moss plants obtained from the spores of the hybrid sporogonia exhibited in some respects a greater variability than the diploid ones derived in a vegetative way from the sporogonia, but they too showed on the whole a strong resemblance to the female parent; a small number of individuals approached the type of the male parent. The diversity observed among the plants developing out of the spores proved that the nuclei of the mothercells of the latter must have been, at least to some extent, of hybrid character.

Wettstein ascribed the antagonistic results of the reciprocal crosses to an influence exercised by the cytoplasm of the female parent; it would be responsible for the almost complete suppression of the characters carried by the male nucleus. This is probably right, but Wettstein's further conclusion that the cytoplasm therefore must be able to produce certain characters on its own account, i.e. without the intermediary of the nucleus, is open to criticism. The hypothesis that the cytoplasm contains a "genetic element", for which Wettstein introduced the name "plasmon", appears to be superfluous, for the observed phenomena do not exclude the possibility that the influence exercised by the cytoplasm of the female parent on the male nucleus, i.e. the influence by which part of the genetic factors carried by the latter are eliminated, may be due to a mechanism that owes its origin to the activity of the nucleus of the egg cell, eventually in collaboration with the nuclei of the surrounding cells. This influence on the nature of the cytoplasm must have been exercised before the moment of fertilization, for if it took place at that moment, there could have been no difference between the results of the reciprocal crosses: in that case the effect of the two nuclei would have been the same, no matter which of them was female and which male. Although we will have to admit that the cytoplasm exercises an influence

on the result of the cross, there is therefore no reason to assume that this influence is due to the presence of autonomous hereditary factors, for the mechanism by which this effect is brought about, might quite well have been called into existence by previous nuclear activity.

Wettstein tried to prove the correctness of his view regarding the presence of autonomous hereditary factors in the cytoplasm in the following way. Among the haploid plants raised from the spores of a hybrid sporogonium developed upon a plant of *F. mediterranea*, a specimen was selected that showed in its leaf characters the rather rarely occurring approximation to the paternal type, i.e. to *F. hygrometrica*. This specimen was fertilized by sperms taken from *F. hygrometrica*, but produced nevertheless a sporogonium of the maternal type, i.e. resembling that of *F. mediterranea*, whereas its own sperms produced on *F. hygrometrica* sporogonia of the *F. hygrometrica* type. The influence of the maternal plasma is therefore unmistakable, but here too there is no proof of the autonomous character of the mechanism to which this influence must be due. The presence of the aberrant individuals approaching *F. hygrometrica* is difficult to account for by any theory. Wettstein assumed that they possessed more or less pure *F. hygrometrica* nuclei in *F. mediterranea* plasm, but in that case it would be difficult to understand why the sporogonia obtained as a result of the fertilization with *F. hygrometrica* sperms would have reverted to the *F. mediterranea* type, for they must have contained the same kind of cytoplasm as the aberrant individuals themselves and also almost pure *F. hygrometrica* nuclei. It seems more plausible to assume that the aberrant individuals were extreme variants, not much different in their genetic constitution from the other ones but accidentally verging to the *F. hygrometrica* type. The results of the crosses carried out with these aberrant individuals are certainly not more conclusive than those of the crosses between normal individuals, and they can therefore not be advanced as arguments against the view that the influence exercised by the female plasma is due to a mechanism that owes its origin to nuclear activity, and they are fully inadequate to prove the autonomous nature of this mechanism.

The differences exhibited by the reciprocal hybrids between some subspecies of *Epilobium hirsutum* and by the reciprocal hybrids between some more conspicuously distinct representatives of the genus *Epilobium* have also been ascribed to the presence of hereditary factors in the cytoplasm, but they too can be explained as the result of previous nuclear activity.

The study of the metroclinous *Epilobium* hybrids is greatly hindered by their sterility, but those resulting from the cross between *E. luteum* as the female parent and *E. hirsutum* as the male one could successfully be fertilized by means of *E. hirsutum* pollen, and as the offspring obtained in this way also produced a progeny when fertilized by the *E. hirsutum* pollen, the number of generations in which the influence of the latter could



be studied, was apparently unlimited. A large number of generations were raised in this way, and on the whole the type of the hybrid remained the same, i.e. it retained the strong resemblance to *E. luteum*, the only difference being that the sterility underwent in the long run a slight decrease.

The preponderating influence exercised on the character of the *Epilobium* hybrids by the female parent is explained by Michaelis and Lehmann in the same way as the corresponding phenomenon in the interspecific moss hybrids was by Wettstein; Michaelis and Lehmann too assume that the character of the hybrid is in the main determined by the genetic constitution of the cytoplasm. In one respect, however, they are somewhat less orthodox, for they hold that the latter undergoes in the long run some influence from the hybrid nucleus; the latter would manifest itself e.g. in the decrease of the pollen sterility. I am not fully convinced of the reliability of the figures on which this claim rests, but if the change really may be taken as significant, an explanation might be found in the assumption that accidentally some new factors are introduced by the sperms or that some of the factors already present undergo a duplication. This, however, is a point of minor importance. The main point is that there is apparently in the case of the *Epilobium* hybrids no more proof for the autonomous character of the factors that are operating in the cytoplasm than there is in the case of the moss hybrids produced by Wettstein. Here too the results can as well be explained by assuming that the cytoplasmatic mechanism by which an important part of the characters carried by the sperm nucleus are eliminated, has previously been induced by nuclear activity.

As stated above, the arguments that have been advanced in support of the view that some of the hereditary characters might be localized outside the nucleus, are all based on the inequality between the results of reciprocal crosses. The arguments discussed above unfortunately proved to be inconclusive. The hypothesis, however, would gain a firmer foundation if special reasons could be found for assuming that some of the characters of the metroclinous hybrids must necessarily be localized outside the nucleus. The characters that determine the green or yellow colour of the leaves and the yellow or orange-red colour of some flowers and fruits, might belong to this category, for these colours are developed by the intermediary of plastids, i.e. by organs that multiply by division and possess therefore a similar kind of individuality as the nucleus. The idea that they might function in the same way as the latter as carriers of hereditary characters, can therefore not peremptorily be dismissed.

In some crosses between entirely green plants and varieties provided with variegated leaves the hybrids proved to be distinctly metroclinous. As the colour of the leaves is determined by that of the plastids, and as the latter are in the sexual cells confined to the female ones, the explanation that this result is due to the localization of the responsible hereditary

factor in the plastids, seems plausible enough. It is possible, however, that the abnormal colour of the plastids in the variegated leaves might not be due to a hereditary factor but to a virus causing a disease of the plastids. It is true that such a virus could not always be isolated, but this may be due to the imperfection of our methods. With regard to the plastids we are therefore in a similar plight as with regard to the cytoplasm: although it can not be denied that these parts might carry hereditary characters, there is as yet no decisive proof that they do. It should, moreover, not be overlooked that the presence of hereditary characters in the plastids would not decide the question of their presence in the cytoplasm.

An argument of an even more hypothetical nature for the assumption that some of the hereditary characters might be localized outside the nucleus, is based on the belief that the hereditary characters are not all of them of the same value. A localization in different parts of the cell might offer a plausible explanation of these differences.

With regard to the characters supposed to be carried by the plastids, we will have to admit that they do not impress us as markedly different from those localized in the nucleus, e.g. from some other flower and fruit colours. With regard to the characters supposed to be localized in the cytoplasm the position, however, is somewhat different, for these characters are often regarded as more fundamentally important than those that have their place in the nucleus. Whereas differences between the latter are held to be responsible for differences of a varietal character, those supposed to be present in the cytoplasm would constitute specific differences.

In discussing the problem mentioned in the preceding paragraph we should always bear in mind that varieties and species are taxonomic conceptions, and that there is no reason to assume a complete correspondence between them and the categories proposed by the students of heredity. Although the variety may be defined, as I have pointed out in the essay on the principles of taxonomy, in a genetic way by identifying the points in which its genetic constitution differs from that of its sister varieties, with the so-called unit characters of the Mendelians, it does not seem possible to find an acceptable genetic definition of the species.

At one time it was thought that the taxonomic value of the difference between two forms could be determined by mating them with each other. If they produced a fertile offspring, the difference was deemed to be of a varietal character; if they proved unable to produce a fertile offspring or if they produced no offspring at all, the difference was thought to be of specific character or of even higher value. This, however, has proved a delusion. It is now known that a large number of universally recognized species produce a fertile progeny when they are mated, and that there is in this respect no fundamental difference between species and varieties. However, we must not overestimate the value of this conclusion, for it can not be doubted that the absence of a constant correlation between the sterility of the hybrid and the degree of taxonomic inequality between

its parents, is partly due to the fact that there are different kinds of sterility. In extreme cases the sexual cells of the hybrid prove to be imperfectly developed, but in other instances no such abnormalities are apparent. That sterility does not always depend on the latter, is well illustrated by the cases of self-sterility met with in some bisexual plants, and by the incompatibility observed in heterostylous plants between the sexual cells produced by individuals belonging to the same form.

The fertility of the species hybrids may also be of different kind. It is not necessary to devote much time to the fertility of the *Hieracium* hybrids of which Mendel had already recognized that they remain true to type. This is due to the fact that the cell from which the embryo develops, is not the product of a reduction division, and possesses therefore the same kind of nucleus as the other cells of the hybrid. Fertilization does not take place, and the fertility of these hybrids must therefore be regarded as the result of a kind of vegetative propagation. More interesting from a genetic point of view is the fertility of *Primula kewensis*, a hybrid of *P. floribunda* and *P. verticillata*, and that of Müntzing's *Galeopsis* hybrid, which resembles the wild *G. tetrahit*. They are, like the *Hieracium* hybrids, fertile and constant, but in contradistinction to the latter, their egg cells must be fertilized. Cytological investigation has shown that these hybrids are tetraploid, i.e. that their nuclei contain twice as many chromosomes as one would expect, which means that at one time the original number must have been doubled. If the chromosome sets of the parental sexual cells are designated respectively by  $a$  and  $b$ , the chromosome set of the hybrid did not remain  $a+b$ , but became  $2a+2b$ . This constitution explains why the chromosomes are all paired. Plants of the type of *Primula kewensis* are therefore no ordinary hybrids but a kind of nuclear chimeras, their nuclei containing the full chromosome sets of both parents. In ordinary species hybrids the parental chromosomes are often unable to arrange themselves in pairs, and as a result of this the reduction division is disturbed, but in the tetraploid individuals this is not so, and here the production of normally functioning sexual cells, each of them provided with the chromosome sets  $a$  and  $b$ , is therefore safeguarded.

The view that species hybrids should always be metroclinous, although perhaps not fully proved, looks plausible enough. However, if it could be proved that the variegated plants discussed above are not merely individuals attacked by a virus, metrocliny would not be confined to species hybrids but would occur in hybrids between varieties too.

The characters by which the varieties differ from each other, rest, as we will see hereafter, on the presence of exchangeable hereditary units, but the characters in which the species differ seem to form a more stable whole. Their cohesion, however, is not always so strong that it can not be broken, and the difference between the species and the variety is therefore in this respect perhaps less fundamental than has been assumed. For the moment, however, we will suppose that the difference between the

specific and the varietal characters is due to a difference in cohesion. The question whether the characters in which the species of the same genus differ, may have their seat in the cytoplasm, can in this case be reduced to the question whether the cytoplasm may be regarded as a sufficiently stable substratum for characters possessing a considerable degree of cohesion. The little we know of the structure of the cytoplasm, certainly does not justify an unreserved negation of this possibility, but there are doubtless weighty arguments against it. We draw attention to the fact that the cytoplasm is the medium in which the influences generated in the nucleus play their game; this would hardly be possible if it possessed an entirely stable constitution. Another solution of the problem therefore sounds more attractive. As we will see presently, there is good reason to believe that the Mendelian or varietal characters are localized in the peripheral part of the chromosomes, and that the characters that show a certain degree of correlation, have their seat in the same chromosome; for this reason it seems plausible to look for characters that are still more firmly united, either at the same place or else in the interior of the chromosomes, i.e. in the latter's axial structure. For the time being it seems, at any rate, permissible to discard the hypothesis of the presence of hereditary characters in the cytoplasm. From now on we will assume therefore that they are all localized in the nucleus.

When the parents differ in a more or less considerable number of characters, the hybrid is, as a rule, more or less intermediate between them, for it resembles in some respects the first parent and in other ones the second. When the parents differ in a few points only, the hybrid may, on the other hand, look entirely like one of them. Its hybrid character is in this case revealed by its offspring. If the latter is obtained either by selffertilization or by interbreeding, and if it consists of a sufficient number of individuals, it appears to comprise always a number of individuals resembling the other parent, and, as a rule, also some that lack one or more of the characters by which the hybrid differed from the latter. This "splitting" among the offspring of the hybrid is the second important phenomenon with which Mendel's investigations have acquainted us. It is best studied in bisexual plants and their varieties, because the hybrids of the latter and the descendants of the hybrid can all be fertilized by their own pollen; this has the advantage that the progeny of each individual can be studied separately.

If the parents, usually designated as  $P_1$  and  $P_2$ , differ but slightly, and if the hybrid, for which we may use the sign  $F_1$ , is similar in aspect to one of them, the offspring of the hybrid, indicated in this notation schema as  $F_2$ , may consist of the two parental types in the proportion 3 : 1, the larger group containing the individuals that resemble the parent whose type reappeared in the hybrid. When a sufficient number of  $F_2$  plants is self-fertilized, it appears that one third of the individuals belonging to the larger group produce an offspring that is entirely true



to type, whereas the offspring of the other individuals belonging to this group consists, in the same way as that of the hybrid itself, of two kinds of individuals in the proportion 3 : 1, the larger group once more resembling the hybrid, the smaller one the grandparent whose type reappeared in the  $F_2$ . The progeny of the  $F_2$  individuals belonging to the smaller group remain true to type.

The offspring of a hybrid that resembles one of its parents, may also show a more complex composition. In that case it comprises two or more new types differing from the other ones by the absence of one or more of the characters by which the hybrid deviated from the other parent. The proportion in which the various types appear, may e.g. be 9 : 3 : 3 : 1, in which case in the mean 9 out of each 16 individuals resemble the parent that transmitted its type to the hybrid, and 1 the other parent, whereas the two remaining groups consist of individuals in which one of the distinguishing characters is absent. When the hybrid resembled in one of its characters the first parent, and in another one the second, the central groups of the  $F_2$  prove to be identical with the parents, whereas the largest group repeats the type of the  $F_1$ , and the smallest one develops a new type characterized by the absence of the distinguishing characters. When from a sufficiently large number of  $F_2$  individuals an offspring is raised, it appears that the latter remains sometimes true to type, viz. in one out of each 9 individuals belonging to the largest group, in one out of each 3 individuals belonging to the central groups, and in all the individuals belonging to the smallest one. All other  $F_2$  individuals produce a heterogeneous offspring, sometimes of the same composition as the  $F_2$ , and sometimes consisting of two types only, in the proportion 3 : 1; in the latter case the composition is therefore the same as in the  $F_2$  of the hybrid discussed in the preceding paragraph.

When the results are not influenced by abnormal circumstances like apogamy, doubling of the chromosome set, or lack of viability in part of the sexual cells, the offspring of a hybrid consists, as we have seen, partly of individuals which produce an offspring of the same composition as that of the hybrid itself and which are therefore to be regarded as genetically identical with the latter, and partly of individuals that are similar to the parents and produce an offspring that remains true to type. In addition individuals may be present in which the characters of the parents appear in other combinations, and in that case the  $F_3$  shows besides the type of splitting observed in the  $F_2$  also simpler ones, e.g. the splitting in the proportion 3 : 1. The explanation of this difference in the manner of splitting is already indicated by the presence or absence in the  $F_2$  of individuals that resemble in some of their characters the first grandparent and in other ones the second; this exchange of characters proves that the latter are not combined in an unalterable whole, but that they are separable. When there are in the  $F_2$  no individuals in which such a recombination of characters is noted, the difference

between the grandparents may, as a rule, be ascribed to the presence or absence of a single, indivisible "unit"; when they are present, it must be due to two or more separable ones. De Vries introduced for these units the name "pangenes", which shortly afterwards was abbreviated by Johannsen to "genes".

Above we discussed the results of a cross between parents differing in a single gene. In the case we had in view, the hybrid resembled one of the parents, and its offspring consisted of two groups of individuals, one three times as large as the other and similar to the grandparent that had lent its type to the hybrid, and one resembling the other grandparent. This is the state of things that is most often met with. The hybrid, however, may also be more or less intermediate between the parents. As indicated above, this may be due to the fact that the parents differed in several characters, and that the characters of the hybrid were partly derived from the first parent and partly from the second. However, a hybrid may also be more or less intermediate between the parents when the latter differ in one gene only. The true nature of the intermediate hybrid whose parents differed in a single gene, is recognized at once when its offspring is studied, for in this case the latter will consist of three different types in the proportion  $1 : 2 : 1$ , the middle group repeating the type of the hybrid, the two smaller ones resembling the parents. This is easily comprehensible. In our earlier example, where the proportion  $3 : 1$  was found, the larger group consisted for two thirds of individuals that were genotypically identical with the hybrid, whereas one third were of the same genetic constitution as the parent that lent its type to the hybrid: in the offspring of an intermediate hybrid whose parents differed in a single gene, these two groups of individuals are of different aspect. The proportion  $3 : 1$ , which is doubtless more often met with than the proportion  $1 : 2 : 1$ , might therefore be written  $(1+2) : 1$ . Genotypically the proportion is always  $1 : 2 : 1$ .

Above we have dealt with hybrids that are in aspect more or less intermediate between the parents, and with other ones that are similar to one of them. Occasionally, however, some of their characters may be either more or less strongly developed than they were in either of the parents. Especially the presence of an increased vigour in the hybrid, which in the case of corn recently has led to a kind of revolution in the breeding methods, has often caused wonder. It is nevertheless not wholly unexpected. The influence of a gene is determined by the nature of the substratum on which it acts, i.e. by the sum of the other genes. In parents differing in a single gene this substratum is, of course, identical, and as it is transmitted unchanged to the hybrid, the result depends in this case on the effect exercised by a single gene more or less. It is possible that the single gene of the hybrid proves to be equipollent to the pair that were present in one of the parents, but it is also possible that its effect remains "infra-optimal". The effect of the gene pair might also be "supra-

optimal", i.e. past the optimum value, and in that case it might even be smaller than that of the single one, but of this no fully convincing examples seem to be known. Where "hybrid vigour" has been noted, the parents differed apparently always in a larger number of genes. As for each gene the combination of the remaining ones forms part of the substratum on which it exercises its influence and which in its turn determines the character and the magnitude of the effect, it needs no special emphasis that this effect may sometimes show unexpected variations, especially when the difference between the parents and the hybrid rests on a rather large number of genes: under such circumstances the hybrid may therefore develop characters that did not manifest themselves in the parents or that manifested themselves in the latter to a minor degree. As a striking example of an entirely new character we may mention the coloured flowers that sometimes appear in hybrids between white-flowered varieties.

Less easily comprehensible than the origin of hybrid vigour is its gradual decline in subsequent generations. If back-crosses with one of the parents are allowed to intervene in the result, there will be a gradual reversion to the type of the latter, and this will, of course, be accompanied by a decrease in the average vigour of the population. If back-crosses with the parents are excluded, the explanation offers greater difficulties. A simple calculation shows that under ideal conditions the proportion between the various kinds of homo- and heterozygotes observed in the  $F_2$  will remain the same in the following generations. This balance may, however, be upset by selective mating and by differences in viability between the various kinds of zygotes. If e.g. the sexual cells of the two parental types mate less easily one with the other than with their own kind, this would lead, in the same way as back-crossing with one of the parents, to a gradual decrease in the number of heterozygotes. In order to find out what actually happens, we might fertilize the hybrid with pollen obtained from an individual which lacks the single genes of the hybrid, for when matings between sexual cells of a definite type are favoured or when some of the zygotes prove to be less viable, this will reveal itself in deviations from the expected numerical equality between the groups of various genetic constitution.

As there seems to be no reason to assume that the final solution of the problem of hybrid vigour will materially alter our ideas on the mechanism of heredity, we will leave it here and return to our analysis of the splitting observed in the hybrid's offspring.

As a rule the offspring of a hybrid consists, as we have seen, not merely of individuals of its own kind but also of one or more groups that show a different aspect. The hybrid therefore does not transmit its character to all its descendants but only to a part. How is this to be understood?

In the egg cell that formed the starting-point of the hybrid, the genes of the male and female parent were brought together. At one time the

sets must have been present side by side, but it is thinkable that they may subsequently have undergone a fusion. In that case the sexual cells of the hybrid too would have been provided with these "hybrid" gene sets, and then the offspring obtained by self-fertilization would have been uniform. As this is not so, the supposition that the parental gene sets undergo a fusion, is apparently wrong. It does, of course, not prove that the gene sets do not affect each other, but for the moment we will assume that the influence they exercise on each other, may be neglected, and we will try to find out whether the observed results can be explained on the base of this supposition.

As the male nucleus introduces into the egg cell a new set of genes, the fertilized egg-nucleus must be provided with a double set. As the nucleus is after each division gradually restored to its former size, it seems plausible to assume that the constitution of the mature nuclei is everywhere virtually the same. The nuclei descended from the fertilized egg-nucleus must therefore all of them be provided with the double set of genes. That the manner in which after each division the restoration of the nuclei to their original size is effected, still remains a mystery, is unfortunate, for so long as we see no light in this problem, our supposition will retain its hypothetical character.

In order to obviate a redoubling of the number of genes at each subsequent fertilization, the number has to be halved before the sexual cells come into action. This halving is supposed to take place during the so-called tetrad division, i.e. in the Metazoa when the sexual cells are formed and in the Seedplants, Ferns and Mosses when the spores come into being: in the latter organisms the sexual cells are produced by the "gametophyte", a body that owes its origin to a further development of the spore; in some other groups the tetrad division follows immediately after the fusion of the nuclei. The most striking feature of the tetrad division is the reduction of the number of chromosomes. The latter is in the four daughter nuclei half as large as in the nucleus of the mother cell and in that of all the latter's predecessors up to the nucleus of the fertilized egg.

As a result of the fusion between the male and the female nucleus the chromosomes are present in pairs, and each time the nuclei prepare themselves for another division, the chromosomes reappear in this arrangement. If we assume that they retain their individuality throughout the organism's whole course of development, one of the partners of each pair must be descended from the corresponding chromosome of the male nucleus, the other one from that of the female nucleus. During the tetrad division the partners, however, are separated from each other, and the sexual cells are therefore provided with a single set. As the genes are to be regarded as material particles, there is good reason to assume that they will be localized in the chromosomes, for the latter form the main content of the nucleus: by the reduction of the number of chromosomes the double set of genes of the fertilized egg will therefore be reduced to a single one.



It seems reasonable to assume that this is carried out in such a way that one of the partners of each gene pair is diverted to one daughter nucleus and the other one to a second, and that when instead of a pair but a single gene is present, the latter goes to one of the daughter nuclei. Whether this happens at the first or at the second of the two divisions that lead to the formation of the tetrad, and whether the daughter nuclei are therefore pairwise identical or whether they may eventually all four be different, is a question of minor importance in which we will not enter.

In the diploid nuclei of a homozygote the genes are all pairwise identical, and this applies also to the majority of the genes that are present in the diploid nuclei of a heterozygote. The products of the tetrad division receive one of the partners of each pair, and with regard to these genes there can therefore be no difference between them. This was to be expected, for if there were a difference, the offspring of a homozygote would not remain true to type either. A hybrid whose parents differed in a single unit-character, must possess in addition to the pairwise identical genes either a pair of unequal ones or else an unpaired gene. The latter is the more plausible supposition, for when a cross between two homozogotic plants of which one is provided with coloured flowers and the other with white ones, gives a hybrid provided with coloured flowers, the supposition that the absence of colour in the white-flowered parent should be due to the presence of a material particle whose activity is in the hybrid suppressed by another particle that is responsible for the production of a pigment, is not only far-fetched but entirely superfluous. The symbolization of the gene that is responsible for the development of the pigment, or of another character of whatever kind the latter may be, by a capital letter, and the indication of the absence of such a gene by a small letter of the same denomination, is merely a matter of convention, for the small letter might as well be replaced by the figure zero or by a dot, or it might be omitted altogether.

When a hybrid whose parents differed in a single gene pair, forms its sexual cells, half of the latter will be provided with this gene, for which we will use the letter *A*, whereas the other half will miss it. As it would serve no purpose to enumerate the genes the sexual cells have in common, the latters' genetic formulas may be abbreviated to *A* and *a*. Now, when the hybrid is self-fertilized, the chance that a sexual cell will meet one of its own kind will be equal to the chance that it will meet one belonging to the other group. If we assume that there is no selective mating and that the zygotes are all equally viable, the offspring will therefore consist of individuals provided with two of the genes *A* (whose formula therefore is *AA*, individuals with one of these genes (*Aa*), and individuals that lack this gene (*aa*) in the proportion 1 : 2 : 1.

If the parents differed in the presence or absence of the genes *A* and *B*, the hybrid will be provided with a single *A* and a single *B* (its formula is therefore *AaBb*), and if these genes are completely independent of each

other, one fourth of its sexual cells will be provided with  $A$  and  $B$ , one fourth with  $A$ , one fourth with  $B$ , and one fourth with neither of them (their constitution therefore may be written  $AB$ ,  $Ab$ ,  $aB$ , and  $ab$ ). When the hybrid is self-fertilized, 16 combinations will be formed of which 9 are different, viz.  $AABB$ ,  $AaBB$ ,  $aaBB$ ,  $AABb$ ,  $AaBb$ ,  $aaBb$ ,  $AAbb$ ,  $Aabb$  and  $aabb$ , and when the result is not obscured by selective mating or by differences in viability, they will appear in the proportion  $1:2:1:2:4:2:1:2:1$  (as  $AA$ ,  $Aa$  and  $aa$  as well as  $BB$ ,  $Bb$  and  $bb$  appear in the proportion  $1:2:1$ , the proportion in which the 9 different genotypes appear, is obtained by developing the square of  $1+2+1$ ). How the 9 different genotypes will look, depends on the effect that is produced by the genes  $A$  and  $B$  separately and in combination. When their effects are separately recognizable, and when both genes are of the kind that already exercises its full effect when present in the unpaired condition, the 9 genotypes will belong to 4 phenotypes appearing in the proportion  $9:3:3:1$ , i.e. of every 16 individuals 9 will, as a rule, be provided with both characters, 3 with the first, 3 with the second, and 1 with neither of them (this proportion is obtained by developing the square of  $3+1$ ). When the effect produced by each of the genes is separately recognizable, but when only one of them is of the kind that already exercises its full effect in the unpaired condition, the number of phenotypes is 6 and the proportion in which they appear, is found by developing the product  $(3+1)(1+2+1)$ , and when neither of them is of that kind, the number of phenotypes is 9 and the proportion in which they appear, is obtained by developing the square of  $1+2+1$ . Less than 4 phenotypes are found when the character depends upon the interaction of the two genes. When e.g. one gene is responsible for the production of anthocyanin in the corolla, and the other one changes the acid reaction of the cell sap in an alkaline one, the presence of the first gene is required in order that the latter may reveal itself, for the red colour of the corolla is in that case changed into a violet one. When the first gene is absent, the flowers are always white, no matter whether the other gene is present or absent. The proportion  $9:3:3:1$  therefore is changed to  $9:3:4$ , i.e. there are 9 plants with violet flowers against 3 with red and 4 with white ones. When one gene is responsible for the production of a chromogen, and another one for that of an oxydase by which the chromogen is changed into a pigment, the activity of each of them alone may remain hidden, and in that case there are but two groups, viz. pigmented and unpigmented individuals, in the proportion  $9:7$ . All these aberrant proportions are nevertheless in good agreement with the supposition that the genes themselves are completely independent and that their distribution over the sexual cells is left to chance. The circumstance that the parental types are always represented among the offspring of the hybrid confirms our hypothesis that the genes themselves remain unchanged.

The proportion in which the various types appear in the offspring of

hybrids whose parents differed in more than one gene, is, however, not always in agreement with the supposition that the genes are completely independent. As the proportion in which in the offspring of a self-fertilized hybrid the various types appear, is often difficult to determine, and as the figures moreover, owing to selective mating, may be unreliable, it is worth while to look for methods by the aid of which the genetic constitution of the hybrid's sexual cells and the proportion in which the various kinds of the latter are produced, can be determined with greater accuracy.

The cells that owe their existence to the tetrad division, differ occasionally in characters that are directly observable. In the hybrid between *Epilobium hirsutum* and *E. luteum* the pollen grains were found to be of four kinds: some proved to be large and ovoid, another group was large and fusiform, a third one small and ovoid, and the fourth small and fusiform. In some of the tetrads all four cells proved to belong to a different type! Where a diploid generation alternates with a haploid one, the cells that owe their origin to the tetrad division, sometimes develop into haplonts of considerable dimensions, e.g. in the mosses, and in that case the differences may reveal themselves in those haplonts.

In the great majority of the living beings the differences in the genetic constitution of the haplonts are, however, not directly recognizable, and in that case we have to base our conclusions with regard to their identity on a study of the diplonts, i.e. on the products resulting from a combination of the sexual cells of the haplont with other sexual cells. To this end originally use was made of the diplonts obtained either by self-fertilization or by interbreeding of the hybrids, but there is another way that is at once more direct and less liable to lead to false conclusions. Instead of fertilizing the hybrid with its own sexual cells it makes use of the sexual cells of an individual that differs from the hybrid in the absence of the genes of which the latter contains but a single specimen.

When a hybrid of the type  $AaBb$ , whose sexual cells therefore are  $AB$ ,  $Ab$ ,  $aB$  and  $ab$ , is crossed with an individual whose genetic formula is  $aabb$  and whose sexual cells therefore are all of the type  $ab$ , the result will be an offspring consisting of four different genotypes, viz.  $AaBb$ ,  $Aabb$ ,  $aaBb$  and  $aabb$ , and when the hybrid produced its four different kinds of sexual cells in equal number, the offspring will consist of four equally strong groups; when the genes  $A$  and  $B$  lead to the development of characters that are separately recognizable, these four groups will also be phenotypically distinct. Self-fertilization of the hybrid would have resulted in the production of  $(1+2+1)^2=16$  different genotypes, which in case the influence of the genes  $A$  and  $B$  was separately recognizable, would have belonged to the same four phenotypes as are obtained by means of the cross with the individual which lacked these genes. As we have seen above, these four phenotypes would in this case have appeared in the proportion  $9:3:3:1$ , which means that in order to ascertain the presence of the individuals belonging to the last group, which is

represented but once among each 16 individuals, we require an offspring four times as large as when we base our conclusions on a cross with an individual with the formula *aabb*, for in that case each of the groups is represented by one individual out of each 4. The cross with the individual *aabb* has, moreover, another advantage: as the latter's sexual cells are all of the same kind, selective mating is, of course, entirely excluded. However, here too the reliability of the results may be impaired by differences in viability between the various combinations. In plants provided with a uni-ovular ovary and in animals whose eggs are fertilized outside the body, the differences in viability between the various combinations can at once be ascertained.

Crosses between a hybrid with the formula *AaBb* and an individual *aabb* have shown that the hybrid's sexual cells *AB*, *Ab*, *aB* and *ab* are not always produced in equal numbers, but very often in the proportion  $n : 1 : 1 : n$ , in which  $n$  may be larger or smaller than 1. The proportion appeared to vary in these cases according to the manner in which the hybrid was formed, i.e. according to the genetic constitution of the parents. If the latter were *AABB* and *aabb*, i.e. when the hybrid owed its origin to a fusion between sexual cells of the types *AB* and *ab*,  $n$  was always larger than 1. If, on the other hand, the parents were *Aabb* and *aaBB*, and the sexual cells therefore *Ab* and *aB*,  $n$  was smaller than 1. The sexual cells of the parental types are therefore always better represented than those in which the genes appear in a new combination. In most cases, moreover, the reciprocal of the value found for  $n$  in case the parents were *AABB* and *aabb*, appeared to be approximately equal to that which was obtained when they happened to be of the constitution *Aabb* and *aaBB*.

Exceptions to the rule that the reciprocal of the value found for  $n$  when the genes are derived from the same parent and that found for  $n$  in case one of the genes is derived from the male parent and the other from the female one, are approximately equal, have been noted in the offspring of some *Zea* hybrids studied by Demerec and in that of some *Pharbitis* hybrids investigated by Imai. In these cases the reciprocal of the value found for  $n$  when the parents were of the type *Aabb* and *aaBB*, fell distinctly behind the value obtained for  $n$  when they were of the type *AABB* and *aabb*. These deviations from the rule may have been caused by factors of secondary importance, like differences in vitality between the various genotypes, but in view of the fact that the reciprocal of the value found for  $n$  when the two genes were divided over the two parents, was seen to fall always behind the value found for  $n$  when they were derived from the same parent, it seems more probable that they indicate a difference of more fundamental importance. Further on I will come back to this point.

As a means to describe the relation between the genes *A* and *B* when the sexual cells *AB* and *ab* are either more or less numerous than *Ab* and *aB*, I will use the terms "attraction" and "repulsion". It is now customary



to speak in these cases of "linkage", but the use of this term should not be encouraged. If  $a$  and  $b$  merely indicate the absence of the genes  $A$  and  $B$ , it is, of course, not allowed to speak of "linkage between  $A$  and  $b$  or between  $a$  and  $B$ ". When individuals provided with the two genes  $A$  and  $B$  occurred more frequently than those provided with one of them, it was originally said that there existed a certain degree of "coupling" between  $A$  and  $B$ , whereas a certain degree of "repulsion" was assumed to be present when individuals belonging to the types  $AB$  and  $ab$  proved to be less well represented than those of the types  $Ab$  and  $aB$ . In the first case it seems more logical to speak of "attraction", for this is the term that is generally applied to relations of this kind. How the presence of attraction or repulsion between two genes is to be explained, is one of the major problems of Mendelian heredity, but it can hardly be expected that the solution of this problem will influence the use of these terms.

The values found for  $n$  when there is attraction between two genes and that found for the reciprocal of  $n$  in case of repulsion are, as stated above, often approximately equal, but the values found for  $n$  when the attraction between different genes is studied, prove to vary considerably.

In some instances values were found for  $n$  that differed but slightly from 1. This might be thought to indicate that the complete absence of attraction or repulsion between two genes is merely a special case, but it can easily be shown that this is not so. Where, as in the fruit-fly and in plants like *Zea* and *Pisum*, large numbers of forms are available for crossing experiments, it was found that the genes between which attraction or repulsion exists, form groups that appear to be completely independent. This means that genes belonging to different groups never show the slightest trace of attraction or repulsion. When attraction is found between  $A$  and  $B$  and between  $C$  and  $D$ , but not between  $A$  and  $C$ , the genes belong to two groups one comprising  $A$  and  $B$ , and the other  $C$  and  $D$ , and there is therefore no attraction between  $A$  and  $D$ , between  $B$  and  $C$  and between  $B$  and  $D$ .

To find a suitable expression for the relation existing between the genes belonging to the same group, we reason as follows. If the attraction between two genes is so strong that their connection can not be severed, or if the repulsion between them is so vigorous that they can not stay in the same cell, the sexual cells will, of course, all belong to the parental types. In this case we may say that the percentage of gene exchange or of "cross-overs", as the genes that enter in a new combination are now usually called, is 0. If there is neither attraction nor repulsion between two genes, the number of sexual cells in which but one of them is found, will be equal to the sum of those in which both are present and of those in which both are absent, i.e. 50 out of a hundred sexual cells will differ from the parental types in the presence or absence of one of these two genes. In this case the percentage of cross-overs is therefore 50. If out of a hundred sexual cells 60 appear with regard to the presence or absence

of the two genes to belong to the parental types and 40 to the new ones, the percentage of cross-overs may be said to be 40, and so on. More than 50 per cent cross-overs would mean repulsion between the genes that in one of the parents were united, or attraction between genes that occurred in different parents, and this is against the rule. The very rare cases in which the new types of sexual cells were reported to be more numerous than the parental ones, form as yet no serious menace to its validity. They may have been caused by a greater viability either of the new types of sexual cells themselves or of the combinations into which they enter. For the moment we may assume that the largest degree of attraction or repulsion may be expressed by 0 per cent cross-overs, and the smallest degree by 50 per cent. For the sake of simplicity we will from now on confine ourselves to those cases where the genes of which the hybrid possesses but a single representative have all been derived from the same parent, i.e. to cases of attraction. *Mutatis mutandis* our considerations, however, apply also to cases of repulsion.

If the attraction between the genes  $A$  and  $B$  finds its expression in  $p$  per cent cross-overs, which means therefore that of a hundred sexual cells  $100-p$  are of the parental types  $AB$  and  $ab$ , and  $p$  of the types  $Ab$  and  $aB$ , and if the attraction between the genes  $B$  and  $C$  is expressed by  $q$  per cent cross-overs, which means that  $100-q$  per cent of the sexual cells are either  $BC$  or  $bc$ , and  $q$  either  $Bc$  or  $bC$ , it appears that the attraction between  $A$  and  $C$  finds its expression in a percentage of cross-overs that is approximately equal either to the sum or to the difference of  $p$  and  $q$ , which means that approximately  $100-(p+q)$  or  $100-(p-q)$  are  $AC$  and  $ac$ , and  $p+q$  or  $p-q$  either  $Ac$  or  $aC$ . When the attraction values for all gene pairs of a group are expressed in this way in cross-over percentages, it appears that the genes can be arranged in a single linear sequence so that the attraction between any two of them is smaller than that existing between either of these and any of the genes that occupy a place between them.

It was stated above that the cross-over percentage for genes that in such a series are separated from each other by intervening ones, is approximately equal to the sum of the cross-over percentages between them and the intervening ones and between the latter themselves, but it would have been more accurate to say that it is either equal to this sum or, more often, smaller, sometimes even considerably smaller. Morgan e.a. found in *Drosophila* for a series of genes for which the names "yellow", "white", "vermilion", "miniature", "rudimentary" and "bar" are used, cross-over percentages amounting respectively to 1.07, 32.1, 4.1, 17.8 and 4.4; if the cross-over percentage between "yellow" and "bar" should be equal to the sum of these values, it would amount to 59.37; in reality, however, it was found to be 46.1. In some other instances the discrepancy between the calculated value and the observed one was even larger. To this point too we will come back.

With regard to the constitution of the sexual cells of a hybrid whose parents differed in two or more genes the following facts will therefore have to be explained: in the first place, that the sexual cells of these polyhybrids are not all of them, like the sexual cells of the monohybrids, identical to the sexual cells of the parents; secondly, that the various types of sexual cell may occur either in equal or in unequal numbers, but that in the latter case the parental types are always better represented than those in which the distinctive genes appear in a new combination; thirdly, that the genes between which attraction or repulsion is found, form groups, and that those belonging to different groups show neither attraction nor repulsion, but are distributed at random over the sexual cells; and fourthly, that the genes of each group can be arranged in a linear sequence, the attraction between them varying inversely with the distance between the positions occupied by them. Further we will have to explain that the repulsion between two genes is never stronger, but apparently not rarely weaker than the attraction existing between them when they have been derived from the same parent, and also that the cross-over percentage observed between two genes that are separated from each other by a number of intervening ones, never exceeds but, as a rule, falls behind the sum of the cross-over percentages observed between these genes and the intervening ones and between the latter themselves.

That the sexual cells of a hybrid whose parents differed in more than one gene are not all identical to the parental ones, proves that the parental gene sets are not to be regarded as structures whose composition is once for all fixed. The circumstance that genes belonging to different groups are apparently distributed at random over the sexual cells, suggests that these groups must be completely independent of each other.

As the only independent units with which we are acquainted within the confines of the nucleus are the chromosomes, the latter are now generally regarded as the carriers of the independent gene groups. This, of course, is a hypothesis, for it is not absolutely sure that the chromosomes really are independent units that maintain their individuality through all subsequent divisions, nor is it fully certain that there are no other independent units within the confines of the nucleus. As our means of discernment are but imperfect, it is, of course, not necessary that we should be able to recognize the latter. There are, however, plausible arguments in favour of the hypothesis that the chromosomes are the carriers of the gene groups. In the following paragraphs we will consider them.

The argument to which usually precedence is given, is in reality not a strong one. It is based on the so-called "individuality" of the chromosomes to which reference already has been made. It is true that in genotypically identical individuals the number of chromosomes is always constant, and that differences between the individual members of the set, like the presence of constrictions and of portions that do not stain, return at every

subsequent division and are apparently fully hereditary. This is in good agreement with the supposition that the chromosomes whose outlines become discernible when the nucleus is about to divide, are virtually the same as those that disappeared after the preceding division, but it does not prove their identity, for what happens to the chromosomes during the time they are invisible is, of course, impossible to make out. It is thinkable that their similarity might be the result instead of the cause of the organism's specific character. The following analogue may serve to make this clear. The androecium of the *Cassia* flower shows in the size and shape of the stamens a similar differentiation as some chromosome sets, and like the latter it is, of course, completely hereditary, but the similarity between the sets of the stamens in the various flowers of the same as well as of different plants is obviously the result of the plant's specific character, and can not be ascribed to a common descent from an initial set. In the case of the chromosomes the latter is possible, but obviously not necessary.

A second argument is found in the differences exhibited by plants in which one of the chromosome pairs is replaced by a triad. Organisms in which all chromosomes occur in groups of three or four, the so-called triploids and tetraploids, do not throw any direct light on this problem, because in these cases all the genes must have increased in number. It is, however, noteworthy that the differences between polyploids and diploids, although sometimes quite considerable and e.g. easily observable in the dimensions of the cells, may also be exceedingly small, so small in fact that it is doubtful whether they are everywhere present. Their absence may be due to the circumstance that the effect exercised by the genes reaches already its highest value in the diploid condition. As we know that most of the genes are of the kind that already exercises its full effect in the hybrid where but one of them is present, this similarity between diploids and polyploids is not surprising. We should, moreover, not forget that the differences observed in the cell size of some of the polyploids need not be due to the presence of one or more extra sets of genes but might be caused by an increase in the amount of some other constituent of the chromosomes or of the nucleus. This possibility should also be kept in mind in considering the differences exhibited by plants in which but one of the chromosome pairs is replaced by a triad.

The best example of the influence exercised by the extra chromosome of the triad was found in the case of *Datura stramonium*. Blakeslee described here twelve different types provided with 25 instead of the ordinary 24 chromosomes. The presence of these twelve different types could be accounted for by assuming that in each of them another pair of chromosomes was replaced by a triad. The convincingness of this result was somewhat impaired by the fact that in reality among the plants provided with 25 chromosomes some more aberrant types were observed. The presence of the latter required an additional hypothesis, which was



found in the assumption that the extra chromosome need not be identical to the two other ones, but may consist either of two lower or of two upper halves. The correctness of this view is, unfortunately, difficult to prove, but we will pass this by. Of more importance is the objection made in the preceding paragraph, namely that the difference need not be due to the extra set of genes but may be caused by some other constituent of the chromosome. The differences observed between the various forms of *Datura stramonium* provided with 25 chromosomes can therefore not be regarded as fully convincing proof of the thesis that each of the chromosomes carries its own genes. In fact, it merely indicates the presence of a difference of some kind between the twelve chromosomes of the haploid set.

A third argument is provided by the circumstance that difference in sex is often correlated with the absence or with the aberrant constitution of one of the chromosomes. The pair of chromosomes of which in such cases one of the partners is either absent or modified in one of the sexes, are usually indicated as the sex chromosomes. The sex chromosome that in one of the sexes is present in duplo, is now commonly designated as the *X*-chromosome; the modified one as the *Y*-chromosome. One of the sexes is in these cases always *XX*, the other one either *XY* or *X*.

In the scheme given in the preceding paragraph one of the sexes is heterozygotic and the other one homozygotic. The latter therefore produces but a single kind of sexual cells, whereas the heterozygotic one yields two kinds, of which one is genotypically identical with that produced by the homozygotic sex, and as the sexual cells of the latter fuse with those of the heterozygote, the result will be that 50 per cent homozygotes and 50 per cent heterozygotes are formed. In this way the maintenance of the numerical equality between males and females in the successive generations finds a plausible explanation. It should, however, not be forgotten that the presence of but one sex chromosome or of two unequal sex chromosomes in one of the sexes proves the latter's heterozygotic constitution, for if this proof were absent, the assumption that one of the sexes is heterozygotic would not have been the only possible explanation. Not everywhere where the successive generations consist of two numerically equal groups of different type, the difference between these types can be accounted for by assuming that one of them must be heterozygotic. As these cases have hitherto received but little attention, a few examples may serve to elucidate my contention.

For several years there appeared in the *Journal of Botany* a short paper in which it was shown that in a certain locality in England about 50 per cent of the arum lilies were provided with a spathe that was dextrorsely contorted, whereas in the other 50 per cent it was contorted in the opposite direction. The author explained this by assuming that the spathes of one kind were produced by homozygotic individuals, those of the other kind by heterozygotic ones. This was a mistake, for the arum

lilies found in a definite locality doubtless owe their origin to a considerable extent to vegetative propagation. That the two kinds of spathe nevertheless appear in approximately equal numbers, is due to the circumstance that both kinds are produced by the same stock. The logical flaw in the reasoning is in this case easily detected, but if the arum lilies did not branch and if they produced but a single spathe, this would have been impossible. The same phenomenon can be observed in grasses with convolutive leaves, where in about 50 per cent of the shoots the right border of the first leaf is seen to overlap the left one in the bud, whereas in the remaining shoots the left border of the first leaf overlaps the right one. Here too the two types of shoot may be found on the same stool, but if the plants do not branch, half of them belong to one type, the other half to the other. In plants with a spiral arrangement of the leaves the direction of the spiral is in about 50 per cent of the shoots similar to that of the corkscrew (helictic) and in the rest opposite to that (antihelictic). If the plant is strongly ramified, the numerical equality between the two types of shoot may be observed in a single individual; if, on the other hand, it is unbranched, each individual, of course, represents one type. In all these cases therefore the presence of two numerically equal groups of individuals has nothing to do with their genetic constitution. In some cases it is known that the question whether a plumula or an axillary bud will develop into a shoot of this or that type is decided by the position which the primordium accidentally occupied in space, i.e. with regard to the direction of gravity. Howsoever this may be, the numerical equality of two alternative types returning in every new generation is in itself no reason to assume that these types are genetically different, and if in the case of the two sexes nowhere a difference in the character of the chromosome set had been found, there would hardly have been reason to assume such a difference here.

The correlation between the differentiation of two sexes and the presence or special development of certain chromosomes does not prove that the latter are the carriers of special genes. Both phenomena might have a common cause, e.g. a difference in the amount of nuclear "substance". In some cases where sex chromosomes are present, there is, however, a correlation between sex and some other characters, and this proved to be more significant than mere sexual dimorphism. We will study the behaviour of these "sex-linked" characters in a cross between two varieties of *Drosophila*.

A white-eyed *Drosophila* male and a red-eyed *Drosophila* female produced a red-eyed hybrid generation, but when these hybrids were mated with each other, the offspring proved to be composed of red-eyed females and of red-eyed as well as white-eyed males. There is therefore a correlation between femaleness and the red colour of the eyes. If we wish to express these results in the ordinary way, we have to choose between the two following schemas:

Schema I

P	mmRR	×	Mmrr
sexual cells	mR		Mr and mr
F <sub>1</sub>	mmRr	×	MmRr
sexual cells	mR and mmRR		(MR) Mr mR (mr) Mmrr
F <sub>2</sub>			

Schema II

P	FfRR	×	ffrr
sexual cells	FR and FfRf		fR fr
F <sub>1</sub>	FfRr	×	FfRr
sexual cells	FR (Fr) FfRR		(fR) fr FfRr and fR ffRr fr ffr
F <sub>2</sub>			

The gene that is responsible for the red colour of the eyes is represented by *R*, and in the first schema the males are supposed to be heterozygotic (*Mm*), in the second the females (*Ff*).

A serious drawback of both schemas is that the dihybridic individuals (*MmRr* in the first and *FfRr* in the second schema) produce but two kinds of sexual cells, those that are placed in brackets being absent. To explain this we would have to assume that the repulsion between the genes *M* and *R* in schema I is so strong that they are unable to stay in the same cell or that the attraction between *F* and *R* in schema II is so strong that they can not be severed. These assumptions are rather strained, for examples of such a strong attraction or repulsion are not known from elsewhere, so that they would place the "genes" *M* or *F* at any rate in a class of their own. That *M* and *R* would repulse each other so strongly that they could not be united, and that *F* and *R* would attract each other to such a degree that they could not be separated is, moreover, hardly believable, for sexual cells of the types *mr* and *fR* actually figure in the schemas. The absence of these types of sexual cell in the hybrids between the white-eyed male and the red-eyed female is therefore insufficiently explained in the schemas I and II. For this reason we will now turn our attention to the solution offered by the chromosome theory. It is given in schema III.

Schema III

P	R R	×	r
sexual cells	R		r
F <sub>1</sub>	R r	×	R
sexual cells	R r		R r
F <sub>2</sub>	R R R r		R r

The advantage of this schema above the two preceding ones lies in the way in which the presence of but two kinds of sexual cell in the male as well as in the female hybrids is explained. In the first two schemas, as we have seen, either a complete repulsion between  $R$  and the "gene"  $M$  or else a complete attraction between  $R$  and the "gene"  $F$  had to be assumed. In the third schema the male parent is provided with an  $X$ -chromosome of the same kind as those forming the corresponding pair in the female parent but lacking the gene  $R$ , and a  $Y$ -chromosome that is supposed to carry no genes and to be unable to receive them. One half of the sexual cells of the male parent receive this  $Y$ -chromosome, which in the scheme is represented by an empty rectangle, the other half the  $X$ -chromosome. The hybrid males are, as the scheme shows, provided with an  $X$ -chromosome carrying the gene  $R$ , and, of course, with the empty  $Y$ -chromosome. As the latter is unable to receive any genes, no exchange is possible between the  $X$ -chromosome and the  $Y$ -chromosome, and the male too produces therefore but two kinds of sexual cells. This is the great advantage of the third schema above the two preceding ones: it gives a plausible explanation of the fact that there are both in the male and in the female hybrid but two kinds of sexual cells. It should however not be overlooked that this advantage is due to a special assumption, namely that the  $Y$ -chromosome is unable to carry genes.

A point that has not always been duly emphasized, is that the fundamental difference between the first two schemas and the third lies in the circumstance that in the first two the difference between the sexes is ascribed to the presence or absence of a gene, whereas the third schema accounts for it by pointing to the equality or inequality between the partners of a definite pair of chromosomes. Both hypotheses explain the numerical equality between the sexes, but whereas for the first one no further arguments can be advanced, the second one finds, as we have seen, corroboration in the fact that it accounts in a plausible way for the behaviour of the sex-linked characters. That femaleness should be due to the presence of two  $X$ -chromosomes, and maleness to that of one  $X$ - and one  $Y$ -chromosome, gives, at least when we make the additional assumption that the latter is unable to receive the gene that is responsible for the red colour of the eyes, an acceptable explanation of the way in which this gene is transmitted to the offspring. As the  $Y$ -chromosome is in some organisms entirely suppressed, the supposition that it is partly or entirely unable to carry genes, is not so far-fetched as it might seem at first view. However, before accepting the hypothesis that the sex-linked characters are produced by genes localized in the  $X$ -chromosome, we will have to find out whether the behaviour of the sex-linked characters can not be explained in a third way, namely by assuming that maleness and femaleness are due to a difference in the amount of chromosome "substance".



To test the hypothesis mentioned at the end of the preceding paragraph we will construct a fourth schema in which the difference between the amount of chromosome "substance" present in the *X*- and *Y*-chromosomes is expressed by the sign +.

Schema IV

P	++RR	×	+	rr	
sexual cells	+R		+r		r
F <sub>1</sub>	++Rr	×		+Rr	
sexual cells	+R	+r	+R	(+r)	(R) r

It is not necessary to complete this schema, for the circumstance that the hybrid male produces but two kinds of sexual cells compels us to assume that the sexual cells with the constitution  $+r$  and  $R$  fall out, and it is impossible to see why this should be so. Complete attraction or repulsion, the factor to which we had to ascribe the result in the first two schemas is, of course, out of the question, for the + sign does not represent a gene. As the fourth schema therefore is unable to account for the observed results, the third appears to deserve preference. This means that the sex-linked characters must be due to genes that are localized in the *X*-chromosome.

When the genes that are responsible for the sex-linked characters are all localized in the *X*-chromosome, the possibility that they form new combinations in the sexual cells of an individual that is heterozygotic with regard to them, is confined to the female. As the latter is provided with two *X*-chromosomes crossing-over of the sex-linked genes can doubtless take place. In the male, however, the sex-linked characters must form an unalterable complex, for the possibility of a crossing-over between the *X*- and the *Y*-chromosome is excluded as the latter is, according to our premise, unable to receive genes. The sexual cells of the male are therefore with regard to the sex-linked characters all of the same two types as the sexual cells to whose fusion that particular male owed its origin, i.e. one half is provided with the *X*-chromosome with its set of sex-linked genes and the other half with the empty *Y*-chromosome. That such a difference in the genetic behaviour of the male and the female really proves to be present, is another and a very strong argument in favour of the hypothesis that the genes to which the sex-linked characters are due, are localized in the *X*-chromosome. However, when we have to admit that one group of genes is localized in a definite chromosome, there is obviously no good reason to dispute the probability that the other groups too will be confined to definite chromosomes.

In schema III the cytological character of the sex chromosomes is assumed to be directly responsible for the determination of sex, but such a direct responsibility is not easily reconcilable with the fact that the cytological character of the male and the female is not in all groups of

organisms the same. In the majority of the insects, in the nematodes and mammals as well as in the dioecious Angiosperms the females prove to be provided with two identical sex chromosomes, the males either with two unequal ones or with a single one, in Lepidoptera and birds on the other hand the two equal sex chromosomes appear to be a character of the male.

The cytological character of the dioecious Angiosperms is in this respect of little importance, for their sexes are apparently not homologous with those of the animals. The fact that the sex organs of the latter develop from cells whose character is already determined at one of the earliest cleavages of the fertilized egg, whereas the sex organs of the plants are differentiated at a comparatively late stage and may arise in various parts of the body, is hardly reconcilable with the idea that they should be homologous, and when the sex organs can not be considered homologous, there is, of course, no reason to regard their products, the sexual cells, as homologous. The name sexual cell refers to a similarity in function between these elements, but morphologically the latter have no more in common than the wings of a bat, a bird and a butterfly.

That sexuality is not everywhere of the same kind will be more readily be conceded when we realize that the ordinary bipolar sexuality with its two sexes, which for the sake of convenience are everywhere designated as male and female, is not the only kind of sexuality with which we are acquainted. In the Basidiomycetes we meet sometimes with a tetrapolar sexuality, a condition that has been explained by assuming the presence of two pairs of hereditary factors behaving like entirely independent genes: individuals provided with both factors mate only with those in which both are absent, and those in which but one of them is present only with those provided with the other one. In the alga *Chlamydomonas* an even stranger kind of sexuality has been observed, for this organism produces several kinds of gametes. At first sight the latter appear to behave like ordinary males and females, but when their behaviour is studied more in detail, it is found that some of the males behave as females with regard to other males that for this reason have been called "strong" males, and that some of the females behave as males with regard to "strong" females. These inconsistencies indicate that the peculiarities in structure and behaviour to which the term "sexuality" is applied, can hardly be everywhere of the same kind.

The conclusion at which we arrived in the last paragraph can, however, not apply to the sexuality of the Metazoa, where the gonads and the sexual cells are clearly homologous structures, and that maleness and femaleness are here in the various main groups and even among the subdivisions of a group like the insects not everywhere correlated with the same cytological structure, offers therefore a serious difficulty. The two possibilities to explain the difference in sex that have already been considered, viz. 1° that it might be caused by the difference in the amount

of nuclear "substance" which finds its expression either in the inequality between the two sex chromosomes or else in the absence of one of them in one of the sexes, or 2° that it might be correlated with the structural peculiarities of the sex chromosomes themselves, can not satisfy us. The first supposition appeared to be improbable, and both of them fail to explain how the same cytological differentiation can in one instance be responsible for the development of a male, and in another group for that of a female. We will have to assume therefore that the differentiation of the sexes is not directly connected with the visible characters of the sex chromosomes but rests on some hidden peculiarity. The visible character of these chromosomes might be mainly, or perhaps even exclusively, of importance to the development of the secondary sex characters. It is in this respect noteworthy that the male birds and butterflies, which resemble the females of the other groups by the possession of two X-chromosomes, show, as a rule, a distinctly higher degree of differentiation than the female birds and butterflies, whereas in the other Metazoa the situation is not rarely reversed, and where this is not at first sight apparent, the high demands that the development of the eggs and of the embryos and the care of the young often make on the female organism might explain the latter's more complete nuclear equipment.

Above some of the main arguments in favour of the chromosome theory of heredity have been discussed. Some more arguments will be brought forward below, but it seems advisable to turn out attention first to the explanation this theory gives of the facts that have been brought to light by the study of the offspring of hybrids whose parents differed in more than one gene.

That the sexual cells produced by these hybrids need not all be identical to those of the parents is easily explainable. As the partners of the chromosome pairs are apparently in the course of the reduction division distributed at random over the tetrads, the genes that are present in different chromosome pairs must also be distributed at random. When the genes *A* and *B* have their seat in different chromosome pairs, the chances that they remain together are apparently equal to the chances that they are separated from each other, and on the average therefore one in each group of four sexual cells will have the constitution *AB*, one *ab*, one *Ab* and one *aB*. However, as the number of genes is far larger than that of the chromosome pairs, the genes whose transmission is studied will often be located in the same chromosome pair. In that case one would expect that but two kinds of sexual cells would be produced, viz. the parental types. In reality, however, everywhere four types of sexual cells appear to be formed, although, as we have mentioned already, not always in equal numbers. As we have seen, they often appear in the proportion  $n : 1 : 1 : n$ .

One might perhaps be inclined to assume that an exchange of genes could only be effected if they were located in different chromosome pairs. In that case the different values of *n* might be due to the circumstance

that the parental partners of the chromosome pairs are not distributed at random over the sexual cells, as we assumed in the preceding paragraph, but that they have a tendency to stick to each other. When  $n$  equals 1, the two chromosomes in which the genes are located would not possess this tendency, but in all other cases the value of  $n$  would indicate the tendency of the chromosomes to remain together. If this were so, one would have to assume that one or more of the parental chromosomes are always distributed at random, but that the remaining ones stick more or less together. In the case of *Drosophila melanogaster* with its four pairs of chromosomes this would mean that when a gene  $A$  was situated in the chromosome  $a$  that is distributed at random, and the gene  $B$  in one of the three other chromosomes, the proportion  $AB : Ab : aB : ab$  would be  $1 : 1 : 1 : 1$ , but when the gene  $A$  was situated in the chromosome  $b$ , and the gene  $B$  in the chromosome  $c$ , the proportion  $AB : Ab : aB : ab$  would be  $n_1 : 1 : 1 : n_1$ , when  $A$  was situated in  $c$  and  $B$  in  $d$ , the proportion would be  $n_2 : 1 : 1 : n_2$ , and when  $A$  was situated in  $b$  and  $B$  in  $d$ , the proportion would be  $n_3 : 1 : 1 : n_3$ . In *Drosophila melanogaster*  $n$  could therefore have no more than three different values ( $n_1$ ,  $n_2$  and  $n_3$ ), whereas in reality a far greater number of values have been observed. Moreover, in the fact that the sex-linked genes are located, as we have seen, in the same chromosome and nevertheless show in the female ( $XX$ ) crossing-over, we have direct proof that the proportion  $n : 1 : 1 : n$  applies to genes located in the same chromosome, and if this applies to the sex-linked genes, there is no reason to assume that it would not apply to other genes. Therefore, we must try to reconcile the presence of four types of sexual cells in the proportion  $n : 1 : 1 : n$  with the supposition that the two genes are present in the same chromosome pair.

To effect the reconciliation alluded to at the end of the preceding paragraph an additional hypothesis is required. It is not enough to know that the genes are situated in the same chromosome pair, but we must be convinced that they are able to pass from one of the partners to the other: an exchange or "crossing-over" of genes must be possible<sup>1)</sup>. If the genes  $A$  and  $B$  were originally present in the same chromosome, its partner containing neither of them, the majority of the sexual cells will be of the types  $AB$  and  $ab$ , but in a certain percentage of the tetrad mothercells the chromosome that contained the two genes  $A$  and  $B$  will have given off one of them to its partner, and part of the sexual cells therefore will be provided with a chromosome containing the gene  $A$  only, i.e. they will be of the type  $Ab$ , and another part will be provided with a chromosome containing the gene  $B$ , i.e. they will be of the type  $aB$ . If one of the partners originally contained the gene  $A$ , and the other one the gene  $B$ , these genes might in a certain percentage of the cells pass

<sup>1)</sup> Another possibility, namely that the genes  $A$  and  $B$  might disappear in some of the sexual cells, will be discussed below.



to the other partner, so that the one that originally contained  $A$  no longer contained either of them, whereas the other one came to possess both: the majority of the sexual cells would in this case be  $Ab$  and  $aB$ , but a certain percentage would become  $AB$  and  $ab$ . In this way therefore the proportion  $n : 1 : 1 : n$  is accounted for.

If we assume that the genes are not specially attracted by each other or by the partner of the chromosome pair in which they happen to have their seat, the highest percentage of crossing-over that could be obtained, would be 50. This value would be reached when the genes were released in all cells, for in resuming their place in the two chromosome partners, the chances that they would enter the one they had left or the other one, would in this case be equal. The fact that this maximum is apparently never reached, and that the hybrid therefore always produces more sexual cells in which the genes occur in the same combination as in the parental ones, would mean therefore that the genes are released in a part of the cells only.

In order to arrive at the conclusion mentioned in the last paragraph, we had to assume that the genes when they are temporarily released do not attract each other, and that they are not more strongly attracted by one of the chromosome partners than by the other. These assumptions appear to be fully justified, for if the genes were attracted by each other or if they were more strongly attracted by one of the chromosome partners than by the other, the attraction between two genes derived from the same parent could not be approximately equal to the repulsion found between the same two genes when they were originally divided over the two parents; it would, on the contrary, always be the same types of sexual cell that were produced in excess. The approximate equality of the values found for the attraction and the repulsion of the same two genes proves that neither chemical affinity between the genes themselves nor chemical affinity between the latter and the axial structure of the chromosome can be the cause of the attraction.

The fact that the genes between which attraction and repulsion are observed form independent groups, is, of course, in good agreement with the chromosome theory. However, when the genes between which attraction and repulsion exist, are located in the same chromosome pair, the number of gene groups will have to correspond with the number of chromosome pairs or can at any rate not exceed the latter. This deduction is unfortunately difficult to verify. It is true that in *Drosophila melanogaster* with its four chromosome pairs four gene groups could be distinguished, but in the only two other objects where a sufficiently large number of combinations have been tested, viz. in *Pisum* and *Zea*, the agreement could not yet definitely be ascertained. In both objects the number of gene groups as well as the number of chromosome pairs are larger than in *Drosophila melanogaster*, and this is at any rate an argument in favour of the theory, although of course, not a particularly strong one.

In some instances the number of genes that are entirely independent of each other, appears to be much smaller than the number of chromosome pairs. In fact, even when the parents differ in a large number of characters, hybridization does not always lead to the appearance of more than a few new types. This may partly be due to lack of viability in the new combinations, but it can certainly not everywhere be explained in this way. In *Oenothera*, where the phenomenon has drawn considerable attention, it was found that the chromosomes do not behave as entirely independent units; it appeared namely that they are not all in the usual way combined in pairs but that the majority are combined in larger groups and form one or more ring-like structures. A free distribution of the chromosomes over the products of the tetrad division is made impossible in this way. The correlation between the formation of chromosome rings and the decrease in the number of types that are represented among the sexual cells may certainly be adduced as an additional argument in favour of the chromosome theory. The phenomena themselves are, however, very intricate, and the details of the process are difficult to explain.

That the genes belonging to the same group may be arranged in a linear sequence according to the percentage of crossing-over existing between them, can be explained by assuming that they all have their place in a single file along the axis of the chromosome. The aspect of the chromosome in adequately stained slides is in good agreement with this supposition, for in suitable objects the chromosomes appear to consist of a series of easily staining discs of various diameter and thickness alternating with thinner parts that do not catch the stain. The chromomeres, as the easily staining discs are called, are supposed to correspond with the genes. That the latter themselves would absorb the stain is improbable, for the only part of the resting nucleus that stains well is the nucleolus, and that during that period the latter should be used as a receptacle for the genes, is hardly conceivable, for if they were shut up in such a small space, they would not be able to perform their function. It seems more plausible to assume that the substances stored in the nucleolus are used during the nuclear division either as a protective envelop for the genes or else as a means to isolate them from the surrounding plasm in order to facilitate the movements of the chromosomes.

In the nuclei of the ordinary cells of *Drosophila* the chromomeres are indistinguishable, but in the cells of the salivary glands chromosomes are found that are several times as large as the ordinary ones, and these enlarged chromosomes show the chromomeres to perfection. They prove to contain an extraordinary large number of them. That the latter should correspond with the not separately distinguishable chromomeres of the chromosomes found in the other cells is, of course, a hypothesis, and at first sight not a very convincing one, for it evidently means that the increase in size is merely a more or less equal distention of the chromosome. An equal distention in all directions would be hardly conceivable in an

organ of such a peculiar structure as the chromosome, but it has been argued that the axial part of the chromosome might consist of a bundle of catenary molecules of the same length as the chromosome itself, and that the links of these chains would be folded in the chromosomes of the ordinary cells like the bellows of a concertina in rest and that they would be stretched in those of the salivary cells. The chromomeres, that are supposed to be threaded on the axis like beads on a string, would in this way be separated from each other in the chromosomes of the salivary cells and become separately distinguishable. If it could be proved that the chromomeres of the enlarged chromosomes really correspond with the invisible ones of the ordinary chromosomes, the fact that the pattern of each of the enlarged chromosomes appears to be constant, would doubtless be of great importance. Now already on this supposed specificity of the chromomeres far-reaching conclusions have been based.

The hypothesis that the position of the chromomeres corresponds with the linear arrangement of the genes based on the crossing-over values determined for any two of them separately, is doubtless attractive and plausible. However, as each hypothesis introduces an element of uncertainty, i.e. a chance to lead us astray, it should not be accepted as an integral part of the theory until it has been tested in other circumstances and until it has shown itself serviceable in the explanation of some other peculiarity. An opportunity to test its probability would offer itself when we succeeded in finding some deviations in the ordinary sequence of the chromomeres or when some of them were found to be missing, for then we would be able to find out whether there existed a correlation between these abnormalities and the crossing-over values between the genes that the affected chromomeres are thought to represent.

In some *Drosophila* individuals the attraction between a number of genes proved to differ from the normal values. The results of the hybrid analysis could best be explained by assuming that the sequence of the genes in a definite part of the series had been reversed, and if our hypothesis is right, the chromosome in which these genes are situated must therefore possess a portion in which the sequence of the chromomeres is reversed. This is, of course, difficult to prove, for the differences between the chromomeres are but small, and they are, moreover, recognizable only when the chromosomes are more or less straight, when they do not cover each other, and when they occupy a more or less horizontal position in the field of vision. Cytological experts, however, assure us that the presence of the "inversion" can be demonstrated.

Other irregularities in the structure of the chromosomes are due to "duplication", i.e. the doubling of a part of the chromosome, and to "deletion", i.e. the disappearance of a portion. Deletion is supposed to be present if a part of a chromosome does not stain. This is a somewhat arbitrary assumption, for the stain is, as we have seen, probably not absorbed by the genes themselves but by a protective envelop. The

latter's absence, however, may be correlated with the absence of the genes. It is, on the other hand, strange that apparently not all varieties with a number of recessive characters, i.e. with an incomplete set of genes, show this deletion, but this is a problem on which further evidence is to be awaited; its solution must be left to the cytologists. At this juncture we will confine ourselves to those cases where deletion actually was observed. In a *Drosophila* strain deletion of a part of the X-chromosome in the cells of the salivary glands proved to be correlated to the absence of a number of sex-limited characters. The hypothesis therefore was confirmed.

Among the evidence based on abnormalities in the structure of the chromosomes, that derived from the presence of "inversions" seems to be the most convincing, but in connection with the difficulty to obtain fully reliable figures for the attraction between the different genes, and also because of the difficulties that are inherent in the cytological investigation, the strength of the argument based on this phenomenon should not be overrated. The hypothesis that the genes are localized at definite points in the chromosome must be regarded as a very plausible one, but the identity of the genes with the chromomeres should not yet be accepted as an established fact.

Instead of assuming that the genes cross over from one chromosome to its partner, we might also suppose that they disappear in some of them and that they may, eventually, be resuscitated in others. This is the base of Winkler's "conversion-hypothesis".

Winkler's conversion hypothesis assumes that in the heterozygotic condition genes may occasionally be suppressed, and that missing ones eventually may be resuscitated. It is based therefore on a similar assumption as that by which de Vries explained his "regressive" and "retrogressive" mutations. If the parental sexual cells were  $AB$  and  $ab$ , part of the sexual cells  $AB$  of the hybrid are supposed by Winkler to be converted in this way to  $Ab$ ,  $aB$  and  $ab$ . This would lead to a proportion  $AB : Ab : aB : ab = \{1 - (p + q + r)\} : p : q : (1 + r)$ . If we assume that part of the sexual cells  $ab$  too were changed, the proportion would become  $\{1 - (p + q + r) + s\} : (p + t) : (q + u) : \{1 + r - (s + t + u)\}$ . This means that the parental types would be present, as a rule, in unequal numbers, for that  $\{1 - (p + q + r) + s\} = \{1 + r - (s + t + u)\}$  or  $p + q + 2r = 2s + t + u$  would, of course, be a great exception. This is a serious drawback of this hypothesis, for although the numerical equality of the parental types among the sexual cells of the hybrid has not everywhere been fully ascertained, there seems as yet no reason to suppose that it would be exceptional. The hypothesis, moreover, would apply also to the sexual cells of a monohybrid, and here the numerical equality of the two groups of sexual cells appears to be firmly established. It seems therefore that Winkler's hypothesis may be discarded, and that we may confine ourselves to the crossing-over hypothesis.



We might perhaps be tempted to ascribe the difference in the number of cases in which the genes cross over from a paternal or maternal chromosome to its partner to a difference in the force by which they are attached to the axis of the chromosome. Although it is not impossible that this force may be involved, it can certainly not be the only cause of the difference. If this were so, the fact that two genes were found to cross over but rarely in each other's company from one chromosome to its partner, would mean that at least one of them was retained with considerable force in its original place, but in that case it would be quite incomprehensible that each of them was at the same time found to pass over comparatively easily to the other chromosome in company of another gene. The frequency with which the chromosomes pass over from one chromosome to its partner is therefore not in the first place determined by the force by which they are retained in their original position but by the force they exercise on each other, either directly or by the intermediary of the axis of the chromosome. The genes that most frequently cross over in each other's company, are therefore supposed to occupy a place in each other's close proximity on the axis of the chromosome, whereas those that pass over less frequently in each other's company, are supposed to be farther away from each other.

Morgan's crossing-over hypothesis explains the crossing-over by assuming that in the chromosomes a fragmentation takes place followed by a reconstruction; in this reconstruction parts of a chromosome derived from the male parent may be replaced by corresponding parts of a chromosome derived from the female parent, and vice versa. As a cytological argument in favour of this "crossing-over" of chromosome parts the "chiasmotype" of the chromosome partners has been adduced. At a certain stage of the reduction division the partners are found to be twisted round each other, and it is supposed that in this stage the chromosomes may readily be broken, and healed in the Münchhausenian way, i.e. by replacing parts of one of them by parts of the other. It is unfortunately so far somewhat difficult to see what magic ointment might effect this cure.

The percentage of chromosomes in which the connection between two genes placed at a considerable distance from each other is severed, is, as has already been stated, as a rule smaller, often even considerably smaller than the sum of the percentages of chromosomes in which the connection between either of these genes and their next neighbours on the inner side and that between the latter and the rest of the intervening genes is broken. This is generally ascribed to "double" or "multiple" crossing-over, i.e. to the presence of one or more extra breaks in the chromosome and to the exchange therefore of two or more portions of the latter against corresponding portions of its partner. In this way genes that were separated from each other by the first crossing-over of chromosome parts are re-united, and this will, of course, happen all the

more frequently the greater the distance between the two genes becomes, for the wider the stretch, the greater the chance that it will comprise another break.

It is, as we have seen in the preceding paragraph, possible to explain why the sum of the percentages of crossing-overs observed between the consecutive pairs of a series of contiguous genes, may be larger than the percentage of crossing-overs observed between the genes located at the opposite ends of that series. The latter can, moreover, never exceed a value of 50. If we assume that in 100 per cent of the cells the chromosome in which our genes are present, breaks in two parts, the chance that it will be healed in the illegitimate way, i.e. with a portion of its partner, will at the most be equal to the chance that it is healed legitimately, which means that the connection between the two genes at the opposite ends can never be broken in more than 50 per cent of the cells. In case a second break occurs, the figure will be the same, for of the 50 per cent that after the first break were healed legitimately, 25 will the second time be healed in the legitimate way and 25 illegitimately, and of the 50 per cent that after the first break were healed in the illegitimate way also 25 will be healed legitimately and 25 illegitimately. Under no circumstances therefore the connection between the genes at the opposite ends of the chromosome will be broken in more than 50 per cent of the cells.

The attraction between the genes must be ascribed to the presence of connections of some kind or other existing between them, either directly or through the intervention of intermediate ones, and perhaps also between each of them and the axis of the chromosome. The concertina-like structure that has been ascribed to the latter might make the presence of extra-connections between the various genes more easily comprehensible.

The hypothesis that extra-connections between the various genes should be present, implies that the figure found for the attraction between two genes will always be larger than that found for the repulsion between them. In case the genes are situated in each other's close proximity, it might even be considerably larger. The attraction between any two genes would according to this hypothesis be due to the existence of connections between them and all the other genes situated in the same chromosome, whereas the repulsion between them would be due to the connections between each of them and those other ones minus the missing one, i.e. minus the gene that has its place in the other partner. If the missing gene happens to be the next one in the series, it would probably mean that some of the strongest ties were absent. The results obtained by Imai in his *Pharbitis* crosses and by Demerec in *Zea*, in which the attraction was always found to exceed the repulsion, might be explained in this way. In *Drosophila* too there are indications that the attraction is not rarely stronger than the repulsion.

The chromosome theory of heredity regards the chromosome as the receptacle of the genes, by which name the material elements of the

hereditary constitution are meant that retain their individuality from cell to cell and from generation to generation.

It makes use of the following additional hypotheses:

- 1°. that the parental chromosomes retain their individuality throughout the vegetative part of the organism's development in all consecutive nuclear divisions;
- 2°. that each chromosome carries a definite set of genes;
- 3°. that during the reduction division an exchange of genes takes place between the partners of each chromosome pair;
- 4°. that the genes are arranged along the axis of the chromosome in single file;
- 5°. that the attraction between two genes situated on the same chromosome, and the repulsion between two genes situated on the partners of the same chromosome-pair diminish with the increase of the distance between the positions they occupy or would come to occupy on the same chromosome.

Winkler's conversion hypothesis does away with the hypotheses mentioned under 3° and 5°, but it is rather vague, and as it is unable to explain the numerical equality of the groups of sexual cells that repeat the types of the sexual cells of the parents, it had to be discarded.

The way in which the exchange of genes between the chromosome partners is effected may be explained in various ways, and the hypotheses that to this end have been proposed can therefore not yet be regarded as essential parts of the theory. The crossing-over hypothesis appears to be the most satisfactory one, but it does not pay sufficient attention to the improbability that the broken axis of the chromosome could easily be repaired, and it is unable to account for the difference that seems to exist between the values found for the attraction between two genes that have their seat on the same chromosome and for the repulsion exhibited by them when they are divided over the two partners. Both difficulties can be circumvented by assuming that the axis of the chromosome is left intact and that the exchange is restricted to parts of the mantle. The way in which the fragmentation and the reconstruction of this mantle takes place remains a difficult problem in which we see as yet hardly any light. The stage now reached by the chromosome theory of heredity is more or less comparable to that which the atom theory occupied before the introduction of Bohr's model of the atom. It allows a satisfactory description and classification of the phenomena but like most conceptions relative to the organic world it remains itself unexplained.

## MORPHOLOGY

The first part of the compound "morphology" comes from the Greek word "morphe", and as "morphe" means form, the term is often translated by "study of the form". The name, however, was badly chosen, for the discipline to which it applies, is not interested in the form of the organism or in that of its parts, but in the general plan of the body, i.e. in the position the various parts occupy with regard to each other or with regard to some common centre or axis. Form, on the other hand, is in the first place, because of its intimate relation with function, an ecological problem, and next, because of its dependence upon physical factors operating in the environment, an object of study to the physiologist. It is true that the branch of physiology that occupies itself with this problem, is often designated as "experimental morphology", but this is a misnomer. As neither the general plan of the body nor the position the various parts occupy in the latter, are in studies of this kind questions of serious concern, the latter have hardly any contact with true morphology.

How irrelevant from a morphological point of view the form of the various parts really is, will be recognized at once when we consider a few examples of morphological classification. In many *Asparagus* species the shoots are provided with flattened lateral appendages that look like leaves. The morphologist nevertheless regards them as axillary shoots because they are subtended by small scales which he is forced to recognize, on account of their position, as the true leaves. The tendrils by the aid of which some of the climbing plants attach themselves to their supports, may also be quoted as a case in point. Although there is in their form often no difference at all, the morphologist divides them according to the place they occupy in the general plan of the body, in cauline and foliar ones. Morphological parts like the leaf and the shoot may, in fact, appear in almost every conceivable form, and it will therefore be clear that it is impossible to distinguish them on account of the latter.

A. P. de Candolle, to whom we owe the first broadly conceived manual of morphology, did not make a sharp distinction between morphology and that part of ecology which deals with the problem of the form. Both subjects were discussed by him under the common heading "organography". His standpoint is clearly expressed in the following sentence found in the preface of his "*Organographie végétale*": "considérée en ce qui tient à la symétrie des êtres, elle", i.e. the organography, "est le fondement de toute la théorie des classifications; considérée dans l'usage des organes, elle est la base de la physiologie; considérée dans ce qui tient à la description exacte de ces organes, elle est le principe de la glossologie et de l'histoire naturelle descriptive."

"Glossology" is a purism by which de Candolle tried to replace the



generally accepted compound "terminology", to which objection can be raised on account of its partly Latin, partly Greek origin, and with regard to this "glossology" and to descriptive natural history in general it must be admitted that they derive part of the terms in their employ from what de Candolle calls organography, i.e. partly from morphology and partly from the study of the form. However, as the serviceability of these terms does not depend upon their origin, it is not allowed to say that these disciplines form the basis of the biological terminology and of descriptive natural history. As this is a point of minor importance, I will not dwell on it, but pass at once to the more weighty remarks with which the sentence opens.

It will be clear that de Candolle confines himself in the first passage to one of the constituent parts of his "organography", for the study of the "symmetry" or, as it is now usually called, of the "plan" or "type" is fully identical with the biological discipline for which Goethe had coined the name "morphology", and it can not be denied that this part of de Candolle's "organography" forms one of the most important pillars of the "théorie des classifications", i.e. of taxonomy.

The second passage, on the other hand, refers to the ecological considerations with which the morphological ones are interwoven, for the use or the function of the various parts, which in this connection are designated as "organs", is, as I have already pointed out, an ecological problem. Ecology, however, has little in common with morphology, but shows on the contrary, as I have shown in my introductory chapter, a strong affinity to physiology, in which it has often, partly or entirely, been included. Although de Candolle's "Organographie" occupies itself mainly with morphology and owes its historical significance to what it has to say with regard to this subject, the name of the book was derived from the ecological considerations with which the morphological analysis is interlaced. Morphology proper, this is a point that can hardly be over-emphasized, does not occupy itself with "organs", i.e. with parts that are classified in accordance with their function, but exclusively with parts that derive their significance from the position they occupy in the general plan of the body.

The name "morphology", which, as stated above, owes its inception to Goethe and has since long been generally accepted, is, as we have seen, entirely misleading, and it is therefore no wonder that attempts have been made to replace it. Recently the name "typology" was proposed, but its use deserves no recommendation, for the word "type", although often used by biologists in the sense of "plan", has in reality a wider application. From zoological side the term "merology" has been introduced. As it is derived from "meros", which means part, it would be more suitable, but as it has found but little recognition, it seems advisable to retain Goethe's term.

Morphology consists, as de Candolle already recognized, of two parts: "Il semble", he says in the preface of his "Organographie végétale" from

which we have already quoted, "que les premiers", i.e. the German morphologists who followed in the footsteps of Jungius and Goethe, "ont mis toute leur attention à comparer entre elles les parties d'un même être, et les seconds", viz. the French, who were mainly influenced by the teachings of de Jussieu and Adanson, "à comparer les parties analogues d'êtres différens". The first school compares e.g. parts of the same plant like bud scales, ordinary green leaves and bracts, the second e.g. the bud scales of different plants. De Candolle himself was of opinion that these efforts should be combined: "Quant à moi", he continues, "je suis persuadé que ces deux branches de la science sont inséparables, et ma *Théorie élémentaire*", this is the title of an earlier work that serves more or less as an introduction to his more elaborate handbooks, "a eu pour but de les lier, en faisant servir chacune d'elles au perfectionnement de l'autre". However, as the comparison of parts occupying a corresponding position in the body of different organisms is obviously of great importance for the determination of the latter's taxonomic position, whereas the results of a comparison of parts developing in the same organism from similar primordia are for this purpose of no value whatever, it can hardly be denied that there is a fundamental difference between these two branches of morphology, and that it is therefore doubtless better to keep them apart.

In later years too the difference between the two branches of morphology to which de Candolle had drawn attention, has not passed entirely unperceived. Whereas the term "homologous", which on Owen's instigation was reserved for morphologically comparable parts, is used, as a rule, as well for parts that occupy a corresponding position in different organisms as for those that develop in the same organism from similar primordia, Haeckel proposed in his "*Generelle Morphologie*" to reserve this expression to parts of the first kind and to use for parts developing in the same organism from similar primordia a new term, viz. "homodynamous".

As the corresponding parts of the various organisms are sometimes present in sets consisting of a varying number of members, it is not always possible to indicate a definite part of one organism as the homologue, in Haeckel's sense, of a definite part of another one. In these cases the term homology can, strictly speaking, be applied only to the sets of homodynamous parts as a whole. However, no serious objection can be raised against an extension of the use of the term homologous to the individual members of the sets when the latter are so similar as to be almost indistinguishable, as e.g. in the case of the ordinary green leaves of a tree. This should be accepted as an admissible simplification. It is, however, difficult to know where the line should be drawn, and a certain caution in the use of the term is therefore advisable. Homodynamous parts like the fore and hind limbs of quadrupeds are doubtless not sufficiently similar to be regarded as fully homologous.

We have defined morphology as the discipline that compares, on the

one hand, parts of different organisms occupying corresponding positions and, on the other, parts of the same organism developing from similar primordia. In this definition the dual character of morphology is clearly expressed. It is possible, however, to bring the second part of our definition somewhat more in harmony with the first. To this end we observe that the similarity between the primordia of the homodynamous parts does not rest on their aspect but, exactly as in the case of the homologous parts of different organisms, on the position they occupy with regard to each other or to a common axis. The primordia of leaves and of axillary shoots, for instance, are up to a rather advanced stage in their development fully indistinguishable, and it is clear therefore that they do not derive their different morphological value from any dissimilarity in shape but exclusively from the position they occupy with regard to each other. In order to be morphologically comparable the primordia must develop in corresponding positions. That the positions occupied by two or more primordia developing in the body of one and the same individual may be regarded as corresponding ones, is, however, not so obvious as that there are corresponding parts in the bodies of different but nevertheless always to some extent similar organisms. When the latter are not too far apart, the common plan on which they are built, is, as a rule, easily recognizable.

The presence of corresponding parts in the body of a single organism presupposes that at least some of the latter's principal parts are built on the same plan, for only in that case subordinate parts of the latter may occupy corresponding positions. If this is admitted, our definition may be brought in the following form: "Morphology is the discipline dealing with the comparison of parts that develop in corresponding positions; these parts may be present in the body of the same individual or in those of individuals belonging to different, although related species. In the first case the main parts of the body and in the latter the bodies themselves are supposed to be constructed on a common plan."

The difference between the two branches of morphology would disappear entirely when the body could be interpreted as a colony of intimately united individuals, i.e. when it agreed in structure with a polypary or with a plant like *Carex arenaria*, on whose long rhizomes numerous rosettes arise that behave as independent individuals. In this case the main parts of the body would be as fully comparable to each other as the bodies of different but related individuals.

For several groups of organisms in whose bodies at first sight no evidence of a colony structure is to be detected, schemas have been developed by which the plan of the body is brought in line with this supposition. In this way in the articulate and segmented animals individuality has been ascribed to the easily recognizable rings and to the usually in the adult less distinct segments; in the seedplants similarly individuality has been ascribed to the main and axillary shoots or, when the analysis was carried a step further, to the internodes with the leaf or leaves that are present

at their top. A similar line of thought has led to the development of the cellular theory, which regards the cellular organism as a kind of cell colony or cell state.

It is not always easy to decide whether an organism is to be regarded as a simple individual or as a colony of intimately united ones. It is true that the difficulty is sometimes but spurious, as e.g. in the case of the Siphonophores. As at least some of the main parts of a Portuguese man-of-war can be homologized with the individuals that are met with in a polypary, there can be no doubt that these organisms are from a morphological point of view to be regarded as colonies. It is sometimes argued that their activities are centrally regulated, but this is an ecological feature and therefore of no value for the morphological interpretation. It might be of importance in an ecological classification, but that the latter would agree with the morphological one, can, of course, not be expected <sup>1)</sup>.

In several instances the problem appears to be unsolvable. This applies e.g. to the organisms that are brought together in the group of the Volvocales. The cells of these organisms are all very similar and show a striking resemblance to unicellular Flagellates, and this is certainly a weighty argument in favour of the view that the body is to be regarded as a colony. The sexual reproduction of these organisms and their power of movement, on the other hand, agree better with the view that they are individuals. In the case of the articulate and segmented animals and in that of the seedplants the argument that the constituent parts resemble free-living organisms, falls away, and the view that these parts represent individuals, is therefore but weakly supported. In the articulate and segmented animals the articulation and segmentation appear moreover at a comparatively advanced stage in the development of the body and they do not extend over all its parts. The segmentation of the Chordata e.g. is primarily confined to the mesoderm.

The cellular theory is founded on the homology between tissue-cells and free-living cells, and this homology has seldom been questioned. It is nevertheless very dubious. If we realize that an amoeba and a mammal are both living beings and therefore homologous, the amoeba can not be regarded as homologous with a cell of the mammal, for that would mean that the mammal would be homologous with one of its cells, which is evidently absurd. We may say that the amoeba is homologous with the

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<sup>1)</sup> The difference between the morphological and the ecological standpoint is well exemplified by the various ways in which the capitula of the Compositae and the flower of *Iris* can be interpreted. To the morphologist the first is an inflorescence and the second a flower, but the ecologist has the right to regard the capitulum of the Compositae on account of its function as a single flower and the flower of *Iris* as a complex structure consisting of three parts, each of them comparable to a single flower; he regards them, in fact, from the same point of view as the pollinating insect would do, at least when it possessed a mind given to analysis.



egg-cell of the mammal, but in that case the egg is not regarded as a mere cell but as the prospective mammal. If the cell of the amoeba is said to be homologous with the cell of a mammal, this is not to be taken literally, for it does not mean that it is homologous with an arbitrarily chosen cell of the mammal but with an idealized one, i.e. with a cell in which the essential characters of all the cells are combined, a cell therefore that is more or less equivalent to a schematized mammal. The expression, however, is apt to create confusion and should therefore be avoided.

There are, as we have seen, no compelling grounds for the theory that organisms in which the main parts are present in the plural, should be regarded as colonies. The idea, moreover, is not everywhere applicable. The circumstance that the phloem and xylem strands of the Vascular Plants are always present in a larger number, is certainly no reason to regard these parts as individuals, and there can be no doubt that there are a considerable number of parts to which no individuality of this kind can be ascribed. However, when it is admitted that the idea is not everywhere applicable, there is, of course, no reason to assume that it forms anywhere a necessary element of our morphological interpretation. For this reason it seems superfluous to spend much time on these rather sterile speculations.

The morphological nature of the various parts is, according to the definition of morphology given above, determined by their position. However, as some of the parts may occupy an anomalous position and others may be lacking, the plan is not always easily recognizable. In such cases the problem may often be solved by an investigation either of nearly related organisms or else of the earlier stages of development, for in one or the other the shifted parts may occupy their normal position, and of the failing ones some vestiges may still be present. If the necessary evidence can not be obtained in one of these ways either, a solution may sometimes be found by application of the rule that the homologous parts themselves are also built according to a common plan, which means that they consist of homologous components. If we can prove therefore that the constituent parts of lower order are homologous, the homology of those of the higher order may be regarded as sufficiently established.

In the preceding paragraphs we paid but little attention to the exact meaning of the expression "corresponding position". This point nevertheless deserves a closer examination, for the question whether the position of different parts may be regarded as corresponding, is not always easily answered. To some of the difficulties that are experienced in this field, I have already hinted in the previous section.

In discussing the question what meaning is to be attached to this expression, it seems desirable to deal separately with the positions occupied by the various parts in the bodies of different organisms (homology s.s.) and with those occupied by similar parts in the body of the same individual (homodynamy).

In the case of homology s.s. the correspondence is, on the whole, easily definable. What kind of determinants for this purpose are used, is perhaps best shown by means of some examples, which, for the sake of clearness, will be taken from a single group of organisms, viz. the Angiosperms.

When the morphologist homologizes the ordinary green leaves of an oak, a buttercup, a lupin, a pea and a mimosa, he bases his conclusion on the consideration that they are all lateral appendages of stems or branches, that they all bear one or more buds in their axil, and that they are preceded and followed by hypsophylls of a similar kind. The definition of their position is therefore in the first place based on the presence of a longitudinal axis, viz. the stem or branch on which they are inserted, in the second place on the polarity of this axis, i.e. the opposition between its apical and basal parts, which shows itself in the position of the axillary buds and sometimes also in a difference between the lower and upper hypsophylls (cotyledons, bud scales and bracts), and in the third place on a relation to other parts, in this case especially to the axillary buds or to the shoots into which the latter may grow out. Instead of a single axis a larger number of them may be involved, but as these axes are, as a rule, all of the same kind, we may for the sake of simplicity confine our attention to one of them.

The lateral insertion on a bipolar axis and the relation to axillary, preceding and following parts are, however, not always sufficient to define the position. In the case of the parts present in a zygomorphous flower or in that of leaves inserted on a shoot that does not show the ordinary radial symmetry, we need at least one determinant more. The first that offers itself as such, is the sagittal plane, i.e. the plane that divides the structure to which the part belongs, into symmetric portions. In lateral shoots and in zygomorphous flowers it is the plane that can be brought through the middle of the subtending leaf and the axis on which the latter is inserted, whereas in main axes that are not radially symmetric and occupy an inclined or horizontal position, the vertical plane that passes through the centre of the axis may, as a rule, be taken. In the very rare instances in which such an axis occupies a more or less vertical position, e.g. in the grasses, the requirements are fulfilled by the plane passing through the centre of the shoot and the middle of the scar that indicates the place where the shoot was originally connected with some other part, i.e. either with the endosperm or, in case it developed from an axillary bud, with the parent shoot.

The plane passing through the axis from which a lateral appendage springs, and the point that is regarded as the latter's centre, does not always divide the lateral appendage in symmetric portions. Examples of such asymmetric parts are to be found in the leaves of the *Begonia* species and in the *Canna* flower, whose single stamen is provided at one side with a petaloid expansion.

When the portions on either side of the sagittal plane are each other's reflected image without being fully equal, i.e. when it proves impossible to bring them in such a position that one is entirely covered by the other, the part is called bilaterally symmetric or dorsiventral. This is the kind of symmetry that is met with in the majority of the leaves and of the zygomorphous flowers.

In the flowers of the Cruciferae there are two symmetry planes. This might be called "quadrilateral symmetry"<sup>1)</sup>. The two symmetry planes are perpendicular to each other, and the portions on either side of them are not only each other's reflected image but also fully equal. Other planes passing through the axis divide the part in equal portions that are not symmetric.

When a part possesses three or more symmetry planes, it is called "multilaterally" or "radially" symmetric. When the number of symmetry planes is even, the portions in which the part is divided, are, exactly as in the quadrilaterally symmetric parts, not only each other's reflected image but also fully equal. When it is odd, the portions are never fully equal.

A satisfactory description of a complicated structure like the flower can not always be based on the symmetry schema alone. In such cases it is especially important to note how the successive parts are inserted with regard to each other. In the flower the various parts are, as a rule, arranged in whorls, and the members of the successive whorls are mostly alternating; sometimes, however, they prove to be superposed or they are arranged according to some other pattern. When the number of parts in the whorls differs, their position is, of course, especially difficult to describe. In such cases a schematized projection on a horizontal plane, the so-called flower diagram, may be very useful.

The preceding considerations lead to the conclusion that parts met with in various organisms are regarded as homologous when the position they occupy with regard to the bipolar axis and the symmetry plane or planes as well as with regard to the adjoining parts, can be described in similar terms. Examples of such homologous parts are our right arm, the right front leg of a dog or of a lizard, the right wing of a bat or of a bird, and the right pectoral fin of a fish. Other examples are found in the exterior stamen on the right side in all flowers with a didynamous androeceum. Not always, however, such a high degree of precision is aimed at. The indications right and left are, for instance, often omitted, because the differences between the right and the left side of the body are usually so slight that it is tacitly admitted that they may be neglected. When the bracts by which the flowers of various plants are subtended, are considered homologous, this is a similar simplification. In this case it is

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<sup>1)</sup> In a posthumous work of J. C. Schoute, this symmetry type is called "bifrontal".

tacitly assumed that the bracts met with in each of the latter are sufficiently similar to be regarded as identical.

The determination of the exact position is not always so easy as in the examples given above. One of the arguments on account of which the flowers of a raceme are considered homologous, is the presence of a bract at the base of the pedicel. This argument, however, is not applicable in the case of the Cruciferac, for the flowers of the latter are not subtended by bracts. We have to confine ourselves here to the rule that parts consisting of homologous components are themselves also homologous, and we base our conclusion in this case therefore on the homology of the perianth cycles, the androeceum and the gynoeceum with the isonymous parts of other flowers. The homology of the latter rests, of course, on their position with regard to the bipolar axis of the flower and to each other, and in the case of the stamens and of the pistil on the connection with such important morphological entities as the pollen sacs and the ovules.

When a part is not found in the position it ought to occupy, a similar kind of reasoning is used as in the case of a missing part. When the abdominal fins of the fishes are found immediately behind the head, they are nevertheless homologized with the hind legs of the land-vertebrates because they are built on the same plan as the abdominal fins of those fishes whose paired fins occupy a similar position as the legs of the land-vertebrates. In this case we apply therefore the rule that *a* must be equal to *c* when both are equal to *b*, the intermediate term being in our example the abdominal fins that occupy with regard to the pectoral fins a similar position as the hind legs of the land-vertebrates do with regard to their fore legs.

The foregoing two examples may for the present suffice to show in what way the morphologist explains deviations from the ideal plan by the aid of some special hypotheses. In the case of the flowers of the Cruciferae he assumes that the failing bracts have been "suppressed", and in that of the fishes with abdominal fins in the anterior part of the body, he claims that these fins have been "shifted". To these hypotheses, which play an important part in morphology, I will come back further on.

When the parts belong to the bodies of different organisms, the definition of what is meant with correspondence in position offers therefore no insurmountable difficulties. In the case of parts belonging to the body of a single individual it is, however, sometimes very difficult to decide what this expression really stands for.

The similarity between the right and the left side of the body is in most organisms so outspoken that the homodynamy of the parts on either side of the sagittal plane needs no special comment.

The question is also comparatively easy to answer when the body consists of a series of comparable rings or segments as in the articulate and segmented animals and in the Vascular Plants, where the stems and branches are composed of internodes that bear one or more leaves at



their upper end. In all these cases the comparable portions of the body contain a part of the bipolar axis and are with regard to the symmetry planes constructed in a similar way. These portions are, like organisms belonging to the same or to related species, built according to a common plan.

Difficulties, however, are met with when the rings or segments do not show such an ideal similarity or when no such parts are present. Instances are found in the fore and hind limbs of the Vertebrates, in the phloem and xylem strands found in various parts of the body of Vascular Plants, and in the mesophyll and the cortex parenchyma of root and shoot in the same group of organisms. In all these cases the position with regard to the central axis and to the symmetry planes passing through the latter plays either no part at all or but a subordinate one, and to decide the question of their homology we are to rely on the position they occupy with regard to other parts and on the presence of homodynamous structural elements. The fore and hind limbs of the Vertebrates are regarded as homologous because they are lateral appendages of the body and because they are built according to a similar plan. The xylem strands in root, shoot and leaf of the Vascular Plants are regarded as homodynamous, in the first place because they belong to the central cylinder or to derivatives of the central cylinder and occupy in the latter everywhere a similar position, and secondly because they contain homodynamous structural elements, viz. the tracheids and tracheae. The mesophyll and the cortex parenchyma of root and shoot are homodynamous because they are bound on the outside by the epidermis and on the inside by the stele or by the meristeles in which the latter sometimes is split; the value that is to be attached to their homologization depends therefore upon the question whether the epidermis and the stele, or the system of meristeles by which the latter sometimes is replaced, may in all parts of the plant be regarded as homodynamous.

In the examples discussed above parts were often considered homologous or homodynamous because they were found to consist of homologous or homodynamous structural elements. If the structural elements met with in a number of organisms prove to be homologous, and if these organisms are therefore built on a similar "plan", they are said to be of a similar "type". The degree of similarity between the various morphological types depends upon the number of structural peculiarities in which they agree, and it forms accordingly a measure of the taxonomic relationship of these types. For this reason morphology, as was recognized already by de Candolle, may be said to form the foundation of taxonomy. If we wish to be precise, we should say that it forms one of the foundations of taxonomy, for the latter may also use attributes in which the morphologist is not interested, e.g. the presence or absence of definite chemical compounds.

According to the degree of similarity observed in groups of organisms

of different rank, the types of these groups differ in their degree of complexity. Beginning with the very specialized types corresponding to the units of the lowest taxonomic rank (varieties, species) they gradually become more generalized when we pass on to more and more comprehensive groups; in the latter the special characters of the lower units are, of course, gradually eliminated. Where, however, does this elimination of characters lead to, and is there a morphological type that may be regarded as common to all living beings?

The latter question has generally been answered in the affirmative, and when a justification of this answer was deemed necessary, it was thought to be provided by the cell theory. If the cells really could be regarded as the fundamental structural elements of the organisms, if, in other words, the cells of all organisms could be regarded as homologous, no objection could be raised against this view. It is, however, by no means sure that all cells are homologous, and it is quite certain that not all organisms possess a body consisting of cells.

Within each group of organisms the homology of the cells rests upon the similarity between their component parts and upon the position they occupy in the body. The cells themselves are usually regarded as individuals. This idea forms, as we have already seen, the basis of the theory. So long as we confine ourselves to free cells, no objection can be raised against this interpretation, but when we extend it to cells that are united into tissues, the presence of middle lamellas and similar structures must be regarded as a serious difficulty, for the latter can not be said to belong to the individual cells. However, an absolute independence of the cells is not required, and against the assumption of a limited degree of freedom no objection can be raised. In the majority of the groups the cells may doubtless be considered homologous because in the cytoplasm and in the nucleus they possess common constituents, and because they develop and multiply in a similar way.

Cytoplasm and nucleus, to confine ourselves to the main constituents, are, however, not everywhere distinguishable, and the cells do not always develop and multiply in the same way; although usually multiplying by division, they arise in some groups by budding. It is therefore by no means certain that the cell types met with in the various groups really are homologous.

That the cells of *Bacteria* and *Cyanophyceae* should be homologous to the cells found in the other groups of organisms, seems hardly believable, for their protoplasm does not show the ordinary differentiation in cytoplasm and nucleus. In the other groups the differences are not so striking, but they are nevertheless obvious enough. The cells of the *Ciliatae* and *Flagellatae* with their pulsating vacuoles, and the animal cells, which, as a rule, lose their individuality at an early stage, are not readily comparable with the cells that are met with in most divisions of the plant kingdom, and in the latter we are confronted with groups like the *Sipho-*

nales and the Phycomycetes, that possess an acellular structure. In the way the term "cell" nowadays is applied, it is merely descriptive and, to make matters worse, rather vague. It surely can not be regarded as a well-defined morphological conception.

As it proves impossible to give a morphological definition of the cell, and as the morphologist accordingly is unable to accept the latter as the common structural unit of the body of all organisms, we will have to find out whether another element may perhaps be regarded in this way. The only one that offers itself for consideration, is the protoplast, but as the definition of the latter has to be based on that of the protoplasm, it is not acceptable either, for the protoplasm can only be described as the seat of the vital functions and is therefore no morphological concept at all. We are therefore forced to admit that the morphologist is unable to indicate a unit that may be regarded as common to all organisms, and it is accordingly impossible to speak of a "general morphology". For the same reason the term "general cytology" is to be rejected.

We have already pointed out that the cells of the various groups of Protozoa can hardly be considered homologous. In other respects too the points of agreement between these groups appear to be so few and of so little importance that it is hardly possible to regard the Protozoa as a natural group. The similarity between the cells of the Sponges and those of the Metazoa appears to be of more importance, and these two groups might perhaps be dealt with under a common heading. However, here too one is very soon at the end of his tether, for the cell layers in the body of the Sponges are on account of their peculiar development hardly comparable to those found in the body of the Metazoa, and there are, moreover, no other points of agreement in the general plan of the body. The morphological analysis therefore begins only after these two groups have been separated. With regard to the Metazoa we may safely say that the morphological analysis does not attain real significance before it confines itself to the subdivisions of this group. So far the most important object for zoo-morphological investigation has been the phylum Chordata and among the latter especially the subphyllum Vertebrata.

After my remarks on the character of the cells of the Bacteria and Cyanophyceae it seems hardly necessary to emphasize that these groups deserve no place in a "botanical" morphology. The Algae, Fungi and Embryophyta have also but few points in common, and the general morphology of this rather heterogeneous assemblage is soon dealt with. The points of resemblance are for a good deal to be regarded as analogies, and are therefore of no direct importance to the morphologist. This applies, for instance, almost certainly to the resemblance between the growing points of the Embryophyta and those met with in some of the more voluminous Algae, to which in the older morphological literature considerable attention has been paid. Difficult to explain is the presence of chromatophores both in the Algae and in the Embryophyta, for it

seems to indicate a nearer affinity between these two groups than one would otherwise be inclined to assume. The agreement in this respect is the more remarkable because of the independent position the chromatophores occupy among the cell constituents. It reveals itself in the way they multiply, and led to an at one time very popular theory according to which they were originally free-living organisms. In a very remote past they would have entered into a partnership with the plants in whose descendants they are now constantly met with. If this were so, their presence in two groups of doubtful affinity would not be so very strange, for we know at least one group of organisms, viz. the Bacteria, of which representatives have entered into a partnership of this kind with plants belonging to different circles of affinity. They are found in the so-called leaf-nodules, that are known to occur in two species of *Dioscorea*, a number of *Myrsinaceae* (a section of *Ardisia* and two small genera that are perhaps not really distinct from the latter) and in three but distantly related genera of the *Rubiaceae* (*Heterophyllaea*, *Pavetta*, *Psychotria*). However, as the chromatophores are apparently unable to multiply outside the cells and as their structure seems to be simpler than that of any of the organisms with which we are acquainted, the difficulties this theory finds in its way, seem to be so great that it can hardly be accepted.

Between the Algae and Fungi the homologies are also of a rather doubtful nature. The presence of plurinuclear cells and that of an acellular structure in some Fungi and in some groups of Algae are probably mere analogies. The derivation of the various *Phycomycetes* from definite groups of Algae, with which they agree in their acellular structure and to some extent in their mode of reproduction, and that of the *Eumycetes* from the *Rhodophyceae*, for which arguments have been found in the alternation of sexual and asexual generations and in the structure of the reproductive organs, can not be regarded as sufficiently founded, as not enough attention has been paid to the possibility of a differentiation along more or less similar lines. That such a parallel differentiation is quite well thinkable, will have to be admitted when we realize that the trichogyne of the *Rhodophyceae* is not only paralleled by that found in some of the *Ascomycetes* but also to some extent by the archegonium neck of the mosses and ferns, the integument neck of the *Chlamydospermae* and the style of the *Angiosperms*.

As a full discussion of the relations between the Algae, Fungi and Embryophytes would occupy too much space, we will content ourselves here with the remark that phyto-morphology is, like zoo-morphology, almost entirely confined to a single group of limited extent, namely to the Vascular Plants, and that among the latter the Phanerogams have always occupied the first place in the discussions.

We need hardly fear contradiction when we assert that botanical morphology has found its origin in the morphological study of the Phanerogams. At present the other groups of Vascular Plants and to



some extent the evascular Embryophytes too share in the attention, but the frequent misapplication of morphological concepts in discussions extending over these wider fields prove that the morphologists but rarely realize that these concepts have been based on the study of a group of limited extent and that they are therefore not necessarily applicable to the wider range of objects that are now drawn within the circle of their attention.

The subsumption of all parts observed in the Vascular Plants under the classical categories root, shoot and leaf, is a good example of this tendency to extend the meaning of a concept obtained in a field of limited size. For the moment I will leave out of consideration that it is fully impossible to subsume under these headings the parts that are to be distinguished in the sexual phase, and that even for a part of such obvious importance as the sporangium no place can be found in this now fully antiquated system. The importance of these parts was overlooked also in the group for which the categories root, shoot and leaf were originally established; this finds its explanation in the fact that many morphologists failed to recognize the great importance of Hofmeister's discoveries with regard to the antithetic alternation of generations and to the homologies existing between the reproductive parts. For the moment this may be left out of consideration; what I wish to point out at this junction, is that the distinction between shoot and leaf was based on the position these parts occupy with regard to each other in the group of the Phanerogams.

In the Phanerogams the leaf can be defined as a lateral appendage of an axis differing from other lateral appendages by the presence in its axil of one or more primordia (buds) from which new axes may develop. As this relation between shoot and leaf is confined to the Phanerogams, these terms have outside this group no morphological meaning. The Clubmosses are the only group outside the Phanerogams in which axillary buds are met with, but here they are an exception, and they are, moreover, not used for the ramification of these plants, which is brought about by a bifurcation of the growing point, but only for vegetative reproduction. In the Horsetails the buds appear in the interstices between the verticillate scales that are designated here in a slipshod way as "leaves", not in the axil of these parts. In the Ferns still another type of branching is met with. The parts to which in these groups the name "leaves" is applied, agree from a morphological point of view in one respect only with the leaves of the Phanerogams, viz. in their character of lateral appendages, and as this applies also to such totally different parts as the axillary shoots by which the leaves of the Phanerogams are accompanied, and to the "leaves" met with in the gametophyte of the evascular Embryophytes and even in some of the larger Algae, this point of resemblance is apparently but of slight importance. A further argument against the homologization of the leaflike lateral appendages in the main groups of the Vascular Plants is found in the fact that these appendages are not

built on the same plan. When the term "leaf" is nevertheless applied to them, it is used in an ecological, not in the morphological sense. The lack of agreement in the structure of some of these parts has already long ago been recognized, but it was not expressed in a satisfactory form. Several authors have tried to show that the strongly divided "leaves" of the Ferns are homologous with shoot systems, but this is in itself illogical, for as the relation between leaf and shoot on account of which these categories are kept apart in the Phanerogams, is absent in the Ferns, the term "shoot" is here from a morphological point of view as meaningless as the term "leaf". The homology between the "roots" met with in all these groups seems to be much better founded, for it rests upon their endogenous origin, on the presence of a calyptra, and on the absence of pluricellular lateral appendages of exogenous origin.

In the same way in which the morphology of the Vascular Plants was often led astray by a totally unjustified faith in the general applicability of concepts based on the study of the Phanerogams, the morphology of the latter often suffered by an uncritical application of concepts developed in the study of the Angiosperms. Examples of such misguided efforts are found in the attempts to homologize the flower of the Angiosperms with parts that perform a similar function in other groups of the Phanerogams, and also in the attempts to homologize the parts by which the pollen sacs and the ovules are borne. To see these problems in their true character, we must regard them in connection with related ones, and it seems desirable therefore to insert here a general outline of the morphology of the Vascular Plants.

A rational morphology of the Vascular Plants will have to be developed in juxtaposition to a morphology of the other groups of the Embryophytes, viz. the Hepatics, Anthoceros and the Musci. In the forefront of its interest it will have to put the antithetic alternation of generations. To this standpoint it will have to adhere, no matter whether the two generations are independent from each other or interdependent in another way than in the evascular Embryophytes, and even when one of them is so completely absorbed in the other that it is more aptly regarded as a phase in the latter's development. As the complete homology of these interdependent phases with the more or less independent generations of the other groups can not be doubted, and as the distinction between "generation" and "phase" is after all more functional than structural, and therefore of more interest to the ecologist than to the morphologist, I do not think it necessary to pay special attention to these differences, and for the sake of simplicity I will therefore in the following paragraphs everywhere use the term "generation".

In the sexual as well as in the asexual generation a distinction is to be made between a vegetative region and a reproductive one. In the asexual generation or "sporophyte" the latter is formed by the sporangia or their homologues, the pollen sacs and ovules, and in these parts a wall

consisting of one or more cell layers is to be distinguished from the contents, which consist of the spores, usually a fairly large number, but eventually, viz. in the case of the "megasporangium", reduced to a few only or even to a single one. In the sexual generation or "gametophyte" the reproductive region consists of the antheridia and archegonia or of structures that are to be regarded as their homologues. In the Phanerogams and also in some of the other groups of Vascular Plants the sexual generation consists of unisexual individuals. In the Phanerogams the male ones are represented by the pollen tubes, the female ones by the embryosacs. The latter remain always included in the ovules and are fed through the intermediary of the latter by the sporophyte. The pollen tube subsists on its way to the embryosac on the tissue through which it passes, i.e. in the Angiosperms on the style and on parts of the ovule, in the other Phanerogams on the latter alone. In accordance with this parasitic mode of life the whole character of the Phanerogamic gametophyte has undergone a change, which manifests itself i.a. in the complete or almost complete suppression of the wall of the sexual organs. The latter are for this reason no longer directly recognizable as antheridia and archegonia.

In the Vascular Plants the vegetative region of the sporophyte possesses in the presence of roots and in that of a vascular system features that are eminently suited for morphological comparison. In the differentiation of the aerial parts in an axis or a system of axes and in leaflike lateral appendages there is, however, as we have seen, a good deal of variation, and the parts that are the result of this differentiation, can not everywhere be regarded as homologous. The shoot-like and leaf-like parts of the various groups are to be regarded as analogous formations, and the idea that it ought to be possible to subsume them all under the headings shoot and leaf, should definitely be abandoned. To use an expression that has become firmly rooted in the morphological vocabulary, they are "organa sui generis". As the latter have a rather bad reputation, it is perhaps not superfluous to add a few words in their defence.

Plant morphologists were originally of opinion that a very restricted number of categories would suffice to inventarize the immense wealth of variation shown by the different groups of plants, and even to-day this belief has many devotees. A strict adherence to this view has, however, often led to strangely distorted interpretations. The attempts to interpret the "stigmarias" of *Lepidodendron* and *Sigillaria* as rhizomes may serve as an example. The authors who defend this view, apparently overlook the fact that the term rhizome applies to underground shoots, and can morphologically therefore only be used in the group in which true shoots are present, i.e. in the group of the Phanerogams. However, even if we should forget for a moment that the *Lepidodendrons* and *Sigillarias* are no Phanerogams and possess therefore no true shoots, there would be no excuse for regarding the stigmarias as rhizomes, for if they were underground shoots, they ought to appear from time to time either with their

top or with a side-shoot above the ground. As they do not fulfil this condition, there is evidently no reason whatever to compare them with rhizomes. They have merely been squeezed into this category because there was elsewhere no place for them!

To arrive at a satisfactory morphology of the various groups of Vascular Plants it will be necessary to introduce a considerable number of new categories. Such a line of conduct has doubtless many advantages, for if it is adopted, several difficulties with which the morphologists have for a long time been struggling, will appear to be spurious; they will be recognized as self-inflicted tortures of a similar kind as the search for the quadrature of the circle. As an example I will cite the difficulties met with in the explanation of the differences in the position of the sporangia in the various groups of Vascular Plants. If the idea that the leaflike parts found in these groups are all homologous, is given up, these difficulties are at once removed. When we realize that the difference between the vegetative and the reproductive region of the sporophyte is morphologically of greater importance than the differences between the various parts of the vegetative region, it becomes clear that according to the way in which the latter differentiates, the sporangia may come to occupy entirely different positions. It is therefore not to be wondered that they are found in the Psilophytes at the end of a stemlike structure, in the Horsetails on special sporangiophores, in the Clubmosses in the axil or at the base of the leaflike appendages, and in the Ferns along the margin or at the back of the leaflike parts.

In the Phanerogams the sporangia, which are known here as the pollen sacs and the ovules, are usually assumed to occupy everywhere the same position. This means that the subregion of the sporophyte in which these parts are brought together and to which usually the term "flower" is applied, would everywhere show the same uniformity of structure as the rest of the vegetative region. However, when we realize that the main points of difference between the various groups of Phanerogams are to be found precisely in the structure of this subregion, this view does not seem convincing.

The parts by which the pollen sacs and the ovules are borne, are generally regarded as homologous with leaves. At one time this idea was supposed to be applicable to all sporangia-bearing parts that are met with in the Vascular Plants, a supposition that found its expression in the term "sporophyll". However, when we admit that the term "leaf" has outside the Phanerogams no morphological meaning, this concept loses its foothold and all the speculations that have been based on it, are set a-drift.

The idea that the pollen sacs and ovules of the Angiosperms are borne by leaves, arose at a time at which the morphologists had as yet no suspicion of the fundamental importance of the sporangium. In the earlier discussions the pollen sacs and ovules played, in fact, no part at



all. The question was in those days formulated in a somewhat different way and sounded more or less like this: are we justified in regarding the various parts of the flower, and among them the stamens and the pistil or, in case the latter proves to be a composite structure, its component parts, as homologous with leaves? It was answered in the affirmative, but the evidence on which this opinion rested, was rather scanty.

In *Nymphaea alba*, it was noted, there is a gradual transition between stamens and petals, and as the latter were thought to be derivable, via the sepals, from leaves, this seemed to prove the foliar nature of the stamens. However, as the petals can in this case just as well or perhaps better be regarded as sterilized stamens, this argument is in reality of no value. No value either can be assigned to the similarity that is to be observed between the so-called mono-carpellary pistils of the Ranunculaceae, especially those of *Caltha*, *Delphinium* and *Aquilegia*, and ordinary green leaves, for it is after all but superficial and of no more significance than the resemblance between the phylloclades of *Asparagus* and true leaves. The teratological transformation of the centre of the flower into a leafy shoot, to which originally also much weight was attached, does not signify anything. It merely shows that the embryonal tissue in the centre of the flower, which normally remains dormant or passes into the adult state, may occasionally resume its activity, and as the embryonal tissue possesses probably everywhere the faculty to develop in various directions, the fact that it produces here occasionally a vegetative shoot, is no cause for wonder.

More recently arguments of another kind have come to the fore. In the discussions on the morphological nature of the stamen much attention has been paid to the deeply divided "microsporophyll" of the Bennettiales. That these "microsporophylls" are leaflike, can not be denied, but this impression may nevertheless be misleading. Some of the fossil relations of the Horsetails were provided with sporangiophores that were deeply split, but the homology of the latter with the simple sporangiophores met elsewhere in this group need nevertheless not be questioned. There is therefore no forcing reason to accept the division of the part by which in the Bennettiales the pollen sacs are borne, as proof of its foliar nature. It may as well be regarded as the product of a process by which the simpler sporangiophores met elsewhere in the Phanerogams are split up.

The argument to which nowadays most weight is assigned in the question regarding the homology of the parts by which the ovules are borne, with true leaves, is of a similar nature. It is found in the leaflike aspect of the "megasporephyll" of *Cycas*. The evidence, however, is rather puzzling, for these "megasporephylls" make a more or less teratological impression, and their position as well as their character are so aberrant that they are more a problem in themselves than a help in the solution of the original one. It is, however, not necessary to enter into details, for just as in the case of the "microsporophyll" of the Bennettiales we may

confine ourselves to the remark that the resemblance with a true leaf may after all be misleading.

The preceding considerations led to a negative result: there is as yet no convincing proof for the thesis that the parts by which the pollen sacs and the ovules of the Phanerogams are borne, are of a foliar nature. In view of the important differences in structure and position exhibited by these parts in the various groups it should, moreover, not be forgotten that they need not everywhere be homologous and that a solution of this question in one of the groups would therefore not necessarily solve the problem for the other ones. Before the characteristics of these parts have been studied in more detail, a final solution of this problem is hardly to be expected. However, even when we have become much better acquainted with them, the issue may remain uncertain. In the rest of the vegetative region the homology between the various kinds of leaves rests upon the presence of axillary buds, but as the latter are never met with in the subregion to which the reproductive parts belong, the only really forcible argument for the foliar nature that so far has been brought to light, is in this case wanting. The value that is to be assigned to arguments of other kinds, is difficult to determine. At present there is, at any rate, no uniformity of opinion with regard to them. In view of the great diversity exhibited by these parts in the various groups, it seems advisable to assume a cautious attitude, and to restrict the applicability of our morphological deductions to the group in which they were obtained. Whether the "stamens" of the Angiosperms are homologous with those of *Ephedra* and with the "microsporophylls" of *Pinus* and *Cycas*, the monocarpellary pistil of the *Ranunculaceae* with that of *Ephedra*, with the cone scale of *Pinus* and with the "megasporephyll" of *Cycas* are in the present stage of our knowledge unanswerable questions.

In the Angiosperms the structure of the stamens is rather uniform, and the slight amount of variability existing between them is not of such a nature that it could shed much light on the morphological character of these parts. The gynaecium, on the other hand, is a rather protean structure, and the peculiarities it exhibits, doubtless deserve a closer inspection. However, before entering into the problem of the latter's interpretation, it seems desirable to pay some attention to the other parts of the sporophyte, and to acquaint ourselves with the way in which the apparently less far-reaching deviations from the normal plan that are met with in these parts, are explained.

In the leaf axil of the Angiosperms we find, as a rule, just as elsewhere in the Phanerogams, one or more buds. When there are more than one of them, they are arranged in one of the two following ways. In the Dicotyledones they are, as a rule, found in a single or, more rarely, in two or more vertical rows, in the Monocotyledones with amplexicaul leaves in one or, less often, more transverse rows. As a rule, not more than one of these buds grows out into a branch. This is the most common way in which in

the Angiosperms branches are formed, but there are three more ways in which the latter may arise. Two of these three modes of branching can in no manner be fitted into our schema, whereas the accommodation of the third mode requires, as we will see, one or, sometimes, two special assumptions.

The two ways of branching that can in no manner be fitted into our schema, are the dichotomy and the ramification by means of branches arising from adventitious buds.

Dichotomy is in the Angiosperms of very rare occurrence. It is regularly observed in some species of the African palm-genus *Hyphaene* and occasionally in some other palms and in the fasciated stems of tulips and fritillarias. The dichotomy of the palms appears to be a process of a similar kind as the splitting of the flattened growing-points of the fasciated stems, and is therefore best regarded as a hereditary anomaly. Branching is in palms very rare; axillary buds, however, are always present: they develop into inflorescences or, when we have to deal with palms provided with a terminal inflorescence, into the lateral branchlets of the latter. The inflorescences of the *Hyphaenes* are axillary.

Adventitious buds may appear on roots, shoots and leaves, either in the normal course of events or when a wound has been inflicted, in which case they often arise in the proliferations formed by the meristems that were exposed by the wound. In those plants where they appear in the normal course of events, they often play an important part in the process of vegetative multiplication, but they do not seem to partake in the normal process of ramification. As neither their occurrence nor their position are bound by any general rule, they are morphologically of little importance.

The third aberrant mode of branching is found in the floral region of some plants. It looks in these cases as if the flowers or the inflorescences are not formed at the top of the shoot or in the axil of a leaf but either extra-axillary, i.e. opposite a leaf, or, in plants with decussate phyllotaxis, inter-axillary, i.e. on one side of the shoot between the opposite leaves. The vine may be quoted as an example of a plant with extra-axillary inflorescences, the *Asclepiadaceae* as a family with inter-axillary ones.

The extra-axillary and the inter-axillary mode of branching can both be reduced to the normal type by assuming that the bud to which the inflorescence owes its origin, does not arise in a lateral but in a terminal position, and that the part of the shoot above the insertion of the inflorescence is the product of an axillary bud originally situated at the base of the latter. In the case of the interaxillary inflorescence we must assume, moreover, that the common base of the inflorescence and the axillary shoot has grown out to the full length of an internode, and that the first internode of the axillary shoot, on the contrary, did not grow out at all. That these two conditions must be fulfilled, is easily seen, for if the common

base of the two buds did not grow out, the inflorescence would make the impression of an axillary one, and if it did not grow out to the full length of an internode, the regular aspect of the sympodial shoot would be disturbed; if, on the other hand, the first internode of the axillary shoot grew out in the ordinary way, the inflorescence would be left behind and would come to occupy a position somewhere between the pair of leaves at the top of the preceding internode and the first pair of leaves of the axillary shoot. In the case of the inter-axillary inflorescence the actual disposition of the various parts is often described in a somewhat different way, viz. as the result of a concrescence between the first node of the axillary shoot and the base of the peduncle. However, it seems more natural to ascribe the unusual situation, as I have done above, to the growth of a transverse zone situated at the base of the two buds. Inter-calary growth-zones of this kind are of common occurrence, whereas the concrescence of originally distinct parts always remains a somewhat strained assumption.

Although the position of the extra-axillary and inter-axillary inflorescences can doubtless be explained in the way indicated above, it might be objected that this interpretation sounds more or less arbitrary. For this reason it seems desirable to look for additional evidence. This is found in the fact that these deviating positions are only met with in circles of affinity in which terminal inflorescences are of common occurrence.

The bud for which on theoretical grounds a terminal position is claimed, may sometimes remain invisible until the axillary bud that is to take its place, has reached a certain size. However, neither the relative size of the two buds nor their position with regard to the top of the axis is from a morphological point of view of decisive importance. The question is decided by the position they occupy with regard to the leaf at their base. When in plants with opposite leaves an inflorescence is found in the axil of a leaf, it is for this reason difficult to make out whether it is an axillary one or, on the contrary, a terminal one that has been driven out of its original position by the rapid development of a shoot in the axil of the opposite leaf. That in the axil of the latter usually a bud is found, does not matter: serial buds are in sympodial shoots of common occurrence. In the Rubiaceae, where the inflorescences are in some circles of affinity terminal and in other ones axillary, there are quite a number of genera where never more than a single inflorescence is found at each node. The floras usually describe these inflorescences as axillary, but in many cases they are undoubtedly to be regarded as terminal ones. Occasionally plants with forked stems are met with, and the latter, of course, owe their origin to the circumstance that instead of one both buds at the base of the peduncle have grown out into a shoot.

Above we have made ourselves familiar with one of the additional hypotheses the morphologist requires for the explanation of deviations from the ideal plan, viz. the possibility that a part may have shifted by



the activity of an intercalary growth-zone into a more or less unusual position. Apart from this hypothesis he may call to his aid the assumption of a partial or total suppression, of a concrescence and, when the number of parts is increased, that of a fissure. The morphologist assumes that a primordium may stop its development at an early stage, and that it need not even become visible, that parts that are supposed to originate as distinct primordia, may fuse, and that, on the contrary, originally simple primordia may split in two or more separate ones.

Splitting of an originally simple primordium is observed e.g. in the case of the compound leaves and in the very rare instances of dichotomous ramification. The suppression of parts is a phenomenon of very frequent occurrence. In many bud-scales and bracts the leaf-blade appears to be lacking, and in the flower it often happens that one or more of the stamens are reduced to staminodes or that they are entirely suppressed.

Structures that are described as the result of a fusion between originally free primordia, are also of common occurrence, especially in the flower, where the sympetalous corolla and the monadelphous androeceum may serve as examples. A fusion between the basal parts of ordinary green leaves is observed e.g. in the genus *Dipsacus*. The morphologist speaks in these cases, as a rule, of a concrescence between the petals, filaments and leafbases, but this term is perhaps better avoided. It is, as I have already pointed out when I discussed the interpretation of the inter-axillary inflorescences, not necessary to assume a real concrescence in these cases. Concrescence between originally free parts, it is true, is by no means rare. It is often observed in shoots and roots that for some time have been in contact with each other, and in horticulture use is made of this possibility in the practice of grafting. However, in all these cases the concrescent parts exercise a certain pressure on each other, and it is very dubious whether such a pressure is present in the parts between which the morphologist assumes concrescence.

We are acquainted with a fairly large number of examples of originally free parts between which afterwards such an intimate connection is established that they can not be separated without suffering damage. The corolla of the *Ceropegia* species looks like a kiosk with large windows; this strange aspect is due to a union between the tops of the tails in which the originally free corolla lobes are drawn out. Even more striking examples are found in the so-called water-calyces. A calyx of this kind forms in the bud a completely closed envelop round the corolla, which for a long time lags behind in its development. In this way a free space is formed between calyx and corolla, and as this space is completely shut off from the atmosphere, its expansion creates a pressure deficit on account of which fluid is sucked in through the walls, especially through the thinner parts of the latter that are represented by the so-called hydathodes or waterglands. The air-tight connection between the calyx lobes is brought about by interlacing excrescences of the marginal cells. A similar con-

nection is also met with in the syngenesious anthers of the Compositae. In all these cases the connection between the marginal cells is doubtless very intimate, but it can hardly be called a concrescence.

Between the petals of a sympetalous corolla there is surely no concrescence at all. The union takes place between the meristematic parts at their base, and it is by no means easy to decide whether at that moment the latter may still be regarded as parts of the petals. Owing to the circumstance that the cells in the gaps between these meristematic parts join in the growth of these parts, a complete meristem ring is formed. This annular meristem may therefore be regarded in two different ways: it may be looked at as the product of a fusion between the basal parts of the petals, but also as an outgrowth of the axis on which the petals are carried upwards. If the latter interpretation is accepted, the corolla tube does not consist of the basal parts of the petals but represents a part of the axis.

That the axis may grow out in the way suggested in our second interpretation, can not be doubted. In fact, the axis may assume even stranger shapes, e.g. in the flat receptacles on which in *Dorstenia* the flowers are inserted and in the fig, which is a hollow axis formed by the activity of a similar meristem ring as plays a part in the sympetalous corolla. Outside the region of the inflorescence too such annular meristems may play a part. Paraboloid growing-points like those of *Hippuris* and *Elodea*, although always figured in the text-books as typical examples of the apical meristem of the Angiosperm, are in fact fairly rare; more or less flat ones are far more common, and in the growing-points of the Cactaceae and of the succulent *Euphorbias* the centre proves to be deeply sunk. This strange aberration is doubtless of ecological importance, for it ensures protection for the most vital part of the growing-point against excessive drought and night frosts. In other plants this part is covered by the young leaves and sometimes by bud scales, but in the Cactaceae and in the succulent *Euphorbias* the leaves remain rudimentary and bud scales are unknown.

As the cells by which in the case of the sympetalous corolla the originally free meristem parts are united, can not be regarded as part of the corolla, the interpretation of the annular meristem that continues their task, as an outgrowth of the axis would seem to deserve preference above the more or less strained assumption of a concrescence. There is, however, one case, viz. that of the style of the syncarpous pistil, in which the intervention of an annular outgrowth of the axis might seem to be excluded. The cells by which in this case the meristem ring is completed, are part of the carpels, and when we regard the latter, as the adherents of the classical theory do, as leaves, this would mean that the style is entirely of foliar origin. It seems worth while to examine this case in some detail.

As a rule, the syncarpous pistil makes its first appearance in the form

of two or more distinct knobs. They develop into the stigmata, which are the only parts in which in the end the original distinctness of the primordia is reflected. In the next stage the cells between the knobs begin to partake in their growth, and in this way the narrow meristem ring is formed that gives rise to the style. This ring subsequently widens and forms at the same time dilatations on its inside, usually just below the spots where the knobs originally met. This leads to the development of the ovary with its parietal placentas or, when the dilatations extend to the centre, with its dissepiments. When we place ourselves on the standpoint of the classical theory, and accept the homology of the carpel with a leaf, we will have to admit that in this case a fusion must have taken place between originally free leaves. It is, however, by no means necessary to accept this theory, which, as we have seen already, is but weakly founded. If we reject it, we will have to regard the parts by which the pollen sacs and the ovules are borne, and perhaps the perianth slips too, as "*organa sui generis*". How is the union between the originally free knobs in this case to be explained?

According to the adherents of the view that the flower parts are not, or at least not all of them, directly comparable with leaves, the vegetative region would be differentiated into two subregions, one consisting of the leafy shoots, and the other comprising the "*sporangiophores*", i.e. the stamens and the pistils, and, perhaps, the parts by which they are enveloped, and this differentiation would be of more fundamental importance than the differentiation in the first subregion of shoots and leaves, and than the differentiation in the latter of an axial part and appendages in the form of stamens, pistils, and, eventually, perianth slips. The differentiation within each of the two subregions might in that case be independent from that in the other.

If we accept the gynoeceum as an "*organum sui generis*", we may interpret it as a meristem proliferation in which the stronger growth of a peripheral zone, eventually supported by the meristematic activity of cell strips extending from one part of the periphery to another, leads to the development of one or more cavities, on whose wall subsequently the ovules are produced. If we place ourselves on this standpoint, we will have to regard the free carpels of the apocarpous gynoeceum as a special case in which the walls of the cavities have undergone a splitting. These free carpels might, however, also represent naked female flowers; to this possibility I will come back below.

In the interpretation of the Angiospermous gynoeceum given in the preceding paragraph the most prominent place is assigned to the formation of the cavities in which the ovules are developed. As the inclusion of the latter in cavities is one of the distinctive characters of the group, it seems to me that it deserves a very prominent place in the latter's morphology. Those who regard the gynoeceum as a compound structure and the carpel as its basal unit, will object that the new interpretation overem-

phasizes the difference between the Angiosperms and the other groups of the Phanerogams, but to this I answer that the difference is indeed so important that it seems hardly possible to overemphasize its value. They will also say that it widens the cleft between the interpretation of the gynoecium and that of the androecium, but as the androecium and the gynoecium are also fundamentally different in some other groups of the Phanerogams, e.g. in the Bennettitales, this objection need not deter us either. There is certainly little reason to assume that the "flowers" met with in the different groups of Phanerogams are all built on the same plan.

If the gynoecium is accepted as an "*organum sui generis*", the rules by which the morphological behaviour of the leaf is bound, are, of course, not applicable to it. The knobs that develop into stigmata need in this case not be regarded as independent units, and there is therefore no reason to ascribe the origin of the style and of the syncarpous ovary to a concrescence of originally free parts. We may confine ourselves to the statement that the whole structure arises out of the top of the growing point, but whether the latter is at that stage still part of the axis, is difficult to decide. This question, however, is perhaps not so very important, as the axis of the flower is evidently not fully homologous to that of the other subregion.

After what has been said on the general structure of the gynoecium, the explanation of the inferior ovary does not offer much difficulty. Here too the opinion that the wall of the ovary is the product of a concrescence between the perianth base and the lower part of the filaments with the carpels is perhaps not the most plausible and certainly not the only possible explanation. We may also assume that the perianth and the stamens are elevated to a higher level by an annular meristem, and that the gynoecium develops on the inside of the cup formed in this way. When we realize that the top of the growing point need not be convex or flat, but that it may also be hollowed out, the difference in structure between the superior and the inferior ovary can easily be explained. Even to those who prefer the old view of the homology between the carpel and the leaf, the inferior ovary presents no more serious difficulties than the syncarpous superior one does.

Before leaving this subject I must return once more to the question of the "concrescence" between originally free parts. We have seen above that this is in the external morphology of the Phanerogams a superfluous hypothesis. However, as it plays an important part in zoo-morphology, e.g. in the skeleton of the lumbar region in birds and mammals and in that of the foot in the Ungulata, it might also play a part in corresponding fields of phyto-morphology, e.g. in the stelar structures. However, as a discussion of this question would take too much time, we will not enter into details.

So far we have occupied ourselves exclusively with the simple parts in which the body is dissolved by the morphological analysis, but morpho-



logy has also to deal with more complex structures. We will confine ourselves here to those that are met with in the Angiosperms.

In the morphology of the Angiosperms the simple parts of the sporophyte are root, shoot, leaf, pollen sac and ovule, and when the homology of the flower parts with leaves is denied, the perianth slips, the filaments and the sterile parts of the gynoecium; those of the male gametophyte or pollen tube are the vegetative and generative nuclei, and those of the female one or embryo-sac the egg-apparatus, polar nucleus or nuclei and, eventually, antipodes. A special position is taken in by the endosperm, which is a kind of undifferentiated sporophyte. Compound parts are bulbs, inflorescences, flowers, stamens, pistils, fruits and seeds. In all these structures two or more of the simple parts are intimately connected into a unit of a higher order. In internal morphology too such compound parts occupy an important place: the simple xylem and phloem strands are, for instance, combined in the complex vascular bundles, meristemes and steles.

In external morphology stamen, pistil, flower, fruit and seed are doubtless the most important compound parts, for they return in all the representatives of the group, and they are therefore as essential as the simple parts. Their definition appears to be beset with greater difficulties than one would perhaps have expected. That of the stamen, which consists, as a rule, of a filament with one or more pollen sacs, is perhaps the simplest one, for if we can make up our mind with regard to the morphological nature of the filament, the rest offers no difficulties. However, if the stamens are united with the gynoecium as they are in the *Asclepiadaceae* and *Orchidaceae*, the definition will have to be modified, and when we are confronted with the strange structures by which in the genus *Rafflesia* the pollen is produced, it proves to be entirely unfit. After what has been said on the interpretation of the structure of the gynoecium, the difficulties with which the definition of the latter is beset, need no special emphasis.

The flower might perhaps be regarded as a special subregion of the sporophyte. It is usually defined as an axis with restricted growth on which are inserted one or more whorls of perianth parts, one or more whorls of stamens and one or more pistils. Some of these parts may be lacking, and instead of in whorls they may also be arranged in spirals. In the so-called "naked" flowers the perianth is absent, and in the unisexual ones either the androecium or the gynoecium is lacking. The number of the parts varies, and a naked unisexual flower may eventually consist of a single stamen or of a single pistil. So long as a bract is present at the base of such a simple structure, it still answers the definition of the flower: an axis of restricted growth provided either with one or more stamens and (or) one or more pistils, eventually surrounded by one or more whorls of sterile parts. The bract, however, is not always present. We have seen already that it is usually absent in the *Cruciferae*, and it may therefore also be absent in inflorescences consisting of naked unisexual flowers

consisting of a single stamen or of a single pistil. A leaf-like part at the base of a stamen or of a pistil need, on the other hand, not represent a bract, for leaf-like parts occur also as appendages of the stamens, e.g. in the flowers of various *Asclepiadaceae*. It is therefore no wonder that it is not always easy to decide whether we have to deal with a single flower or with an inflorescence consisting of unisexual flowers of this very simple type. A classical example of such a controversy is the interpretation of the cyathium of the genus *Euphorbia*. The stamens are here halfway up provided with an articulation, and on account of the latter and also because of the fact that just above this articulation occasionally some small scales are met with, they are regarded as flowers, the minute scales representing the perianth, and the part beneath the articulation the pedicel. The arrangement of these structures in uniparous cymes is another, and as it seems, decisive argument in favour of this interpretation. However, if the latter is accepted for such a structure as the cyathium of *Euphorbia*, it is difficult to see why it should not be applicable to some other "flowers" in which an aberrant arrangement of the stamens and of the pistils is found. The spiral arrangement of the stamens and pistils observed in the "flowers" of the *Polycarpicae* is certainly as uncommon as the arrangement of the "stamens" of the *Euphorbia* cyathium in uniparous cymes. How this problem is to be decided in this case, is at this moment difficult to say. I have merely mentioned it, because it shows that the definition of the flower offers more difficulties than is usually assumed.

The problems with which we are confronted in the definition of the fruit, find their origin in the fact that the latter is in its present delimitation more an ecological than a morphological concept. In the ecological sense the fruit comprises all those parts that owe their origin to the further development not only of one or more pistils but also to that of the adjoining parts, at least in so far as they are intimately connected with the first and assist them in their function, i.e. in the distribution of the seeds. To the morphologist a fruit that develops entirely out of the gynoecium, is a true one, and all other ones are "pseudocarps" or spurious fruits. When the latter are studied more in detail, they appear to form a very heterogeneous assemblage. The group comprises structures that are equivalent with inflorescences, e.g. the ananas, the mulberry and the fig, and structures like the fruit of *Anacardium occidentale*, which consists of the strongly swollen, pear-shaped pedicel and the much smaller true fruit which is known as the cashew nut, further the strawberry with its fleshy receptacle strewn with small nuts, the cynarrodion or rose-hip, where the fleshy part is formed by the hollow receptacle, and the pome, where it consists mainly of the wall of the inferior ovary, which may be interpreted as another form of the hollow receptacle. Among the dry fruits too spurious ones are met with. The wings of alate fruits, for instance, may be formed by calyx or perianth lobes or by an outgrowth of the ovary, but they may also be a dilatation of the pedicel or a sclerified bract.

It is often difficult to know where the line should be drawn. The globose inflorescences of *Buphane*, an African genus of *Amaryllidaceae*, develop into infrutescences that are thrown off as a whole, and are then, with their long and stiff fruit stalks pointing in all directions, blown away as "steppe-witches", which in their race over the "veld" gradually shed their seeds. As these infrutescences behave as a whole, they might well be regarded as pseudo-carps.

The subdivision of the true fruits is also an ecological one. It rests on the edibility or inedibility of the wall: on account of this character they are divided in fleshy and dry fruits. The line is often difficult to draw, and that the distinction is from a morphological point of view of hardly any value, follows from the fact that the fruits of nearly related plants often belong to different groups. The further subdivision of these groups is neither morphologically nor ecologically of any value. That it is morphologically entirely worthless, has often been overlooked, for not rarely conclusions have been drawn with regard to the affinity of a plant from the presence of fruits that are known by the same name as those occurring in other ones. For this reason the *Proteaceae* genus *Brabeium* of the Cape has been regarded as related to some South American *Proteaceae* because its fruit is like the fruits of the latter a drupe. Among the other South African *Proteaceae* this kind of fruit is unknown. The conclusion, however, is certainly false. A more detailed investigation shows that there exists a considerable difference in structure between the fruit of *Brabeium* and the drupes of the South American genera, and that it can therefore not be homologized with the latter.

Morphologically well-defined fruits are met with in families like the *Cruciferae*, *Malvaceae*, *Umbelliferae*, *Acanthaceae*, *Labiatae*, *Boraginaceae* and *Compositae*, in a subfamily like the *Pomoideae*, and in genera like *Aristolochia* and *Trapa*. A satisfactory morphological classification of all these fruit types would have to comprise a much larger number of groups than at present are recognized, but such a classification lies perhaps more in the domain of the morphology of the various families than in that of the *Angiospermae* as a whole.

The preceding considerations will have shown that the morphology of the various main groups of the Plant Kingdom, and even that of the best studied group, the *Angiosperms*, is by no means, as is often assumed, a discipline that has already long ago reached its final goal, and that since then has been transmitted in a nearly unaltered form from one generation of botanists to the other. On the contrary, in this field too, large stretches of ground remain to be broken, and in many instances the investigations will have to enter into greater detail before a final conclusion can be reached. Far from being a sphere of thought belonging to the past, morphology is still as full of life as it has ever been, and the other biological disciplines, taxonomy and genetics in the first place, can only benefit by its further development.

## PHYSIOLOGY

Taxonomy, morphology and heredity, the three biological disciplines dealt with in the preceding essays, form a kind of biological trivium, to which the twin disciplines, physiology and ecology, may be opposed as an even more homogeneous group. In the latter our interest is centered on the life either of the individual or of groups of individuals, whereas our biological trivium occupies itself with the plan on which the organism is built. Taxonomy tries to grasp the plan's diversity, morphology analyses it, and heredity traces the way in which it is transmitted in successive generations.

When we say that the life of the individual is the domain of physiology, and the life of groups of individuals that of ecology, we should realize that the term is in the first instance used in the literal sense, in the second in a metaphorical one, and that in the latter case its application therefore is apt to be more or less misleading. The groups to which it is applied, impress us as being alive because the individuals of which they consist, are living. It can, of course, not be denied that the life of these individuals is one of the conditions of the persistence of the groups, but considered as a whole, the groups can not be said to show the characteristic features of life. Their existence has no well-defined beginning or end, nor does it show a gradual differentiation. In fact, so long as conditions remain the same, the groups persist in a virtually unchanged state. What happens when the conditions change, depends upon the composition of the groups. If the latter consist of genetically identical or nearly identical individuals, i.e. if they are species, they will, as a rule, die out, but when we have to deal with groups consisting of organisms living under the same circumstances, i.e. when they are associations, then their composition will undergo a change, and they will either pass into other associations or dissolve. In the latter case the constituent species, in so far as they are not weeded out, are distributed over the adjoining associations. In the life of neither of these kinds of groups there is, moreover, anything that might be compared with the faculty of multiplication, and as there is no change so long as the circumstances remain the same, it is obviously impossible to speak of growth either, and when there is no growth, respiration and the corresponding katabolic processes can surely not be regarded as essential features. It would therefore be better to avoid the metaphor, and to confine ourselves to the statement that physiology and ecology occupy themselves with the way in which individuals and groups of individuals persist.

A closer consideration of the persistence of the individual and that of a group of individuals reveals, as we have seen, a noteworthy difference. The persistence of a group of individuals is potentially unlimited, i.e. so long as conditions remain the same, there is no reason why it should



come to an end. The individual, however, is "mortal"; "the span of its life is but brief".

It is true that some kinds of individuals, viz. the unicellular organisms, are often spoken of as potentially immortal, which means that they remain alive so long as nothing untoward happens. However, the use of this expression, which enjoys a somewhat undeserved popularity in biological circles, is open to criticism. It can hardly be doubted that the individual unicellular organism ceases to exist when it splits, for there is apparently no reason to identify one of the products of the division in preference to the other with the original individual. We will, on the contrary, have to admit that the moment of splitting is the end of its individual existence, i.e. of its life. When the unicellular organisms are said to be immortal, they are therefore not regarded as individual living beings, but as links in an endless "living" chain. However, when we apply the term "life" to this chain, we use it, just as in the case of the species and the association, in a metaphorical way. The chain is said to live because its links are living, but the features on account of which the latter are regarded as living beings, are but of secondary importance when we regard the chain as a whole. The chain, in fact, represents the species, and its immortality is of the same kind as the immortality of the latter.

The chain of unicellular organisms might also be compared with the "germ tract" of the Metazoa, and this comparison shows perhaps even more convincingly that the use of the term "life" is in this case better avoided. The "germ tract" is a morphological abstraction introduced to explain the "continuity of the germ plasm", i.e. the unchanged transmission of the genetic structure from one generation to the next, and it is supposed to comprise all those cells that are involved in the production of the animal's eggs and sperms. It needs no special emphasis that these cells possess no independent existence. In this respect they are in the same position as the other cells of which the body of the Metazoa as well as that of the multicellular plants is composed, and in their case too the use of the term "life" must be regarded as metaphorical. It can, of course, not be denied that the cells undergo a change at the moment of death, and that a "living" cell is doubtless as sharply distinct from a "dead" one as a living organism from a corpse, but this does not prove that the "life" of the cell is fully identical with the life of the individual organism. With the exception of the fertilized egg, which may be regarded as a potential organism, the cells are all specialized and mutually dependent parts of the body, i.e. parts that lack some of the latter's characteristic faculties. Contrary to the current opinion their divisions too are not directly comparable to the process of multiplication as met with in the organisms themselves, for the most characteristic feature of the multiplication of the latter is that new individuals are produced by which the type of the parents is repeated, and this does not necessarily apply to the products of the cell division, which may develop in totally different

ways. The application of the term "life" to the period of existence of the cells must, in fact, be regarded as a most unfortunate extension of its original meaning; it is bound to lead to confusion.

The definition of "life" as the period of existence of the individual organism, can not be regarded as satisfactory so long as there may be some difference of opinion with regard to the meaning of the expression "individual organism". Our next task therefore will be to find out how the latter is to be defined. This is by no means easy, as in the use of this expression too we meet with a good deal of confusion. In fact, physiologists and morphologists use it in entirely different ways.

With regard to the term "life" it can hardly be doubted that it was first used in connection with man, and that its use has gradually been extended to other kinds of organisms, but with the term "individual" this was perhaps not so, for it means "indivisible", and "indivisibility" is obviously not a feature that occupies a dominant part in our mental picture of the human being. However, we have not to consider the original meaning of the term, but its application in biology, and here we may be sure that it was used, just as the term "life", first of all in connection with man and the larger animals, and that its use was gradually extended from the latter to other kinds of organisms. So long as the animals with which man was acquainted, belonged all to the free-living kind, no difficulties were met with. The latter, however, began to manifest themselves when animals were discovered that at the base proved to be connected into a kind of common stool. Examples of such "colonies" were found among the Coelenterata and Bryozoa and afterwards in a somewhat different form among the Tunicata. They owe their origin to a similar kind of vegetative reproduction as is found in many plants. The members of such colonies are morphologically comparable to each other, to their common parent and also to their free-living relations, and the morphologists therefore came to the conclusion that they too were to be regarded as individuals. So long as they are provided with all those organs that are characteristic for their free-living relations, and exercise all the latter's functions, this conclusion is acceptable to the physiologist also, but difficulties arise when the members of the colony, as e.g. in *Hydractinia*, begin to show a far-going differentiation in structure and function, for in such cases the various kinds of polyps are from a physiological point of view no longer sufficiently independent to be regarded as distinct individuals. Such colonies behave as an individual of a higher order, and the various kinds of polyps of which they are composed, are in these cases no more than subordinate members comparable to the tentacles, the intestine and the sex organs of their free-living allies. In *Hydractinia* the physiological individuality of the colony is still somewhat ill-defined, for the number of its parts is not fixed, nor is its size and shape definitely limited, but in the Siphonophores we meet with colonies in which the centralization is carried to a much higher degree of perfection, and although

these compound structures remain from the morphological point of view colonies, they are to the physiologist indivisible wholes, i.e. individuals. In fact, they are born, develop and die exactly like the free-living Metazoa for which the term "individual" was already at an earlier date generally accepted.

If the use of the term is extended to plants, its meaning is even more difficult to define. The way in which the more voluminous plants develop, is doubtless much more like that of a polypary than like that of an individual in the original sense of the word, and morphologists have therefore often tried to identify the body of such plants with colonies. In the Phanerogams individuality was from this point of view first claimed for the branches, afterwards for the internodes with the leaf or leaves belonging to them. The physiologist and the ecologist, however, have no reason to regard either of these parts as independent units, and to them the plant is an indivisible whole.

Our investigation into the use of the term "individual" leads to the conclusion that physiologists and morphologists apply it in an entirely different way. The morphological point of view, however, does not interest us here, and we will confine ourselves therefore to the standpoint of the physiologist. To the latter there can be no question of individuality unless all or at least part of the vital functions are provided for. At first sight this conclusion might seem rather disappointing, for we started our investigation in order to find out whether the definition of life as the period of existence of the individual might be regarded as a suitable one, and now we find that the physiological definition of the individual in its turn requires a consideration of the vital functions. The definition of life as the period in which at least part of the life functions are fulfilled, might at first sight seem a mere tautology. However, when emphasis is laid on the fact that at least part of them must be provided for and if the latter can be defined with sufficient precision, it is not entirely meaningless.

In my introductory essay I have summarized the vital functions under three headings: 1°, the faculty to grow and develop by means of substances that are prepared by the organism itself from materials derived from the environment, 2°. the faculty to carry out movements by the aid of energy obtained by the decomposition of substances prepared by the organism itself or, eventually, by other organisms and procured from the latter, and 3°. the faculty of reproduction. The two first-mentioned faculties are probably present in all parts of the organism that exceed a certain minimum value, but the last one is, as a rule, confined to special organs, and is therefore for the definition of the individual of more importance <sup>1)</sup>.

<sup>1)</sup> In the colonies of the social insects the faculty of reproduction is restricted to a comparatively small part of the individuals; the workers lack it, although they too possess organs of reproduction, be it in a rudimentary condition. The insects that are living together in such colonies, have apparently lost part of their

Reproduction originally meant the production of new organisms that repeated the features of their parents. The resemblance between parents and descendants, however, is not always so complete that the latter may be said to repeat the features of the first. In the case of unisexual organisms there is already a slight discrepancy, for the male descendants can not be said to resemble their female parent in all respects nor the female descendants the male parent, but the dissimilarity becomes much more significant when, as in the Aphids, generations of female and male individuals alternate with generations or successions of generations that are entirely composed of female ones with moreover a somewhat different aspect, and there is hardly any similarity at all when, as in the ferns, generations of diploid, asexually reproducing individuals alternate with generations of haploid, sexually reproducing ones, which show an entirely different structure and mode of life. It is therefore not allowed to confine ourselves to the statement that the descendants repeat the type of the parents, but we will have to add "or of some previous ancestor". In the case of hybrids the individuals belonging to the same generation combine, moreover, characters of both parents or, when the hybrids belong to a group in which an antithetic alternation of generations is found, of the two grandparents.

The difference between a fern prothallium and the fern plant that develops from the fertilized egg-cell in one of the latter's archegonia, is, from the physiological as well as from the morphological point of view, much more important than the difference found between any two fern plants or between any two fern prothallia. On account of their genetic relation the prothallium and the fern plant that develops on the latter, are nevertheless in the opinion of the morphologist but stages in the development of the same organism. The physiologist and the ecologist, however, regard them in an entirely different way, for to them form and function are of far greater importance than a common line of descent. In their eyes a treefern is more readily comparable to a Cycad or a palm, a stemless fern to the rosette of a biennial Umbellifera, the fern prothallium to the thallus of a liverwort or of a lichen than the fern is to its own prothallium.

This attitude of the physiologist is of special importance when we wish to understand the commonly accepted division of physiology in three branches, viz. general, comparative and special physiology.

Special physiology occupies itself either with a single species or else with a group of species of limited extent. Such groups may be composed of organisms that have no other connection with each other than their importance to man. This applies e.g. to veterinary physiology, which confines its attention to the vital phenomena observed in the domestic animals, and agronomic physiology, which occupies itself with the life "individuality", but we would doubtless go too far when we denied them all individuality.



of the cultivated plants, eventually with a passing glance at the accompanying weeds and parasites. Human physiology is an example of a branch of physiology that confines its attention to a single species. Animal and plant physiology may be quoted as examples of disciplines that comprise much wider fields. Human physiology, veterinary and agronomic physiology do not interest us here; they belong to the domain of applied science. Animal and plant physiology are to our purpose of greater importance, but for the moment we will leave them apart, because we will have occasion to return to them when we consider the aim and scope of general physiology.

Comparative physiology studies the similarities and dissimilarities that are exhibited by the physiological processes in the various groups of organisms. The expression "group of organisms" is, unfortunately, not always used in the same sense, and this explains why books that pretend to deal with comparative physiology, are often for a large part devoted to ecological problems. Comparative physiology should confine itself to groups of organisms that belong together on account of taxonomic relationship, whereas the study of groups consisting of organisms occurring under similar circumstances should be left to the ecologist. Comparative physiology tries to establish a correlation between the physiological character of a group and its taxonomic position. It studies e.g. the respiration of the fishes, and contrasts the latter with that of the Tetrapoda in order to emphasize the physiological peculiarity of the group; subsequently it may also consider less nearly related groups. In the same way and to the same end it compares the autotrophy of the Algae with the heterotrophy of the Fungi. The correlations are, however, not always obvious, and it is even by no means rare that we obtain the impression that they are entirely lacking. This is well exemplified by the way in which the faculty to wind round a support is distributed, and for this reason it is worth while to discuss the latter in some detail. I will confine my attention here to its occurrence among Phanerogams, as the corresponding phenomena in other groups have not been sufficiently studied.

Circumnutation and the faculty to wind round a support are found in the shoots of plants belonging to a fairly large number of Phanerogamous families. The affinity between the latter is often but remote, and several of them are more nearly allied to families in which the faculty to wind is entirely wanting. In some of the families, e.g. in the Convolvulaceae and Menispermaceae, it is a nearly general feature, but in other ones, e.g. in the Leguminosae, it proves to be restricted to a few genera. The absence of the faculty in some of the members of a taxonomic group and its presence in other ones may perhaps be explained by assuming that it remains in the first in a latent condition. Its presence in distantly related groups might be ascribed to the circumstance that it is not everywhere of the same kind, and that differences of a more or less fundamental nature may remain hidden behind a superficial resemblance.

The latency of a character must be due either to the absence of some internal or external factor that is required for its manifestation, or else to the presence of a factor by which the latter is prevented. In the *Convolvulaceae* with procumbent or ascending instead of winding shoots the character of the shoot is doubtless for a large part determined by external factors, for if these plants are cultivated in a humid soil and in subdued light instead of under the climatic conditions of their natural habitat, they assume, as a rule, the mode of growth that is characteristic for the family. The species of *Quamoclit*, on the other hand, are under ordinary circumstances high-climbing plants, but seedlings raised in a hothouse in the subdued light of our winter, developed into low plants that flowered and fruited without having produced a single winding. That the faculty to wind is not everywhere of exactly the same nature, need not be doubted either. In the winding *Monocotyledones* the part of the shoot in which the faculty to wind resides, has, at least so long as it is not hindered in its movement, the form of a semi-circular arc; it is, in other words more or less evenly bent over its whole length. The free-moving top of the *Dicotyledonous* twiners, on the other hand, is as a rule nearly straight, i.e. it is bent at the top and at the base only. This difference in form was found to be correlated with a difference in behaviour on the clinostat.

In comparative physiology, just as in morphology, a distinction should be made between homologies and analogies, and here too the establishment of homologies should be the proper aim of our endeavours. It does not seem necessary to enter more deeply into this subject as a comparative physiology of this kind is at the moment but little developed. What nowadays passes under this name, is, as has already been stated, mostly ecology. Comparative physiology and ecology, it is true, occupy themselves both with the behaviour of the species, but the ecologist regards them as constituents of associations, not as members of a taxonomic unit of higher order. We find, in fact, in the field of comparative physiology the same confusion of thought as was originally met with in morphology, which perhaps may be regarded as the comparative discipline par excellence. There too the earlier investigators did not make a sharp distinction between constitutional and functional similarity.

With regard to the real nature of general physiology too there is much confusion of thought. This appears, for instance, in the wide-spread belief that general physiology is identical with cell physiology, an idea that was based on the assumption that the cell is the common unit of all living beings, i.e. on the cell theory. As I have already pointed out in the introductory chapter, this theory, which was originally a morphological conception, will have to be abandoned, as the division of the body in cells is certainly no general feature of all organisms. From the physiological point of view it has hardly any meaning at all, for even where the body consists of cells, the functions of the latter are by no means always readily comparable. In the *Metazoa*, moreover, cells are in most parts of the body

but a passing phase in the development, but even the persistent and sharply defined cells that in the multicellular plants form the greater part of the body, are not such important elements as has often been assumed. It can not be denied that the cell-wall plays in this instance some part in the maintenance of the turgor, but this part should not be over-estimated. A large portion of the cell walls, viz. all those on which from both sides the same pressure is exercised, are in this respect completely superfluous. The turgor rests in reality almost entirely on the tension existing between tissue layers of different constitution. More important is the part which the protoplasmic lining of the cellwalls plays in the absorption and secretion of various products, but that the individual cells of the plant should always act as independent units in the metabolism, is nevertheless a mere assumption. On the one hand there is the possibility that parts of a smaller size may in some instances, e.g. in the case of the chloroplasts, play a more or less independent part, and on the other hand we should realize that the carrying on of certain functions may require the co-ordination of a comparatively large number of cells. The term "cell-physiology" therefore has no well-defined meaning, and is better avoided.

In recent times it has become customary to experiment more or less at random with all kinds of living beings, especially, of course, with those that for some reason or other are regarded as "suitable objects", and the results of this promiscuous experimenting are often presented as general physiology. In reality such an erratic treatment merely leads to a fragmentary ecology. General physiology should take its task more seriously; it should confine its attention to those phenomena that are common either to the whole range of living beings or, at least, to a large part of the latter. To find out what these phenomena are, is by no means easy; a somewhat closer examination will soon convince us that there is much analogy and but little identity in the phenomena that are commonly regarded as occurring in all living beings. It will be worth while to enter here in some detail.

Among the features that are common to the life of all organisms we have mentioned in the first place the faculty to grow and develop by the aid of substances that the organism itself builds up from constituents derived from the environment. These constituents may enter the organism either over its whole surface or through a part only, and they are passed on until they reach the place where they are required in the metabolism. Entrance as well as passage may be due to diffusion, but it may also be a mass movement. A mass movement of a diluted watery solution is met with in plants that are partly exposed to the atmosphere, for in this case the evaporation on the surface of the exposed part will cause a saturation deficit in the plant, which in its turn will give rise to a suction force that will exercise its influence everywhere where water can be drawn in. However, as the conditions for the origin of such a suction force are

present only in a single group of organisms, viz. in those whose body is partly exposed to the desiccating influence of the atmosphere, its study falls outside the field of "general" physiology. The latter has to restrict itself to the entrance and distribution of substances by way of diffusion and, eventually, to the devices by which this process can be accelerated.

With regard to the kind of substances that enter the organism and are passed on in the latter, there is no absolute uniformity either. The naked protoplasts of the animal body are able to absorb fats, but the cellulose walls by which the protoplasts in the majority of the plants are enclosed, prevent the entrance of these products. In plants therefore a first selection is made by these walls, which, as is well known, may be of different constitution, for in the Fungi they consist of chitin, and in the rest of the plants of cellulose and related substances. Whether a substance will enter into the protoplasts themselves, depends, of course, on its faculty to permeate the latter's surface layer, which differs in its constitution from the inner parts. This layer, however, is not everywhere of exactly the same kind. Inside the protoplasm a large number of substances are produced, and the amounts of the latter as well as their composition vary from one species to the other. The way in which these products arrange themselves inside the protoplasm, depends i.a. on their surface tension, and this is the reason why the so-called "lipids", a class of substances that are present in all cells, accumulate in the surface layer. Differences in the chemical constitution of these substances would account, at least partly, for the differences in "selectivity". Another cause for the presence of differences of this kind is found in the faculty to form insoluble products either in the protoplasm or in the vacuole. As calcium may be precipitated in the form of its oxalate, an organism that is provided with the faculty to produce oxalic acid, will doubtless be able to absorb more calcium ions than an organism that does not produce this acid, and in whose cells the calcium ions therefore remain in solution. The general character of the mechanism by which the entrance of the various products is regulated, is doubtless one of the study objects of general physiology, but a detailed investigation of the differences in selectivity must be left to the ecologist.

How different the devices by which the entrance of a substance is regulated, may prove to be, is well exemplified by the way in which the intake of water is kept within bounds. It is well known that the fresh-water Protozoa absorb more water than their protoplasm can contain, and that they expel the surplus by the aid of their pulsating vacuoles, a curious kind of structures, of which the mechanism is not well understood. In the fresh-water Algae the accumulation of such a surplus is prevented by the presence of the cell wall; with every amount of fluid that enters the cell, the pressure on this wall undergoes an increase, and as the tension in the latter increases of course at the same rate, after some time a balance will be struck between the force by which the water



is sucked in, and the force by which it is driven in the opposite direction. As the devices by which the water balance inside the cell is kept up, are therefore not everywhere of the same kind, their study would fall outside the range of "general" physiology.

That a large number of substances are formed in the inside of the various organisms, is well known, and that but a comparatively small part of these products is common to all of them, needs no special emphasis either. General physiology is, of course, interested in the latter only. To this group belong proteins, fats and carbohydrates, but also some other products like the lipids that have their seat in the surface layer of the protoplasts, and the enzymes and co-enzymes that play a part in the synthesis of the various substances and in the changes the latter undergo when they are broken down in the katabolic processes, or when they are temporarily split in more easily transportable ones.

The katabolic processes by which the aerobic organisms obtain their energy, differ at least in their final stages considerably from those observed in the partly or entirely anaerobic ones, and the latter too show among themselves a wide range of diversity. It is true that the general character of these processes is everywhere of the same kind. This is well seen in those cases where the basic material is dextrose. The latter is first of all phosphorylated by means of the enzyme phosphatase, and then the process continues with a series of successive dehydrogenations, enzymatic reactions by which hydrogen atoms of the phosphorylated dextrose are transferred to so-called co-enzymes that in their turn are dehydrogenated by other enzymes, the concluding step in the case of the aerobic organisms being the enzymatic oxidation of the last member in the series of hydrogenated substances by means of oxygen obtained from the medium in which the organism lives. The co-enzymes are apparently not everywhere of the same kind, and the same applies to the intermediate products; in the anaerobic organisms the end products too vary a good deal.

Of the use that is made of the energy set free in the katabolism, very little is known. One of the processes that depend upon this energy is the protoplasmic streaming, and the latter might perhaps be regarded as a common feature of all organisms, but even this is not quite certain. The movements inside the dividing nucleus may also be regarded as depending upon this internal energy supply, but they are, of course, confined to organisms in which nuclei are present. The fact that the transport of organic products ceases when the oxygen supply is stopped, and that under these circumstances growth and nearly every kind of movement come to an end, seems to prove that for these processes too energy has to be supplied by the protoplasts. The way in which this energy transfer is effected, still remains a mystery.

The faculty of reproduction too assumes entirely different aspects in the various groups. With reproduction the physiologist means the production of new individuals. A process like cell division therefore is from

his point of view not directly comparable with reproduction, for the daughter cells possess, as a rule, no individuality; only where the body consists of a single cell, the latter's division can be regarded as a reproductive process. The standpoint of the physiologist with regard to reproduction and the organs by means of which the latter is effected, is entirely different from that of the morphologist. From a morphological point of view the embryosac mothercell of the Phanerogams is a megaspore, i.e. a reproductive cell, and the embryosac itself a new individual. To the physiologist, however, the embryosac mothercell is not fundamentally different from the other cells of the young ovule, and the embryosac remains a part of the motherplant; in his eyes the latter's reproduction is effected by means of the seeds. Even the morphologically as well as genetically very important difference between a normal and an apogamic embryo is to him of minor importance.

Vegetative reproduction is not very interesting to the physiologist either. With regard to these processes his standpoint differs materially from that of the ecologist. To the latter the importance of the fact that sterile hybrids may be able to maintain themselves in this way, and that dioecious and heterogamous plants of which but a single specimen was introduced, have sometimes spread in their new habitat over areas of a very considerable extent (*Elodea canadensis* in Western Europe, *Eichhornia crassipes* in several tropical countries), is obvious, and the spreading of these clones is to him a striking example of the importance of this way of reproduction. In the reproduction by means of runners and of scions the main points of interest to the physiologist are the production of roots and in the case of grafts the concrescence between the tissues of scion and stock, and for the study of these problems he is not bound to these objects. When the physiologist therefore speaks of reproduction, he confines himself, as a rule, to reproduction by means of spores or eggs or, eventually, of seeds. It are, however, not only the reproductive parts themselves in which he is interested, but also the stages by which their production is preceded, i.e. the transition from the vegetative phase into the reproductive one. With regard to these changes we will have to admit that they may have a common base. That the latter may consist in the formation and transmission of definite products, follows from experiments in which shoots of so-called short-day plants were grafted on long-day ones, for in that case the latter assumed in the vicinity of the place of concrescence the character of the short-day plant, i.e. it began to flower when it was kept under conditions that were suitable to the flowering of the latter but unsuitable to that of a plant of its original character.

The most important limitations of "general" physiology are doubtless due to our insufficient knowledge of the common substrate of the physiological processes. This substrate is the "protoplasm", but this is so far little more than a name to cover our ignorance, for beyond the fact that it is the substrate of the physiological processes, we know practically

nothing of it. Its structure is said to be of a colloidal nature, but this does not mean very much, for the colloidal structures vary a good deal, and so long as we do not know what substances actually are involved, the problem of its structure can hardly be solved. It looks, moreover, as if the expression "colloidal" structure is no fully adequate description of the intricate mechanism by which the physiological processes are carried out. Even the substances that play a part in the development, maintenance and regulation of this mechanism, are but very imperfectly known to us. In order to study the structure of the mechanism itself, it has to be broken down, but as it has so far proved impossible to reconstruct the protoplasm out of these *débris*, this analysis has not brought us much further.

One of the protoplasm's main functions is the production of the various substances that play a part in the organism's manifold physiological activities; enzymes and hormones especially are in this respect of paramount importance. It can hardly be doubted that a large number of these products return in all organisms, and the study of these substances and the way in which their production is regulated, belong therefore to the chief objects of general physiology. It is, on the other hand, very probable that the protoplasm contains in the various kinds of organisms also products of a less general nature. The supposition that some of the latter are confined to a single species or variety, finds a strong support in the outcome of the serodiagnostic investigations.

The substances that are generally present in the organism, are apparently formed out of a comparatively small number of simpler substances, viz. proteins, fats, carbohydrates, vitamins and some anorganic salts. Plants provided with chlorophyll or with one of the other coloured substances that belong to the latter's circle of affinity, and also some groups of Bacteria possess the faculty to synthesize the basic organic compounds themselves. In the majority of these plants this faculty is confined to special parts of the body, and the rest of the body is, just like the organisms that lack this property, dependent upon a supply of these products. The production of the raw proteins, fats, carbohydrates and vitamins is therefore no study object of general physiology but of the physiology of particular groups. It also plays a prominent part in ecology; in fact, we might say that the transformation of the anorganic constituents of the environment into organic compounds and vice versa forms one of the latter's central problems.

The preceding considerations will have shown that "general" physiology, although not so many-sided as is often assumed, comprises nevertheless a large and varied number of subjects. It should, however, be borne in mind that our knowledge of the latter is, on the whole, rather unsatisfactory. There is doubtless much to be said in favour of the practice to begin a course in the physiology of some group of organisms, no matter of what kind, with a few lectures on general physiology, but it would be a mistake to regard the latter in its present state as a fund of general

rules from which the special ones required in the physiology of the particular groups could be obtained by inference. In giving it a prominent place in our exposition, we should not forget that it is in reality but a preliminary synthesis of our knowledge of a few special cases, and that the number of the latter is as yet in most instances far too small.

Better known than the features that are common to all organisms, are some of those that are confined to groups of a more restricted size. Several of these special features are more striking and, moreover, more easy of access to the analyst than the general ones, and this is doubtless one of the reasons why animal and plant physiology are to many biologists more attractive subjects than general physiology. Their nature is rather different from that of the latter, and this finds its explanation in the way they came into being. Both started from speculations on the function of structures that drew attention by their peculiar aspect, and on the how and why of an unexpected behaviour, and they took their departure therefore from a point diametrically opposite to that from which afterwards general physiology took its flight. The animal physiologists concentrated their attention at first on such specialized structures as the organs of locomotion and as the circulation and respiration organs of the Vertebrates, and plant physiologists were first of all attracted by the exceptional behaviour of the *Mimosa* leaves and by the curious structure of the dead elements in the wood of the seedplants, which, although originally regarded as respiration organs of a similar kind as those of the insects, were soon recognized as the channels along which the transport of water takes place.

Owing to their historical development neither animal nor plant physiology are at present exactly what they pretend to be, viz. a really comprehensive survey of the physiological functions in the groups with which they are dealing. This, however, is unavoidable. It is easy to see that a general physiology of the animal world and a general physiology of the plants could not differ very much from a general physiology of all living beings. As the division of the organisms in animals and plants is purely conventional, it can not be expected that the physiology of these groups will show special features that are common to all their representatives. In reality neither animal nor plant physiology try to be such general disciplines; on the contrary, they both occupy themselves most often with phenomena that are confined to special groups and for which no equivalent can be found in the other ones. In plant physiology this applies e.g. to the devices by which in the more voluminous land plants water is transported, and in animal physiology to the means by which in the larger animals the circulation is kept up, and by which air is passed in and out of the respiratory organs. It would doubtless be better to split these disciplines up, and to relegate the study of such problems to the physiology of the group in which they occur. Water is transported on a larger scale in the Vascular Plants only, and the study of this problem



belongs therefore to the physiology of the latter. In a physiology of the Vascular Plants there would, on the other hand, be no place for a study of the "chemosynthesis", the formation of carbohydrates by means of energy obtained by the oxidation of anorganic products, a process that is confined to some groups of Bacteria.

The haphazard way in which subjects of such an entirely different nature are dealt with in most handbooks of plant physiology, is rather confusing to the student. From a methodological point of view it would doubtless be more recommendable to divide the ordinary course in plant physiology in a course dealing with the physiology of the Vascular Plants and in a course of comparative physiology of the whole organic world. In the department of botany the latter might be adapted to the special requirements of the botanical student by special emphasis on the physiology of the Bacteria and Fungi. A course in the physiology of the Vascular Plants is, of course, an indispensable part of the curriculum of the agricultural student, and a comparative course on the anabolic and katabolic processes in the whole organic world would form the necessary foundation for a sound ecology of the communities with which he will have to deal, and which comprise not only the cultivated plants but also the weeds and parasites by which the cultures are infested, and the organisms that live in the same soil and influence the latter's structure and composition.

In animal physiology such practical points of view often recede into the background, and here the investigations are guided for a greater part by purely scientific interest, i.e. by man's insatiable curiosity. Only where the investigator concentrates on the phenomena of life in man himself and in his domestic animals, his aim may be said to be directed in the first place on a practical object.

In the following considerations I will confine myself to the physiology of plants, and mainly to that of the Vascular Plants, because I am better acquainted with this branch of physiology than with the other branches, but remarks of a similar nature could doubtless be made with regard to the subjects with which the other branches are dealing.

We have already repeatedly mentioned the three main features of life, and it seems plausible to bring them here once more to the fore and to assume that a logical subdivision of physiology, no matter with what group the latter is dealing, would have to be based on these three features. The first part would have to deal therefore with the absorption and assimilation of food, and with the concomitant phenomena of growth and development, the second with the katabolic processes, i.e. with the processes in which kinetic energy is liberated, and further with the movements that are carried out by the aid of this energy and with the other uses to which the latter may be applied; and the last part would occupy itself with the phenomena connected with reproduction.

Although I do not believe that weighty arguments can be adduced against this subdivision, it can, on the other hand, not be denied that it

makes in the present state of our knowledge a somewhat artificial impression. There can, of course, be no doubt that growth and development depend upon a supply of food, but the way in which the latter is provided and the transformations it has to undergo, are by no means clear, and in the study of these phenomena this side of the problem has received so far but little attention. The study of growth and development has confined itself almost entirely to a descriptive treatment and to the influence exercised on these processes by external circumstances, e.g. by differences in temperature, in humidity and in the manner in which the plants are exposed to the light. If we leave out the basic nutrients, it appears that the number of substances whose influence on growth and development has been investigated, is but small, and that the place they occupy in the metabolism and the way in which they exercise their influence, are, as a rule, but imperfectly known.

An even wider gap separates our knowledge of the processes by which kinetic energy is liberated, from that of the processes in which the latter is used. We know that a large part of the organism's activities, i.e. all the movements that are carried out by living parts, no matter whether they rest on changes in turgor or in the rate of growth, come to an end when the katabolic processes are stopped, but although this may be regarded as a confirmation of our conviction that they are in one way or another connected with the latter, it sheds no light on the nature of this connection.

Another point that should be taken into consideration, is that the energy used by the organism need not all be produced by the latter itself. This applies in the first place, of course, to the energy required for those movements that are independent of the presence of living protoplasm, e.g. to the cohesion movement shown by the annulus in the wall of the fern sporangium and to the imbibition movements exhibited by capsule valves, the involucre bracts of some desert Compositae and similar structures. The so-called transpiration stream in the vessels of the wood may also be quoted as an example of a movement for which the plant itself does not need to supply the energy, for this movement depends, at least so long as the atmosphere is not fully saturated, for a large part upon a suction force arising in the transpiring surface, and as the maintenance of the transpiration rests, of course, upon a supply of heat, and as the whole amount of the latter may eventually be obtained from without, it will be clear that the water transport does not necessarily require a supply of energy produced by the plant itself.

It can not be doubted that energy absorbed from without also plays a part in phenomena that are dependent upon the presence of a living and active protoplasm. In these cases, however, the nature of its action often remains obscure. This applies e.g. to the supply of light energy that is responsible for the production of a phototropic curvature. In view of the fact that the relation between the absorption of light by the reacting

part and the way in which the curvature is formed, has usually been misunderstood, this phenomenon deserves a closer examination.

In experiments mainly performed with oat seedlings the strength of the curvature was found, at least between certain limits, to be proportional to the amount of light absorbed by the reacting part, but as the curvature appeared to be accompanied by a decrease in the rate of growth and consequently, as growth belongs to the processes that require a supply of energy, in the consumption of energy, the absorbed energy is apparently not used for the production of the curvature itself. We will have to assume that the absorption takes place by the intermediary of some photo-chemical system, but what subsequently happens with the absorbed energy, remains a mystery. The photo-chemical system is apparently after some time restored to its former condition, which means that the absorbed energy is released. It is thinkable, of course, that it leaves the plant at once in the form of heat, but even when this were so, we would still have to account for the decrease in the consumption of energy that manifests itself in the decrease of growth. The way in which the growth of the reacting part is affected by the change in the photo-chemical system, is as yet not fully known. An indication may perhaps be found in the fact that at least one of the hormones that play a part in the maintenance of growth, was itself found to be photo-sensitive. Howsoever this may be, it seems fairly sure that one of the intermediate stages in the development of the curvature is the production of a substance by which the transport of the growth-hormone to the reacting zone is blocked. So long as the photo-chemical system is not entirely put out of action, this block will be more effective in the side turned towards the source of light than in the opposite one.

The proportionality between the strength of the curvature and the amount of energy absorbed by the sensitive part of the reacting organ has been brought into the field against a pronouncement made by Pfeffer to the effect that any disproportionality may exist between the magnitude of the so-called "stimulus" and that of the reaction. This objection, however, is unfounded, for Pfeffer did not mean that the magnitude of the stimulus is irrelevant, nor that there is no relation at all between the latter and the magnitude of the reaction, but merely that the reaction may be "disproportionally" strong. That his theory nevertheless is to be rejected, is due to the circumstance that it regards the release of a certain amount of energy as the essential feature of the reaction, and as we have seen above, such a release of energy certainly plays no part in the processes leading to the phototropic curvature. This does not mean that his theory may not be applicable in some other instances, for it is by no means sure that all the phenomena which Pfeffer ascribed to "stimuli", are of the same kind, but merely that it can not be accepted as a general rule. In animal physiology such a sudden release of energy is doubtless a quite common phenomenon; as an example we may quote the contraction of

the stimulated muscle. In plants it plays a part in the seismonastic reactions.

According to Blaauw's theory of phototropism the phototropic curvature is to be regarded as the "direct" result of the absorption of light energy, but this interpretation can not be accepted either. What happens with the absorbed energy, is unknown, but as the development of the curvature does not require an extra supply of energy, the absorbed energy is apparently not used for this purpose.

Because of the great importance that has always been attached to the so-called "product-rule of phototropism", it seems worth while to make a few remarks on this topic. According to this rule the amount of unilaterally incident light of definite quality that is required to produce a just visible curvature, is independent of the intensity of the illumination. We may express this also by saying that the product of the light intensity, and the time during which the reacting part is to be exposed to the light, has in this case a constant value. The rule rests on a few data communicated by Fröschel and on a much larger number of figures given by Blaauw. The latter are usually quoted, and it can not be denied that they form an imposing series. Unfortunately they can not all be right. As the curvature gradually shifts from the top of the growing zone towards its base, the length of the curved part will be the greater, the longer the reacting part was exposed to the light or, in other words, the weaker the intensity of the illumination was. However, a curvature that is just visible when it remains confined to a small portion of the reacting part, becomes invisible when it is spread over a larger stretch. For this reason Blaauw's figures pertaining to illuminations with light of a weak intensity and consequently of long duration, can not be right. This has apparently not escaped the attention of later physiologists, for Blaauw's table has occasionally been reproduced by them in an abbreviated form, the results obtained with the weaker sources of light being omitted<sup>1)</sup>. This, however, is not allowed, for the lack of reliability of a series of figures can not be made good by omitting those that are obviously wrong. I would not have mentioned this when the figures obtained by Blaauw in his experiments with weak light had not been adduced by others in support of the view that the photo-chemical substrate would already react to a single light quant. It is not my intention to enter into this question, but I am bound to point out that the figures on which the conclusion was based in this case, are unreliable.

From phototropism the attention naturally shifts to geotropism. Here we are confronted with an even more difficult problem than in the case of the phototropic curvature. The only direct effect of a change in the position occupied by a part with regard to the direction of gravity or, eventually, of the centrifugal force, seems to be a transposition of particles

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<sup>1)</sup> E.g. by Weevers, *Fifty Years of Plant Physiology*, Amsterdam 1949, p. 168.



whose specific weight differs from that of the semi-fluid protoplasm in which they are embedded. Haberlandt directed attention towards the presence of large amyllum grains in most of the parts that are able to react on changes in their position, and although the indispensability of the latter could not be proved beyond all doubt, the fact that the cell layer in which they are found, is, as Bose's measurements with the electric probe have shown, more intensely affected than any other one, and the circumstance that no other mechanism could be detected of which it seemed plausible to assume that it could play a part in the perception of a change in the organ's position, are strong arguments in favour of Haberlandt's "statolith" theory.

The question in which way a displacement of particles like the amyllum grains might cause the local changes in the rate of growth to which the geotropic curvature owes its origin, is difficult to answer. That these particles would be responsible for the changes because of the slight pressure they exercise on the layer of protoplasm on which they rest, does not seem probable. They might act, however, either indirectly through the intermediary of enzymes or hormones adsorbed on their surface or else, in case they are represented by amyllum grains, directly by their influence on the carbohydrate metabolism. There are, however, still other difficulties. In order to explain the origin of the curvature, we will have to assume that in the cells of the part by which the change in position is registered, the protoplasmic lining of the inner and that of the outer tangential walls possess a different constitution. If this were not so, the effect in the opposite sides of the organ would be the same, and there would be no curvature. That the top and bottom layers too must be different, follows from the fact that the so-called sine rule is no fully adequate description of the way in which the plant reacts to a temporary stay in positions in which its axis includes angles of different size with the direction of gravity. Originally it was assumed that the time in which it ought to be kept in such a position in order to react with a curvature of definite strength, was inversely proportional to the sine of the angle between the direction of gravity and the axis of the reacting part or, in other words, to the length of the component that is obtained by constructing a rectangular parallelogram with the axis of the reacting part as one of the sides and a vector representing gravity as the diagonal: the vector perpendicular to the axis is in this case the component we are looking for. Afterwards it was found that the result could be described more accurately by the use of the formula  $a \sin \alpha + b \cos \alpha$ , in which  $a$  and  $b$  are coefficients that can experimentally be determined. This formula tells us that the longitudinal component, i.e. the component in the direction of the axis, also exercises some influence on the result. In most instances the influence of the longitudinal component is but weak, but in the case of the *Dicotyledonous* twiners it was found to be of considerable importance; it explains why the overhanging shoots that have failed to find a support,

soon stop their growth. In order to account for the influence of the longitudinal component we will have to assume that the protoplasmic layer at the upper and that at the lower end of the "statocysts" are also somewhat differently affected by the presence of the "statoliths".

In the case of the phototropic curvature it is easy to see that energy, i.e. light energy, is absorbed from without, but in the case of gravity there is apparently only a redistribution of energy inside the reacting part. This raises another problem. By exposing etiolated seedlings to an omnilateral illumination followed by a unilateral one, it can be shown that the plant's sensitivity to light undergoes a decrease during the illumination. This is comprehensible enough as the primary effect of the latter is a change in the photo-chemical system; the velocity with which this reaction takes place will, of course, slow down when the amount of the photo-chemically active substance decreases. We may now ask whether the plant's sensitivity to the geotropic stimulation too will undergo a decrease during the time it is exposed to the latter's influence. In the case of a geotropic stimulation that is due to a change of the organ's position with regard to the direction of gravity itself, this problem is for the moment unsolvable, for so long as we are bound to the surface of this planet, it is, of course, impossible to eliminate the influence of this force. Instead of gravity, however, we might use in our experiments the centrifugal force, for the latter is known to affect the organism in the same way. It would not be difficult to construct a centrifuge on which during part of the time the apparatus is in action, the plants are slowly rotated round their axis. By the aid of such an apparatus they might first be exposed to a stimulation that affects them successively from all sides. This could not lead to curvatures, but it might, in the same way as an omnilateral illumination, decrease their sensitivity to the stimulus; this decrease would manifest itself when the plants subsequently were exposed to a unilateral stimulation. To this end we would merely have to stop the rotation of the plants round their own axis. If their sensitivity had been reduced by the preceding omnilateral stimulation, the effect of the subsequent unilateral one would, of course, be smaller than it would be in untreated controls.

In the case of the centrifugal force it is, however, by no means sure that the preceding omnilateral stimulation will cause a decrease in the plant's sensitivity. It is quite possible that it does not affect the latter at all. That the pressure exercised by the specifically heavier particles on the viscid medium in which they are embedded, could have much influence, is, on account of their small size, hardly conceivable, and if, as we suggested above, the stimulus would consist in an action carried out by chemically active particles, it is even more difficult to see why the intensity of the force by which the translocation of these particles is effected, would make any difference, for in this case the magnitude of the reaction would be determined by the length of time during which the

particles are retained in their unusual position and, eventually, by the mass of the substrate on which they exercise their action and which, on account of the latter, will undergo a diminution. It might be objected that in this case the effect of the centrifugal force would merely depend upon the length of time during which it acts on the plant, and not on the product of the latter and the intensity of the force, but it should not be overlooked that the product rule has only been proved for stimuli causing a comparatively weak reaction, and for such stimuli its validity is comprehensible enough, for in their case the translocation of the specifically different particles may remain incomplete, and so long as it is not complete, the time during which the centrifugal force will have to act in order to effect such an incomplete translocation, must, of course, be the longer, the weaker the force is. What will happen when the stimuli exceed these comparatively low values, will be difficult to find out, because in order to produce such stimuli, the centrifugal force will have to be increased to such a high intensity that it will almost certainly damage the internal structure of the plant, and under such circumstances a normal reaction is, of course, not to be expected.

If the interpretation of the geotropic reaction given in the preceding paragraph should prove to be right, it would mean that this reaction differs in a far more fundamental way from the phototropic one than has hitherto been assumed. The only point in which they would agree, would be found in the way in which local changes in the metabolism lead to differences in the rate of growth that reveal themselves in the form of a curvature. As other reactions that become apparent to us in the form of tropistic curvatures, might also show fundamental differences in their initial stages, it seems worth while to pay some attention to them too. We will confine ourselves, however, to those that have most often been mentioned in the literature, viz. to thermotropism, chemotropism, hydrotropism and thigmotropism.

As the rate of growth depends i.a. upon the temperature, local differences in the latter inside a growing organ must, at least if they can be kept up for a sufficient length of time, of necessity lead to curvatures, which, so long as the temperature inside the reacting organ remains below the optimum, will always be directed away from the source of heat. As the difference in the rate of growth would come to an end as soon as the difference in temperature inside the organ had disappeared, these curvatures would differ fundamentally from the geotropic and phototropic ones, which continue their development long after the stimulus has ceased to act. It has, however, been suggested that heat might also be absorbed in the plant in a similar way as the radiations that are responsible for the phototropic curvature, and in that case a reaction more readily comparable to the latter might be expected. Whether it ever acts in this way, is as yet uncertain.

Chemotropic reactions are brought about by substances of various

composition that are unequally distributed in the medium. Pollen tubes and fungus hyphen are suitable objects to demonstrate their presence, but roots too are chemotropic. The way in which these curvatures are brought about, is unknown, and it is even uncertain whether they continue their development in the same way as the phototropic and geotropic ones when the stimulus ceases to act, i.e. when the reacting organ is transferred to a medium in which the stimulating substance is either absent or evenly distributed.

As water too is a chemical, hydrotropism might be regarded as a kind of chemotropism, but water occupies in so far a special position as in contradistinction to the substances by which the ordinary chemotropic reactions are brought about, it is always already present in the reacting part in considerable amounts. This means that the parts which are supposed to be hydrotropic, must be able to react to comparatively irrelevant changes in their water content, and this seems hardly probable. It is, moreover, rather strange that the so-called hydrotropic curvatures turn, as a rule, their concave side towards the source from which the water is supplied, whereas one would expect that the absorption would cause an elongation of the absorbing cells, and consequently a curvature in the opposite direction. Hydrotropism, therefore, is a rather mysterious faculty. The idea that the root should be hydrotropic, is doubtless a remnant of the old Aristotelean teleology. Teleologists of that stamp regarded the root as an organ whose task it was to provide the plant with water, and they supposed that it would be entrusted to this end with a special sense by which it would be enabled to reach those parts of the soil where water could be obtained. Even after it had been recognized that the downward direction of its growth depends in the first place upon the regulating influence of gravity, this conviction persisted. It was apparently even strong enough to dull the critical faculty of investigators of such high standing as Sachs and Molisch. These physiologists based their opinion that the roots are hydrotropic on experiments in which these organs proved unable to free themselves from the underside of an inclined slab that was kept in a humid condition, so long as the angle of the inclination did not exceed a certain limit, i.e. so long as the gravitational stimulus was unable to overcome the stimulus that bound them to the inclined surface. They tacitly assumed that this second stimulus was a hydrotropic one, and paid no attention to the possibility that the inclined surface might exercise its attraction on the root not because of its water content but because of some other particularity. I could show that a dry surface too exercises an influence on the root, and that the attraction is even the stronger, the drier the surface is kept. This suggests the possibility that the reaction may be due to the unevenness of the surface, for the latter undergoes, of course, a decrease when the inequalities are covered by fluid. The reaction that binds the root to the inclined surface, might therefore be a thigmotropic one. For the



aerial roots of the epiphytic Orchids the presence of this kind of sensitivity had already long ago been reported, and a more general distribution of this property would therefore not be surprising.

Molisch tried to prove the hydrotropism of the root also in another way, namely by placing it between a wet surface and a dry one, but the results of these experiments were very irregular and are therefore unconvincing. Moreover, even if a repetition on a sufficiently large scale should reveal a slightly stronger tendency to turn towards the wet side, this would not prove that the reaction really is to be regarded as a hydrotropic one, for on account of the evaporation the temperature of the wet surface will, unless it is artificially heated, always be lower than that of the dry one, and this difference in temperature too might explain a somewhat faster growth on the drier side.

Thigmotropism is not confined to roots. In fact, it has already long ago been recognized as a characteristic property of the tendrils, and it is also known to be present in the tentacles of *Drosera*. It is sometimes assumed that the contact causes lesions, and that the reaction is in reality a kind of chemotropism, the stimulating substances being formed by the wounded cells. The thigmotropic curvatures of the tendrils continue to increase in the same way as the phototropic and geotropic ones when the primary cause of the reaction no longer exists. If the stimulus by which the thigmotropic reaction is provoked, should prove to act through the intermediary of one or more substances formed in the wounded cells, this similarity in behaviour would be easily comprehensible, for such substances would, of course, be apt to continue their activity after the contact had been broken. In thigmotropism, therefore, the primary cause of the reaction might be, exactly as in phototropism, the production of some substance by which in some way or other the normal rate of growth is changed. A similar interpretation was suggested above for the geotropic reaction.

Before leaving the subject of the tropisms I want to discuss a problem with regard to which the ideas developed by Pfeffer and his school are still almost generally accepted, although it can hardly be said that they rest on a sufficient foundation. I mean the belief that the direction of the curvature depends upon the strength of the stimulus, the effect of strong stimuli being diametrically opposite to that of weak ones. In the case of the phototactic and chemotactic reactions of the free-swimming micro-organisms, swarmspores and spermatozoids, this reversal of the direction is a well-established fact, but in all other cases there is either no indication at all of such a reversal or, if there is, the way in which it takes place, is so entirely different, that it can hardly be placed upon the same line. Before entering into a discussion of this problem, we should do well to realize that the real nature of the change in the behaviour of the cilia and flagella on which the reversal of the movement of the free-swimming micro-organisms, swarmspores and spermatozoids rests,

has as yet not been elucidated. However, as it is hardly conceivable that this change will be directly comparable to the changes in turgor and in the rate of growth that play a part in the production of the tropistic curvature, we can not expect that the behaviour of these organisms will throw much light on the latter.

The chemotropic and phototropic curvatures are the only tropistic reactions of which it is known with certainty that they may show a reversal of their direction when the strength of the stimulus exceeds a certain limit; in all other instances such a reversal is either improbable or at least not definitely proved. The chemotropic reactions are difficult to study, and there is in their case but little hope that a satisfactory insight into the nature of the reversal will soon be forthcoming. The phototropic reactions, on the other hand, are comparatively easy of access, and they offer therefore a better opportunity for the study of this phenomenon.

A unilateral administration of large amounts of light may lead to curvatures in a direction opposite to the normal one. These anomalous curvatures are sometimes preceded by a normal one, in which case the reacting part temporarily assumes an S-shape. A particularity of these anomalous curvatures is that they never reach a considerable extent, and that they persist for a short time only. It appears, moreover, that the amount of light which in one case was found to produce an anomalous curvature, would lead in another case to a curvature in the normal direction: we now know that this depends upon the length of time during which the amount is administered. When the latter exceeds a certain limit, the curvature is always of the ordinary kind; it was found to be the stronger, the more time it took to administer the full amount. The explanation of this curious behaviour is to be sought in the changes the photo-chemical system undergoes in the time during which it is exposed to the light. A more or less sudden fall in the photo-sensitivity proves to be followed by a very gradual recovery, but when the illumination is continued, the latter remains incomplete; the degree of sensitivity that ultimately is reached, appears to depend on the intensity of the illumination; the weaker the latter is, the nearer the level to which the sensitivity ascends will approach the original one. As in this way the original situation is more or less restored, the chance that a curvature in the normal direction will be formed, increases. This partial recovery of the photo-sensitivity must, of course, be due to a process that tends to restore the photo-chemical system, but on account of its slowness this process can not be regarded as a mere reversal of the primary reaction. It is apparently a more or less independent reaction or, perhaps, a chain of reactions, in which the decomposition products of the photo-chemical system are not necessarily involved. A discussion of the way in which under certain conditions the interaction of these processes in the opposite sides may lead to a curvature in the wrong direction, would take too much space.

For our present purpose it is enough to realize that the length of the period during which the amount of light is administered, is a factor of great importance. As we have stated above, the same amount of light that causes the appearance of a curvature in the wrong direction when administered within a comparatively short time, may cause a curvature in the normal direction, and even a very strong one, when it is provided in the form of a much longer but proportionally weaker illumination.

The considerations of the preceding paragraph mainly served to emphasize the difference between the almost instantaneous reversal of the tactic movements of the free-swimming micro-organisms, a reaction by which the character of the movement itself is, so far as we can see, not affected, and the changes the phototropic reaction undergoes under the influence of variations in the intensity as well as in the length of the illumination; the reversal in the direction of the curvature appears to be bound to entirely different conditions, and it can certainly not be regarded as instantaneous. From an ecological point of view it is noteworthy that this faculty to form a curvature in the opposite direction is apparently of no importance whatever in the life of the organism, but from a physiological point of view this is irrelevant.

The foregoing survey of the tropistic reactions is far from exhaustive. Our main purpose was to find out whether these reactions are sufficiently alike to be dealt with in the same section. With regard to the question of their dependence upon a supply of energy, we came to the conclusion that energy may or may not be supplied from without, but that even when it is supplied from without, it is not necessarily used for that part of the reaction which manifests itself in the form of a curvature. In the case of the phototropic reaction the total growth proved to be reduced, which means that the amount of energy required for the continuation of the growth process, has actually undergone a diminution. What happens with the energy which was supplied from without and absorbed by the photo-chemical system, and to the unused rest of the amount that otherwise would have been consumed, is unknown. The geotropic reaction, on the other hand, proved to be an example of a tropistic reaction that is carried out without a supply of energy from without. That the rate of growth of a shoot placed in the inverse position may be smaller, in the case of a Dicotyledonous twiner even considerably smaller, than that of a shoot in the normal position, shows that the reaction may nevertheless be accompanied by a change in the rate of consumption of the plant's own energy. We may add that in the case of the seismonastic reactions we have to deal with a quite different process, for here the administration of a comparatively small amount of energy leads to the release of a considerable amount of the energy stored in the reacting part.

Other differences in the character of the changes brought about in the form or in the movement of various organs or organisms under the influence of the external circumstances, are seen in the so-called "transmission" or

"conduction" of the "stimuli". In the case of the tropistic reactions the shifting of the curvature in a distal direction seems to rest on the shifting of the local deficit in the amount of growth-hormone to which the first appearance of the curvature was due. In the zone where the latter first became visible, this deficit is gradually reduced and at last totally abolished by a fresh supply issuing from the top, but in the meanwhile a similar deficit begins to make itself felt in the adjoining part, which is cut off from the supply issuing from the top and where the store therefore gradually diminishes. As the rate of growth and therefore also the consumption of the growth-hormone shows a gradual decrease in the direction of the base, the latter will experience the consequences of the deficit last of all, i.e. at a time at which the supply of growth-hormone to the zones above it has already been re-established. The way in which this transport of the growth-hormone takes place, is not yet quite clear, but so much is certain that it shows a decidedly polar character, the movement in the distal direction being much stronger than that in the apical one. This is apparently a similar problem as that with which we were confronted in our analysis of the geotropic reaction, where we had to assume the presence of a constitutional difference between the protoplasm that lines the inner and outer tangential walls as well as between that which lines the apical and basal walls of the cells by which the stimulus is perceived; in the question why the geotropic and phototropic reactions of roots and shoots take place in different directions, we probably find another analogon. However, as in the present state of our knowledge a discussion of this problem could hardly lead to definite conclusions, we will not enter into details. What interests us here, is that the transport of the growth-hormone is a rather slow process. In the case of the seismonastic reactions of *Mimosa* there appear to be two ways in which parts situated at some distance from the point where the stimulus is applied, are affected. There is a rather slow transmission in which these parts are stimulated by means of a substance of as yet unknown composition that is ejected by the directly affected cells and apparently transported with the ascending sap through the vessels of the xylem bundles. Besides this way of transmission there is also a "high-speed" conduction, of which the mechanism is as yet entirely unknown. It reminds one of the conduction of an excitation through the nerves in the animal body; the rate of transmission is of about the same order of magnitude as that found in the nerves of the more sluggish animals.

The preceding discussion dealt with phenomena that do not seem to fit very well into any of the three subdivisions of physiology proposed above. The tropistic reactions are, on account of the fact that their outward manifestation rests on local changes in the rate of growth, usually dealt with in relation to the latter. They are in this case regarded as special instances of the changes which the rate of growth undergoes under the influence of external circumstances. As light is known to



exercise such an influence on the rate of growth, it is only natural to assume that unilaterally incident light will lead to a curvature. This, however, does not mean that our knowledge of this effect of light on the rate of growth will enable us to calculate the strength of the curvature, for in case of a unilateral illumination the average rate of growth in the side turned towards the light need not be the same as that found in the case of a plant that is from all sides exposed to light of the same intensity (more properly, in which the average intensity in the whole section is the same as that in the front half of the unilaterally exposed one), nor is the average rate of growth at the back side of the unilaterally exposed plant necessarily the same as it would be in a plant that is from all sides exposed to light of the same intensity (more properly, in whose interior the average intensity is the same as that in the back half of the unilaterally exposed plant). When the reaction of the photo-chemical system leads to the formation of a block by which the transport of the growth-promoting hormones is retarded, the transport in a unilaterally exposed part might be deflected towards the side in which the block is slightly at a disadvantage, and in this case the retardation of the rate of growth might become disproportionally strong in the side turned towards the light. It is noteworthy, however, that the influence of this factor would remain confined to the magnitude of the curvature, but that it would not affect its direction. In the case of the geotropic curvature there is no change in the external circumstances, but only in the distribution of products with a different specific weight in the interior of the body, and in order to explain the way in which the redistribution of these particles might affect the rate of growth, we had to assume a quite special structure of the organ in which the stimulus acts, viz. a difference in the constitution of the protoplasm lining the exterior and interior walls of its cells, and also a similar difference between their poles. The nastic movements shown by dorsiventral parts may also be due to unequal growth, but they are not all of them of this kind: in organs provided with pulvini they are, as a rule, due to reversible changes in turgor. As turgor changes are known to play a part in the growth process, these reactions too are usually dealt with in relation to growth. However, it is by no means sure that the turgor changes in the pulvini are of the same kind as those observed in the growing parts. The tactic reactions of the free-swimming micro-organisms, the swarmspores and the spermatozooids are, on account of a rather superficial resemblance to the tropisms, usually also included in the same category, but this is doubtless quite arbitrary, for these reactions certainly do not depend upon changes either in the rate of growth or in turgor.

Another way to come to a subdivision of physiology would be to deal first of all with the processes that take place between the organism and the environment, viz. with the absorption and secretion of various substances by the surface layer and with the absorption and emission of energy, and then with the processes that go on in the interior of the body,

viz. with the changes the various substances and the captured energy undergo. In each of these two main divisions we might deal separately with processes in which the living protoplasm is involved, and processes that are independent of the latter. It would, of course, also be possible to use this criterion for the main division, and to base the subdivisions on the place where the processes take place. However, it seems doubtful whether a classification of this kind would satisfy our sense for order. As an illustration of the conflicts to which it would lead, I will take the water transport through the tracheae and tracheids of the Vascular Plants, a subject on which a few remarks have already been made. In this case the movement may rest entirely on the saturation deficit that is due to the loss of water by transpiration, a process that requires a supply of heat. The latter may be provided from outside the plant, but part of it may certainly be produced by the plant itself. Moreover, the water transport does not always depend upon this saturation deficit; it may also be due to the activity of the living cells by which the transport channels are surrounded, and by which they are connected with each other; when the atmosphere is saturated with water vapour, the activity of these cells is sometimes revealed in the excretion of water drops. In the water transport through the tracheae and tracheids we meet therefore with a process that is partly dependent upon forces residing in the cell walls and in the water itself and partly upon the activity of the protoplasm. We may say, therefore, that it rests partly on a loss of water at the surface and partly on forces that are active in the interior. It would accordingly have to be dealt with in each of the four subdivisions, and this certainly is impractical.

As the subdivisions based on theoretical considerations are as yet not satisfactory, it seems preferable to content ourselves for the time being with an empiric classification. We might have special sections e.g. for the absorption of food, for its assimilation, for the transport problem, for the katabolic processes, for growth, development and reproduction, and for the various kinds of movements. However, the provisional character of these sections, especially that of the latter, which comprises, as I have shown above, rather heterogeneous elements, should not be lost out of sight.

## ECOLOGY

### THE STUDY OF THE ORGANISM IN ITS ENVIRONMENT

In the previous essay ecology was defined as the discipline that deals with the differences in the mode of life displayed by the various kinds of organisms. We might also say that it studies the relations between the species and their environment, for the differences in their mode of life rest, of course, on differences in the way in which they react on the conditions offered by the latter. Other authors have called it the study of the adaptations, but the term "adaptation" has, as I have already pointed out in the introductory chapter, more than one meaning, and is therefore apt to cause confusion. We have seen that it is used in the first place to indicate the individual's faculty to adapt itself to changes in its environment, but it also serves to describe the fact that each kind of organism is "adapted" to the environment in which it is commonly found, which means that it thrives better in that habitat than anywhere else. It will be worth while to study these two meanings of the term at somewhat closer range.

The individual is doubtless in many instances able to adapt itself to some extent to changes in its environment. When the rate at which the changes are effected, is sufficiently slow, the organisms are often able to continue their existence under circumstances that otherwise would have proved fatal. This is seen e.g. when a brackish pool gradually dries up, for in that case it appears that some of its inhabitants may hold out for a long time, and come to endure a degree of salinity by which they certainly would have been killed when it had suddenly been imposed.

Little is known of the way in which adaptations such as those meant in the preceding paragraph are brought about. Occasionally, however, we may catch a glimpse of the mechanism which is at the back of it. As an example we will discuss the adaptation to the osmotic value of the medium. It is a well-established fact that organisms provided with vacuoles gradually adapt themselves to some extent to a decrease as well as to an increase in the osmotic pressure of the medium in which they live, by a corresponding change in the osmotic value of the fluid contained in their vacuoles. This is the reason why the bursting of the cells observed in seaweeds that are suddenly immersed in fresh water, does not take place when the seawater is gradually diluted. However, we should not overlook that the bursting of these cells is but a subsidiary effect caused by the sudden expansion of the vacuoles. The circumstance that organisms without vacuoles are killed just as well, shows that the real nature of the change must be looked for elsewhere, viz. in the protoplasm. Another point we should not lose out of sight, is that we do not know whether this kind of adaptability is operative in every instance, no matter of what

kind the change in the environment may be. Many biologists are inclined to regard adaptability as a general property of the living organism, but the evidence on which this conviction rests, seems entirely inadequate. However, a discussion of this problem would carry us too far out of our way.

The choice of the term "adaptation" for this kind of adjustment was perhaps not a fortunate one. Whatever its original meaning may have been, there can be little doubt that the biologists borrowed it from popular psychology, and that they were attracted to it because the adjustment of the organism to changes in its environment suggested to them a mental, perhaps even a voluntary process. However, there seems to be no sufficient ground for such an assumption. The adjustment of the osmotic pressure inside the cell to that of the surrounding fluid need not be interpreted in this way, as it may be due to the endosmosis or exosmosis of substances of which the concentration inside and outside the vacuole differs. Moreover, this kind of "adaptation" is not confined to living organisms. Examples of a similar phenomenon are found also in the world of the non-living, e.g. in the way in which a rubber thread adjusts its structure to a stress: when the latter is very strong, the length to which the thread is extended before it snaps, is less than when the stress is less strong and the extension accordingly slower.

It seems plausible to assume that the faculty of the individual to adapt itself to definite changes in its environment, enables the species to colonize a larger area that otherwise would have been possible. Differences in the degree to which this faculty is developed, may therefore play a part in the "struggle for life". Specific differences of this kind are, however, not the only object of study of the ecologist, and they are certainly not his main concern. Not the way in which the individual "adapts itself" to its environment, but the way in which the species proves "to be adapted" to the latter, i.e. the manner in which the species maintains itself in its special environment, is the principal object of his study, and when we say that the organisms are "adapted to" their special environment, we certainly do not mean that this condition has been reached as the result of a "process of adaptation".

It is true that in former times "adaptability" has often been regarded as a faculty which is inherent in the species too. This assumption implied that the latter were able to change their genotype, for an adaptation of this kind would only be possible when the offspring of the adapted individuals were able to adapt themselves still further. Their variability therefore would not fluctuate round the same mean as that of the generation to which their parents belonged, but around a mean that had shifted in the direction in which the latter had deviated from the original mean. It seems, however, that in multicellular organisms such a shifting of the mean is possible only in species that are genotypically heterogeneous, and even then only to a certain extent. In such "populations" changes



in the environment may doubtless cause a change in the numerical representation of the various genotypes, but such an "adaptation" comes to an end when the population has been reduced to a single "pure line" or to a group of the latter that react in the same way on the conditions of the environment. In genotypically homogeneous material adaptations of this kind seem to be out of the question. Under the influence of some external circumstances, e.g. of the action of poisons like colchicine or of irradiations to which the organisms normally are not exposed, the genotype may certainly undergo a change, but the manifestations of such changes show, so far as we can see, no correlation whatever to the cause by which they are brought about, and can therefore not be regarded as adaptations.

Genotypical changes such as those meant at the end of the last paragraph are often due to a disturbance in the normal course of the nuclear division leading to the production of germ cells with an aberrant number of chromosomes. The zygotes formed by the fusion of these cells are but rarely viable, and when they are, the individuals into which they develop, may prove sterile. When, however, in the course of their development a doubling of the chromosome number takes place, there seems to be a good chance that they may prove fertile.

As polyploids seem to be more common in some climatic zones than in others, it has been suggested that ordinary climatic variability too may cause this kind of aberration. This, however, is by no means sure, for the greater frequency of polyploids in a definite region might well be the result of a difference in the climatic requirements of diploids and polyploids, i.e. it might be due to the selection that is always exercised by the environment on the composition of a population.

The theory that the species would be adaptable, may the more confidently be discarded as its adherents have to admit that such adaptations are not directly demonstrable. They ascribe this to the extremely slow rate with which they would take place, but this seems somewhat far-fetched. It will therefore be better that we confine our attention to those factors whose action is directly observable or for whose presence definite indications can be found.

Ecology, as was pointed out already, has many points in common with physiology, but whereas the latter, at least when our delimitation is accepted, centers its attention on the individual, ecology deals with groups of individuals, i.e. with species and with communities. However, as the number of individuals of different constitution is almost unlimited, and as all differ to some extent in their mode of life, it is clear that the physiologist will have to confine himself to those phenomena that are of more or less general occurrence; these he will try to analyse as fully as possible. The study of the differences in behaviour between the various species he will leave to the ecologist, who will also have to restrict his sphere of interest, and who confines himself to those features which he

regards as directly responsible for the species' presence in a definite environment, a choice that will always remain difficult and, may be, even somewhat arbitrary.

In the study of the physiological qualities that determine the occurrence of the species in their various environments, emphasis may fall either on the taxonomic relationship of the organisms or on the similarity and dissimilarity of the habitats in which they are found. In the first case we may speak of systematic ecology, in the latter of habitat ecology. As these fields are both still enormously wide, they will have to be subdivided. The systematic ecologist will, as a rule, restrict his attention to a part of the organic world, and in this way we come to a division in zoo- and phyto-ecology, and to the ecology of smaller groups like the Vertebrates, Insects, Vascular Plants, etc. The habitat ecologist will, as a rule, restrict himself to habitats of a definite type, like water or land, deserts or forests, or he will apply himself to a study of the habitats represented in an area of more or less limited extent. Systematic ecology especially has many contacts with physiology; habitat ecology, on the other hand, verges on bio-geography, but whereas the latter aims at a classification of the habitats, the ecologist tries to find out why the organisms are bound to definite habitats. As a rule, he puts himself on the standpoint that the physiological requirements of the various organisms can be recognized, at least to a large extent, by their structural peculiarities. Haberlandt's "physiological anatomy" is, according to our definition, in reality ecology.

In the preceding paragraph we have expounded why the study object of the ecologist is, in our opinion, not formed by the individual but by groups of individuals, i.e. by species and communities. However, before acquiescing in this decision it seems desirable to pay some attention to the meaning the ecologist attaches to the terms species and community. With regard to the first the difficulty does not lie in the delimitation of the individual species: this is a problem on which the ecologist may have his own views, but of which the final decision rests with the taxonomist. What I mean, is this: is the species to the ecologist merely the sum of all those individuals that from his point of view may be regarded as genotypically identical, and is the community merely the sum of all the individuals that are present in a definite environment, or do these concepts imply to him something more?

It is a well-established fact that an aggregate may possess features that are not present in its components, and for this reason the aggregate is often said to occupy a "higher level of organization". Some evolutionists go a step further: in their trend of thought the aggregate is for this reason a more recent development. This interpretation, however, is not convincing. Even if we restrict our attention to those aggregates that are most often adduced as examples of different levels of organization, viz. the atoms and molecules, this view does not seem justified, for it is by

no means sure that the molecules are more recent developments than the atoms nor that the latter in the course of time have been preceded by electrons, i.e. that the world at one time consisted entirely of free electrons, and in a subsequent stage of free atoms, to become at last the tumbling-place of the molecules. As atoms, apart from those of the inert gases, as soon as they are set free, enter into new combinations, i.e. form molecules either of the original or of a new kind, we would have to assume that this faculty to form compounds was at one time absent, and this is hardly conceivable. It is possible, of course, that the conditions for their combination were not always present, but so long as we stick to the conviction that the faculty to form the combinations is present, the fact that the latter are not necessarily formed, is of no importance. Another point is, that even in this case the assumption of different levels of organization seems open to criticism. The adherents of this view apparently overlook that molecules, atoms and electrons are mathematical abstractions, and that they possess therefore only such attributes as can mathematically be grasped, viz. mass, extension, velocity and energy, and we will therefore have to admit that their differences can only be of a quantitative character. This scheme has therefore no place for new qualities. When we confine ourselves to atoms and molecules, we will, moreover, have to concede that there can be no general difference in their level of organization, for in one group of substances, viz. in that of the inert gases, there is complete identity between the two.

Another point we should not leave out of view, is that the new features that make their appearance when a new substance is formed, can not be interpreted as the result of differences between the latter's molecules and the atoms out of which these molecules were built up. We may say that a water molecule is formed out of one oxygen atom and two hydrogen atoms, but as the attributes of these atoms with which we are acquainted, all belong to the group mentioned above, this is for our purpose of little importance. What we observe is that oxygen and hydrogen combine under certain conditions in the volumetric proportion 1 : 2, or in the weight proportion 8 : 1, to form water vapour, and we will have to admit that the latter possesses qualities that were absent in the reacting substances, as, we will have to add, it also lacks some of the latter's properties, but the oxygen and hydrogen that entered into the reaction and of which the qualities are compared with those of the reaction product, certainly are aggregates of a similar kind as the latter.

It must be admitted that the existence of different levels of organization is thinkable, and may even be regarded as an attractive hypothesis, but even if they exist, it is by no means sure that we will ever be able to obtain an insight in their real character. As the activity of our sense organs apparently is based on the perception of changes inside their own structural elements, and as the latter are of a molecular character, it seems doubtful whether differences in other organization levels than that

of the molecule, will ever be directly recognizable to us. Their presence may be inferred, like that of an electric current, which is not directly recognizable to us either, but their features will probably always remain obscure.

The organisms have been regarded as representing another level of organization than the objects that form the world of the non-living, and this view may be maintained even if the idea that the electrons, atoms and molecules represent distinct levels, should have to be abandoned. If it is accepted, the position which the individuals occupy within the confines of the species is to be regarded as similar to that which the molecules occupy in the structure of a chemical substance, for in the same way as the molecules the individuals represent the parts that can undergo no further division without losing their particular character. However, after what has been said above, it will need no special emphasis that the really characteristic features of the living being's organization will be difficult to define. It should, moreover, not be forgotten that there may exist intermediate levels, for beside the homogeneous substances there are also heterogeneous ones, e.g. igneous rocks, and even such intricate aggregates as machines. However, as the latter are unthinkable without the intervention of man's intellectual activity, they belong only to a certain extent to the world of the non-living. The special attributes of the living organism, which some have called the "supermachine" or the "machine that reproduces itself", have been discussed in our previous essay, and it can not be denied that their peculiar character forms a strong argument in favour of the living organism's autonomous nature, which is only another way of expressing our conviction that it represents a different level of organization. At the same time we should bear in mind that we do not know why these attributes are confined to the organic world, and we will have to admit that some of them may after all be present in some parts of the world of the non-living too.

The genes and the protoplasm have sometimes also been regarded as representing such special levels of organization, but this does not seem probable, for as they are outside the organism entirely unknown, they are evidently integral parts of the latter. The presence of such highly specialized constituents as the genes and of a medium with such a peculiar character as the protoplasm may doubtless be regarded as a weighty argument for the living being's autonomous nature, but it does, of course, not prove it. In the world of the non-living there are doubtless groups of aggregates which differ considerably in their general character, but which nevertheless need not be regarded as representing different levels of organization. If it could be shown that the organism's attributes themselves are of a higher order than those observed in the various groups of non-living aggregates, the problem of the organism's position would be solved, but it is hardly to be expected that such proof will soon be forthcoming.

Theoretically it is, of course, possible that the species and the com-



munity may possess qualities that can not be understood from what we know of the qualities present in the individual organism. The presence of such special qualities, however, will be difficult to prove. It is, on the other hand, comparatively easy to show that several of the individual's characters recede into the background when the species or the community are regarded as a whole. In the individual the assimilatory and dissimilatory processes are, at least during the period of development and reproduction, never fully balanced, for growth as well as reproduction require a surplus of assimilates; in the species and in the community, however, there is often a nearly perfect equilibrium between assimilation and dissimilation, and as there is in that case no surplus of assimilates, there is nothing that could be compared with growth or multiplication. This is, of course, no general rule, for the species and the communities often show differences in their seasonal aspect, and such differences may doubtless be due to disturbances in the balance between assimilation and dissimilation. They are apparently the result of a synchronism in the physiological behaviour of the individuals, and here as elsewhere in the domain of ecology our first task therefore will be the study of this behaviour. The dissimilatory processes lead to the liberation of kinetic energy, which is used in the individual for movements of various kinds, some of them hidden inside the body, while others manifest themselves in displacements either of the whole body or of parts of the latter, but in the species or in the community as a whole outward signs of movement are often entirely wanting. The species generally remains where it is, and migrations on a larger scale seem to be restricted to a comparatively small number of living beings, where they assume, as a rule, a seasonal character. Such migrations are stimulated by changes in the conditions of the environment, and when they are carried out by groups of individuals, the latter's joint action will be due, at least partly, to correlations existing between the reactions of the individuals separately.

It is here perhaps the right place to pay some attention to the difference between the standpoints taken in by the ecologist and the taxonomist with regard to the species.

The main object of the taxonomist with regard to the species is to discover the features by which it may be distinguished from its nearest allies, and to see in what points it resembles the latter and other, less nearly related species. He starts his study with the analysis of a single specimen, and when he has satisfied himself that it differs in important points from previously studied specimens, he accepts it as a representative of a new species. When more material becomes available, the quality of this particular specimen may prove to deviate considerably from the average of the species, i.e. from the latter's "ideal type". The study of the first specimen, the "nomenclatural type" was, of course, only a preparatory step, and the circumstance that the taxonomist always has to return to this particular specimen when doubt is cast on the distinctness

of the new species from a previously described one, is merely the result of the exigencies of a stringent nomenclature, and should be no reason to overestimate its value in the study of the specific characters. The more important part of the taxonomic investigation begins when the student has obtained a considerable number of specimens, for then he will be able to make himself a picture of the "ideal type".

The ecologist is not directly interested in the "ideal type" of the taxonomist. His first object is to find out what place the species occupies in nature, i.e. he will try to determine the extent of the area occupied by the whole set of individuals and the character of the habitats in which they occur. The taxonomist is interested in this features only in so far as some knowledge of the ecological requirements of the species may help him to distinguish it from its nearest allies. To the ecologist this is, however, but the first step; his real aim is to find out why the species is bound to this area, and to this end he will have to study its physiological behaviour. The results of this study will form a physiological counterpart to the taxonomist's picture of the "ideal type".

In the preceding paragraphs we have already indicated some of the points in which the field of study of the ecologist deviates from that of the physiologist, but in several other respects too there are differences. The latter rest partly on the circumstance that the ecologist studies the behaviour of the organisms under normal conditions, whereas the physiologist is not bound in this way, and partly on the circumstance that the competition between individuals of the same as well as of different kind, which is one of the main concerns of the ecologist, is left entirely out of consideration by the physiologist. The latter may find that the individuals belonging to a certain species keep alive between 0° and 50° C, but the temperature range in which the species actually maintains itself, will doubtless be less wide. This is due to the circumstance that a species can only compete with other species when the conditions offered to it do not differ too much from those that are most suitable to it, for the farther they are removed from the ideal ones, the greater the chance that they will prove more favourable to some of its competitors. This, however, does not mean that the conditions must be evenly distributed round the optimum: the ideal conditions are, in fact, under natural circumstances not always realized. With regard to the nature and the amount of food too the range in which the individual can be kept alive in the physiological experiment, i.e. when it does not have to compete with other individuals, is wider than it is for the species living in its natural environment.

Individuals, however, are not always competing with each other: they may also co-operate. For individuals of the same species this is shown to some extent by animals living in herds, and to a higher degree by those that are united in colonies. It is not necessary to enter here into details, as this kind of relation between individuals belonging to the same species

seems to be confined to animals, and is even here by no means common, at least if we leave out of consideration the care for the offspring shown by one of the parents or by both, and the relations existing between males and females during the mating time. Moreover, if we realize that organisms living in herds or colonies have given up part of their independence, it is clear that their place in our schema may be taken over by the higher units of which they have become members, and in that way co-operation is reduced to a factor of secondary importance. At another place in this book we have already referred to the fact that the members of such colonies may be so completely interdependent (Siphonophores) that the colonies practically behave as single individuals. In such cases the co-operation between the members of the colony has become a matter of internal organization, and when we study the part played by such species in nature, we may confine ourselves to the behaviour of the colonies as a whole, and leave the individual activity displayed by their members out of consideration. Where the interdependence of the members of a group is less complete, co-operation as a distinct factor may come somewhat more to the fore, but it can hardly be doubted that mutual indifference and competition are more usual.

The interrelations between the various organisms are the study object of the synecology or coenology (sociology). The latter, it is true, has not yet proceeded very far beyond the descriptive stage, and contents itself, as a rule, with a preliminary classification of the communities, and in that case it is better included in biogeography, but if it is to be kept up as a more or less independent branch of ecology, as some of its devotees prefer, it should certainly turn its attention to the way in which the various communities obtain their specific character, which manifests itself in their heterogeneous composition and in the more or less constant proportion of their constituents. This promises to be a wide and thorny field.

Considerable difficulties are already met with when we try to find an explanation of the heterogeneousness of the communities. By way of example we will here consider the situation in a tropical forest. It is easy to see that the space between the roots must be a suitable place for the development of micro-organisms, that on the ground between the stems of the trees a herbaceous or fruticose vegetation may establish itself, that the bark of the stems and branches offers a foothold to epiphytes, and that all the living parts are exposed to the attacks of herbivorous animals and to the possibility of an infection by parasites, but not so obvious is the explanation of the heterogeneousness displayed by the trees themselves. In fact, one wonders why in the long run one of the species does not become completely dominant and ousts the other ones. It is doubtless true that the open spaces created by the downfall of the larger trees, are not always colonized by seedlings of the tree species that is most abundant in the near vicinity, but by those of species that prove

to be better adapted to the changed conditions now prevailing in this part of the habitat, but this observation offers no fully satisfactory explanation of the persistently heterogeneous composition of the tree canopy, for one would expect that the seedlings of the dominant species would in the end simply overwhelm their competitors by their number. That this stage is apparently never reached, may be due to the circumstance that in the neighbourhood always stretches are found that, either on account of the composition of the soil or on account of their exposition, bear a different association. From these stretches seeds may reach the open spaces in the adjoining community.

The competitive value of the various species can, of course, only be determined by a thorough study of their behaviour under various conditions. This is the domain of "autecology", and the results of these studies will have to form the foundation on which the study of the communities, the "synecology" or "coenology", will have to be built up.

The preceding considerations will have shown that autecology does not only study the physiology of the various species by growing them under different climatic and edaphic conditions, but that it also has to take into account the influences exercised on them by the organisms with which they are associated. These influences may be of various kinds. When we have to deal e.g. with a Phanerogamous landplant, we will have to consider how its roots have to compete with the roots of other plants, and, may be, how they are hindered by the excretions of the latter, further how they respond to the damage inflicted on them by animals and parasitic fungi, how they benefit by the changes the soil undergoes by the action of micro-organisms how their oxygen requirements are more easily satisfied when tunnel-boring animals are present, etc. With regard to the plant's aerial parts we will have to see what influence the shade cast by the neighbouring vegetation may have, how it profits or suffers by the presence of the windscreen formed by the latter, what the influence of the exhalations of some of its neighbours may be, what the results are of the damage done by animals feeding on them and by the parasites by which they are infected. Then we will have to take into account how this particular plant depends for its pollination on the visits of one or more kinds of animals or, when it happens to be a wind-pollinated plant, how the action of the wind is influenced by the surrounding vegetation. With regard to the distribution of the seeds we will have to find out how the latter depends upon the presence of definite animals, on wind or water, and, in the case of dehiscent fruits, on the heat of the sun and on the amount of water vapour in the atmosphere, factors that in their turn are influenced by the surrounding vegetation.

The autecologist feels, of course, the need to classify the objects of his study. He will do that more or less along the lines set out in the preceding paragraphs. With regard to the purely physiological factors he will divide the organisms according to the temperature range in which



they occur (megathermous, mesothermous and microthermous organisms), the light intensity they prefer (heliophilous and sciadophilous organisms), the relative length of day and night they require in the various stages of their development, and especially for the formation of their reproductive organs (long-day and short-day plants), their dependence or independence of the presence of oxygen (aerobic and anaerobic organisms), and their food requirements.

With regard to the food requirements botanists and zoologists use a different terminology. The botanist distinguishes in the first place between autotrophic and heterotrophic organisms. Organisms that subsist on the mineral substances present in their environment, and that are in this respect therefore not directly dependent upon the presence of other organisms or of products formed by them, are called autotrophic and organisms that require at least part of their food in the form of organic compounds, are heterotrophic. The heterotrophic organisms he divides in saprophytes and parasites; the first use organic substances that are no longer part of a living being, where as the latter subsist on organic food that they obtain, at least partly, from the body of a living host. This classification has never appealed to the zoologists, who use the term parasites in a more restricted sense.

Saprophytes are especially important because they decompose organic remains; in this way they return to the soil the mineral nutrients that are continually taken away by the autotrophic plants. A detailed discussion of this problem would occupy too much space, but it seems desirable to draw attention to a misapplication of the term that is more or less sanctioned by custom. I mean its use for a group of heterotrophic Phanerogams that live in symbiosis with definite Fungi. These plants are obviously unable to obtain their organic food directly from the surrounding soil, i.e. in the way in which the bacterial and fungal saprophytes obtain it. They are, in fact, entirely dependent upon the endotrophic Fungus, and the way in which they acquire their food from the latter, is the same in which e.g. a broomrape obtains it from the plant on which it parasites. These colourless mycorrhiza plants are therefore true parasites. The main points of difference between a plant like *Monotropa* and a broomrape are found in the taxonomic position of the host and in the way in which they are attached to the latter. In view of the totally different structure of the hosts, this difference in the mode of attachment can, of course, not be regarded as surprising.

Parasites are found as well among Bacteria and Fungi as among Algae and Phanerogams. The bacterial and fungal parasites are often able to live in a purely saprophytic way, and even the obligatory parasites among them might perhaps be able to obtain part of their food from other sources if the latter could be made available to them, but under the circumstances in which they live, this is obviously impossible. This applies even more forcibly to the Phanerogamic parasites. The latter are usually divided

into holo-parasites, which obtain all their food from the host, and hemi-parasites, which draw it partly from other sources. These hemi-parasites are, in contradistinction to the holo-parasites, provided with chlorophyll, and they are therefore able to synthesize at least part of the organic food they require. Would they be able to synthesize all their organic food, they would have no right to the name parasites, for this name is, according to the definition given above, reserved for heterotrophic organisms. This is rather unfortunate, for the term is preferably applied to such plants as the Loranthaceae and the Rhinanthaeae, which absorb part of their food by means of haustoria from the living tissues of other Seed-plants, but are provided with chlorophyll, and if it could be shown that they obtain only anorganic food from their hosts, they would certainly have to be included in the group of the autotrophic organisms. The name might with more justice be applied to such plants as the Leguminosae, which obtain their proteins partly from the root nodules, i.e. by the intermediary of the bacteria that are living in these nodules, and also to the green plants that are provided with endotrophic mycorrhiza. The insectivorous plants are more or less comparable to these groups, for they too obtain at least part of their proteins from living beings. Organisms like the bacteriophilous species found in the Rubiaceae genera *Pavetta* and *Psychotria* and in the Myrsinaceae genus *Ardisia*, where the association between the Seedplant and the symbiotic Bacteria is so intimate that it is difficult to dissolve, are perhaps better regarded as parts of a compound organism, but if they are taken separately, the position of these Seedplants with regard to their Bacteria must be regarded as similar to that of the Leguminosae, for they may doubtless obtain a certain amount of organic food from the Bacteria. Seedlings of *Ardisia* that had been deprived of the symbiotic Bacteria, did not develop normally, and this has been regarded as an indication that the Bacteria provide them with a growth-hormone. However, as the means by which the seeds were freed from the Bacteria, were rather drastic, their abnormal growth may have been due to this treatment. In the time before this hereditary symbiosis was established, these plants must have produced a sufficient amount of growth-hormone, otherwise they would not have been able to maintain themselves, and we would have to assume therefore that this faculty was subsequently lost. This seems a somewhat strained supposition. I am afraid that we are here confronted with a survival of the belief in the adaptability of the species and with that of its counterpart, the compensation theory, according to which parts and faculties that no longer are required, are doomed to disappear.

Because of the prominent position the autotrophic plants occupy in the various communities, their subdivision is one of the main concerns of phyto-ecology.

Part of the autotrophic Bacteria occupy a special position, because they reduce carbon dioxide by means of energy obtained by the oxydation

of various, for each group specific, substances, and because the latter form therefore an important item on their food list. In this respect they differ considerably from the other autotrophic organisms, for whom several of these products are of no value or even harmful. However, as a detailed discussion of the metabolism of these Bacteria, and of the place they occupy on account of the latter in the various communities, would take us too far out of our way, we will confine our attention in the following considerations to the organisms that reduce carbon dioxide by means of energy derived from the light that is absorbed by their chromatophores. This group comprises the Green and Purple Bacteria, the Algae and the Embryophyta (Mosses and Vascular Plants). We will deal here with the Vascular Plants only. However, as the latter's carbon-dioxide assimilation itself is not very interesting from the ecological point of view, we will now pass on to a discussion of the rest of their food requirements.

Among the various substances required by the Vascular Plants water occupies a prominent and quite unique position, as it is not only one of the basic materials for the synthesis of the organic compounds of which the body mainly consists, but also because it serves as a solvent for the other nutrients, and as a means of conveyance for the latter. The last-mentioned function plays especially in the larger landplants an important part, and the system of channels along which the solutions are conveyed, determines for a great deal the character of these plants.

As the cell-walls bordering on the intercellular spaces are soaked with water, water vapour will continually diffuse into the latter. This process will go on so long as the atmosphere in the intercellular spaces does not become saturated, and as the water vapour passes from the intercellular spaces through the stomata and lenticels into the surrounding air, it may take a long time before the saturation point is reached. On account of this particularity water is the only substance taken up by the plant of which also large amounts are given off. Between the amount of water lost by "transpiration" and the amount absorbed by the roots and transported to the transpiring surface there must, of course, be a kind of balance, and the maintenance of this balance is one of the main problems in the life of the individual species.

So long as the atmosphere with which the cellwalls are in contact, is not saturated with vapour, transpiration goes on. The cellwalls in their turn withdraw water from the protoplasts and by the intermediary of the latter from the vacuoles. When this loss is not balanced by a new supply, it is apt to lead to wilting, i.e. to a loss of turgescence. The latter leads sooner or later to an irreversible change in the protoplasm, which in the end causes the plant's death. The various protoplasts met with in the same plant and morphologically similar protoplasts found in different plants show in this respect marked differences. In most seeds the water content sinks in the normal course of development to an extremely low level, much lower in fact than the level at which the protoplasts in other

parts of the plant usually succumb, and of the differences existing in this respect between various kinds of plants striking examples present themselves. Lichens, Mosses and Filmy Ferns (species of *Hymenophyllum* and *Trichomanes*) may shrivel to such a degree that they look beyond all hope of recovery, but they resume nevertheless their normal aspect as soon as they are wetted. Such a high power of resistance against desiccation is doubtless exceptional, but a mere loss of turgescence, on the other hand, is probably nowhere immediately fatal. It would be extremely valuable to know the degree to which the faculty to recover from the wilted condition is developed in the various kinds of plants, but as its determination is a time-consuming and rather monotonous task, it is hardly to be expected that a really representative collection of data will soon be forthcoming.

Another aspect of the problem has proved more attractive. It concerns the differences in structure that may have a bearing on the plant's faculty to live on a comparatively dry soil. The power to hold out on such a soil may apparently be increased in two ways, viz. by a reduction of the transpiration and by a more effective absorption of water.

Submerged waterplants that are taken out of their natural element, wilt very rapidly, but landplants that are deprived of the means to take up water, retain their freshness, as a rule, much longer, although they show considerable differences in this respect. Usually two groups are distinguished, viz. easily wilting mesophytes and more resistant xerophytes. These names are not fully adequate, for the name "mesophyte" merely indicates a plant growing in a place where a sufficient amount of water is available, and the name "xerophyte" similarly applies to plants living in a comparatively dry environment. If a "xerophyte" possesses the means to absorb more water from the latter than its competitors, e.g. because its root system drains a larger area or descends to a greater depth, the structure of its aerial parts need not differ from that of a "mesophyte", and in that case it would wilt just as easily as the latter when it was deprived of water. This, however, is a more or less theoretical case, for plants that are provided with a root system of this kind, possess, as a rule, also some of the contrivances that tend to reduce the rate of transpiration. A more important point to bear in mind is that wilting, as stated above, does not necessarily lead to the death of the plant, and when we wish to estimate the chance of a species to maintain itself in a comparatively dry environment, the faculty to endure for some time a loss of turgescence should also be taken into consideration.

Loss of water by transpiration will lead less rapidly to a deficit when the extent of the transpiring surface is small in comparison to that of the absorbing surface, and it is therefore no wonder that the root systems of xerophytes often occupy much more space than their aerial parts, and that the vegetation of dry regions therefore is always an open one. This predominance of the subterranean over the aerial parts is, however, not



found in all xerophytes. In several of the so-called succulents the root system is but poorly developed. These plants are often confined to habitats of a peculiar kind, e.g. to crevices in rocks, where a large root system would find no room. These crevices act as reservoirs for the rain that falls on the rocks and also for the dew, which may be quite heavy in these bare regions, where the nights are often extremely cold. Some of these "chasmophytes", moreover, are able to absorb the dew that condenses on their surface.

Before entering on a discussion of the structural peculiarities that tend to reduce the absolute value of the transpiration, it seems worth while to pay some attention to the way in which the latter so far has been estimated. This is all the more desirable as some authors have come to the rather paradoxical conclusion that the transpiration of xerophytes is often of the same order of magnitude as that of mesophytes. If this were true, it would mean that the various contrivances whose presumable effect on the rate of transpiration we are about to discuss, would be of little or no avail. However, before acquiescing in this conclusion we will try to find out whether the data on which it was based, really are trustworthy.

The transpiration rate has usually been estimated per unit of surface area. In physiological experiments that are undertaken to study the influence of external circumstances, and for which either parts of the same individual or else individuals belonging to the same species are used, no objection can be raised against this practice, which recommends itself by its simplicity. However, when we wish to compare the transpiration of plants with an entirely different structure, the method is totally inadequate. It is quite possible, at least when the experiments are made in a wind-still room, that in determining the transpiration per unit of surface in a mesophyte and in a xerophyte we arrive at values that are more or less of the same order of magnitude, but this means very little, because in a xerophyte the surface is, as a rule in proportion to the volume of the transpiring part considerably smaller than in a mesophyte, and as it are the contents of the plant cells that are affected by the transpiration and not the surface of the plant, this way of calculating the transpiration rate is, of course, inadmissible.

It would doubtless be better to calculate the transpiration rate per unit of volume, but this method too has its drawbacks. The latter are found in the circumstance that not all elements of the part whose transpiration we are studying, are equally concerned in this process. Dead elements, like the sclerenchyma and the cork tissue, are in this respect of no direct importance, and those with but little protoplasm, like the epidermis and the so-called water-tissue, are also of little avail. The space occupied by these elements is, however, in the body of xerophytes, as a rule, larger than in that of mesophytes, and when we calculate the transpiration rate on the base of the volume, we are therefore apt to overestimate the effect of the structural peculiarities of the xerophytes.

Theoretically the best way to compare the transpiration of various kinds of plants would be to calculate it per unit of protoplasm, as it is the condition of the latter with which we are concerned. Unfortunately it is impossible to determine the amount of protoplasm with sufficient accuracy. Chemical analysis gives us the total amount of organic substances, but the latter comprise besides protoplasm also storage materials and secretion products. The amount of organic material present in the cellwalls and that represented by the principal storage products, starch and oil, may separately be estimated, and by subtracting the values found for them from the total amount of organic material, at least a first approximation of the amount of protoplasm may be gained. Another method would be the estimation of the nitrogen content. As such estimates have not yet been carried out, the reduction of the transpiration rate by the development of special structures can as yet not be expressed in reliable figures.

The transpiration takes place partly through the cuticle and the cork layers at the surface of the transpiring parts and partly through the stomata and lenticels, which serve as exits to the system of intercellular spaces and set the air inside the latter in communication with the atmosphere outside the plant. In connection with this dual character of the mechanism of transpiration there are, generally speaking, also two ways in which the transpiration can be reduced. That through the cuticle can be diminished by a thickening of this pellicle and, eventually, by the secretion of a wax layer on top of it, and that through the cork layers by which the older parts are covered, by an increase in their number. As the cuticle as well as the cellwalls of the cork cells contain but very little water, and even in a fully saturated condition they lose the latter but slowly; it will be clear that this loss will be the smaller the thicker these layers are.

A reduction of the far more important transpiration through the stomata and lenticels may be obtained by a decrease of their number and of their width, and in the case of the stomata by the presence of a hair felt on the epidermis. The latter's effect is twofold. In the first place it creates a wind-still space above the stomata, which means a lengthening of the way along which the water molecules have to pass before they come into the open, and in the second place it reflects a greater part of the incident light, so that the temperature inside the leaf does not rise so much as it otherwise would have done, and as the vapour tension in the intercellular spaces therefore is lowered, the diffusion gradient is reduced. Inside the plant the diffusion may be retarded by the narrowness and great length of the intercellular channels, which, of course, are the sooner saturated the greater the surface by which the water molecules are given off, and also by the presence of a cuticle in the outer part of these channels or by an invagination of the part of the epidermis in which the stomata are situated. By means of the two last-

named devices the transpiration of the cells bordering on these openings is eliminated, and this is the more important as the diffusion gradient reaches its highest value in this part of the leaf. A lengthening of the intercellular channels means, of course, a greater thickness of the leaf; it is therefore a feature of common occurrence in leaf succulents.

In some xerophytes the decrease of the water content in the leaves leads to a deformation by which a further loss is almost completely stopped. This happens e.g. in the leaves of many xerophytic grasses. In these leaves the chlorenchyma, i.e. the tissue formed by the green cells, is usually arranged in the form of cylindrical sheaths round the vascular strands. These sheaths are separated from each other at the upper side of the leaf by longitudinal rows of large, thin-walled cells that are free from chlorophyll. When the loss of water by transpiration is not balanced by a new supply, the water content of these "hinge-cells" is seen to undergo a considerable decrease, and this shrinkage of the individual cells is, of course, accompanied by a contraction of the whole upper side, and leads therefore to a rolling up or, when there are but two rows of hinge-cells to a folding up of the blade. When this movement has proceeded so far that the margins overlap, transpiration is almost completely stopped, for as the stomata are in these grasses confined to the same side of the leaf as the hinge cells, they now open into a cavity that is almost completely shut off from the outer air.

In the rolled-up blades of the grasses the walls of the hinge-cells appear to be folded, and this proves that the cells are no longer turgescient. This loss of turgescence might be the direct effect of the loss of water by transpiration, and in that case the condition of these cells might be described as an initial stage of wilting. It should be realized that cells which lose their turgor by wilting do not behave in exactly the same way as cells that are immersed in a hypertonic solution, i.e. in a solution whose osmotic value is higher than that of the fluid inside the vacuole. During "plasmolysis" the cells contract until their walls are completely distended, and when still more water is withdrawn, the protoplast frees itself from the distended wall, the space between the latter and the receding protoplast being filled by the plasmolysing fluid. When a cell loses its turgor by wilting, i.e. in an atmosphere in which no water is present, the protoplast, on the other hand, does not free itself from the wall as soon as the latter is distended, but adheres for a shorter or longer time to the distended wall, and draws the latter into folds. This is, as stated above, what we observe in the hinge-cells, and it might therefore be interpreted as a direct result of the loss of water by transpiration. It should, however, not be overlooked that the folding may be due to another cause. Instead of in the form of vapour the water might have left the cells in the form of fluid. This would have happened when a pressure had been exercised on the cells, and such a pressure might have been caused by an unequal shrinking of the sclerenchyma strands on

the upper and lower side of the blade. In this case too the folding of the walls could only have taken place after they had become distended, i.e. after the cells had lost their turgor. It seems that as yet no full certainty has been reached on this point.

A similar mechanism as that found in the blade of the xerophytic grasses recurs in a very curious form in the South-African resurrection plant, *Myrothamnus flabellifolius*. The sessile, hand-nerved blades of this shrublet are inserted upon short-shoots. When their water content sinks below a certain level, they close in the way of a fan, and as the upper side of the joint at their base undergoes at the same time a stronger contraction than the lower side, they are pressed against the branchlets. The plant assumes in this way a leafless, dead aspect. Indeed, dead shoots look exactly like these desiccated living ones, and unfold in the same way as the latter when they are immersed in water.

The noxious effect exercised by the closure of the stomata on the supply of carbon dioxide to the chloroplasts is in some plants reduced by a modification of the way in which the respiration ordinarily takes place. These plants produce during the night organic acids (the Crassulaceae e.g. malic acid), which, of course, in contradistinction to carbon dioxide, remain inside the cells. When these plants are once more exposed to the light, these organic acids gradually disappear, while carbon dioxide is split off. The latter can at once be used for the synthesis of new carbohydrates. What interests us here, is that the amount of carbon dioxide that has to be supplied from without, is in these plants drastically reduced, and that this kind of metabolism is apparently met with in several kinds of succulents.

The transpiration rate increases with the temperature. The effect of this factor reveals itself in the difference in aspect shown by the vegetation on the opposite slopes of a mountain ridge stretching in the direction from east to west. Above the equator the cool northern slopes bear, as a rule, a more mesophytic vegetation than the warmer southern side, whereas below the equator it is on the contrary the southern slopes that bear the more mesophytic flora.

The rise in temperature inside the plant may be kept in check by a reduction of the irradiation. This reduction may be obtained either by a change in the position of the leaves, which may assume a more or less vertical position, upright in many herbs and shrubs and pendulous in some trees, e.g. in *Eucalyptus*, or else by the development of a strongly reflecting surface, e.g. a white felt formed by dead hairs whose cells are filled with air, or a layer of white wax. A similar function has been ascribed to the atmosphere of ethereal oil by which on a hot day so many plants of the macchia are surrounded, but it seems that the effectiveness of this device has been overrated.

The disastrous effects of a transpiration by which more water is withdrawn than the roots can replace, may to some extent be neutralized by



the presence of a water reserve. This latter is usually contained in large, thin-walled cells containing little or no chlorophyll and a very thin layer of protoplasm only. The cell juice is not rarely more or less slimy, but the significance of this feature is still a matter of debate. Plants that are provided with this kind of water reservoirs, are called succulents.

Water reservoirs may also be present outside the plant in the form of cups or niches formed by the leaves, either individually or in groups (some epiphytic ferns, *Asclepiadaceae* and *Bromeliaceae*) or inside the plant in parts that have lost their living contents (velamen of the root in epiphytic Orchids). The dead sheaths by which the lower parts of the so-called tunic grasses and the stems of the *Velloziaceae* are surrounded, may also help to collect water. The thick mantle by which the stems of the latter are enveloped, consists of an enormous number of sheaths, and the fact that it is traversed by numerous adventitious roots, suggests an actual use of the water that is drawn in between the sheaths by capillarity. These mantles are also a very effective protection against the often recurring field fires; in the South-African savanna the stems of these plants, which attain a high age, are on account of these fires always blackened. In the tunic grasses these mantles may have a similar function. As they are bad conductors of heat, they also protect the vital parts of these inhabitants of the savanna against the often excessively high temperatures that prevail during the day in the surface layer of the bare soil and in the air immediately above the latter.

The water reservoirs of the succulents occupy different positions. In stem succulents, like the *Cactaceae*, *Stapelieae* and succulent *Euphorbias*, the aqueous tissue is found for the greater part or even exclusively in the often very bulky stems. Their leaves are usually small and short-lived, and when they persist, they often become hard and spiny. Their function as organs for the assimilation of carbon dioxide is taken over by the green parts of the stems and branches. So long as the latter are but moderately swollen, as in the *Asclepiadaceous* genus *Secamone*, in *Euphorbia tirucalli* and in the *Rhipsalis* species, they retain their cylindrical form, but as the chlorenchymatous surface layer of a swelling stem retains its original thickness and increases therefore less rapidly in volume than the inner part, there comes a time that it is no longer able to provide the latter with the necessary assimilates. The shoots of the more outspoken stem-succulents assume either a flattened, a prismatic or a ribbed form; this increase in surface is, of course, of importance in the assimilation of carbon dioxide, but it causes also a higher transpiration.

In the leaf-succulents the greater part of the aqueous tissue is found in the leaves. Examples are provided by the *Crassulaceae*, the *Mesembryanthemeae* and some of the *Liliiflorae* (*Aloinae*, *Agavoideae*). As the succulent leaves are comparatively heavy, they require an extra support: in most cases they are arranged in rosettes resting on the ground; more rarely they are inserted on creeping or decumbent stems, and in the even

less frequent arborescent forms they are borne by thick stems and branches.

Corms and bulbs may also serve as water reservoirs, and the amount stored in these parts is sometimes large enough to allow the production of new stems (potatoes) or flowers (*Colchicum*, *Sauromatum*) even if the plants are kept completely dry. A corm of the South-African *Asclepiadacea* *Raphionacme divaricata* Harv. stored on a shelf in my laboratory produced four years consecutively flowering shoots, although it did not receive a drop of water. The corm, which at the beginning weighed several pounds, lost during this time more than half its weight.

Seeds contain, as a rule, but little water, and do not germinate unless they are in a position to absorb moisture. An exception is formed by the so-called viviparous seeds, which germinate before their connection with the mother plant is severed. They are a characteristic feature of the *Rhizophoraceae* and the *Avicennias* of the mangrove forests, but they are not confined to them. The difference between these seeds and those of the *Crinum* species, of which some grow on the sea shore and others in the savannas of the interior, is perhaps but a gradual one. The large seeds of the latter germinate when they are taken out of the withered, papery capsules, even when they are kept in a completely dry environment.

Succulents are especially common in semi-deserts, and in these regions they are often, apart from a little dew, the only source of liquid for the herbivorous animals. Protection against the latter is sometimes provided by the presence of distasteful substances, by the development of prickles or by a withdrawal in the soil. Good examples of such buried plants are the *Lithops* species and some other *Mesembryanthemaeae*. The leaves of these plants are obconical and they are sunk so far into the soil that the flat top is about level with the surface. The possibility that they are damaged by the tongue of a grazing animal is therefore very small indeed. The flat top contains no chlorophyll, and the light passing through this "window" reaches, via the aqueous tissue in the centre, the layer of chlorenchyma which lines the epidermis of the buried part. The tops of these leaves sometimes show another peculiarity, viz. a rather striking resemblance to veined pebbles, and this has been interpreted by some botanists as "mimikry". However, as grazing animals apparently rely more on their nose than on their eyes for the distinction of objects in their immediate vicinity, it does not seem likely that they would be deceived by this resemblance. These animals are probably much better plant collectors than their human colleagues!

Before leaving the subject of the differences in the water requirements, we must turn our attention for a moment to those regions where the climatic conditions are such that but during part of the year the plants are in a position to obtain a sufficient supply of water. This applies in the first place to tropical regions where during part of the year a dry monsoon prevails. The plants that are found in these countries develop

their new foliage at the beginning of the wet season. Some of the trees are provided with leaves of a mesophytic character, and in that case they shed their foliage when the wet season is over; other trees possess leathery leaves, and the latter are evergreen. The undergrowth of the monsoon forest consists for the greater part of mesophytes, and withers in the dry season. A similar kind of vegetation is found in the temperate region, where in the winter the roots are unable to absorb enough water, especially when the temperature of the soil sinks beneath the freezing point. In subtropical countries with winter rains and a dry summer growth and development are mainly confined to the cold season. The vegetation consists partly of more or less mesophytic herbs whose aerial parts wither at the beginning of the dry season, and partly of evergreen xerophytes, among whom small-leaved sclerophyllous scrub plays an important part. This kind of scrub is apparently a growth-form especially suited to conditions that allow but a slow growth.

In the preceding paragraph reference was made to the influence exercised by a low temperature on the faculty of the plant to provide itself with the required amount of water. It is also worth noting that the influence of such low temperatures when prevailing throughout the year, is the same as that of a permanently deficient precipitation, and that deserts are therefore not confined to dry subtropical regions, but occur also in the higher parts of the globe, e.g. on table lands at high altitudes (Tibet). The most luxurious type of vegetation, the rain forest, on the other hand, demands for its development not only a relatively high supply of water but also a comparatively high temperature. Sometimes a great abundance of epiphytes is regarded as the most characteristic feature of the rain forest, but when this criterion is accepted, this type of vegetation can not be said to reach its fullest development in the tropical lowlands, i.e. in the regions where the mean temperatures are highest, for the abundance of epiphytes is far more imposing in the forests covering the slopes of the tropical and subtropical mountains, where the temperature is lower but the atmosphere more humid. As a moist atmosphere is a necessary condition for the development of a rich epiphytic flora, it is no wonder that the latter often reaches its most exuberant development at an altitude where the forest itself already begins to show a less vigorous growth. The exuberance of the epiphytic flora at these higher altitudes is, however, more one of mass than of diversity, for it consists almost entirely of a limited number of Bryophytes and Ferns.

Water is a nutrient of which even the most outspoken xerophytes require amounts that are, in comparison to those of the other nutrients, enormously large, and it is therefore no wonder that this substance is often in the position of the "minimum" nutrient, which means that it is often the decisive factor in the struggle for life. At first sight this may seem strange, as in agricultural practice the supply of the other nutrients proves to be a matter of grave concern, but we should not forget that

the harvester continually removes large quantities of these substances which under natural circumstances would have been returned to the soil. However, under natural conditions too a shortage of the mineral nutrients is not entirely unknown. Virgin soil is always very poor in dissolved minerals, and fixed nitrogen is in the latter often completely absent. This, however, is but a passing phase, for the shortage usually disappears within a comparatively short time.

The gradual improvement of a virgin soil is reflected in the "succession" of the plant communities. The pioneers are a few species of micro-organisms scattered over the area. Gradually, however, the vegetation increases in density and height, and, as a rule, also in diversity of composition, until it reaches its "climax". The latter is the type of community that is characteristic for the climatic conditions of the region.

Sand dunes are to a certain extent comparable to virgin soils, but although they may doubtless be deficient in mineral nutrients, their unsuitableness to plant growth is, at least partly, due to the fact that their soil is unable to retain the water that falls on it. The succession on these dunes is, especially in dry climates, often extremely slow.

Perhaps of more general interest are soils that owing to the composition of the rocks from which they are derived, are permanently deficient in some of the necessary mineral nutrients, e.g. phosphate. The vegetation of such regions remains, of course, always behindhand. The effect of deficiencies of this kind is fully comparable to that observed in agricultural practice on insufficiently manured soil.

The so-called edaphic differences observed in the natural vegetation of climatically similar areas rest, as a rule, not on deficiencies but on an excessively high concentration of some substance in the soil solution or else on an unsuitable hydrogen-ion concentration.

The best-known example of a substance that influences the character of the vegetation when present in an unusually high concentration, is sodium chloride.

The effect of salt in the soil rests at least partly on the high osmotic value of the soil solution. The higher this value is, the stronger the force required to withdraw water from the solution, and when such a large force is not available, the absorption will, of course, be less than in an ordinary soil. For this reason the saline soils are sometimes designated as "physiologically dry", a term that has also been applied to cold soils.

In one respect there is a very important difference between a "physiologically dry" soil of the saline type and a physically dry one. When a plant withdraws water from a soil that contains but a limited amount of the latter, the decrease of the available store is relatively important, and it becomes therefore increasingly difficult for the plant to obtain a sufficient supply. This does not apply in the same degree to a saline soil. It is true that the withdrawal of water causes an increase of the salt concentration in the immediate vicinity of the roots, but there is no shortage,



and as the diffusion gradient created by the withdrawal of water causes a movement of the water molecules in the direction of the roots, the concentration round the latter does not undergo any further increase. The structure of the "halophytes" is therefore not necessarily xerophytic. In the neighbourhood of salt lakes, or of saline depressions that owe their origin to the drying-up of such lakes, the soil is, of course, not only saline but also comparatively dry, and in that case the halophytes prove to be provided with similar structural peculiarities as the plants growing on the non-saline soil of the surrounding steppe. The trees of the mangrove forests that in a moist tropical country fringe the banks of the rivers at their debouchment in the sea, are, on the other hand, hardly more xerophytic in structure than several of the trees that grow in the rain forest at the back of the mangrove.

A special problem of the halophytic vegetation is the succulence shown by most of its representatives. It is well known that this peculiar structure is not confined to halophytes but occurs also in many xerophytes, and it is therefore no wonder that it has been used as an argument in favour of the view that the halophytes should be regarded as a special kind of xerophytes. It is, however, by no means certain that the succulence of the halophytes is directly comparable to that exhibited by some of the inhabitants of the drier regions. If this were so, it would be difficult to understand why the typical succulents of the semi-deserts in the interior are never met with on the seashore, nor the halophytes in the non-saline semi-deserts. Especially the latter circumstance seems significant, for it is well-known that several of the halophytes are by no means fastidious in their climatic requirements. Moreover, if the composition of the vegetation on a saline soil really was determined by the latter's "physiological dryness", the absence of other kinds of xerophytes would be unexplainable.

Several investigators have observed that non-halophytic plants obtain a more or less succulent structure when they are grown in a saline soil. The bearing of this discovery is not fully clear, but as a working hypothesis we might assume that plants provided with this faculty are more apt to survive on a saline soil, and in that case the hereditary propensity to succulence which most halophytes doubtless possess, would place the latter in a more favourable position than their competitors. That the degree of succulence may vary in true halophytes too, is well shown by *Clerodendron inerme*, a Malesian halophyte. This shrub shows a most remarkable seasonal dimorphism, the leaves that are produced during the dry monsoon being thick and fleshy, whereas those that are formed in the wet season remain more or less mesophytic.

The main property of the halophytes is doubtless their power of resistance against high concentrations of sodium chloride. It is developed to a very different degree in the various kinds of plants. It is doubtless highest in some Bacteria and Cyanophyceae, which are able to maintain

themselves in brines of a concentration far higher than that found in sea water, and which are apparently seldom absent from the surface of the mud flats and of the sandy shores by which the sea and the larger inland salt lakes are surrounded. It is also developed to a high degree in seaweeds and in submerged Phanerogams of the *Zostera* type. These are, in fact, the most perfect "halophytes". The plants to which the name usually is applied, i.e. those rooting in a saline soil, are probably never exposed to such high concentrations, at least not with the parts that are apt to suffer from the salt. Their aerial parts, it is true, may be covered with crusts of salt left by the evaporation of the drops of sea water with which they are continually sprinkled, but these parts are protected by their cuticle. In those saline soils that are inhabited by plants, there are several factors at work that tend to keep the concentration of the salt solution in check. Mud flats inhabited by plants are found only in the estuaries of the larger rivers, and the water by which they are periodically flooded, is therefore always between salt and fresh. The mangrove forests of the tropical and subtropical regions prove to be confined to parts with a high precipitation, and rains, of course, tend to decrease the salinity of the soil. On sandy or rocky coasts the Vascular Plants never descend below the ordinary high-water mark, which means that they are confined to those parts where the soil is exposed to the diluting influence of the rains; the few times that it is inundated with salt water, are separated from each other by such long intervals that the degree of salinity does not reach a very high value.

Before leaving the subject of the halophytes it seems worth while to return for a moment to the mangrove forests, because the latter are doubtless the most remarkable of all halophytic associations. A closer investigation, however, reveals that their two main peculiarities, the viviparousness and the presence of aerial roots, have nothing to do with the salinity of their habitat. Neither of them is confined to this association, although it must be admitted that they play nowhere else such a prominent part. Their absence from other halophytic associations as well as the circumstance that they are occasionally met with in representatives of associations growing on other soils, prove that there exists no direct relation between them and the salinity of the soil. It can, on the other hand, not be doubted that the mangrove plants profit by them. When a small and leisurely expanding seedling finds itself in the soft mud within reach of the waves, its chances to obtain a firm hold are doubtless very small, and the way in which the long fusiform seedlings of *Rhizophora*, *Bruguiera* and *Ceriops* are like aeroplane bombs driven by their weight into the mud, is certainly quite effective; it is, moreover, not paralleled elsewhere. The viviparousness of other mangrove plants is less striking, and apparently hardly more effective than the possession of non-viviparous seeds provided with large embryos would have been. Such large embryos are found in most of the drift seeds, no matter whether they belong to

seashore or to streambank species, but they are not confined to them.

The presence of aerial roots is in more than one way helpful to the mangrove plants. It need not be doubted that they provide the subterranean part of the root system with oxygen, of which there is a shortage in the water-logged soil; differences in temperature arising in the dark-coloured mud and from there transmitted to the roots, will accelerate the relative speed of the gas exchange between the very spacious intercellular system of these roots and the outer air, the expansion of the gas being followed by an expulsion of the surplus, and the contraction by the inhalation of a fresh supply. This, however, is not the only function of the aerial roots. The soft mud does not form a solid substrate for these trees, and owing to the oxygen deficiency of this mud, the roots are, moreover, unable to penetrate to any great depth. A storm therefore would easily uproot these trees if they were not specially protected against such an emergency. This protection is provided in the first place by the great length of the horizontally spreading roots, which far exceed the radius of the crown; these roots form a kind of raft on which the stem is mounted. The stability of these rafts is further increased by their mutual connections, the roots of each tree being interwoven with those of the surrounding ones. The presence of proproots and of negatively geotropic spargel roots weaken at the same time the impact of the waves, and lessen therefore the danger that the soil is washed away and that the horizontal roots which are quite near the surface, are undermined.

Far less striking in their general aspect than the halophytic associations are the associations that are found on soils in which some other salt is present in an unusually high concentration. Best known among them are the communities growing on soils that are particularly rich in ammonium salts and nitrates. The effect exercised by high concentrations of these salts is in so far similar to that exercised by a strong solution of sodium chloride, that but a limited number of plants is able to withstand it. These "nitrophilous" communities are found in the neighbourhood of human settlements, especially farms, and consist partly of plants belonging to families that are also met with on saline soils (*Chenopodiaceae*, *Cruciferae*), and partly of representatives of families that seem to avoid the latter (*Solanaceae*). More typically "nitrophilous" than these *Phanerogams* are some *Fungi* (*Mucorineae*) and *Mosses* (*Splachnaceae*), which occur only on dung. As our knowledge of these communities has as yet hardly proceeded beyond the study of their composition, we will not enter into details.

Above we have already indicated that the hydrogen-ion concentration of the medium constitutes also a factor of importance. This is very convincingly shown by the behaviour of micro-organisms in artificial cultures, for the *Fungi* show, as a rule, a stronger growth in acid media, the *Bacteria* a better growth in alkaline ones. On account of the fact that the acid soil of bogs and fens bears another kind of vegetation than

the adjoining areas with a neutral or alkaline soil, it is usually assumed that differences of this nature are also present in the idiosyncrasy of the various kinds of Vascular Plants. This argument, however, is in itself unconvincing, for these soils differ also in other respects: the acid soils are at the same time poor in mineral nutrients, they are badly aerated, and in periods of drought they retain their water so strongly that the roots are soon unable to withdraw it from them. Special experiments are required to determine the effect of each of these differences separately. Experiments of this kind have not yet been carried out on a large scale, but there seems to be no reason to doubt that the reaction of the medium too is for these plants an important factor. In view of the facility with which the H- and OH-ions penetrate into the protoplasm, this is certainly not unexpected, but the preference shown by the various kinds of plants either for an acid or for an alkaline medium remains difficult to explain. So long as we are not more intimately acquainted with the structure of the protoplasm and with the differences existing between the latter in the various kinds of organisms, there is little hope that we will be able to solve this problem. This applies, of course, also to the differences in adaptability shown by various kinds of organisms. The adaptability proves to be largest in Bacteria and Fungi.

Another difficult problem is that of the so-called "calciphilous" and "calciphobous" plants, i.e. of the plants growing respectively on soils that are rich in calcium carbonate and on soils that contain but relatively small amounts of the latter. As soils that are poor in lime, usually owe their origin either directly to the weathering of siliceous rock or to a deposit of sand, the calciphobous plants are also called "silicicolous", the calciphilous ones, to remain in style, "calcicolous". That the silicicolous plants should have a preference for silica, does not seem probable, as the latter is a rather inactive substance. However, the value of this argument should not be overrated, for silica is not the only form in which the element silicon may be present, and it can not be doubted that some plants are able to store compounds of this element in considerable amounts, which proves that they possess the means to absorb them. In the case of the Diatoms, where these compounds help to build up the scales within which the protoplast is enclosed, silicon may certainly be regarded as an essential element. The faith in the experiments by the aid of which classical plant physiology pretended to prove not only the necessity but also the sufficiency of but ten elements, has severely been shaken since the importance of the so-called "trace-elements" was discovered, and although there seems as yet no reason to enter into the train of thought of the Mexican botanist Herrera, who regarded silicon as an element second only to carbon in its importance to the living organism, the possibility that its significance has been underestimated, must doubtless be admitted.

The dominance of the calciphilous plants on soils with a high content of calcium carbonate is apparently due to the elimination of competitors



that are either less tolerant with regard to the Ca-ion or less able to maintain themselves in an alkaline medium. The degree to which these two factors are responsible for the result, might vary in different cases, but we are as yet but imperfectly informed with regard to this point. Other factors too might be involved. Some of the so-called calciphobous plants of our moors and similar habitats were found to possess no special aversion for calcium; it appeared that they could be grown in soils containing large amounts of lime provided that the other mineral nutrients were present in small quantities only.

Some of the calciphilous plants may deposit considerable amounts of calcium salts either on their surface, in their cell walls or in their vacuoles. The most spectacular results of this activity are the reefs which from palaeozoic to recent times have been built up by a number of seaweeds. A high degree of tolerance with regard to the Ca-ion must be present in the lichens living on the surface of lime-stone rocks and especially in the endolithic species that are embedded in the latter.

Our survey of the field of ecology is in one respect rather disappointing. A large part of the facts on which our exposition is based, are already to be found in Warming's "Oecology of Plants" and in Schimper's "Plant Geography upon a physiological basis", works dating in their original editions from 1895 and 1898. That since then but little has been added to our knowledge of the fundamental facts, is doubtless for a large part due to the circumstance that the physiologists have turned their attention to problems whose solution is of little or no importance to the ecologist, and to the fact that most ecologists nowadays confine their activity to the description of the almost innumerable communities that are spread all over the world, and on the changes the latter undergo in the course of time. This is an almost endless task, and even when there was hope that it could ever be completed, it is hardly to be expected that the results would materially widen our ecological insight. What really is needed, is a thorough study of the autecology of a restricted number of organisms, for this seems to be the only way by which in this field progress can be achieved.



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