BIOMORPHOLOGY IN GENERAL

BY

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During the last years of his life SCHOUTE was engaged in the composition of a large, comprehensive work on biomorphology. At his early death in Jan. 1942 only the beginning of this work had been put in writing: a chapter on the general principles of biomorphology and a second one on the symmetry of organisms, which, however, was not wholly finished. It was the wish of SCHOUTE that these two chapters, which contain his ideas about biological symmetry and a wholly new classification of the symmetry in organisms should be published after his death.

On my request his pupil Dr R. VAN DER WIJK who is at present his successor as professor in systematical botany at this University had the kindness to finish the manuscript and to prepare it for publication. Only some parts of the second chapter have been slightly altered by him. These parts are indicated by asterisks.

W. H. ARISZ.
State University of Groningen

Jan. 1949.

CHAPTER 1.

GENERAL PRINCIPLES.

§ 1. Introduction.

Morphology being the study of forms, its domain is not restricted to the biological sciences, but it forms part of other sciences as well, for instance, of mathematics, cristallography and geology.

The morphological branch of biology, or biomorphology, has always been recognized to be of primary importance in biology, as it has to come before any study of living beings in other directions. For it has not only to provide the biologist with the indispensable means to distinguish and to recognize the innumerable species and varieties, but without an adequate knowledge of the forms no study of the vital phenomena is possible, as the latter are all connected in some way or other with the external or the internal forms of the living body.

The necessity of a biomorphological study therefore being evident, yet opinions may diverge about the way in which it has to be undertaken, and about the aims it has to serve. In the present chapter, accordingly, some of the most important topics relating to these questions will be dealt with.

§ 2. Static and dynamic biomorphology.

In literature the view has often been held that biomorphology has to refrain from any causal analysis of the morphogeny and that it should be merely descriptive.

No more than elsewhere in this introductory chapter, will an attempt be made to review the numerous expressions of such a view; only one of the most recent and at the same time of the most distinct ones will be quoted, namely that given by FREY–WYSSELING in his fascinating volume on the submicroscopic morphology of the protoplasm (1938, p. 6), where he writes that biomorphology, being independent of the factor time, merges into developmental physiology as soon as time is introduced and accordingly developmental changes of forms are considered; the idea of a dynamic morphology is even characterized as being a mistake.

Of course such a narrow conception of biomorphology is consistent in itself, and from a logical point of view no objections can be raised. Yet it will not be adhered to here, and biomorphology will be taken in a broader sense, as involving developmental morphology and where possible even a causal analysis of morphogeny. In other terms, biomorphology will be taken as a dynamic and not as a static science. The same view has always been held by the majority of morphologists and was defended again by SINNOTT in his paper: "Morphology as a dynamic science" (1937) and by SCHUSSNIG in his volume on "Formbildung" (1938, I, see p. 2).

For there are two practical reasons which may induce us to include "developmental physiology" in biomorphology, and as neither the etymology of the term, nor historical [1]) or theoretical arguments can be objected, it may be preferable to do so.

The lesser of these two practical arguments is that the reduction of biomorphology to a static science would deprive it of nearly all its scientific interest. Indeed, a static biomorphology is not able to investigate the forms as the expression of vital phenomena, to the great detriment of its biological value.

No problem would arise any more in biomorphological investigations and even the tracing of a life cycle would be excluded, as it would only be permissable to study the spatial relations of an organism at a definite stage of its life; and the distinction between analogous and homologous organs would of course be wholly excluded, as containing phylogenetical and developmental elements.

A clear image of the nature of a static biomorphology would be presented in the Bertillonnage of criminals by the registration of their fingerprints, a method which, though being an invaluable instrument in the hands of the police, hardly offers any scientific interest, exactly on account of the fact that it considers the pattern of the lines of the skin as a geometrical, not as a vital phenomenon.

For external plant morphology in particular, we may say that in the static form it would be restricted to the study of such topics as the distinction between elliptical and lanceolate leaves.

But, as already observed, there is a still more important practical objection. Indeed, the reduction of biomorphology to a mere skeleton as sketched above, however regrettable in view of its glorious past, would be balanced by a corresponding gain of the transferred chapters in developmental physiology and in phylogeny.

We may be sure, however, that for some time to come the physiologist will not be able to handle the intricate problems of morphogeny. Physiology in our days prefers with good reason the study of those vital processes which are relatively of the least degree of complication, as assimilation, dissimilation, growth, tropisms, transport and the like.

Even here it has met with the greatest difficulties on account of the fact that the phenomena have proved to be much more complicated than had been anticipated. And if physiology has attained so many brilliant

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[1]) As is well known, the term morphology was framed by GOETHE (1807) in: "Die Absicht wird eingeleitet", who wrote: "Wollen wir also eine Morphologie einleiten, so dürfen wir nicht von Gestalt sprechen, sondern, wenn wir das Wort brauchen, uns allenfalls dabei nur die Idee, den Begriff oder ein in der Erfahrung nur für den Augenblick Festgehaltenes denken. Das Gebildete wird sogleich wieder umgebildet, und wir haben uns, wenn wir einigermassen zum lebendigen Anschauen der Natur gelangen wollen, selbst so beweglich und bildsam zu erhalten, nach dem Beispiele, mit dem sie uns vorgeht."

results in these fields, this is only due to the strenuous exertion and the genius of a great number of investigators. But the analysis of morphogenetic processes, being to all appearance of still greater complication, cannot yet be carried out, and so for the present time little help is to be expected from the physiologist.

On the other hand the morphologist in studying and comparing forms cannot help observing numerous regularities and rules, resulting from and pointing to the laws governing the physiological processes of morphogeny. It is true that the "causal analysis", instituted by the morphologist, goes neither far nor deep; yet it may sometimes pertain to the very last processes in the long chain of the extremely complex phenomena. Such knowledge as he may gather by his own methods is not to be disregarded, the less so as the physiological methods are not appropriate for gathering it.

The ideal should be that in a remote future the physiologist, after having elucidated the basic vital phenomena, and approaching gradually the more advanced steps in the concatenation of processes, will some day meet the morphologist who has been dealing with the last links. It is only then that biomorphology will have received its full physiological basis, but as far as the present author sees it, morphology has to be carried on in the mean time with a "physiological background", *i.e.* that its conceptions have to be shaped in such forms that they may one day be expressed in physiological terms.

§ 3. **Biomorphology and idealism.**

Many biologists, in the present as well as in the past, have been inclined to attribute the origin of the admirable forms of life to other laws than those prevailing in dead matter. In this chapter the historical details about the change of view in this respect, will not be mentioned, only the principle will be made mention of.

In doing so it will not be necessary to describe the numerous shapes in which these idealistic principles have been clad, whether they were mystical, vitalistic, teleological, typological, holistical or of still other descriptions; the essential point for us is that by the authors in question form is not considered to arise in a causal way by the sole action of physical and chemical processes, but that in living matter, in addition to the physical laws, ideal or spiritual, at any rate immaterial forces are supposed to work.

This metaphysical (and endless) question will not be discussed here; instead only the private opinion of the present author will follow.

In my opinion all supernatural conceptions are to be avoided in natural science, as they only tend to mar the progress of our knowledge. For by their cheap and seeming solutions of the problems they keep many investigators from trying to find a scientific solution of the same problems.

Perhaps I may add that I am personally convinced that all these views are only the outcome of misconceptions about the metaphysical problem of the relation between spirit and matter. All scientists, starting consciously or unconsciously either from a materialistic or from a dualistic metaphysical system will somewhere come up against the insurmountable barrier between spirit and matter, no reasoning being able to explain how matter can be moved by an immaterial spirit, and conversely how matter can ever act on such a spirit.

And as nevertheless our daily experience shows that our mind is influenced by observations, and continually influences matter by its will, the whole insolvable problem is disregarded and dissimulated.

Once so far, the way is open for the introduction of spiritual forces in the explanation of physiological processes.

The only metaphysical system which is able to solve the fundamental problem is psychical monism, as founded by G. TH. FECHNER, and as elaborated by G. HEIMANS (1905). It is not the place here to give a complete exposition of this system, but it may suffice to remark that it considers the psychical phenomena as the only existing reality, matter being nothing but a notion of our mind, formed on account of those conscious phenomena which we recognize to have no adequate causes in our mind, but which are due to sensorial observation. The supposed objects which are taken to be responsable for the origin of these observations, are considered to be other (psychical) realities, only outside the domain of our own mind.

In this system spirit and matter accordingly are parallel series, being two sides of the same reality. Consequently matter can be described by natural science without any regard to psychical processes and even without the possibility of introducing any psychical processes in the concatenation of causes and events.

Even our own psychical phenomena, if they were ever observable for an ideal scientist, would prove to be nothing but physiological brain processes, without a single idealistic, teleological or other immaterial element in them.

It is on account of these arguments that in the present chapters no idealistic elements will be acknowledged in explanation of biological forms.

Partly this critical attitude of mind will be approved by all modern botanists, in as far as we are dealing with the curious statements of the old Nature Philosophers. So nobody will any longer agree with WILBRAND who wrote in 1821 (p. 417) that as all vital phenomena are expressions of a general stream of life, running from the Universe through the earth, the longitudinal growth of plants accordingly symbolizes the circular course of the earth round the sun and the daily opening and closing of flower buds the rotation of the earth round its axis.

Most biologists, however, still readily accept a number of other idealistic views which, though not burdened by the nonsensical details of Nature Philosophy, and clad in a modern and more appealing dress, yet clash in the same way with physiology.

So for instance with the symmetry of organisms. Assumptions about its causes, if made at all, usually amount to supposed inner tendencies of an immaterial kind.

Such an "explanation" which is detrimental to the progress of science should not be accepted, and for lack of better an admission of our ignorance should be preferred.

In the case of organic symmetry however a positive attack will be made below, in Chapter 2, in the form of an attempt to replace the idealistic view by a rational one. Two other problems for the solution of which similar endeavours will be made are the nature of the fundamental plan or type (Grundplan, typus) of organisms and the question whether there exists a special Size-Factor. The fundamental plan is often held to represent the general organization scheme of an ancestral form, persisting and making itself felt during development in some mysterious way, or by others it is held to be a metaphysical idea. The other problem, about the Size-Factor, has to be discussed on account of BOWER's view that the relation between size and form of organisms itself is able to influence form, is also morphoplastic (1930, p. 210), and that the same relation is causal (1939, p. 603). Both problems will be dealt with in § 6.

§ 4. Morphogeny; morphogenetic factors and their effects on the living body.

The fact that individuals of the same species, and especially kindred individuals, show such astonishing similarities both in external form and in internal organization, has always drawn everybody's attention and is ascribed to heredity.

Now there is a fundamental difference in the mode of hereditary transmission between two categories of forms, the one being transferred in a direct way to the offspring, the other being formed anew in each individual.

The former group, though rather limited in number, is extremely important, as it comprises a number of structures of the living protoplasts: the submicroscopical structure of the cytoplasm, the chromosomes, the plastids and probably several other ones.

These structures, having once been formed during phylogeny, and as a rule having been modified a number of times, multiply by growth and fission and in such a way can be transmitted.

The latter group, however, which is far more numerous, contains several cell forms too, but owes its great extension to the complicated external and internal organs and parts of multicellular organisms. To give a few instances, the anatomy of wood, the morphology of the flower or the structure of the human brain are not present as such in the zygote.

In these cases it is not the form which is inherited, but the power to realize such a form. And as genetics has taught us, for the realization of any differentiation the presence of one or more special genes is wanted.

The way in which such forms are laid down is still unknown for the greater part. What we know is that from the genes special influences emanate, influences which have been recognized in several cases to be chemical substances; perhaps they always are. They have been studied in a number of zoological objects as *Drosophila, Ephestia, Triton* and other *Amphibia,* and in botanical objects as *Acetabularia* and *Zea Mays.*

Moreover it is certain that these morphogenetic influences act as stimuli and provoke morphogenetic processes of some description or other as reactions in the living protoplasm. Evidently the protoplasm can react in various ways, and it is these powers which are brought into action by the stimuli. Accordingly the same stimulus may induce various products in various objects (lenses of different structure in different *Amphibia,* SPEMANN 1936, p. 58) and different stimuli may induce the same structure in the same species (induction of neural plate in *Amphibia* by various fatty acids, SPEMANN p. 152).

Of the morphogenetic processes themselves the real nature is hardly known. Their outward appearance, distribution, size, progress on the other hand may be freely investigated. These observations teach us in the first place that as a rule these processes pertain only to a restricted, more or less sharply delimited area. Indeed cases in which the same process is activated all over the body are rare: as such we may mention the plasmodia of *Myxomycetes* proceeding to fructification, or the filaments of *Spirogyra* when all their cells turn into gametes.

It is this power of local activation of morphogenetic processes which enables organisms to attain their complicated forms and structures, and even a slight progress in our knowledge of the way in which it acts will constitute a distinct gain for our morphological insight.

The extent of the activations is usually rather accurately determined and for activations of the same process it is more or less the same. Those of different processes may, however, be widely divergent in extent; as very small areas we may quote the protoplasmic parts forming the units of sculpturing of Diatom shells.

In multicellular organisms the larger areas may be delimited in such a way that the individual cells either wholly belong to them or fall outside them. In other cases it is the protoplasm as a whole in which the area is formed, without any reference to cell limits. The latter condition is the prevailing one in plants.

Once being active, a morphogenetic process may continue for a long, or even for an intermediate time (meristems). Usually, however, it is discontinued after a certain lapse of time. The reason for this discontinuation is generally unknown; exhaustion as well as the action of "stopping" stimuli may be supposed.

Below, in § 6, some remarks will be made about the distribution of morphogenetic processes. As to their effects on the organism, we may say that these vary so much and in so many directions, that no survey will ever be able to account for their endless wealth.

In general, however, we may distinguish between some groups of effects, presenting some contrasts between each other.

In the first place the effect may be a differentiation of the protoplasm, so that the living parts, or their products, locally assume characters deviating from those at other places. Mechanical tissues and glandular tissues may be mentioned as instances, each occurring in a great number of varieties.

In the second place it is not the quality of the protoplasm which is modified, but its growth.

First there may be local stimulations or local retardations of growth.

The former phenomenon may lead to the origin of new organ primordia, especially when connected with differentiation; the latter may modify the shape of the whole body in various ways, and in an extreme form it may cause abortion of certain parts or organs.

There may be also a furthering of growth in a single direction, or even a limitation of growth in that direction. This phenomenon will be called here growth polarization, irrespective of the differentiation at both ends of the growth axis, which may be the same, as in a *Spirogyra* filament, or which may be different, as in any root or shoot. This will be distinguished as isopolar and heteropolar growth polarization.

In botany the term polarization is often restricted to the heteropolar cases. This practice will not be followed here, in accordance with the fact that in other natural sciences isopolarity is often implied in the conception, as for instance in the term polarized light.

These phenomena of differentiation, growth localization and growth polarization may be combined in any conceivable way, and as each of them is variable in character, in localization and in extent, an inexhaustable wealth of forms may be produced in this way.

The duplicity in the mode of origin of organic forms, described in this paragraph, though seldom if ever mentioned in morphological literature, has to be considered as a fact of great importance.

That a direct transmission of part of the structures is necessary is obvious. As FREY–WYSSELING sets forth (1938, p. 288, 289), the various complex structures of the living protoplasm cannot be reproduced without the help of equal structures. Accordingly no elaboration of the structure of an organism could ever take place without a certain available basis to start from, a basis in which all the various structures of the protoplasm are represented.

If on the other hand the morphogenetic powers of the organisms were confined to the multiplication of inherited structures, the full-grown body would always be more or less homogeneous, as is for instance the case in *Oscillatoria,* which approaches the indicated condition. For the complex organization of higher organisms this system of elaboration of form would be very inappropriate.

The advantage of the existence of genes, being roughly comparable to models or designs in a construction factory, is therefore evident; it makes possible the production of a great number of forms in those places where it is wanted. In many cases forms are even transmitted without being realized at all. In a Fern prothallus for instance the power to produce ramenta or sporangia is undoubtedly present and it may betray itself even in rare teratological cases (SCHOUTE in VERDOORN, 1938, p. 132); yet in the normal course of events it is never activated.

A few remarks are finally to be made on the remarkable fact of the inclusion of all genes in the nucleus, a condition absent only in *Bacteria* and *Cyanophyceae*, where the number of genes may be low. As soon as the number is high, their congregation in the nucleus has great advantages.

In the first place the transmission of a sample of each of the kinds of genes to any daughter cell is ensured by the linear arrangement of the genes in the chromosomes, combined with the wonderful mechanism of mitotic division.

The same necessity of an equal transmission exists of course for all the other hereditary structures of the cytoplasm, as for instance the plastids. For the latter the problem is met in other ways, either by a concatenation of plastid division and cell division, as in all cells of Algae with a single plastid, or by the presence of a good number of plastids in any cell, so that a cell division cannot fail to allot some of them to each daughter cell.

It is, however, clear that for the numerous kinds of genes the second solution would be decidedly inferior to that of mitotic nuclear division.

In the second place the condensation of a succinct but complete set of genes in the nucleus allows of the production of extremely small reproductive organs, a single nucleus and a small amount of cytoplasm being only required. This fact is of great importance both for the propagation of the species and for the facilitation of fertilization.

In the third place the full advantage of sexual reproduction, being the realization of all combinations of casual variations in the inherited structures, can only be attained by the nuclear division process, the accurately working division mechanism being applied, during the heterotypic division, to the segregation of whole chromosomes instead of their fission products. In such a way the segregation of any pair of homologous genes, and the incorporation of one of the partners in each of the daughter nuclei is ensured, so that the resulting haploid nuclei only convey the genes in the form which was present in one of the parents; without the inclusion of the genes this most important result could never have been attained.

§ 5. **Organs; homology and analogy.**

The term organ is frequently used to designate any specially differentiated part of the body. Originally the word means tool or instrument, and this has often induced the authors to limit its use to the parts the function of which was supposed to be known.

We find for instance already in JOHN RAY (RAYUS, 1686, p. 5) that a homogeneous part of a plant which only has to provide its own nutriment ("saltem nutritionem suam procurat") is to be contrasted as a "pars similaris" to a "pars organica" ...... "quae praeter sui nutritionem aliam aliquam actionem habet, quâ vel aliis partibus, vel toto corpore inservit".

Later biologists, however, did not fail to recognize that unless the body in a colony lacks every differentiation, any part may have some special function and that it is at any rate extremely difficult to recognize the complete functions of any special part. Moreover it was soon recognized that the functions of clearly corresponding organs in related species may be different, which was called a change in function (for plants see De Candolle, 1813, p. 91) and that to all probability there are parts without any function, the so-called rudimentary organs. For these reasons the use of a term in which the functional element was implied might seem rather unwieldy.

Notwithstanding this objection the term organ continued to be used freely, be it without a satisfactory definition; in practice it is used for all parts of living bodies which contrast more or less with their surroundings in shape, consistency, colour or any other feature.

It is therefore proposed here to define the conception of the term as indicating any part of an animal or plant which has a separate origin.

In the case of such parts as the chromosomes which are directly transmitted from one generation to another, and which accordingly multiply in the living body so that each new individual may get its share, any of these parts that is separately transmitted is therefore to be called an organ.

And for those parts the structure of which is elaborated anew, any part of a body is to be considered an organ which owes its shape and other characteristics to a local activation of a morphogenetic factor or of a set of such factors. So the human arm is an extremely complex organ, consisting of very large number of smaller organs, in many gradations; in the same way an inflorescence is a complex organ, with a similar gradation in sub-organs.

This way of defining the term organ in connection with the origin and not with the function has the great advantage that it is more natural, as there is a causal relation between the factors ruling the origin of an organ and its established form, whereas such a relation does not exist between the established form and the function. Indeed many well-formed organs never come in function, the necessary conditions for functioning not being present, for instance sexual organs of animals and plants, when fertilization does not take place. Moreover it is clear that the possibility of a "change of function" is connected with this lack of a causal relation.

The conception of the term organ as given above has moreover the advantage that it allows us to obtain a better understanding of the meaning of the notions of homology and analogy, notions which are familiar to any morphologist, but the theoretical view of which is not quite clear to everybody.

As is generally acknowledged, two organs are homologous if they are different, but of "common descent", and they are analogous if they are more or less similar, while being of "different descent".

It is, however, not quite clear what this "descent" means. A petal though being homologous to a foliage leaf, has an independent origin, its very first visible stages being different from those of leaves; we cannot say that a petal arises from a leaf.

For directly inherited organs like genes or plastids however, the common descent is neither mysterious nor hypothetical; on the contrary it is a hard fact. For instance: the widely varying forms of chloroplasts of the *Conjugatae* have all been formed by multiplication of a single ancestral form which in the course of phylogenetical evolution underwent numerous small changes in various directions, changes which were preserved in the offspring.

And for organs which are newly formed by morphogenetic factors the conditions are really only slightly different. It is true the organs are not inherited themselves, but the morphogenetic factors are, or at least the genes with which they are related.

The tail of the *Anura* is strikingly different from that of the *Urodela* by its disappearance during metamorphosis. Yet in its larval form it is brought about by morphogenetic factors which no doubt are of the same "descent" in both groups.

Many authors restrict the term homologous to those cases in which the organs perform different functions, while being of common descent: the foliage leaves of related species therefore are not called homologous. Other authors exclude parts of the same organism from homology 1). These two conceptions will not be followed; the definition adopted here is: homologous are organs of common descent, or induced by morphogenetic factors of common descent. So the corresponding gene in two sister nuclei falls under the concept of homology.

If only the origin and not the function is considered here in determining homology, a different course has to be followed for analogy.

For if the function should be disregarded here, any two organs of different descent would be analogous. So our definition of analogous should be: more or less similar in connection with a similar function, but yet of a different descent.

Against the definitions as given here, the objection may be raised that the descent of an organ or of its morphogenetic factors is never known, so that they can never be applied with any certainty.

Our answer is that in many cases we have good arguments to believe that descent has really proceeded in a certain way, but that in all cases the certainty of our judgment on homology and analogy is proportional to our knowledge of phylogeny.

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1) For a detailed discussion of these views cf. MOLL, 1934, p. 347.

Nobody will doubt the homology of our nails and the hoofs of animals or that of the pappus of the *Compositae* and the calyx of other *Dicotyledons*, and no more do we doubt the analogy of the sarcotesta of *Cycas* and the sarcocarp of *Prunus*.

But we cannot tell whether the leaves of the *Musci* and the microphyllous *Pteridophytes* are homologous or simply analogous, by lack of information about the phylogenetic relation between these two groups.

§ 6. Fundamental plan; biological axes; size-factor.

A. Fundamental plan. The temporary and the local morphological processes are not brought about in an arbitrary or haphazard way; on the contrary their distribution and extension are as a rule strictly determined, in space as well as in time.

In the developing embryo of a Vertebrate for instance, a great number of different local processes take place in a rigid order and with definite spatial relations; in a flower calyx, corolla, androecium and gynoecium are laid down in an invariable order with definite places for the different members.

The successive processes are evidently connected by very stable relations, in an accurately defined though unknown way, and it is by this concatenation that the fundamental plan of type, the general scheme of organization is established.

A first idea presenting itself is that the origin of such a fundamental plan is regulated by the nuclei. For as the plan consists of a harmonious conjunction of ontogenetically formed structures, each of which is due to the stimulation by gene substances from the nuclei, the distribution of these stimuli might account as well for the whole scheme of organization.

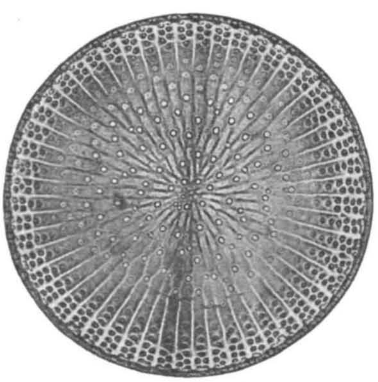

Fig. 1. *Stictodiscus Buryanus*, one valve. From collection KINKER (property of the Bot. Lab. of the State University Groningen).

On second thoughts there are, however, insuperable difficulties for such a view. If in a single uninucleate cell, such as *Stictodiscus Buryanus* (fig. 1) the numerous local ornamentations which have all been formed by special protoplasmic organs, show a complex and regular distribution, this cannot be simply the effect of the emission of some chemical substances, diffusing equally. Here we cannot avoid the assumption of arranging forces in the cytoplasm itself.

And if, as is the case here, these ornamentations are of two kinds, with definite spatial relations, we come to the conclusion that there must not only be interactions between the homologous localizations, but that the two kinds of formations must also act on each other. From our figure we may even conclude that the strong radial bars must have been laid down first, and that the small alveoles must have been induced in the interstices.

On these and other facts the following hypothetical conception may be based, that the proper arrangement of organs in the cells and tissues is determined by processes in the cytoplasm; that the nuclei act chiefly as stores of genes and respond to stimuli from the cytoplasm by the emission of the proper gene substances, without ever taking the initiative.

These supposed stimuli emanating from the cytoplasm may be produced in the morphogenetic processes which are already going on, and the linkage between two kinds of organs may be due to the fact that the morphogenetic processes of the one, stimulate the nuclei to emitting the gene substances for the building of the other organ. The nature of such stimuli may be similar to that of the gene substances. Probably both of them may prove to be hormones; for the present they will be spoken of here as gene substances and reaction substances, in order to convey that the latter are due to the vital reactions in the cytoplasm following on the stimulating effect of the gene substances.

We shall now try to check the above suppositions by a discussion of the actual conditions in some organisms, and for more than one reason we shall begin with the zygote in *Fucus*. By the researches of ROSENVINGE, WINKLER, KNIEP and others this object is better known than most other; a survey is given by OLTMANS (1923, 3, p. 74). The first differentiation to be formed in the zygote is the rhizoid which appears about 17 hours after fertilization, but which is induced in the 13th or 14th hour. The place in which the rhizoid is laid down is normally determined by light, at the side turned from the entering light. In the dark the zygotes germinate in any direction, unless they are in contact with old thallus pieces, in which case the rhizoid is turned towards the contact place. No treatment before or after the induction time is of any influence on the side of germination.

Before the induction the zygote has no polarity as yet; the gene substance for rhizoid formation must have been emitted in the interval between fertilization and the induction, and must have spread all over the cytoplasm. The relative darkness, or the chemical changes due to the contact with the thallus pieces, have probably no other effect than increasing locally the susceptability to the cytoplasm for the gene substance, and so they may bring about the localization.

The vital processes in this new localization have more than one consequence. In the first place no other rhizoid is formed in other parts. This may be due to an attraction of the gene substance by the rhizoid, and of its consumption during its vital processes. In the second place the emission of a stem-forming gene substance is probably the effect of the emission of a reaction substance by the rhizoid. And in the third place the stem apex is localized opposite the rhizoid, in a place which was not determined beforehand. About the forces which bring about the latter localization little is to be said; we only know that it is a special case of a most frequent group of phenomena, that the distribution of later differentiations is influenced by those which are already present. These influences may be brought about in the youngest stages of the differentiations by mutual repulsions, attractions or directive influences, and though we have to admit that nothing is known as yet about such directive forces, the resulting arrangement often compells us to admit their existence.

In the case of *Fucus* we had to suppose that the rhizoid prevents the originating of other rhizoids anywhere in the zygote. In other objects the influence of some differentiation is much more restricted, and if the involved gene substance equally spreads over the whole cell, a number of homologous differentiations may arise. This is for instance the case in the pollen grains of *Cucurbita*, represented in fig. 2, where two kinds of organs are formed at the surface, the operculate places of exit and the little spines.

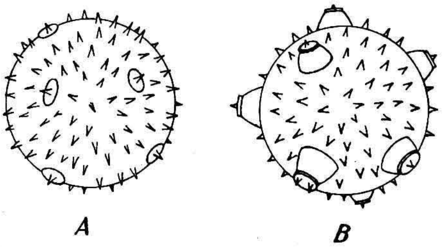

Fig. 2. *Cucurbita Pepo*, two pollen grains. A. dry. B. wetted. From V. MOHL, 1834, Taf. IV, fig. 16.

Two kinds of gene substances must have been emitted, simultaneously or succesively, and each of them has given rise to a number of localizations. A certain evenness of distribution may be due to the consumption of the gene substances in a small field around any localization, and we shall recognize below that for the places of exit repulsing forces have to be admitted also. Between the two kinds of organs no other relation seems to have existed than that the spines keep clear of the places of exit; this may be due to a succession in time, the spines coming later.

In still other cases two such intermingled organ categories show obvious spatial relations, as in the pollen grains of *Alisma Plantago-aquatica* (fig. 3). The distribution of the places of exit is similar to that in *Cucurbita*, but the small granulations in the exine form pentagonal or hexagonal frames around them and moreover radial rows inside these frames; a clear instance of the directing influences of one organ category on another.

If the views given here should be mainly correct, and if the fundamental plan is the outcome of the phenomena of organ formation under the influence of gene substances from the nuclei, of the emission of further gene substances under the influence of reaction substances and of mutual directing influences of the organs in the cytoplasm, the origin of the fundamental plan itself may be considered as a complicated physiological process.

Fig. 3. *Alisma Plantago-aquatica,* pollen grain. From WODEHOUSE, 1936, p. 537, 4.

According to this conception the fundamental plan is neither a reminiscence of an ancestral structure, nor an immaterial idea, and it is not the fundamental plan of the species or of any other taxonomic group which is the primary fact, but the real fundamental plan is that of the individual organism.

However, as the individuals of the same species are usually astoundingly similar in the fundamental plan, we can describe the common features as the plan of the species. And in doing so we may disregard the rare individuals with smaller or greater departures from the normal scheme, the so-called monstrosities or teratological cases.

These departures may have various causes: changes in the concatenation of the factors, as in a calycanthemous flower; or in the spatial relations of the different activations, as in a situs inversus viscerum, or in a pleiomerous flower; or the departures may be due to changes in the factors themselves, or to an insufficient action of the factors, as in albinos, in the case of a hare-lip in man, and so on.

These differences between the monstrosities and the normal cases strongly remind us of the differences between related species, and accordingly what is teratological in one species, may be normal in another.

Fundamental plans in the sense of the above views are not limited to species, but the common features in the construction of the members of a larger taxonomic group, indicating similarities in the concatenation of their morphogenetic factors and in these factors themselves, together establish a fundamental plan of the whole group. The larger the group, the smaller the number of common features will be; on the other hand it has been generally recognized that phylogenetically and taxonomically those features are the most important which are common to the more comprehensive groups.

Whether in a group a certain characteristic will be "important" or not in this sense can never be told beforehand; experience has amply shown that the same feature is most important in one group and is quite unimportant in another. This depends only on the degree of persistency with which the feature has been transmitted in the particular group during its phylogeny.

No fundamental plan has been studied more intensively and with better results than that of the *Vertebrates,* and one of the unintended consequences of this fact has been that many biologists have been inclined to look at the pecularities of this special fundamental plan as typical for the other plans, as a standard to judge them by.

Now in the fundamental plan of the *Vertebrates* the spatial relations are the most essential features, while the differentiation of the different parts is extremely variable; evidently the concatenation of the morphogenetic factors is very stable, whereas the factors themselves are liable to important changes. A number of the spatial relations are even the same in all *Vertebrates,* so for instance the reciprocal position of the medullary groove and notochord.

There is, however, no reason why in other phyla the morphogenetic factors should not be more stable than their concatenation, and in plants this is really often the case. As a striking instance the *Florideae* may be advanced, which undoubtedly possess a number of homologous organs in their monospores, tetraspores, gametes, thallus parts protecting and enveloping the latter, and their auxiliary cells; all these organs, however, are produced in various positions in the plant, even so much so that a fundamental plan of the whole thallus hardly exists.

In more than one case botanists who were not aware of these facts have actually been led to erroneous conclusions by their overestimation of the importance of the spatial relations, under the impression of the zoological instance.

B. Biological axes. Above we remarked that it is a frequently occurring phenomenon, that the distribution of organs formed later is controlled by previously formed differentiations. This control is nowhere better expressed than in what will be called here biological axes, being those lines in the organism in or around which all the more important organs are placed in definite positions, either in consequence of a general growth polarization, or of the strong influence of two differentiations placed at the end of the line.

As such biological axes have evidently a great influence on the fundamental plan, they have to be discussed here in full.

The cell of *Stictodiscus,* one valve of which is represented in fig. 1, has a biological axis uniting the centres of the two equal valves, and the arrangement of all the ornamentations of the valve expresses this very well. In this case the axis is isopolar. The more frequently occurring case is, however, the heteropolar axis, of which *Volvox* may give an illustration (fig. 4). Here we find an anterior or sensitive pole, going ahead in the movement through the water, and a posterior or generative pole. Though on the whole built in the same way, the cells of the sensitive pole have much bigger stigmas than those of the generative pole; both the sexual and the asexual reproduction are confined to the latter.

Between the two instances given here there is moreover the difference, that the axis in *Volvox* is clearly the outcome of the antagonism between two fields with different morphogenetic powers; we may suppose different gene substances in them.

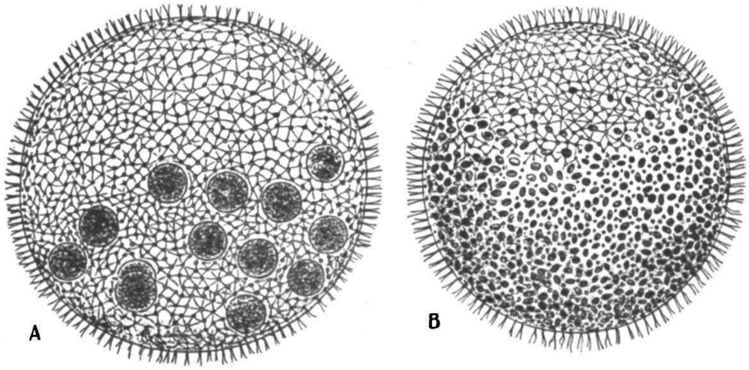

Fig. 4. *Volvox aureus,* two individuals. A, with oogonia. B, with antheridia. From OLTMANS, 1922, I, p. 224.

In *Stictodiscus* on the other hand the axis is not due to any differentiation at the ends of the axis, the polarity being present before the valves, or before the protoplasmic parts in charge of their formation; the axis is here the result of a special growth polarization, and the valves are only incidental differentiations, placed in the axis.

Hence we have to distinguish between growth axes, due to growth polarization, and differentiation axes. And as both may be isopolar or heteropolar, we get already four kinds of biological axes in this way.

The heteropolar growth axis may be instanced by *Achnanthes* (fig. 5)

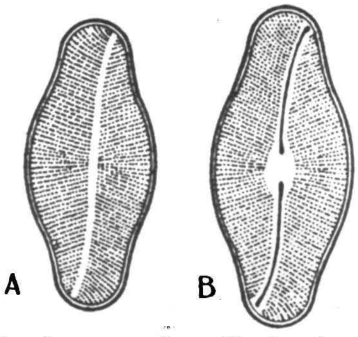

Fig. 5. *Achnanthes flexella.* A, upper valve without raphe. B, lower valve with raphe. From ENGLER and PRANTL 2nd ed. 2, 1928, p. 269, fig. 358, A, B.

or any other form belonging to the *Monoraphideae* under the Pennate Diatoms, in which one valve bears a true raphe, the other at the utmost a rudimentary raphe. If, as occurs in some *Achnanthes* species the cells remain united in threads, all cells turn their raphe to the same pole of the thread. The heteropolarity of the growth axis is expressed moreover by a flexure of the cell, the valve with the raphe forming a re-entering, that without raphe a salient angle to the outside while the chloroplasts lie against the valve without raphe.

And as instances of isopolar differentiation axes we have the pollen grains of the majority of *Dicotyledons,* as in fig. 6, where two equal poles of a special organization are separated by an equatorial zone with the places of exit and the grooves, the latter running in meridional directions.

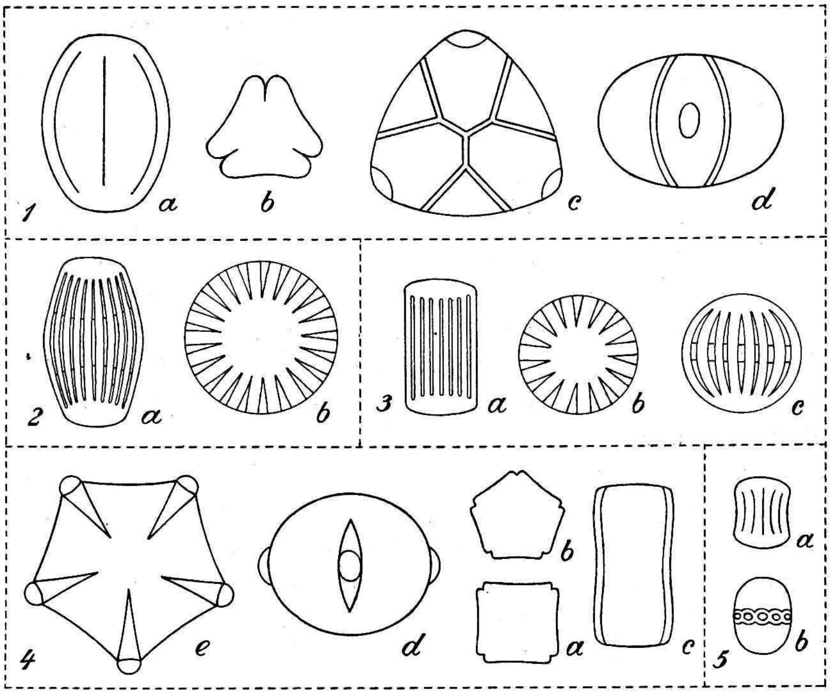

Fig. 6. Pollen grains of Dicotyledons, with a biological differentiation axis. 1. *Vinca herbacea:* a, b, dry; c, d, wetted. 2. *Polygala myrtifolia:* a, dry; b, wetted. 3. *Monnina xalapensis:* a, dry; b, c, wetted. 4. *Viola tricolor:* a, b, c, dry; d, e, wetted. 5. *Symphytum officinale:* a, dry; b, wetted. From v. MOHL, 1834, pl. V and VI.

To these four kinds of biological axes we have finally to add a fifth one, that of the segmentation axes which are always heteropolar. They arise by the development of a certain morphogenetic process in a protoplasmic field, followed by a second one next to it of the same kind, a third one at the other side of the second and so on, a repetition of the same process in a linear order. Such a row of homologous differentiations forms a biological axis, theoretically of an infinite extension.

As a simple instance of such a segmentation axis we have the acrogenous formation of conidia in *Cystopus* (fig. 7), where the protoplasmic field in which the basipetal abscission of conidia takes place is regenerated continuously by growth. By far the most cases, however, are found in the animal kingdom, where the metameres of *Arthropoda* and *Vertebrata* are formed in this way.

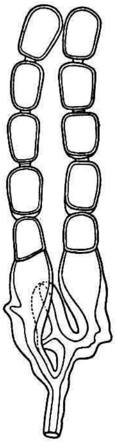

Fig. 7.
Cystopus Portulacae, conidia.
From de BARY, 1884.

It need not be said that in nature the various kinds of biological axes may be blended in any way. Stems and roots have growth axes which at the same time are differentiation axes; the *Vertebrates* have segmentation axes which are also differentiation axes.

The conception of axes as given here is not new; in fact the distinction of axes in organisms is as old as biology itself. Up till now these axes have, however, not been recognized as being due to biological processes, and moreover they have been confounded with such lines in organisms which, though not being biological axes, may be distinguished as symmetry axes in a mathematical sense. In our § 13 the difference between biological and mathematical axes will be pointed out accordingly.

The number of biological axes may be limited to a single one, as in most of the instances given above. Their formation may, however, be repeated a number of times, and, moreover axes of a different description may also develop in the same organism.

The repetition of homologous axes in organisms may be found for instance in any branching system of stems or of roots, and as cases of an addition of new axes of another description we may mention the development of leaves on stems, or of hairs on any plant organ.

In these cases the distribution of all secondary axes is checked by the morphogenetic processes in their parent axis, and hence the oneness of the fundamental plan is warranted. The regular shape of a solitary *Abies excelsa* for instance may be brought back to the repeated control of the twigs by their parent branches.

On the other hand in those cases in which a secondary axis of another kind is formed, a wholly different mode of complication may be reached if the new axis does not rule over a new region of its own in the organism, but if it is present in the same protoplasmic region as a primary axis. This condition is exemplified by *Rhoicosphenia curvata* (fig. 8), a near relative of *Achnanthes,* with the same heteropolar growth axis and where the same flexure of both valves is found, but a second contrast is to be seen in the direction of the raphe, the two narrow ends of the cell having distinct different organizations. Evidently at these two ends, the poles of the sagittal axis of Diatomologists, different gene substances are present, so that the morphogenetic processes must be different too.

In a mathematical sense we may distinguish even a third axis in this *Rhoicosphenia*, perpendicular to the two others. But as there is no growth polarization in that direction and there is neither any indication of special influences of the pole of this axis, on each other or on other parts of the body, there are no reasons for assuming a biological axis there.

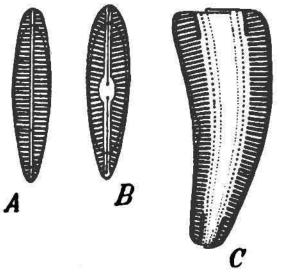

Fig. 8. *Rhoicosphenia curvata*. A, upper valve without raphe. B, lower valve with raphe. C, girdle view. From ENGLER and PRANTL, 2nd ed. 2, 1928, p. 287, fig. 390, A, B, C.

Other instances of organisms with two biological axes in the same region are all dorsiventral flowers, and the great majority of animals. In rather rare cases a third axis is clearly present, as in those dorsiventral animals in which the right and the left side have assumed different features, by a new contrast between different gene substances at those sides; the flatfishes are well-known in this respect.

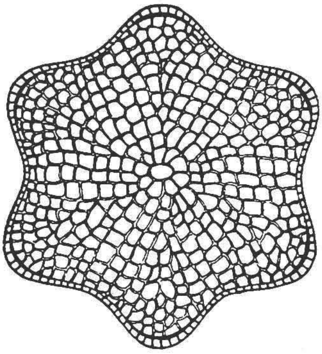

Fig. 9. *Triceratium reticulatum*, sixlobed valve. From ENGELR and PRANTL, 2nd ed. 2, 1928, p. 240, fig. 291, A.

More than three biological axes in the same field do not seem to occur in any organism. In a six-lobed *Triceratium* (fig. 9) we might assume, it is true, a single isopolar growth axis, and three equal isopolar axes perpendicular to it, intersecting at 60°. But we had better describe the cell as having only the isopolar growth axis, around which six local differentiations have been formed at equal distances; in the genus the number varies from 3 to 9, and as soon as the species varies with 5 of them, the three so-called isopolar axes are replaced by five heteropolar ones.

This vagueness in the distinction of biological axes does not interfere with the naturalness of the conception, as it is a matter of course that the higher the number of local differentiations in an organism, the less each of them is likely to dominate the whole organization.

In all the cases in which two or three biological axes occur in the same field it is possible to recognize an order of precedence amongst them, and accordingly we may distinguish between a primary or main axis, a secondary axis which is checked by the main axis, and eventually a tertiary axis, dominated by the two others.

As a rule the axes of different order are perpendicular to each other. This may, at least partly, be understood as follows. Secondary and tertiary axes are usually, and perhaps always, differentiation axes. Now the two local activations of morphogenetic factors must assume strictly opposed positions with respect to the main axis, by their own mutual influences, and if they are placed at the same level by the influence of the main axis, the secondary axis must be at right angles to the main axis.

Of course there may be complicated relations, bringing about a different way of crossing; an instance will be mentioned in § 16 for *Nitzschia*.

Biological axes, being the outcome of ontogenetic processes, are laid down at a certain developmental stage, and stop their influences at another stage. In a thorn of *Crataegus* for instance growth ends by the transmutation of the vegetative cone. In such a thorn numerous results of the polarizing factors remain in the organic structure, and accordingly we still describe such a thorn as having a heteropolar biological axis. Strictly speaking, we should distinguish between the axis as present in the growing stages with its physiological processes, and the results in the adult condition in which these processes may have ceased to exist. However, as our knowledge in this respect is still very defective, both groups of phenomena will be described here as representing a biological axis.

In some cases a protoplasmic region in which an axis has come to an end, may turn into the field of activity of a new and different axis. An outstanding example of this kind is furnished by the *Pennate* Diatoms, where the auxospore has a biological axis in the direction called by Diatomologists sagittal axis, and where after the formation of a frustule a new axis comes into action which is perpendicular to the first one.

In such cases the distinction between main and secondary axis is less clear; it may perhaps be advisable to follow here the common use of Diatomologists, to call the new axis main axis, and to recognize that a former has been replaced by a new one.

The considerations given above may prove sufficiently that biological axes are of paramount importance for the elaboration of complicated fundamental plans. Indeed the fact that a few differentiations dominate the distribution of several others, which in their turn again may localize others, and so on, ensures a stabilization which could hardly be reached by any system in which such a hierarchic organization was lacking.

Special stress may further be laid on the circumstance that any axis itself is the outcome of the activity of a very few differentiations. A larger number would of course be liable to meristic variation, but that this is unknown in growth axes which are due to a single differentiation and that in the heteropolar differentiation the two different poles are seldom multiplied, is not strange; the two-headed monstra in animals at least are only poor instances of the latter.

The isopolar differentiation axis is somewhat more exposed, though two is still more stable than any higher number. In fact we may observe a "tripolar" sagittal axis in some Pennate Diatoms. The normal bipolar sagittal axis takes its origin in the development of two equal differentiations in the auxospore. Now if in rare cases an auxospore forms three of them, it gets a triradiate shape, and as this form is transmitted to all vegetative cells derived from it, a clone with a "forma trigona" (fig. 10) is the outcome.

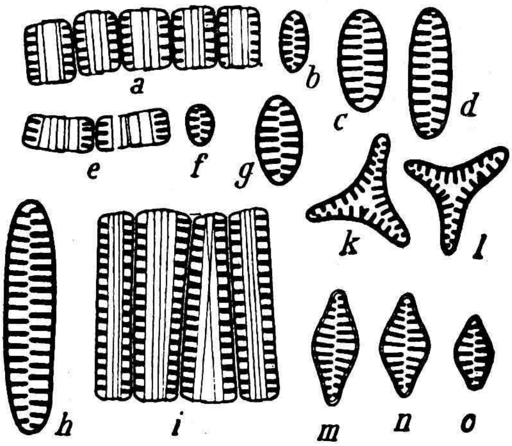

Fig. 10. Forma *trigona* of *Pennate* Diatoms. *Fragillaria pinnata, a-i,* normal form; *k-l,* var. *trigona; m-o,* var. *lancettula.* From HUSTEDT, 1924, VII, 2, p. 161. Similar trigonal forms are pictured for *Fragillaria construens,* p. 159, *Raphoneis nitida,* p. 177 and *Centronella Reichelti,* the latter with the difference that the trigonal form is not the exeptional, but the normal form of the species.

A last remark on biological axes is that, if all later formed axes are localized by those already present, the question arises how the first axis of the whole body may be determined.

The answer has to be that undoubtedly this occurs in various ways. In *Fucus* we saw that it takes place either by chance or by different stimuli from without. In other cases those stimuli emanate from the parent generation; in the *Bryophyta* for instance the apical pole of the sporogonium develops at the side of the archegonium neck. And in *Equisetum, Tmesipteris* and *Isoetes* the stem pole is formed at that side, whereas conversely in the *Lycopods* it is the root pole which arises in that place (cf. BOWER, 1935, p. 524). And the isopolar main axis in pollen grains, where present, is determined by the position of the cell in the tetrad, one of the poles pointing to the tetrad centre.

In all these cases we may for the present stick to the view that the gene substances are spread uniformly in the cytoplasm, and that the susceptibility to these of the protoplasm is locally enhanced at the places indicated above, by the influence of external stimuli.

c. Size-factor The views given above about the fundamental plan may enable us to shed some light on the origin of structural differences between organisms of different sizes.

It has been repeatedly remarked in biology that GALILEI's principle of similitude which reigns everywhere in nature, is of great importance in the bodily organization of living beings; indeed the fundamental plans of related organisms of different size, such as cat and tiger, or *Poa annua* and *Phragmites communis,* are amongst all their more or less important differences invariably distinguished by such features as cause their bodies to be up to the claims of their sizes; a detailed account with many good examples of the differences in mechanical construction of small and big organisms was given by d'ARCEY THOMPSON (1917) [1]), whereas BOWER (1930) paid especial attention to the differences in complication of the external and internal surfaces in organisms of different sizes, the complication in the big forms being indispensable for an efficient physiological interchange.

BOWER, moreover, points out that these differences occur not only between representatives of different, but also of the same species, when they happen to be of different sizes, and even between small and big homologous parts of one single individual.

As an instance one of the numerous figures given by BOWER is reproduced here, representing the stele of seven roots of different size of *Danaea nodosa,* in which the xylem is drawn in black, the sclerotic pith as a dotted area (fig. 11).

The explanation of the latter cases has, of course, to be another one than that for the differences between two species. Indeed, any species the construction of which is not in full harmony with the needs resulting from the normal sizes of its individuals, lags behind in the struggle for life; we may therefore expect that by natural selection only those forms have been preserved, the fundamental plan of which ensures an efficient organization, at least for the middle-sized individuals.

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[1]) The 2nd edition was published during the war in 1942.

For the constructive differences of small and big members of the same body such an explanation, of course, is not available, and BOWER therefore concludes to an effectiveness in the development of the size-factor itself, and he enounces the working hypothesis that the relation between size and form should be a causal one, in so far as "it induces by change such mature forms as shall tend to maintain a due proportion of surface to bulk". (1930, p. 220).

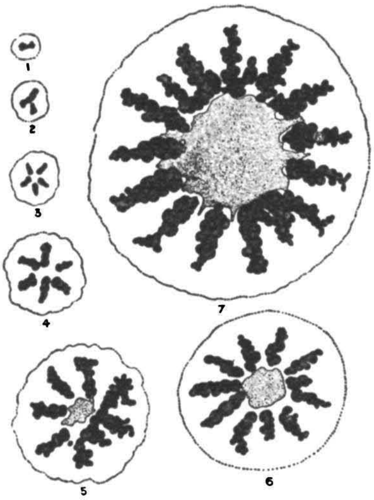

Fig. 11. *Danaea nodosa*. Transverse sections of stele of roots of different size, all drawn on the same scale, from sporelings (1, 2), young plants (3, 4) and adult plants (5-7). Xylem black, sclerotic pith dotted. From BOWER, 1930, p. 167.

And as the vascular tracts are laid down in the apical region, long before the adult size has been reached, there is supposed some anticipatory, or proleptic, sensitiveness to the incidence of similarity (1930, p. 221).

These assumptions, in which an idealistic element is not to be mistaken, may be replaced by a more natural view, on the basis of the above considerations about the fundamental plan.

For in all cases in point we meet main organs of varying sizes, inside which a variable number of subordinate organs are formed; in most instances the extraordinary variation in size of the main organ is connected with the gradual elaboration of a Fern sporeling or a Monocotyledonous seedling.

In these young plantlets the developmental stages of the first organs are all shortened and stunted by lack of materials. For the induction and development of the subordinate organs the case is, however, somewhat different; the common rule that the different activations of the same morphogenetic process give rise to homologous organs of about the same size meets here with few difficulties. If only the activation areas are of about the same size in weak and in strong principal organs, the outcome will be that their number will be accordingly lower in the weak organs where a smaller protoplasmic area is available for them.

This applies to the roots described by BOWER, as well as to the stem of *Pteris* with its increasing complexity (BOWER, 1930, fig. 2, p. 9) and to the Fern leaves with increasing elaboration (see for instance ORTH (1938)). At any rate the assumption of an anticipatory sensitiveness becomes superfluous in this way, as it is evident that the plant is able to realize different degrees of complexity if only the morphogenetic factors for the subordinate organs are such that their activations always occupy a more or less constant, limited area.

§ 7. Summary.

1. The first task of biomorphology is the description of all life forms; any study of vital phenomena in whatever direction has to be based to a smaller or greater extent on such descriptions.

2. A second and scientificially much more important task of biomorphology is the study of these forms as expressions of vital phenomena themselves. This study implies the origin of any structure and its changes during life-time, and if possible it attempts to shed some light on the causes ruling the morphogenetic processes.

3. In explaining morphogeny no idealistic principles are to be accepted, only physiology being able to offer the required basis.

4. The forms of living beings are for a minor part directly inherited from the parent generation; most forms, however, are formed anew in any individual.

Directly inherited parts multiply in the living body by fission; the newly formed structures are elaborated in the cytoplasm by vital reactions on the stimulating effect of gene substances emitted by the nuclei.

These reactions may be of various extension and of different kinds, being either local differentiations or stimulations or retardations of growth. A limitation of growth to a single direction is called here growth polarization.

5. The duplicity in the hereditary transmission of structures ensures important advantages.

By the existence of genes it becomes possible to transmit the powers of reproducing complex structures to such places where they are wanted, and by the inclusion of the genes in the nuclei it is possible to condense these powers in a very small compass and to form extremely small reproductive organs, the more so as by the mitotic division every nucleus receives a complete set of genes, only a very small sample of each gene being present.

Finally during the heterotypic division the mitosis facilitates the realization of numerous new combinations of casual variations in the genes, a fact by which the chance to obtain progressive changes of the species is enhanced.

6. The term organ, though universally used in biomorphology, has not yet been defined satisfactorily. It is therefore proposed here to call organs those parts which are separate units in the direct transmission, and also those which arise under the influence of separate gene substances, or of a set of such substances.

7. Accordingly the terms homologous and analogous organs are defined as follows:

Directly transmitted organs are homologous when they have a common ancestor, irrespective of the circumstance whether they have retained the same shape and the same function or not. They are called analogous when they are of different descent and yet have certain features in common, in connection with a similar function.

Organs formed under the influence of gene substances are called homologous, when the stimulating gene substances are either identical, or when the emitting genes are homologous. They are analogous when they share certain features, in connection with a similarity of function, though being induced by substances from phylogenetically unrelated genes.

8. The fundamental plan (Type, "Grundplan") of an organism is ascribed here to the concatenation of a number of physiological processes.

The view is proposed that, whereas any new differentiation is a vital reaction on the stimulus of gene substances, the emission of new gene substances in its turn is due to a stimulation of the genes in question by other substances of analogous description which are emitted by the differentiations.

9. According to this view the fundamental plan is a real process, no immaterial idea, and any individual has its own plan. In a variation or a teratological case the plan is therefore different from that of normal specimens.

As, however, the fundamental plans of related organisms have much in common, we may describe the fundamental plan of a species, or of any other taxonomic group; in more comprehensive groups the number of common features diminishes rapidly. Those features which are common to very comprehensive groups are phylogenetically and taxonomically the most important.

10. The same features which are important in one group, may be unimportant in another. The great importance of the spatial relations in the *Vertebrates* is a special pecularity which is not necessarily found in other phyla; in some plant groups these spatial relations are even of very slight importance.

11. In the elaboration of fundamental plans an important rôle is played by what is called here biological axes, being lines in the organisms in or around which more important parts are placed in definite positions. By these axes the distribution of most further differentiations is controlled.

These axes may arise in different ways, and though their features may be combined in any conceivable way, we have to distinguish between five kinds of biological axes: isopolar growth axes, due to growth polarization, heteropolar growth axes, due to growth polarization in combination with a differentiation of the two poles, isopolar differentiation axes, due to the antagonism between two equal differentiations placed at the poles, heteropolar differentiation axes, due to the antagonism between two unequal differentiations, and segmentation axes, due to a continued formation of homologous differentiations in a linear order.

12. The same organism may develop a number of biological axes, those axes which are formed in the protoplasmic region of an earlier axis being localized by that axis.

In most cases the newly formed axes develop a protoplasmic field of their own. Two or three axes may, however, be developed in the same field, and from the dependence of one axis on the other we may distinguish in such cases between a primary or main axis, a secondary, and possibly a tertiary axis. As a rule these axes are perpendicular to each other.

13. By the hierarchic relation between the different biological axes and the control of the distribution of other differentiations by each of them, the fundamental plan of an organism may get a distinct stability.

14. Organisms of different sizes, belonging to nearly related species have always such hereditary differences in their fundamental plans as to meet the requirements of GALILEI's principle of similitude by the construction of their bodies.

15. Organs of different sizes belonging to individuals of the same species, or even to the same individual, are often different in structure so as to meet the same principle of similitude in the same way.

This is reached in a very simple way by a more or less constant size of the local processes for the formation of the subordinate internal organs, so that in the large main organs a greater number of them is induced.

The assumption of a special size-factor, with a causal influence on the arising structure, as advocated by BOWER, is therefore not required.

CHAPTER 2.

ORGANIC SYMMETRY.

§ 8. Introductory.

As mentioned in § 3, an attempt will be made here to break a way for the replacement of the usual idealistic explanation of organic symmetry by a causal view.

An indispensable step to be made in behalf of such an aim, is the reviewing of the available body of facts presented by the various groups of organisms, in the hope of recording facts, regularities or laws which enable us to trace the causal basis of the symmetry phenomena.

But as symmetry is not limited to organic life, and occurs also in other domains of nature, we may compare the symmetry found in animals and plants to that occurring in inorganic nature, and as, moreover, mathematics gives a general survey of all symmetry forms which may exist in space, we may investigate to what mathematical groups the forms realized in organisms and in inorganic bodies belong.

The following paragraphs will accordingly deal with the definition of the term symmetry (§ 9), the symmetry elements in mathematics (§ 10), in inorganic nature (§ 11), and with the causal basis of organic symmetry (§§ 12—13), while in the further parts of the chapter the method of describing organic symmetry will be discussed (§ 14), and three groups of organic symmetry will be treated (§§ 15—17).

§ 9. Definition of the term symmetry.

In course of time different meanings have been conveyed by the term symmetry, a word which has not been framed by a scientist but which was in common use with the ancient Greeks.

In their language *symmetria* indicated both a due proportion and a mensurability, the literal translation being together-measuring. *Symmetros* was used for fitting, or moderate, or not too big, not too far, and *symmetreō* for to compute by comparison, to measure out, and in the passive form for to agree with.

In modern sciences, especially in crystallography and in mathematics, a derived meaning has been generally adopted, namely that something consists of two equal parts which are distributed in such a way that the spatial relations between the parts are the same for any part.

The advantages of the adoption of this definition in biology are obvious, as in this way all results obtained by the mathematical theory may be freely used in biology.

A very few biologists have indeed acted accordingly, as did in botany A. FREY (1926, p. 87) but on the whole we may say that the biologists have been rather lax in this respect, and that usually they did not pay much attention to the meaning of the term symmetry. Therefore, though impressed by the achievements of mathematics, and far from being recalcitrant, they only followed from a long distance, and sometimes even used ill-defined or ambiguous concepts.

No blame is to be laid in this respect on A. P. DE CANDOLLE, one of the very first biologists to use the term symmetry, who defined it as the "système général de l'organisation" (1913, p. 92) or as "l'ensemble qui résulte de la disposition relative des parties" (ibid. p. 93). Symmetry accordingly was for DE CANDOLLE what we call now the fundamental plan, and in those days in which the mathematical theory of symmetry did not yet exist, there was no objection to this conception.

Some modern authors, however, usually give a rather ambiguous meaning to the term, in applying it to the repetition of equal parts as well as to the spatial relations in general.

This practice is followed by GOEBEL, who begins the chapters on symmetry relations in his Organographie (1898, p. 53—121; 1913, p. 185—312; 1928, p. 209—424) with the statement that symmetry embraces "ganz allgemein die raümlichen Beziehungen der Pflanzengestaltung" and who deals accordingly in these very extensive chapters with a great variety of morphological topics, but who includes also descriptions of radial, dorsiventral and bilateral symmetry.

This leads to uncertainty about the meaning of the term in many cases, and may induce some authors to write such sentences as we find in LEWIS (1923, p. 5): "Symmetry is here to be considered in the wide and non-mathematical sense of a balanced and harmonious relation of parts of organs, and as displayed in three main types: bilateral, radial and spiral symmetry."

Other authors, especially zoologists, reduce the meaning of the term to the special form of symmetry of nearly all higher animals, where the only symmetry element is a symmetry plane, normally placed in a vertical position. This practice is not only based on the wide-spread occurrence of dorsiventrality in the animal kingdom, but moreover on the fact that the notion of symmetry in daily life is chiefly limited to that of dorsiventrality, the form met in our own body and in most buildings as well as in many articles of daily use, where it is valued, partly as an aesthetic element, and further as meeting the requirements of a natural equilibrium.

At any rate the use of the term symmetrical in the sense of dorsiventral is often found in zoological text books, and a most curious instance of repugnance to including radial symmetry in the conception of symmetry is given by G. JÄGER in an old paper of 1857, who wrote p. 338 that he was as averse from considering an *Echinoderm* as symmetrical "als mich Jemand von der Symmetrie eines Kreises überzeugen kann, indem er mir sagt, er bestehe aus zwei Halbkreisen".

In the present chapter the mathematical definition of symmetry will be accepted.

§ 10. Symmetry in mathematical figures.

Any mathematical figure in which two or more equal parts are present in such a way that the spatial relations of one part to all the others are identical for any part, must needs posses one or more elements, being either symmetry axes, symmetry planes or symmetry centre.

Symmetry axes are lines around which the equal parts are distributed in such a way that after certain movements of the figure around or along the axis the figure coincides with itself, as the expression runs. A plane is a symmetry plane, when the equal parts are placed at both sides of it in such a way that those at one side are the mirror-image of those at the other side. A symmetry centre is a point with the special feature that any line passing through it meets in both directions, at equal distances, corresponding points in the figure.

As some knowledge about these elements is required for our purpose, the three groups of symmetry elements will be considered in some detail, but a mathematical treatment will be avoided as much as possible, and there where instances of forms will be given, natural objects will be chosen by preference instead of mathematical bodies, even though the latter should be superior as to the exactness of their symmetry.

As the nature of all symmetry is different in finite and infinite figures, we shall have to say some words about the latter category too, though at first it might seem quite superfluous, all earthly bodies and surely all organisms being of finite dimensions.

Yet a body of finite dimensions may show some features which may be better understood when considered as parts of an infinite structure. This is always the case with internal symmetrical structures if they are entirely independent of their own outer boundaries.

All crystals exhibit this condition. Their essential characters follow from an arrangement of the constituent particles in a space lattice and this lattice is theoretically infinite. Between a rough diamond in the shape of a pebble and a beautifully cut and ground specimen, of a quite regular shape, there is no difference in the crystallographical symmetry features.

A. Symmetry axes. In finite figures only one kind of these elements may be realized, namely rotation axes.

In a figure with a rotation axis the equal parts are repeated n times around the axis, at equal angular distances and on circles. By a rotation of the figure around the axis, through an angle of $360^\circ : n$, it accordingly assumes a similar position as it did before.

The number n may vary from 2 up to ∞, but must always be a natural, also a whole number. Objects from nature with an approximate realization of a rotation axis are isomeric flowers (Fig. 12, *Ornithogalum umbellatum*; a ternary rotation axis) and hens' eggs (an isotropous rotation axis, *i.e.* an axis with an infinituple repetition of infinitesimal equal parts).

Fig. 12. *Ornithogalum umbellatum.* Floral diagram. From EICHLER, 1875, I, p. 154.

Two or more rotation axes may be present in the same body; several *Pennate Diatoms* have three dimeric rotation axes, intersecting each other diagonally (Fig. 13, *Plagiogramma elongatum*) and in a sphere there is an infinite number of isotropous rotation axes.

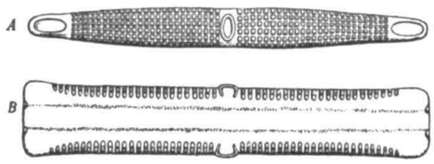

Fig. 13. *Plagiogramma elongatum.* A, valve; B, girdle view. From ENGLER and PRANTL, 2nd ed., 1928, p. 261, fig. 234.

In infinite figures the conditions are rather different. We have to distinguish between no less than three groups of infinite figures, according to the infinite extension in one, two or three dimensions of space; the difference between these three groups may be very roughly illustrated by some biological objects.

A comparison with one-dimensionally infinite figures is allowed for organisms, with an unlimited growth in one direction, like a root, or a tape-worm. Analogies to two-dimensionally infinite figures are not nearly so wide-spread amongst living beings. Yet a protoplasmic layer of a limiting surface, like a tonoplast, may be mentioned, or, to give an instance of a larger size, but of a less striking kind, a forest, or a grass-plot, both considered as entities. For an approach to a three dimensionally infinite figure a *Sarcine* colony may be taken, or, much better, all crystals.

In infinite figures no less than three kinds of symmetry axes may be present, which may be distinguished as rotation axes, translation axes and screw axes.

1. *Rotation axes in infinite figures.* Rotation axes may be present in one-, in two- and in three-dimensionally infinite figures, but their characteristics are different from those in finite figures as soon as they are perpendicular to a plane of infinite extension.

Those which are perpendicular to a finite transverse section have the same properties as in finite figures; for instance in a growing root a single isotropous rotation axis is present, and in a five-ribbed *Cereus*-stem we distinguish a quinary axis, at least if we disregard the scattered areoles on the stem surface.

Those rotation axes, however, which are perpendicular to an infinite plane differ in two important respects; they lose their fixed position, only their direction remaining fixed, and their repetition number *n*, instead of being variable from 2 to ∞, is limited to one of the four values 2, 3, 4 and 6.

No mathematical demonstration of the general validity of these rules will be given here; for three-dimensionally infinite figures it may be found in any treatise on crystallography. The facts themselves may only be brought nearer here to the biological reader by some simple instances.

In a forest or in a grass-plot no symmetry is present at all, the constituent elements being distributed without any regularity. In a planted wood, or in a potatoe field, the individuals as a rule are planted regularly, at equal distances in straight rows.

Now our fig. 14,1 makes it clear that if the individuals are planted in

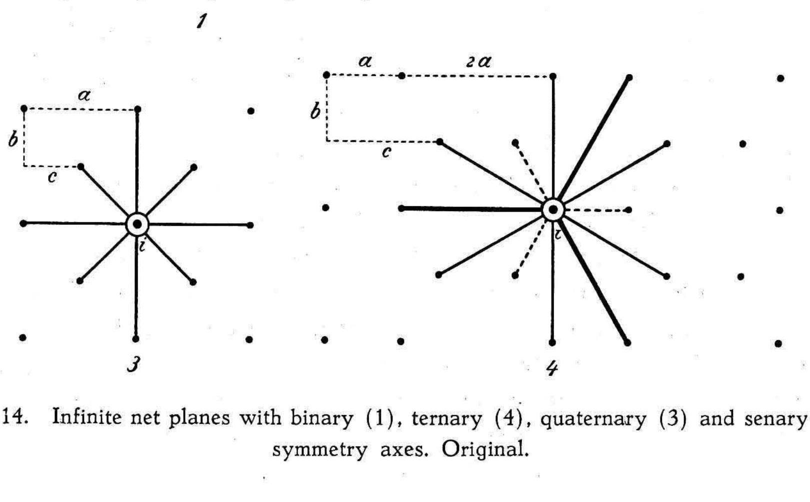

Fig. 14. Infinite net planes with binary (1), ternary (4), quaternary (3) and senary (2) symmetry axes. Original.

the rows at equal distances a, and if the rows are placed at equal distances b and if finally the shift of any row as compared with the adjoining rows is constant over a distance c, the system must, irrespective of the chosen values for a, b and c, have a binary rotation axis, without a special position.

For we may turn the system which is part of an infinite pattern, around any arbitrarily chosen individual i through 180° and the result will invariably be identical to the system before turning.

By choosing suitable special values for b and c, the symmetry of the system may be increased; in planting practice c is usually taken to be $\frac{1}{2}a$, as in fig. 14,2 and 14,3, by which two symmetry planes are added.

The binary axis itself may moreover be promoted to a quaternary or a senary rotation axis, being therefore in a sense doubled or tripled. In order to get a quaternary axis, we may for instance take both b and $c = \frac{1}{2}a$ (fig. 14,3), or we might have taken $b = a$ and $c = 0$; a senary axis arises by taking $b = \frac{1}{2}a\sqrt{3}$ and $c = \frac{1}{2}a$ (fig. 14,2) or $b = \frac{1}{2}a : \sqrt{3}$ and $c = \frac{1}{2}a$.

Finally a system with a ternary rotation axis can never be the result of a homogeneous combination of rows of equidistant individuals, as this always implies the presence of a binary axis. It may be obtained, however, either by omitting every third row, or by omitting every third individual in the rows, so that the distances in the rows are by turns a and $2a$. Our fig. 14,4 has been drawn after the second mode, b being chosen equal to $\frac{1}{2}a\sqrt{3}$ and $c = 1\frac{1}{2}a$. The result is that any individual i has three nearest neighbours at a distance a, three farther ones at $2a$ and six intermediate ones at $a\sqrt{3}$, all arranged in a most regular way.

So far about the possibility of binary, ternary, quaternary and senary rotation axes; that quinary rotation axes are impossible if perpendicular to a plane of infinite extension, may be made clear as follows:

If we surround a given central point A by 2, 3, 4, or 6 points in the most symmetrical way (fig. 15, 1—4) the results are a line, a equilateral triangle, a square and a regular hexagon. The last three figures may fill up the plane with nothing but their equals, as indicated in fig. 15. This is due to the fact that their angles, being 60°, 90° and 120° are aliquot parts of 360°. Regular pentagons, however, having angles of 108°, cannot fill up a plane (fig. 15,5), and the same may be said about the regular heptagon (fig. 15,6), with its angles of 128° 34′, and of all higher regular polygons, the angles of which range from 135° to not quite 180°.

Another way of illustrating the impossibility of numbers of repetition n higher than 6 in infinite systems, is calling to mind that 7 or more points, equally surrounding a centre and lying therefore on a circle, are nearer to each other than to the centre, so that the spatial relations of the centre to all other points of the system can never be identical to the relations between one of the surrounding points and all the others.

2. *Translation axes.* A translation symmetry axis involves that the equal parts are repeated at equal distances in a way corresponding to a rectilinear shift in a direction of infinite extension, the character of the perpendicular plane being irrelevant.

A biological equivalent is present in the segmentation of an earthworm, if we disregard the ends of the animal, or in a stem with nodes and internodes, if the internodes are of equal length, and if the leaves are placed in superposed whorls, as in *Sphenophyllum.*

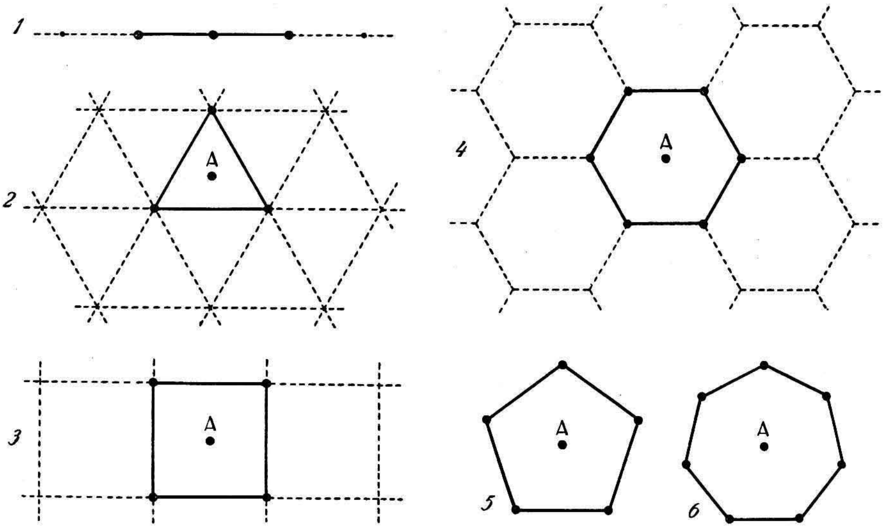

Fig. 15. A point *A* surrounded by 2—7 similar points in a symmetrical way. Only in the cases with 3, 4 and 6 surrounding points a regular polygon is formed, which can fill up the plane with nothing but its equals. See moreover the text. Original.

3. *Screw axes.* A screw symmetry axis is a combination of a rotation and a translation axis, the equal parts being placed in a screw line around the axis.

A shoot with a spiral phyllotaxis and with internodes of equal length, provides an example.

B. Symmetry planes. Symmetry planes in finite as well as in infinite figures divide the figure into two halves which are each other's mirror-images; these mirror-images may be identical in every respect, or they may differ in the way of a right and left hand.

In agreement with what we recognized for symmetry axes, these planes lose their fixed positions in figures which extend infinitely in the dimension perpendicular to the plane. In crystals accordingly all symmetry planes have only fixed directions, no fixed positions.

C. Symmetry centres. For our purposes these elements are hardly of any interest; the only remark to be made here, is that in finite figures only they have a fixed position.

D. Combination of symmetry elements. A figure may have a single symmetry element, being either a symmetry axis (fig. 16, contort corolla of *Blumenbachia Hieronymi*), or a symmetry plane (the human body) or a symmetry centre (fig. 17, holohedral triclinic crystal).

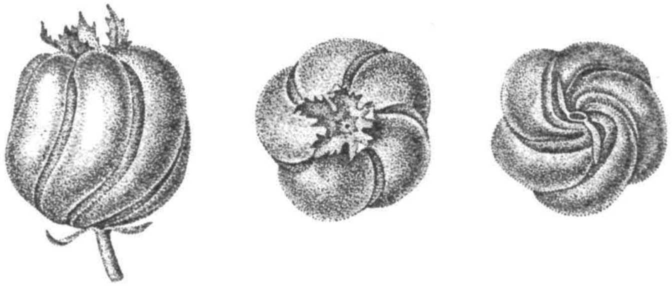

Fig. 16. Contort corolla of *Blumenbachia Hieronymi.* Original.

As, however, the equal parts of a figure must be distributed in harmony with all symmetry elements of the figure, it is obvious that there must be close relations between the different symmetry elements of a figure, and often even the presence of a certain combination implies the presence of other elements.

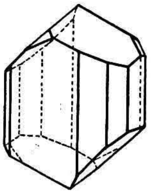

Fig. 17. Holohedral triclinic crystal of copper-sulphate (5 H_2O). From JAEGER, 1917, p. 56.

The existence of two, orthogonally intersecting, binary rotation axes, for instance, implies the presence of a third one, perpendicular to the plane of the other two, and if a symmetry centre is added to these elements, three symmetry planes appear at the same time. This form of symmetry is realized for instance in several *Pennate Diatoms*, as in *Plagiogramma elongatum* (fig. 13).

Figures having the same symmetry elements, and therefore the same distribution of their equal parts, are said to form together a symmetry class. The 32 symmetry classes of crystals are to be understood in this way; these classes are, however, not specific for crystals, but they are common to all three-dimensionally infinite figures.

In the same way the possible classes of finite figures may be registered; their number is, however, much greater and even endless, on account of the fact that rotation axes in these figures may have any repetition number.

A general survey of types, or groups of classes, was given in 1917 by JAEGER, who distinguishes between 14 types without, and 7 groups with isotropous axes (1917, p. 73 and 88).

Of course figures belonging to the same class of symmetry may have entirely different forms; nobody has any difficulty in distinguishing between a lobster and a turtle or between a primrose flower and a starfish.

§ 11. **Organic symmetry compared with symmetry in inorganic nature.**

The phenomena of both organic and inorganic symmetry have one most important feature in common which distinguishes them from mathematical symmetry; the occurrence of every symmetry element in nature is due to the previous action of natural causes; it is the outcome of actual processes, whereas in mathematics neither causes nor events exist, the lordly will of the mathematician determining all the elements of any figure.

Another common feature of all symmetry forms in nature is that they are all subject to, and therefore in agreement with, the mathematical laws of symmetry, which embraces all symmetry forms possible in space. Accordingly, the differences in symmetry of natural objects are either gradual, the realization of the symmetry being more or less accurate, or they are due to the fact that different symmetry classes are approximated.

In our discussion we shall first deal with the comparison which is most important for our purposes, *i.e.* that of organic symmetry with crystal symmetry; in the second place organic symmetry will be compared with that of physical phenomena.

A. Comparison with symmetry in crystals. The differences in symmetry between organisms and crystals may be brought under the following four groups:

1. *Symmetry axes in organisms may have any number of repetition; in crystals this number n can only be 2, 3, 4 or 6.*

Especially the lack of quinary axes in crystals, and their more or less predominant occurrence both in the animal and the vegetable kingdom, are facts at which the old morphologists have often wondered (FREY, 1926, p. 97).

It is clear, however, that the difference is only the expression of the fact that the symmetry of organisms is that of finite figures, whereas that of crystals is based on the features of infinite space-lattices.

The only biologist who, to my knowledge, ever touched upon this fundamental truth, is FREY (l.c.) who rightly added that the difference is not an essential one between organic and inorganic matter, but that it is nothing but the outcome of a different mode of distribution of equal parts. The same symmetry as found in crystals may accordingly be observed in organisms if the distribution of equal parts changes.

However, FREY made the mistake that he took continuous space-filling as the condition for crystal symmetry, instead of the occurrence of a space-lattice. Hence of the two instances alleged by FREY one was wrongly chosen, namely that of the fruit-bearing capitulum of *Helianthus*. For the contact between the achenes is immaterial for the symmetry of the system, and the capitulum with the scattered arrangement of the bracts has no symmetry element whatever. And his other instance, the comb of the honey bee is formally quite right, its equal cells being regularly added one by one in the way of two combined net-planes with a ternary symmetry axis, perpendicular to the planes. An obvious biological remark is, however, that the comb is no organism, but a fabric, in the same way as our industrial wares.

In view of the importance of the question it is worth while therefore to quote better instances.

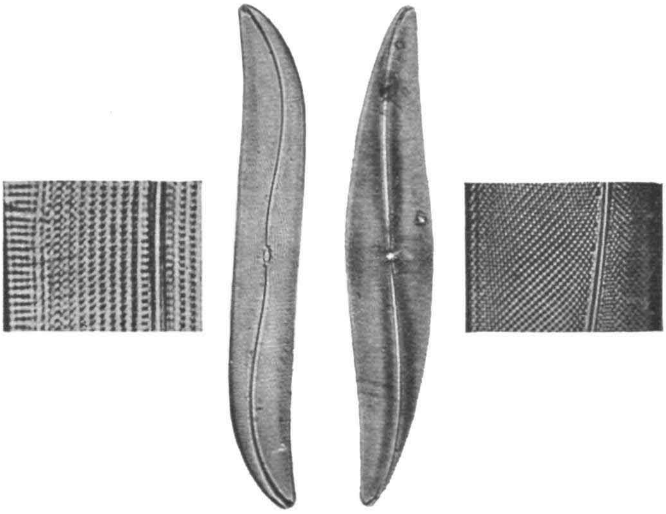

Fig. 18. A. *Gyrosigma balticum*. Valve, the areolation higher magnified.
B. *Eupleurosigma*. Valve, the areolation higher magnified. (Collection KINKER).

These may be found in a convincing form in the well-known sculpturing of the frustules of *Pleurosigma*, a sculpturing which occupies the major part of the valves on both sides of the raphe and which consists of a great number of equidistant transverse rows of small puncta or alveoli.

These alveoli are equidistant in the rows also, and the mode of junction of the alveoli in the adjacent rows is strictly determined too, the patterns are to be considered, as parts of infinite and regular net-planes, having a binary symmetry axis as indicated in § 10 sub A (fig. 14).

Now the vast genus *Pleurosigma* contains two sharply distinguished subgenera, which are sometimes even considered as distinct genera: *Gyrosigma* (fig. 18, A) and *Eupleurosigma* (fig. 18, B) which differ exactly in the mode of junction of the rows of alveoli. As CLEVE puts it, *Eupleurosigma* is characterized by "small puncta disposed in transverse and oblique rows. No longitudinal lines" (1895, p. 32) and *Gyrosigma* by "puncta disposed in transverse and longitudinal rows" (l.c. p. 112).

In other terms, the alveoles of adjacent transverse rows alternate in *Eupleurosigma* (the value c in fig. 14 being $= \frac{1}{2}a$), whereas they are superposed in *Gyrosigma* ($c = 0$).

In *Eupleurosigma* the binary axis accordingly may become quaternary (for $b = \frac{1}{2}a$) or senary (for $b = \frac{1}{2}a\sqrt{3}$), whereas in *Gyrosigma* it can only become quaternary (for $b = a$), but not senary as the condition $c = \frac{1}{2}a$ is not to be realized there. And as in both subgenera the relation $a : b$ varies freely, all these conditions and no other are met in nature.

The fact that only one kind of symmetry axes in infinite figures, the ternary axes, is lacking in these objects, is moreover wholly accounted for by the circumstance, recognized above in § 10, that a system with a ternary rotation axis can never be the result of a homogeneous combination of rows of equidistant points.

At any rate these few instances are undeniable proof of the existence of infinite symmetry in organisms; of course the question why, with a very few exceptions, organic symmetry bears a finite character, will be considered below.

2. *The repetition number n of a rotation axis in an organism is not always the same, but may vary in two different ways, both of which are unparalleled in crystals.*

In the first place we have the wide-spread so-called meristic variation, *i.e.* the fact that the usual number of repetition may be replaced in organisms by a higher or a lower number. Occasionally a star-fish may have four arms, and a rose six petals, instead of only five.

In the second place the same axis may have different values for n in the different parts of its course. As a striking instance we may quote the shoot of *Equisetum Telmateia* described by CHURCH with the following numbers of leaves at the successive internodes: 11, 13, 14, 17, 20, 20, 22, 24, 27, 28, 29, 30, 29, 30, 26, 26, 26, 23, 23, 21, 19, 16, 14, 12, 10, 8, 6, 6, 4, 3 (1904, p. 147).

Evidently this difference from what we find in crystals is related to a notable difference in the causes which bring about the symmetry in both domains, and especially to the lack of a general space-lattice throughout the living protoplasm.

3. *Symmetry elements in organisms occupy fixed positions; in crystals only their directions are determined.*

Remarkably enough this difference seems never to have been remarked in literature; it clearly depends on the features of finite figures, the surface of which are subject to the symmetry rules, and on those of infinite figures, which theoretically have no surfaces at all, their practical limits being always incidental.

In fact any fragment of a crystal contains all the symmetry elements.

In organisms on the other hand the symmetry nearly always contains the outer boundaries of the body too, and hence the symmetry elements occupy fixed positions. In a longitudinal section of a root tip for instance there is only one, the median, section which contains the axis.

It is only in the rare cases of minor details, arranged symmetrically in a certain area, without regard to the boundaries of the whole, such as we met in the alveoli of *Pleurosigma*, that the symmetry elements have no fixed positions, but only fixed directions.

4. *Symmetry is realized to a much greater perfection in crystals than in organisms.*

In an oak leaf the individual lobes of the right and the left side do not correspond in size or in position; both halves of a leaf are only built after the same plan in a general way, not in details. Analogous conditions, though often on a smaller scale, are always found in organisms; the capillary veins of our right and left little finger do not correspond to each other one by one, and so on.

As remarked above, this difference does not pertain to the class of symmetry to which an organism belongs, but to its realization; it has of course to be accounted for by features of the morphogenetic forces.

FREY writes about this topic: "Die Prinzipien der Drehung, Spiegelung usw. liefern in der Biologie keine Symmetriegesetze, sondern nur allgemeine Richtlinien, nach denen die Anordnung gleichwertige Elemente erfolgt. In der Mineralogie dagegen, wo die geometrische Symmetriebetrachtung in der Strukturlehre der Kristalle die grösste Bedeutung erlangt hat, erweisen sich alle Symmetriebeziehungen als gesetzmässig. Dies rührt daher, weil dort die distinkten Punkte, deren gesetzmässige gegenseitige Lage studiert wird, den Raum lückenlos erfüllen. Die lückenlose Raumerfüllung is die notwendige Bedingung dafür, dass Symmetriegesetze auftreten" (1926, p. 96).

These views are not to be accepted, as there is no direct relation between space-filling and symmetry. The only fact is that, if symmetry is realized, any symmetrical form may occur in finite figures whereas in infinite figures, and accordingly in space-lattices, a restricted number of symmetry classes is only possible.

Further we may remark that the symmetry of crystals, notwithstanding the astonishing degree of accuracy which it presents to our observation is no more rigorously realized in the mathematical sense than organic symmetry. Perhaps no crystal will ever be free from the inclusion of some alien atoms, which of course destroys all real symmetry, and even if it were free from such alien parts, the movements of its atoms and of the constituent parts of the latter clash at any rate with the requirements of mathematical symmetry.

Beyond these four points of difference a fifth has been described by CROW, who wrote (1928, p. 208): "The most noticeable difference between symmetry in the living and in the non-living is that whereas the latter only involves figures bounded by plane surfaces, the forms of organs and organisms, *i.e.* of living things and their parts, introduce numerous curved surfaces."

This undeniable fact does not pertain to our topic, however, as symmetry is not concerned with actual shape. A globular antheridium of *Chara* with its eight octants has the same symmetry elements as an Egyptian pyramid, namely a heteropolar quaternary rotation axis and four symmetry planes; and an orange with eight pegs belongs to the same symmetry class as an eight-sided chinese pagoda.

Moreover crystals are not always bounded by plane surfaces. The fact is that theoretically infinite space-lattices, having to be discontinued somewhere in this finite planet, may get an irregular boundary, as for instance, any rough diamonds do. In other cases, under favourable conditions of growth, crystals may "develop" their characteristic faces, being planes of the space-lattice. During its growth a crystal often changes its form by the appearance of new or the disappearance of existing faces. Conversely organisms may form more or less plane faces, as for instance the adaxial side of many leaves.

Of course the fact that, on the whole, the organisms have curved surfaces, has to be accounted for by the features of the morphogenetic forces. This will be discussed in § 12.

B. Comparison with symmetry in non-crystalline matter. In those cases in which physical bodies and physical phenomena exhibit symmetry elements, it is often possible to understand to some degree the causes underlying the symmetry.

As such a group of forms we may mention all phenomena due to an emission of forces, or of matter, from a centre. The circular ripple of the water caused by the fall of a stone into a pond, is an instance of a form with a single isotropous symmetry axis, and the spherical emission front of light from a source of light is one with an infinite number of isotropous axes.

Other cases are the bodies the form of which is determined by surface tension, being spherical, as small raindrops or soap bubbles, or being flattened spheres as small oil drops floating on water; related forms are heavenly bodies which are either spherical under the influence of gravity, or rotation ellipsoids under the combined influence of gravity and centrifugal force.

These instances are all finite forms with isotropous axes; of finite forms with non-isotropous axes two other instances may be quoted, namely that of the chambers in a froth and that of basaltic columns. In these two cases the causes of symmetry are different. In the froth the form and the arrangement of chambers are due to surface tension. As was shown recently by S. T. Bok (1940) in those froths in which the chambers differ greatly in size their shape is more or less globular, the smaller elements finding room between the larger globes; if on the other hand the chambers are about equal in size they have to assume the shape of pentagonal dodecahedra, with slight curvatures of the walls so as to allow of a space filling.

The arrangement of basaltic columns on the other hand is not determined by surface tension. The splits in the rock on cooling are due to a shrinking tension of the outer layers, and they are all formed in the direction of the temperature gradient, but otherwise without any regularity, the origin of any split being independent of the places of other splits.

As, however, any split by its appearance removes temporarily and locally the shrinking tension, their distribution in course of time must become more or less even, though not symmetrical, and as they all extend until they meet other splits, the outcome is that prismatic bodies are formed, with a varying number of sides of unequal breadth. In nature the columns are reported to have from 3 to 9 sides, those with 5 or 6 sides being rather frequent. Those which accidentally have about equal sides, form of course an approach to the symmetry of a quinary or senary rotation axis, but not the slightest approach is made to an infinite symmetry pattern.

These two instances are in so far important for us as they illustrate the fact that for the origin of a general symmetry in a large collection of elements a common cause ruling the distribution is required.

§ 12. Considerations in literature about the causal basis of organic symmetry.

It is a curious fact that the problem of the causal basis of organic symmetry has hardly ever been raised in literature.

The old morphologists contented themselves, as might have been expected, with assuming a tendency to symmetry in living matter, without discussing origin and nature of such a tendency.

As an instance von MOHL may be quoted, who wrote in 1845 on: "den grossen und weit verbreiteten Einfluss des Strebens nach Symmetrie auf die Form" and on: "den Kampf, in welchem dieses Streben nach Symmetrie mit der durch die spiralförmige Stellung der Blätter erzeugten Neigung zu regelmässiger concentrischer (radially symmetrical) Ausbildung der Pflanzen steht" (p. 26).

After the gradual development of biomorphology as a natural science some authors felt the urgency of a physiological explanation, though other authors continued to be satisfied with the assumption of a tendency to symmetry.

GOEBEL for instance, even in the last edition of his Organography, wrote about "zweifellos innere Symmetrieverhältnisse des Vegetationspunktes . . . welche für die Anordnung der seitlichen Organe massgebend sind" (1928, p. 253) and these views have been adhered to up to the present day by several of his followers. Whether these inner causes are material or not, is not indicated, but at any rate we can hardly call this an explanation.

And in a paper by LEWIS of 1923 we read the rather vague statement: "Symmetry in organisms is presumably the result of various tension diffusions, effects of gravity and other physical causes", but this is followed by the enouncement that: "From the preponderance of symmetrical forms in nature, it may be assumed that there is a special tendency to produce them." (p. 7).

In this respect a far more preferable point of view is taken by THOMPSON, who wrote in 1917 1) that the assumption of an inner determinant, a "Gestaltungstrieb", would be of infinite help to us if we might postulate it in the explanation of organic symmetry, but that it does not follow by any means that the morphogenetic forces in question are not essentially physical forces (1917, p. 486; 1942, p. 732).

Among the authors feeling the urgency of a physiological explanation and endeavouring to indicate the way to find it, we may mention in the first place those who hoped to derive it from the molecular constitution of the protoplasm. CHURCH for instance wrote in 1920 that: "the study of Formal Morphology may be regarded as that of the .... directive effect of living matter following the laws of Geometry; the ultimate expression of which may again come under the head of molecular arrangements and groupings, with the laws which determine them" (p. 5), and following this line and thought CROW wrote: "It is, therefore, possible to infer as CHURCH has already done in his work on leaf arrangement a molecular protoplasmic basis or correlate for the phenomena of organic symmetry, just as the facts of crystal symmetry are found to depend on or to be correlated with the special features of the first fine structure of solids elucidated by means of the Röntgen rays." (1928, p. 209).

After what we found in § 10 above it is clear that these views are to be discarded; indeed if organic symmetry should have been based on a regular arrangement of protoplasmic molecules, the symmetry features of organisms should have been those of infinite, and not those of finite figures. Here again THOMPSON is on the right track in refraining from an explanation of organic symmetry by the assumption of a space-lattice, exactly on account of the fact that after HAECKEL's observation certain Radiolaria have the form of a regular pentagonal dodecahedron, a form to which the space-lattice theory would be inapplicable. His conclusion is therefore that "symmetry of crystallization ... has no close parallel, but only a series of analogies, in the protoplasmic symmetry of the living cell". (1917, p. 486; 1942, p. 732).

Quite another explanation in which the form of molecules plays a rôle may be mentioned for curiosity's sake: in 1939 RASHEVSKY gave a suggestion for the origin of dorsiventral organisms and for "bilateral assym-

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1) The second edition was published in 1942 after the death of SCHOUTE. Some words of the citations are altered in the second edition, but the ideas of THOMSON, mentioned by SCHOUTE, have remained the same.

metry" (sic), starting from the idea that enantiotropic molecules should be present, shifting under the influence of an electric field either to the right or to the left side of the body according to their steric configuration. In those cases in which the mixture of these molecules is a racemic one, the body becomes dorsiventral, but if one of the two enantiotropic forms prevails, the corresponding half of the body will grow stronger. (p. 200).

No doubt RASHEVSKY is right in calling these views "purely abstract speculations".

The only author giving noteworthy suggestions about a possible causal basis of organic symmetry is, as far as I know, once more THOMPSON. In his chapter on the forms of cells he writes the following about the influence which surface tension may have on the form of protoplasm: "Among the forces which determine the forms of cells, whether they may be solitary or arranged in contact with one another, this force of surface tension is certainly of great, and is probably of paramount importance" (1917, p. 205; 1942, p. 351).

He points out that by this force the form of a drop or a bubble is ruled, and he is inclined to assume a direct connection between surface tension and organic symmetry, as is expressed in the following sentences: "In all cases where the principle of maxima and minima comes into play, as it conspicuously does in the systems of liquid films which are governed by the laws of surface tension, the figures and conformations produced are characterized by obvious and remarkable symmetry. Such symmetry is in a high degree characteristic of organic forms, and is rarely absent in living things, save in such cases as *Amoeba,* where the equilibrium on which symmetry depends is likewise lacking. And if we ask what physical equilibrium has to do with formal symmetry and regularity, the reason is not far to seek; nor can it be put better than in the following words of MACH's: " "In every symmetrical system every deformation that tends to destroy the symmetry is complemented by an equal and opposite deformation that tends to restore it. In each deformation positive and negative work is done. One condition, therefore, though not an absolute sufficient one, that a maximum or minimum of work corresponds to the form of equilibrium, is thus supplied by symmetry. Regularity is successive symmetry; there is no reason therefore, to be astonished that the forms of equilibrium are often symmetrical and regular." " (1917, p. 209; 1942, p. 357).

Now it is a fact that in some cases a symmetrical form in an organism is really due to surface tension. Eight ovules of *Fucus,* developed in one oogonium by partition of the mother cell, each assume a spherical shape on becoming free, though beforehand their form was rather irregular. The symmetry of these ovules therefore rises with a sudden leap from a low grade, if any, to the highest possible grade, by the action of surface tension only.

THOMPSON remarks further that other, non-spherical forms may be the outcome of local changes of the surface tension, a lowering of the tension allowing the turgor to bring about a local extension of the cell. The budding of the yeast cell is described as an instance, and is considered to occur "because at a certain part of the cell-surface the surface tension has more or less suddenly diminished". (1917, p. 213; 1942, p. 363).

Against this view it might be remarked that there is no proof of the thesis that the budding is initiated by a local change in surface tension: it might be just as well that in the protoplasm local growth develops much stronger expansion forces than elsewhere so that locally the surface tension is easily overcome.

But even if THOMPSON were right in the assumption that change in surface tension is the first stage in any outgrowth, this would not touch the very centre of the great problem of the causes of organic symmetry. For it would still remain a mystery why these local changes in surface tension should occur in a symmetrical way. Why should for instance numerous limbs of animals arise always in exactly corresponding places of right and left sides, and why should they develop corresponding organisations there?

The real importance of surface tension for the problem of organic symmetry is that it can explain why certain initial stages of organisms as spores and zygotes may have a spherical shape, but it does not go further, the real problem remaining that of the regular distribution of equal parts.

Now as these equal parts in organisms are all formed by growth and by differentiation, and their distribution is the effect of their ontogeny, the causes of organic symmetry must ly hidden in these ontogenetical processes.

It is clear, of course, that growth alone, without differentiation can never be a cause of symmetry. Homogeneous growth, if it were to occur in organisms, cannot even produce a new form, let alone new symmetry, it only increases the size of an existing form. Only heterogenity of growth creates new forms; growth in itself provides the necessary protoplasmic substratum.

The causes of organic symmetry must therefore be found in the processes ruling the distribution of the local processes of differentiation, of growth localization and of growth polarization, distinguished above in § 4, and as we recognized already that the processes are usually concatenated by physiological processes, which in their entirety we have called the fundamental plan, we may say that the symmetry has to be the consequence of the features of that fundamental plan.

In endeavouring to defend this thesis we have to acknowledge that hardly anything is known about the physiological processes of the fundamental plan. In many cases we have some knowledge about the hereditary transmission of the genes which are to be considered as the realisation of these processes, but what we know about the processes themselves is extremely meagre. In some cases we know that a certain organic compound is involved in it, that such a substance is indispensable for it, and that, if artificially introduced, the corresponding processes are brought about, but this is not yet equivalent to a knowledge of the vital process itself.

But that a complete and physiological analysis is not available, does not mean that we cannot get some notion about the general trend of the forces bringing about the regular distribution and indeed a morphological analysis of the final results may sometimes enable us to draw important conclusions about the morphogenesis.

However, all attempts in literature to give a solution of our problem, to find the causes of organic symmetry, have been in vain. Therefore a fresh endeavour will be made in the next paragraph.

* § 13. New considerations about the causal basis of organic symmetry.

In the foregoing paragraph we recognized that though surface tension must be responsable for a minor part of the organic symmetry, the chief part of it must be due to other causes and from what has been advanced in § 6 we understand that organic symmetry is largely a feature of the fundamental plan.

Indeed the directly inherited structures of organisms, if they are symmetrical at all, owe this for the greater part to surface tension, as vacuoles or plastids, but the main question of the origin of organic symmetry must be why newly formed organs are distributed in a symmetrical way.

In numerous cases we know that these organs are laid down from the beginning in a symmetrical order, as for instance the limbs of animals, but we know just as well of rearrangements which may bring about symmetry. In *Amphioxus* for instance the mouth which lies in het median plan in the adult, is laid down at the left side, representing originally, according to some investigators, the left ear.

Our problem is therefore a double one: why the original places are often distributed symmetrically, and why rearrangements may often be exactly of such a nature as to bring about symmetry; the answer to both questions has to be sought in a study of the fundamental plan.

In our § 6 we recognized that biological axes play an important rôle in the elaboration of most fundamental plans; accordingly the present § 13 will be divided in three parts: A. On symmetry in organisms without biological axes. B. On symmetry in organisms with biological axes. C. Final considerations.

A. Symmetry in organisms without biological axes. Organisms without any biological axis are always of a simple structure and usually small; often they are more or less spherical by surface tension, as the zygote of *Fucus*. Instances of larger size are the plasmodia of *Myxomycetes*, which by their amoeboid movements are lacking all symmetry.

A striking symmetry, not due to surface tension, may be present as soon as in the organism a number of local organs is formed, which are distributed in a regular way, and as we meet here our problem in a very simple form, it is worth while to consider it with every attention.

In the first place we shall return to the pollen grains without a biological axis already discussed in § 6 (see fig. 2 and 3). For the little spines of *Cucurbita* (fig. 2) we found that no symmetry was present, a certain evenness of distribution being due to the fact of the uniform spreading of the pertaining gene substance(s) and the small size of the localized reactions of the protoplasm. Accordingly this unsymmetrical distribution presents no difficulties. For the places of exit the case is different, however; here an unmistakable symmetry may be attained. In fig. 19 we reproduce two pollen grains of *Corydalis* (= *Fumaria*) *capreolata* from von MOHL's admirable work of 1834. One grain has 12 pores placed according to the faces of a rhombic dodecahedron, the other 6 according to the faces of a cube. Here a remarkable symmetry is therefore attained. However, what von MOHL does not mention is that these two forms had been selected exactly for their symmetry. TAMMES, investigating the same species more than a century later, reports that on 200 grains the distribution of the number of pores was found to be:

pores:	6	7	8	9	10	11	12
frequency:	125	6	29	5	3	2	30

The grains with 7, 9, 10 or 11 pores showed no symmetry at all. Yet the pores were not distributed in the same irregular way as the spines mentioned above, or as the plant hairs which in their distribution lack all symmetry, but, and this is characteristic for pollen grains in other species too, the minimum distances between the pores were always about equal. So we had a certain rule, but no symmetry.

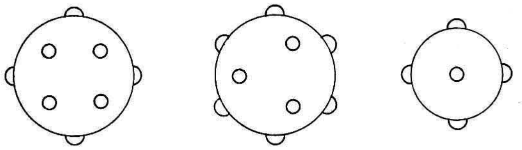

Fig. 19. *Corydalis (Fumaria) capreolata.* Two pollen grains, one with 12 (A and B) another with 6 (C) places of exit. From VON MOHL, 1834, pl. IV, fig. 5.

In grains with 8 or 12 places of exit the symmetry was moreover variable: 8 pores were either arranged according to the faces of an octahedron, or of a tetrahedral trapezohedron, and 12 pores according to the faces of a rhombic or a pentagonal dodecahedron.

These facts may be explained in a very simple way if we suppose that the localization of the pore formation are placed originally more or less evenly, by the fact that each of them absorbs the pertaining gene substance from their area, but that, moreover, by mutual repulsing forces a much higher degree of symmetry is attained in these cases in which the number of pores allows it.

The probability of these suppositions is still increased by the following facts. First TAMMES describes that, in this and other species, the number of pores is correlated with the size of the grains. So he comes to the conclusion that a place of exit is not formed before a certain space is cleared for it on the surface, and that the number of pores therefore depends only on the extent of the available space, the minimum distance of the pores indicating the diameter of these required areas.

Secondly TAMMES shows that the curious distribution of frequencies, with its tops on 6, 8 and 12, is in harmony with his view, on account of the irregular way in which the possible number of equal and touching circles on a sphere increases with the diameter of the sphere. (1930, p. 68).

The predominance of the numbers 6, 8 and 12 is therefore not limited to *Fumaria capreolata*. In the long lists given by FISCHER (1930) of pollen forms in various plants we find for plants with pores all over the surface, that in most species the number is variable, and that between 4 and 15 all indications of the variability are such as 4—8, 6—8, about 8, 8—10, 10—12 or about 12, in which the said numbers largely prevail.

As, however, no regular polyhedra exist with more than 20 sides or 30 ribs, it is clear that pollen grains with more than 30 pores never have more than a certain regularity, but no true symmetry.

In fact the seeming regularity, due to the constancy of the minimum distances between the pores can be a very striking one. TAMMES gives a photo of a grain of *Ipomoea purpurea* (our fig. 20) in which some pores are surrounded by 5, others by 6 other pores; yet the arrangement is rather regular. And similar conditions are met in the excellent drawings made by von MOHL by means of a mirror. 1)

In those pollen grains in which the pores are distributed symmetrically, it is of course possible to indicate a number of symmetry elements. In a grain like that in fig. 6,1, A, we have three quaternary and four ternary symmetry axes, 9 symmetry planes and a symmetry centre. At the same time it is clear, however, that such symmetry elements have only a mathematical, not a biological character, as there is nothing in the living body which is particularly related to them, and as they are lacking in quite similar grains of a slightly different size, grains which are in no way inferior or less viable: it is the regularity of the distances between the pores which is due to biological causes, not the symmetry.

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1) It is only in free-hand drawings of other authors, in which ornamentations had been filled in arbitrarily, that this law, being not known to the author, has been disregarded. The worst example in this respect is probably E. HAECKEL, who in quite other objects — the Radiolarians — but which are subject to the same stereometrical laws, pictured several spherical organisms (1862, pl. 9 fig. 1–5; 10 fig. 1–3; 13 fig. 7; 14 fig. 3, 5; 24 fig. 1), all having a uniformly extending hexagonal ornamentation all over the surface, as in our figure 21. Mathematically speaking, these drawings represent monstra.

B. Symmetry in organisms with a biological axis. Fig. 22 represents a *Centric Diatom* inserted in the collection KINKER

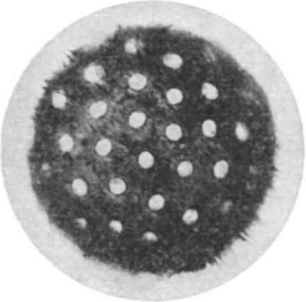

Fig. 20. *Ipomoea purpurea,* pollen grain. From TAMMES, 1930, pl. 1.

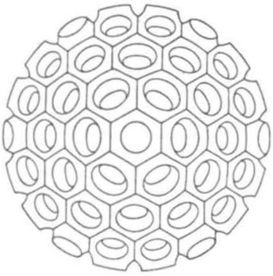

Fig. 21. *Ethmosphaera siphonophora.* Surface view of the silicious skeleton. From HAECKEL, 1866, pl. 2, fig. 16.

under the name *Melosira selecta,* a form with an isopolar growth axis. The valves show a great number of alveoles, united in short and winding rows, filling up the central area in an even, but wholly asymmetrical way. The morphogenetic processes for these alveoles must have been concatenated in some way or other, or probably the rows are laid down first as continuous stripes, in which by a second process the alveoles are formed. The only influence of the axis on these rows is that the space allowed to them is a circular one around the axis.

Fig. 22. *Melosira selecta.* Surface view of valve. (Coll. KINKER).

Similar rows of alveoles are found in many other *Centric Diatoms,* and in many cases these rows show a radial arrangement, at least in the peripherical part of the valve. In fig. 23 of *Stictodiscus Truani* this is very conspicuous, though the rows are very short; in fig. 24 of *Coscinodiscus nitidus* and in fig. 1 of *Stictodiscus Buryanus* they are much longer, and in fig. 25 of *Coscinodiscus* sp. they extend as far as the centre. Obviously the rows are laid down here centripetally, starting from the margin of the valve.

In the two last mentioned objects there is moreover a new regularity in the arrangement of the alveoles which is lacking in fig. 23; the alveoles of adjacent rows are in those figures alternating, so that "parastichies" in both directions may be observed. This result must be due to mutual influences between the local activations for the alveoles in the adjacent rows; a complication by which a better proximation to symmetry is attained.

Finally in our figure 26 of *Coscinodiscus lineatus* the symmetry is again much more perfect on account of the fact that the rows are arranged in hexagonal pattern, an infinite symmetry system therefore.

Fig. 23. *Stictodiscus Truani.* Surface view of valve. (Coll. KINKER).

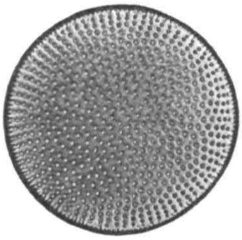

Fig. 24. *Coscinodiscus nitidus.* Surface view of valve. (Coll. KINKER).

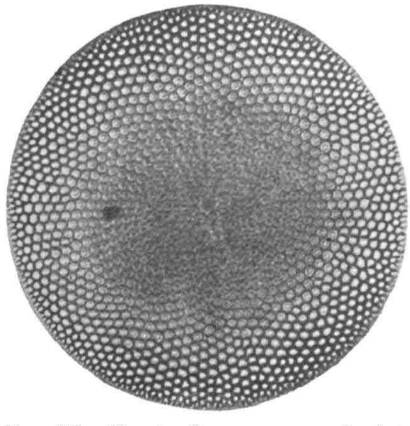

Fig. 25. *Coscinodiscus spec.* Surface view of valve. (Coll. KINKER).

Fig. 26. *Coscinodiscus lineatus.* Surface view of valve. (Coll. KINKER).

Here again we get the impression that the symmetrical distribution itself of the local activations of morphogenetic factors is never controlled by special physiological processes, but that it is the combined action of a number of processes which brings about the fundamental plan, and with it all relations and regularities which under given circumstances may lead to a certain approximate symmetry.

This agrees with the general experience of taxonomists that symmetry itself is not always of great systematical value; dorsiventral flowers and peloria may arise on the same plant, and in the natural group of Diatoms almost all classes of organic symmetry are represented.

From the instances given above of organisms of different groups without and with biological axes, we get the same impressions: localizations of growth may be influenced by each other, but this is not necessary and similar localizations may have different influences simultaneously. If the localizations are not similar and not at the same time, the influences are also different, but in this case often the large localizations determine the place of the small ones. The biological axes are only instances of this last case on a large scale.

Now it must be possible to explain the different aspects of organic symmetry. It is already clear for the organisms without biological axes. In the following part of this paragraph we shall try to explain it also for the organisms with biological axes.

From the above considerations and from those of § 6, B, it follows that biological axes are by no means identical with mathematical symmetry axes, and the use of the same word axis in both conceptions might even be criticized.

But as the term axis in biology is older, and is in common use, though in a more general sense than above, and as its use in mathematics is a derived one, the original meaning of axis being axle, no new term will be introduced here, but we shall only point out the differences between the two conceptions.

As we recognized already, biological axes may at the same time be symmetry axes, as in *Aulacodiscus*. Yet, properly speaking, there is only an approximation of the biological axis to the features of a symmetry axis, but never an indentity. The biological axes, being due to physiological processes, can never be perfect, and a mathematical axis, as existing only in the imagination, is always perfect.

In many other cases biological axes, however, have essential features which are either alien, or even contradictory, to the nature of symmetry axes.

Alien to the nature of a mathematical symmetry axis is the torsion found in some biological growth axes. The stem of the Characeae for instance is not only always twisted, but on elongating it rotates the free tip (GIESENHAGEN, 1897, p. 164). Now a mathematical axis, even if it is a screw axis, can never be subject to torsion itself.

As incomptabile with the character of symmetry axes we have to mention two features, namely curvatures of the biological axes, and a lack of symmetrical repetition of equal parts along or around them.

Curvatures of biological axes are indeed rather frequent, and they may be of various descriptions. Several examples will be given in § 15—17, but here it may suffice to recall the lunular cells of many *Closterium* spp. with a growth axis in the shape of an arc of a circle, and of that of the genus *Eucampia* (fig. 27) where the growth axis is a screw line.

The mathematical theory of symmetry is not able to deal with curved axes; in the lunular *Closterium* it can only consider a dimerous symmetry axis which is perpendicular to the growth axis and lies in the same plane as the arc of a circle; and in *Eucampia* it describes a screw axis passing through the centre of the coils of the screw and touching no cell anywhere.

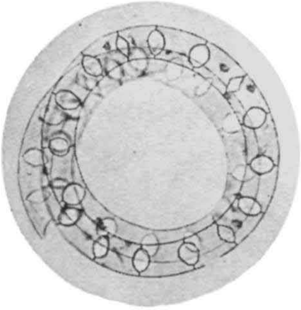

Fig. 27. *Eucampia zodiacus.* The individuals form a screw line. (Coll. KINKER).

Biological axes without symmetrical repetition of equal parts around of along them, are, for instance, present in all dorsiventral organs; a dorsiventral flower may illustrate this. In such a flower the main biological axis passes through the pedicel and the thalamus. But as the anterior and the posterior flanks of the flower are differentiated in different ways, we have to turn the flower around this axis over 360° in order to get it in a corresponding position. In other terms, this finite axis is no rotation axis.

As biological axes control the arrangement of the principal local differentiations, they cannot only form approximations to symmetry axes, but they can moreover bring about approximations to symmetry planes.

Any organism with an isopolar biological axis has of course a symmetry plane perpendicular to this axis, and both iso- and heteropolar biological axes bring about an infinite number of symmetry planes passing through the axis, if there are no other activations or morphogenetic factors.

All such symmetry planes are mere mathematical consequences of the spatial relations, without biological importance of themselves.

The same conclusion holds more or less true for all other symmetry planes, as will be made clear by a discussion of the symmetry plane in dorsiventral organisms. In a dorsiventral flower of *Viola* for instance, we have to assume the activity of two heteropolar biological axes, one being the growth axis, the other being a differentiation axis at right angles to the first. The latter is due to the activation of two different sets of morphogenetic factors at the anterior and at the posterior side of the vegetative cone. Accordingly at the anterior and the posterior flanks all homologous floral parts develop differently, whereas those at the lateral sides are according to their position more or less exposed to the influence of the one or the other of these sets.

By such a distribution of four poles, the right and the left side of the region have to become each other's mirror-image, as may be demonstrated as follows:

Be in fig. 28,1 the line AB a heteropolar biological axis, the heteropolarity of which is indicated by its black and white ends. If in an organism with such an axis there should be no other local activations of morphogenetic factors, the body would be constructed similarly at all sides of the axis, as is indicated by the circle around AB; and the same diagram may do for any organism with a radial symmetry, as all other local activations in it are dominated by the axis, and distributed either regularly around it by their own mutual influences, or in an irregular way if such mutual influences are lacking.

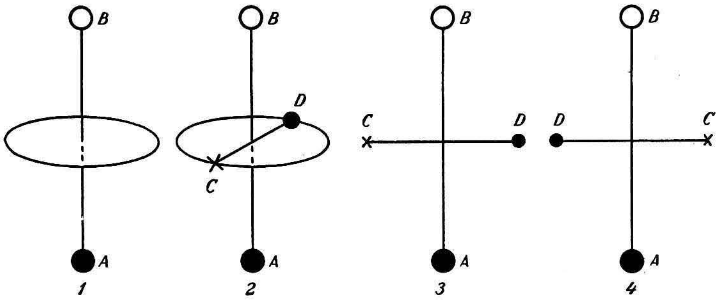

Fig. 28. Schematic representation of an organism with radial symmetry (1) and of another with dorsiventral symmetry (2). 3, 4. The symmetry plane of the latter (2) as seen from both sides. The heteropolarity of the axes is indicated by a black and a white circle at the poles, resp. by a crosslet and a black circlet. Original.

In fig. 28,2 a dorsiventral organism is represented in a similar way, the secondary axis being placed on the circle in the form of two additional poles C and D, which are indicated by a crosslet and a black circlet. In our instance, the dorsiventral flower, these two poles are extended by the longitudinal growth of the main axis into longitudinal lines, which are parallel to AB, but in any case the four poles fall in the same plane, by the mutual repulsing of C and D.

Viewed from either side this plane shows a different arrangement of the four poles, as represented in fig. 28,3 and 28,4: the two are not to be interchanged, as they are mirror-images. Now if we consider two other longitudinal planes, parallel to this one, and situated at equal distances from it at either side, the influence of the four poles differs in the latter from that in the middle one in degree, but not in reciprocal positions. All morphological features which are controlled by the four poles in the two lateral planes must therefore be arranged as in mirror-images, or in other terms, the middle plane is a biological symmetry plane.

The conception of biological axes, as given here, being quite natural, it might be asked why it has not been given earlier, by previous authors.

In fact we find that it has been vaguely felt and indicated by a few morphologists, but it has always been overgrown and suppressed by the mathematical notion of the symmetry axes.

One of these authors was the zoologist G. JÄGER who wrote in 1857 that the real difference between radial and dorsiventral symmetry consisted in the uniaxial character of the former and the biaxial character of the latter. His definition of an axis was the line connecting essientially different points, and from his rather clumsy further exposition it follows clearly that he had recognized one of the kinds of the biological axes, namely the differentiation axis. In radial organisms he found one axis of this description, the two other dimensions being isopolar and in dorsiventral organisms he saw two axes and one isopolar dimension.

His views were quoted and partially accepted by HAECKEL. In his own elaborate system of organic symmetry HAECKEL enounced, however, another conception of axis.

On the one hand he recognized the more important biological axes, even though they are no symmetry axes. He knew that most organisms possess a main axis, and that this axis may be curved; on the other hand he did not distinguish between these and mathematical axes. The result was a curious confusion.

In dorsiventral organisms for instance three axes are described, the main axis, one between the dorsal and the ventral side, and one between right and left. The two former are biological axes and do not exist in the mathematical theory; the third is a mathematical symmetry axis of the second order, which is not a biological axis.

Similar confusions are found in the work of several later biologists, especially in those of the followers of HAECKEL. This is due, no doubt, to the great impression the mathematical infallibility makes on every scientist.

The only instance of authors who took exception to the notion of mathematical axes in organisms seem to have been KLEINENBERG (1887) and especially SPENGEL (1905). The latter wrote (p. 643) that the assumed axes are stereometrical, not biological. The three axes which are supposed to exist in the human body should meet in a point but this point does not exist.

But as SPENGEL failed to replace the mathematical by a biological conception of the axes, he could not disentangle himself from the mathematical idea without biological meaning, and his conclusion was that an axis is only present in radial, and a symmetry plane in dorsiventral animals, the difference being due to the number of equal parts.

c. The main features of organic symmetry. In order to prove that the above views may afford a basis for a biological understanding of the phenomena of organic symmetry, a discussion of the main features of that symmetry will be given here. As such features we shall treat successively 1. the imperfect character of symmetry in organisms. 2. the frequent changes of symmetry in organisms. 3. the finite character of organic symmetry. 4. the almost universal occurrence of symmetry in organisms. 5. the dominance of a very few symmetry classes in organisms.

Before entering into these separate topics we may briefly remark that the curved surfaces presented by symmetrical organisms in which CROW saw the most important difference between symmetry in living and that in non-living matter (cf. § 11 sub A) are no longer a problem for us. Indeed all organic forms, whether symmetrical or not, are usually bounded by curved surfaces, a fact which may be due, at least for a part, to surface tension. And as organic symmetry is derived here from the distribution of material influences, emanating from distinct protoplasmic parts, there is no reason whatever to expect flat surfaces.

Fig. 29. *Urtica baccifera.* Contact print of leaf. From ETTINGHAUSEN, 1858, pl. 24, fig. 4.

1. *The imperfect character of organic symmetry.* As an instance of normal degree of perfection in its symmetry the leaf of *Urtica baccifera* may be taken, represented in fig. 29, being a reproduction of a contact print from nature. We see that neither the leaf teeth, nor the primary or secondary veins or the veinlets have the same distribution at both sides. The fourth primary vein at the left for instance is inserted on the midrib somewhat over the fifth vein on the right.

Symmetry in the mathematical sense of the word is therefore entirely absent. Yet no botanist will hesitate to call a leaf like this symmetrical, on account of its fair approximation to dorsiventrality. The actual condition may be described as follows: the two heteropolar biological axes, dominating the leaf architecture, are the growth axis extending between blade apex and leaf insertion and the differentiation axis between the abaxial and the adaxial side, the latter axis being controlled in its position by the heteropolar growth axis of the shoot.

The right and the left side of the leaf accordingly have to become mirror-images, as explained above, but this goes only so far as the right and left side of the blade are equal fields for the development of a number of different organs, as leaf teeth, veins and veinlets. In these two fields these organs develop by the same forces in a similar mode, but there are no factors bringing about a correspondence of any organ at the left side to a similar one of the right.

Of course there might be mutual interactions between right and left side, with the effect that the distribution is symmetrical, but the cases in which such interactions are lacking as they are here, are extremely numerous, and in all those cases its result is an arrangement which mathematically is clearly asymmetrical, but biologically is described as symmetrical.

Similar considerations might be inferred for organisms without biological axes. In the *Fucus* zygote for instance, the spherical symmetry as induced by surface tension goes only as far as this tension reaches, the distribution of the protoplasmic parts not being subject to it.

2. *The frequent changes of symmetry in organisms.* One of the most noticeable features of organic symmetry is its lack of stability.

In the first place we have the wide-spread meristic variation, amounting in a mathematical sense to the realization of forms belonging to different symmetry classes. Our fig. 30 of *Aulacodiscus* gives an instance.

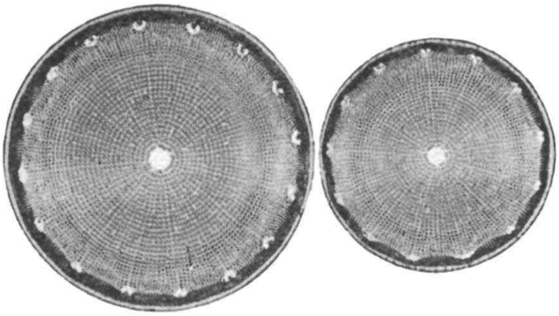

Fig. 30. *Aulacodiscus oreganus* f^a *sparsius punctata.* A with 16, B with 13 marginal spines (Coll. KINKER).

In the second place the same individual may successively assume different symmetrical forms, belonging to different groups. A zygote of *Echinus* has a spherical symmetry; the *Pluteus* larva developed from it, is dorsiventral, and the adult *Echinus* is radial. In the third place the different organs of the same individual may belong to different symmetry groups. The shoot of *Fumaria capreolata* is radial, its flowers are dorsiventral and the pollen grains have a spherical symmetry.

In the fourth place homologous organs of the same individual may sometimes show similar differences. The lateral flowers of the *Labiatae* are dorsiventral, but the peloria which develop in many species incidentally at the inflorescence apex, and even normally in *Mentha aquatica*, are radial (fig. 31, *Nepeta macrantha*).

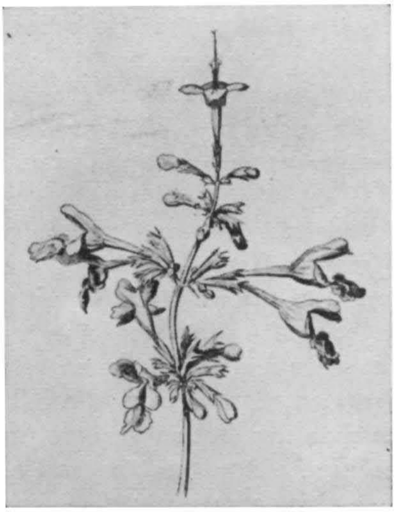

Fig. 31. *Nepeta macrantha*. Upper part of inflorescence with tetramerous pelory. From PEYRITSCH, 1878, pl. 6, p. 92.

In the fifth place we have to assume phylogenetical changes in the normal symmetry forms of organisms. The dorsiventrality of *Spatangus* is no doubt derived from a radial symmetry of a regular sea-urchin and a peloric race of *Linaria vulgaris* with nothing but radial flowers has sprung from the normal species with dorsiventral flowers.

Such a range of variation presents serious difficulties for any conception of organic symmetry as the outcome of the sub-microscopical structure of the protoplasm, or of the activity of special symmetry genes; it seems to indicate that organic symmetry is not nearly so deep-rooted in its subject as crystal symmetry.

On the other hand these phenomena fit in very well with the conception of organic symmetry as part of a fundamental plan. The meristic variation is explained by the assumption that the minor local activations require a more or less constant protoplasmic area, so that the changes in the symmetry of an individual during its development, and also the different symmetry forms of its various parts, are obviously due to the fact that the fundamental plan comes only gradually into action, different sets of morphogenetic factors being successively activated in different parts of the individual; the terminal peloria must become radially symmetric if the sets of factors for the second biological axis, which in lateral flowers is orientated with respect to the positions of subtending bract and parent shoot, are not activated at all by lack of these landmarks; and finally the phylogenetical changes are evidently brought about by changes in the hereditary output of the species, the result of which is a change in the nature or in the distribution of the morphogenetic factors.

3. *The preponderantly finite character of organic symmetry.* Though, as we saw, symmetry forms of infinite character may occur as rare exceptions, in the great majority of organisms no other than finite symmetry forms are met. Accordingly the symmetry elements in organisms have nearly always fixed positions and the symmetry axes are not in any way restricted in their repetition number *n*. This remarkable fact, for which no explanation has been given as yet, may be understood by the following considerations.

As we saw, organic symmetry is usually controlled by biological axes. Now these axes, if being differentation axes, are always of a finite character, as they are due to the reciprocal influences of two dominating localizations of morphogenetic factors. Accordingly the symmetry controlled by such axes must also have a finite character.

Growth axes and segmentation axes on the other hand have a one-dimensionnally infinite character. But as they are perpendicular to a finite cross section, they too have a fixed position and an unlimited repetition number. Moreover these axes occur rarely in the pure form as the growth axes in *Diatoms*. Usually they show at the same time the features of differentiation axes, as for instance the heteropolar growth axis in a root, or the segmentation axis in an earth-worm; these axes are therefore in every respect finite.

In organisms without biological axes the symmetry may be due to surface tension. This is again a finite symmetry, as being connected with surface form.

A third mode in which symmetry may arise is by the formation of a number of equal local activations with a regular distribution. Symmetrical forms of such an origin are also finite in character, unless the distribution of the equal parts is independent of the size of the field in which they are laid down.

In pollen grains, where the available area determines the number and the arrangement of the places of exit, the symmetry must therefore be finite; in *Pleurosigma* on the other hand where the distribution of the same alveoli is independent of the limits of the field, a symmetry of infinite character is actually realized.

Cases in which a number of subordinate organs are formed without any relation to the boundaries of the field are by no means rare; we may for instance point out plant hairs as organs which are formed at the surface of various organs, and, to give also an instance of a three-dimensionnal field, the formation of capillary vessels in the tissues of the vertebrate embryo. But in nearly all these cases the arrangement is wholly asymmetrical, only more or less even, just as the splits in the basaltic magma on cooling. To this fact we shell return below sub 4.

4. *The almost universal occurrence of symmetry in organisms.* The above considerations may perhaps have shown that *if* the different local activations of morphogenetic factors have such and such special features, and *if* they are concatenated in a definite way, symmetry of the organism may be the outcome, but they do not touch the question why the fundamental plan actually has in the great majority of organisms such properties, that a fair amount of symmetry is realized, at least in broad outlines.

Without a solution of this fundamental problem the only form of organic symmetry the origin of which is clear, is the spherical form due to surface tension, but all symmetry of the more complex forms would remain enigmatic as before.

Here we may advance two points of view, namely (a) that symmetry is often nothing but a lack of differentiation, and (b) that organic symmetry may often be furthered by natural selection.

(a). Similarity of parts representing a lower biological stage, and differentiation a higher one, many features of organic symmetry are simply to be taken as a lack of forces to realize further differentiation.

In support of this thesis we may first point out the circular form of many fairy rings of toadstools, if growing in a homogeneous soil. A mathematically high grade of symmetry is reached here in an incidental way.

Another striking case is afforded by peloric flowers, mentioned already above sub 2, where the inactivation, or the loss, of some morphogenetic factors increases the symmetry considerably.

The radial symmetry of a root, or of a stellate hair in *Malva*, are the direct outcome of this same lack of differentiation.

Above we mentioned the fact that all botanists usually call a leaf as pictured in fig. 29, dorsiventral, which implies the presence of a symmetry plane. This, for a mathematician inadmissable description is no doubt due to the (unconsciously) recognized absence of any differentiation between the two lateral sides. 1)

(b). As a rule all form features of organisms influence one or more vital functions, and those features on which symmetry is based make no exception. If this holds true, these features may be more or less perfectly adapted to those purposes, and it is therefore clear that natural selection, by wiping out all forms with a symmetry form — or without any symmetry — which are less fit for the struggle of life, may further some forms and check others, while a third group of forms will not be affected.

In those pollen grains in which the places of exit are formed all over the surface, we recognized already that a certain regularity was the outcome of the mutual repulsing forces, a regularity which under special bulk relations may incidentally pass into symmetry. The regularity is evidently of some biological interest, as it facilitates the germination of a grain at

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1) An other instance is the calyx of the rose, of which the biologist says that it is symmetrical, whereas there is mathematically no symmetry at all.

the side which is nearest to the stigma. But the symmetry itself is of no advantage.

This result may in a sense be extended to all cases of organic symmetry; wherever it occurs, it is not the symmetry itself that matters, but certain consequences of the approximation to symmetry.

The advantages of such an approximation may be of various descriptions, but for no group are they perhaps so evident as for freely moving dorsiventral animals. Indeed a bird with unequal wings, or a deer with a notable difference in strength of right and left limbs would clearly be at a great disadvantage.

Now it is the more remarkable that we know that the external symmetry in those animals is not simply due to lack of differentiation between right and left side. In the useful compilation by W. LUDWIG on the "Rechts-Links-Problem" (1932) an astonishing number of cases of true differences between right and left side is enumerated. The author introduces the term dissymmetry (perhaps better to be written dyssymmetry) for all secondary asymmetries in origininally dorsiventral bodies in consequence of an unequal differentiation of mirror-like parts (p. 387), and he brings long lists of these dyssymmetries in almost all groups of animals.

Indeed we get the impression that almost all dorsiventral animals have one or more organ systems whose structure essentially infringes upon the general dorsiventrality of the body. Yet in nearly all cases the body remains dorsiventral as seen from the outside; especially the organs for locomotion are not affected.

Even stronger: in such cases where the activity of different sets of morphogenetic factors at both sides might impair the locomotion, we see that by superimposed growth processes the appearance of symmetry is saved, of course it is theoretically only the shadow, not the substance which is saved, but physiologically this makes no difference.

A good instance is furnished by the Narwhal, in which the left canine tooth of the upper jaw is developed as a tusk and by an asymmetrical growth of the skull shifts to the median plane. Better than long reasoning this case shows that the fundamental plan, in passing through the sieve of natural selection, is impelled to provide for all the required features, those of a certain approximate symmetry included.

Now we may be sure that just as the appearance of symmetry is restored here, the original symmetry of so many organisms which is the effect of lack of differentiation, is often prevented from being disturbed by the same natural selection. This may be illustrated by the well-known fact that the right and left limbs of man are not quite equal, the right limbs being usually somewhat stronger and heavier (LUDWIG, 1932, p. 255, 262) and as VAN GIFFEN proved statistically in recent as well as in prehistoric cattle that the right humerus and the right femur are somewhat larger than the left partners (after researches not yet published). And as the right and left limbs themselves are not subject to any dyssymmetry, these small differences are probably due to the influence of one or more dyssymmetrical internal organ systems. These influences must be kept in narrow bounds by regulating processes, the biological importance of which is evident.

In other cases where the demands of locomotion are less urgent, a useful dyssymmetry of organ systems may be displayed openly, as for instance the unequal pincers in several large Decapod Crustaceans (LUDWIG, 1932, p. 202), and there where the dyssymmetry is no impediment but even useful, it may become most conspicuous, as in flat-fishes.

So far about the relation of symmetry forms to locomotion. Other symmetry features are connected with statics, with the equilibrium; these features seem to be less important, and no instances of supernumerary processes for the restoration of a disturbed equilibrium have come to my knowledge.

In the dorsiventral shoots of *Begonia* the sides of a leaf are very unequal; yet the leaf stalk bears the blade just as well. And in the radial shoots of *Musa* the large leaves are distinctly inequilateral, a feature which is connected with the leaf vernation. Here a slight deviation in the direction of the petiole which may be brought about under the influence of stimuli emanating from pressures and tensions, removes any inconvenience, just as a man carrying a weight on one shoulder, or a stork standing on one leg, have no difficulties in keeping their equilibrium.

A last point to be discussed here is the fact mentioned above sub 3, that numerous equal local activations in the same field are as a rule not arranged symmetrically, but only more or less evenly. This may perhaps be understood by the following considerations: In the first place we know that such a symmetrical arrangement might only be reached either by shifts in an originally asymmetrical distribution, or by succesive formation, starting from a certain centre, at equal distances from each other. In the second place the advantage of a symmetrical arrangement might in most cases be very small or naught. So it may be natural that most organisms lack the complicated measures for the realization of such a symmetry.

In the case of *Pleurosigma* it is perhaps not difficult te point out the (exceptional) importance of a far-reaching approch to symmetry. According to HUSTEDT (1930, p. 33) we have to consider the alveoli as small pores through which fluids may pass, and on the ground of physical arguments he draws the conclusion that a diameter of .3 to .2 micron must be of great advantage, whereas pores under .1 micron are useless. As the transport capacity of these minute pores must be exceedingly small, the symmetrical arrangement may be the solution of the problem how to condense a maximal number in a minimal field.

Our conclusion about the wide-spread occurrence of organic symmetry is therefore that three groups of causes bring it about; in the first place surface tension, in the second place the occurrence of biological axes, combined with a similarity by lack of differentiation of the minor local activations controlled by these axes, and in the third place the biological advantages which are often reached by an approach to real or to imitated symmetry, advantages which may have been fixed by natural selection.

5. *The predominance of a very few symmetry classes in organisms.* A most remarkable feature of organic symmetry is that, though the number of classes of finite symmetry is theoretically endless, only two of these classes actually occur on a large scale, namely the radial and the dorsiventral symmetry. A number of instances representing other classes will be given in §§ 15—17, but these are all more or less exceptional.

It is, however, difficult to understand that these two leading symmetry classes have great advantages over the others. In both we have a heteropolar main axis which meets the requirements of sessile as well as of freely moving organisms, one of the poles being attached to a substratum and the other being free, or the one going in front, the other in the rear.

Of these two the radial symmetry in which all sides around the main axis are formed in the same way is the most appropriate for orthotropic sessile organisms, and dorsiventrality excellently suits the requirements of plagiotropic sessile and freely moving organisms.

And if indeed organic symmetry is part of the fundamental plan, and is exposed as such to a never-ceasing natural selection, a predominance of the most useful forms is to be expected, and we understand why it is dorsiventrality that prevails in the animal kingdom and why in plants both symmetry classes are wide-spread.

§ 14. Classification of organic symmetry; terminology and description.

A. Earlier classifications. In view of the preponderance of radial and dorsiventral symmetry, especially in al higher animals and plants, most biological text books deal only with these two and with a third form, usually called asymmetry. These three are distinguished by the fact that they may be divided into symmetrical halves, successively in more than one way, in one way, of not at all.

The common instances for the asymmetrical group are flat-fishes and the flowers of *Maranta*. If our knowledge of the asymmetrical form is restricted to these instances, we may say that all three groups of organic symmetry agree in having a heteropolar main axis.

The same or similar views are found in the papers of several authors on organic symmetry. The first to give it in full was E. MEYER (1832), who even added that radial symmetry is biologically the lowest grade, as being due to a single organic contrast, the dorsiventrality with its two contrasts being the higher, and the assymmetric form which he termed diaphoric, being the highest grade with three contrasts. Our biological axes are clearly foreshadowed therefore in this paper.

Other authors are T. CH. SCHNECKENBERGER (1836), H. MOHL (1845), and, though they give a different definition of asymmetrical, H. G. BRONN (1858) and E. VON FREYHOLD (1874), whereas AL. BRAUN (1842) and

G. JAEGER (1857) specially dealt with the two leading symmetry groups, leaving aside the asymmetrical forms.

K. GOEBEL gave a somewhat different classification (1880, p. 357; 1884, p. 141 and in several later papers) by omitting the asymmetrical group and replacing it by what he, following SACHS' suggestion, called the bilateral group, a form which had been described already for the Ctenophores by F. MÜLLER as biradial symmetry (1861), and is called bifrontal symmetry below.

It is, however, clear that such a limitation to a few symmetry groups is only in place in elementary textbooks, but not in a general morphology, as a number of other symmetry forms are found in *Protozoa* and in *Thallophyta*; a general classification is therefore required.

Such a classification is not to be derived from the distinction between longitudinal and lateral symmetry which was introduced by P. GROOM (1909) and which was adopted afterwards by GOEBEL (1928, p. 209) and by TROLL (1937, p. 16), the longitudinal symmetry implying the distribution of equal parts along the axis, the lateral that around it.

For as there exist symmetrical organisms without any axis, this distinction can never meet the requirements of a general classification. Moreover the distinction is not at all to be accepted. The fact that an organism possesses a biological axis, controlling the distribution of one or more kinds of local activations, brings along with it that these activations may be localized, evenly or symmetrically, in whorls around the axis, or spirally or in a straight line along it. These different arrangements do not constitute separate forms of symmetry, but they are related consequences of the presence of the same axis, and must be brought to the same symmetry class.

A genuine general classification of organic symmetry had, however, been given as early as 1866 by E. HAECKEL in his "Generelle Morphologie" (1, Ch. 13, p. 400—527), and this elaborate system was based on the presence of biological and mathematical axes, as mentioned above in § 13 B.

In a general way, however, this system has not been adopted by biologists. It is true, some of them have admitted part of his views and have taken up a few of his numerous technical terms, so for instance HERTWIG and CLAUS amongst zoologists, in their textbooks, and O. MÜLLER amongst botanists, in his description of the symmetry of *Diatoms* (1895).

By the influence of these authors fragments of HAECKELS system have even come more or less in general use; the bulk of his system, however, has fallen into oblivion. This has probably not only been due to the intricacy of his classification [1]), or to the barbaric and inexpressive

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[1]) Comprising two classes, two subclasses, two orders, four suborders, four families, nine sub-families, nine genera, four subgenera, twenty six species, four subspecies and two groups of organic symmetry.

technical terms [1]), but chiefly to the unhappy mixture of biology and mathematics in which both aspects of the topic were impaired. This was already alluded to above, but one more of the consequences may be mentioned here.

As a natural consequence we may see that more than one author, in borrowing terms from HAECKEL, lost his way in the tangle: in CLAUS–GROBBEN we find (1932, p. 92) *monaxonous* used where *diplopolous* is meant, and O. MÜLLER writes (1895, p. 224) *heteroaxonous* where *stauraxonous* should have been used.

In the body of Man for instance HAECKEL distinguishes three axes, two heteropolar, and a transverse isopolar one. Biologically this is one too many, the transverse axis having no biological sense, and mathematically it is two too many, neither the main nor the sagittal axis coming under mathematical consideration.

Moreover, as HAECKEL is entirely meristic in his conception of organisms; considering them as a union of separate elements, he included the number of the constituent parts amongst the symmetry features. So the dorsiventrality of Man was that of the group *Eudipleura,* on account of the two parts, right and left half, but *Nereis* was brought to another group, the *Eutetrapleura,* as the setae occur in ventral and dorsal groups at both sides. He should, however, have been aware of the truth that symmetry deals only with the general principles of the distribution of the equal parts, not with their form or with their actual number.

Half a century later the crystalographer F. M. JAEGER wrote his interesting volume "Lectures on the principle of symmetry" (1917), in which he gave a complete system of all classes of finite symmetry, possible in space, and in which he pointed out that the majority of these possible classes are represented in the forms of animals and plants.

Written by one of the leading authorities in his branch, this system does not suffer from any of the faults of HAECKELs work, the survey being as clear as it is mathematically irrefutable.

As the number of finite symmetry classes is endless, in striking contrast to the limited number 32 of infinite symmetry classes, JAEGER brings them to 14 groups which he denotes successively as

$$\mathrm{C}_n, \mathrm{D}_n, \mathrm{T}, \mathrm{K}, \mathrm{P}, \mathrm{C}_n, \mathrm{C}_n^{\mathrm{V}}, \mathrm{C}_n^{\mathrm{H}}, \mathrm{D}_n^{\mathrm{H}}, \mathrm{D}_n^{\mathrm{D}}, \mathrm{T}^{\mathrm{H}}, \mathrm{T}^{\mathrm{D}}, \mathrm{K}^{\mathrm{H}}, \mathrm{P}^{\mathrm{I}}.$$

In these symbols *n* stands for a number varying from 1 to ∞, any value indicating a separate symmetry class. Of the majority of the groups JAEGER

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[1]) For instance there are four terms: *Haplopola, Homopola, Isopola* and *Autopola* which are meant to convey successively: an isopolar main axis without further axes; an isopolar main axis with equal and isopolar perpendicular axes; a heteropolar main axis with an even number of equal and isopolar perpendicular axes; a heteropolar main axis with two unequal homopolar perpendicular axes. The four antithetic terms are *Diplopola, Heteropola, Anisopola* and *Allopola.* It cannot but be extremely difficult to memorize all this.

finds instances in biological literature, and several of them are instances of a number of classes.

In view of these results, the author writes in his introduction: "Indeed, the principle of form-symmetry in its strict formation has been neglected too long already in the morphological and systematical description of the biological sciences; or at least: its scanty applications have been too rudimentary and insufficient in almost all cases. In this respect it is most necessary that the obsolete and unwieldy definitions of form still in vogue in these sciences, should be finally abandoned for a rational system of description, in which the doctrine of symmetry is the trustworthy guide." (1917, p. 3).

It might have been expected that this constructive criticism would have met with general approval and that the offer of a mathematically irrefutable method to improve the state of things would have been cordially accepted. On the contrary we see that it has never appealed to biologists, who without any reply continued their own way. This attitude may seem obstinate and incromprehensible, but on closer examination it becomes nevertheless rational, as the disadvantages of new methods were indeed preponderant.

In the first place: the mathematical theory does not know about causes and events, and can therefore not pay attention to the morphogenetic facts, to what is essential to the biologist.

In the second place, and this is no less important, the mathematically absolute notions of the theory do not correspond to anything in nature, the organisms having only approximations to symmetry. In describing organic symmetry we have accordingly always to disregard the deviations from the mathematical form, and in this process of disregarding the mathematical theory is helpless, any deviation whether great or small taking away all symmetry. Now small deviations may be morphologically much more important than large ones, so that the biologist in judging whether any deviation may be overlooked or not, has to rely on his own resources.

It is therefore no wonder that descriptions of organic symmetry, made on a theoretical basis, are sometimes perfectly inacceptable for a biologist, as the following instances may demonstrate.

Dorsiventral bodies are denoted by the symbol $\overline{C}_1$ which means that a single axis C is present, without any repetition of equal parts around it; any part, on turning, occurring only once (1) in every revolution. This axis is, however, of the second order ($\overline{C}$), so that a symmetry plane is perpendicular to the axis. We see therefore that the mathematical theory, much more consistently than HAECKELS description, disregards both the biological axes, and that it considers only a mathematical axis to which nothing in the organism corresponds.

Radial bodies are brought to various classes. The diagram of *Aspidistra* (fig. 32) is given as an instance of class C_4^V, having a heteropolar quaternary symmetry axis and four symmetry planes passing through the axis. But if the same plant happens to produce a ternary flower, this belongs to another class C_3^V. And the related *Paris quadrifolia* belongs to class C_4, which is part of another group C_n, as having no symmetry planes. (fig. 33).

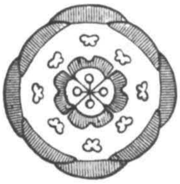

Fig. 32. *Aspidistra elatior.* Floral diagram. From JAEGER, 1917, fig. 63.

Fig. 33. *Paris quadrifolia.* Floral diagram. From JAEGER, 1917, fig. 22.

In the latter group C_n, however, we find also the class C_1 to which all wholly asymmetrical forms belong, as there is no repetition of equal parts; the axis in this class has no position, and any line may be taken as such.

Our conclusion is therefore that the trustworthy guide of the mathematical doctrine neglects what is most important for a biologist, it lays weight upon what is unimportant for him, it unites what is heterogeneous and separates what belongs together; moreover it remains silent on the most important question in how far an organism is symmetrical or not.

B. A new classification of organic symmetry. As therefore neither of the two earlier systems answers the purpose, a new classification is proposed here which is based on the essential biological features.

It distinguishes twelve classes of organic symmetry, which will be denominated and defined here, and which will be dealt with in detail below in §§ 15—17. In fig. 34, 1—12 they have moreover been represented diagrammatically.

Class 1. **Asymmetry.** No biological axes, no regularity of form. Plasmodium of *Fuligo septica.*

Class 2. **Spheroidal symmetry.** No biological axis, but a spherical main form, with or without regularly or evenly distributed local differentiations. Egg-cells of *Fucus*; pollen grains of fig. 2 and 3.

Class 3. **Discoidal symmetry.** An isopolar main axis, with or without regularly or evenly distributed local differentiations around it. *Spirogyra*; pollen grains of fig. 6.

Class 4. **Trabal symmetry.** An isopolar main axis and an isopolar secondary axis. *Plagiogramma,* fig. 13.

Class 5. **Unequal-sided trabal symmetry.** An isopolar main axis, and isopolar secondary and a heteropolar tertiary axis. *Amphora arceolata,* fig. 35.

Class 6. **Pontal symmetry.** An isopolar main axis and a heteropolar secondary axis. *Asterionella japonica,* fig. 36.

Class 7. **Unequal-sided pontal symmetry.** An isopolar main, a heteropolar secondary and a heteropolar tertiary axis. *Nitzschia Ungeri*, fig. 37.

Class 8. **Radial symmetry.** A heteropolar main axis, with or without regularly or evenly distributed local differentiations around it. *Botrydium granulatum*; *Hydra vulgaris*.

Class 9. **Bifrontal symmetry.** A heteropolar main and an isopolar secondary axis. Shoot of *Opuntia*; *Ficus indica*; *Ctenophora*.

Class 10. **Unequal-sided bifrontal symmetry.** A heteropolar main, an isopolar secondary and a heteropolar tertiary axis. *Cocconeis notata*, fig. 38.

Class 11. **Dorsiventral symmetry.** A heteropolar main and a heteropolar secondary axis. Flower of *Viola*.

Class 12. **Unequal-sided dorsiventral symmetry.** A heteropolar main, a heteropolar secondary and a heteropolar tertiary axis.

The choice of these classes has been determined by what actually occurs in nature, by the existing combinations of biological axes.

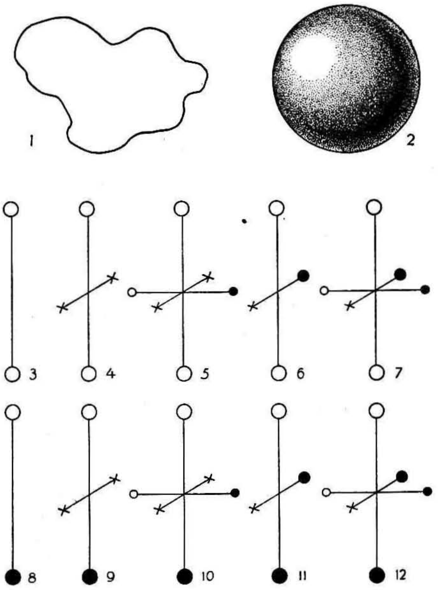

Fig. 34. Schematic representation of the twelve classes or organic symmetry. 1. Asymmetry. 2. Spheroidal symmetry. 3. Discoidal symmetry. 4. Trabal symmetry. 5. Unequal-sided trabal symmetry. 6. Pontal symmetry. 7. Unequal-sided pontal symmetry. 8. Radial symmetry. 9. Bifrontal symmetry. 10. Unequal-sided bifrontal symmetry. 11. Dorsiventral symmetry. 12. Unequal-sided dorsiventral symmetry. Isopolar axes are indicated by two equal poles, heteropolar axes by black and white poles, the secondary heteropolar axes by a crosslet and a black circlet at the poles. Original.

Other combinations might be possible, in the first place those with more than three biological axes. In § 14, B it has been mentioned already that probably such organisms do not exist, and below in § 16, C some instances will be discussed of organisms in which according to the outer form four axes might occur, but it will be indicated why it is better to assume only one biological axis in this and similar organisms.

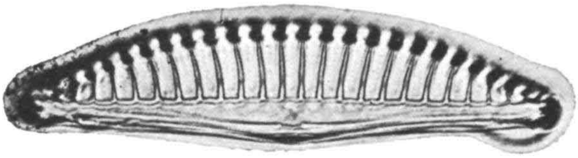

Fig. 35. *Amphora lanceolata.* Valve. (Coll. KINKER).

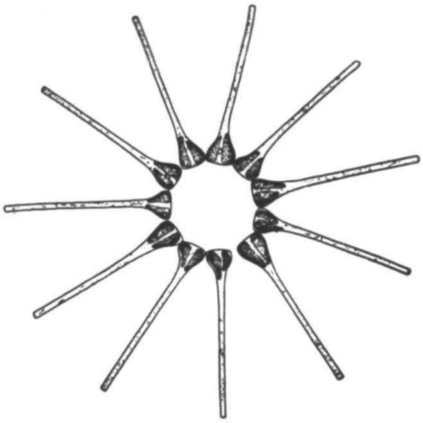

Fig. 36. *Asterionella japonica.* Colony the individuals in girdle view. From HUSTEDT, Rabenhorst, VII, 2, p. 256.

Moreover not even all possible combinations of three biological axes have been distinguished as symmetry classes, all four possible forms with an isopolar tertiary axis having been omitted. This was done on account of the consideration that even if such organisms exist, which is uncertain, their distinction from the corresponding classes without a tertiary axis (our classes 4, 6, 9 and 11) would be most difficult. For in these classes the ends of the transverse direction are already equal by lack of differentiation, as demonstrated above with the aid of fig. 29 for dorsiventral organisms.

The classification given here has the disadvantage, like other natural classifications, that transitional forms occur.

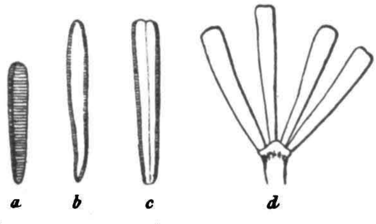

Fig. 37. *Nitzschia Ungeri.* a. valve. b, c, girdle views of different sides. d. colony. From GRUNOW, 1870, T 1, fig. 1.

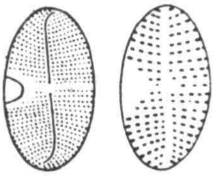

Fig. 38. *Cocconeis notata.* Two valves, the lower with a raphe, the upper without a raphe. From HUSTEDT, Rabenhorst, VII, 2, p. 353.

The body of Man is a transition between dorsiventral symmetry and unequal-sided dorsiventrality. This is connected with the fact that the dominating influences of certain localizations of morphogenetic factors may be of any degree of importance and strength, so that all gradual transitions exist between biological axes and simple relations between less powerful localizations. That especially tertiary axes may show such transitional stages is self-evident.

About the names of the classes the following remarks may be made. The requirements being conformity to the common use wherever possible, simplicity, clearness and above all avoidance of ambiguity, most terms in use in literature give difficulties.

Some were taken up, but in a restricted sense, namely asymmetry, from which the dorsiventral as well as the unequal-sided dorsiventral symmetry were excluded; radial symmetry from which the discoidal, and dorsiventral symmetry from which both the unequal-sided trabal symmetry and the pontal symmetry were separated, against the common use.

Spheroidal and discoidal symmetry, being more or less new terms, were taken in a somewhat wider sense than might have been expected from the very words, as all polyhedral forms were included into the former, and all triradiate, quadriradiate etc. forms in the latter class.

None of the new terms is to be taken literally; the only correspondence between the organic form and the object after which the symmetry class is named is the occurrence of certain symmetry elements, in the same way as the discoidal symmetry class comprises forms with a long main axis and a small transverse section as well as flat discs.

The new terms trabal (*trabs* = beam) and pontal (*pons* = bridge) symmetry were chosen on account of the familiar character of these objects, a beam having three different isopolar axes, while a bridge has two isopolar axes and one, the vertical, which is heteropolar. 1)

Finally the new term bifrontal symmetry has been derived from the Roman god *Janus bifrons,* whose head was a good instance of this symmetry class.

No use has been made of the inexpressive and ambiguous term bilateral which indicates dorsiventrality for most zoologists and which is used by GOEBEL and his followers for bifrontal, while the vague terms asymmetrical and irregular for dorsiventral have also been discarded.

The term radial is retained, but only on account of its general use, as it does not convey the presence of a heteropolar main axis, and would in fact be more appropriate for designating spheroidal symmetry. As the argument of frequent use cannot be applied to the term biradial, introduced by F. MÜLLER for bifrontal (1861), this was dropped.

Finally the two terms actinomorphous and zygomorphous were also left out, as they had no advantages over radial and dorsiventral, and are not nearly so much used.

In the classification as given here, the important distinction between finite and infinite symmetry does not find expression. This may be justified by the following considerations.

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1) Of course only the form of a swing-bridge, not of a lift-bridge is to be thought of. The lift bridge forms an instance for the unequal-sided pontal symmetry.

As has been recognized above, both infinite and finite symmetry is found in organisms. In these symmetry forms there are of course always mathematical symmetry elements, and as we saw, these elements differ according to the finite and infinite character of the symmetry. Of symmetry axes notably we recognized that they do not occupy fixed positions if they are perpendicular to a plane of infinite extension.

Now biological axes, as being physiological processes, always occupy definite positions, and hence we may conclude that any symmetry which is due to the activity of a biological axis has to bear a finite character. This holds even true in those cases in which the axis itself is more or less infinite in its extension, as in growing stems and roots, or in tape-worms. For in these instances the organism is only comparable to a one-dimensionally infinite figure, so that the longitudinal axis has all the features of a finite axis, it can have any repetition number, and occupies a definite position.

A two-dimensionally infinite system on the other hand, in which the mathematical symmetry axes have no definite places, as in the ornamentation of *Pleurosigma,* cannot be related to any biological axis. These cases accordingly do not concern the general symmetry of the organism, but are only of local influence.

Our conclusion is therefore that our classification is, as it should be, a survey of all symmetry forms which may be controlled by biological axes, whether finite or infinite.

c. Terminology. For the description of organic symmetry we need not only a classification of the different forms, but moreover a uniform terminology for designating the biological axes, the directions in, the sections through, or the planes in the organisms, and further for the various sides of the organism.

In literature a special nomenclature exist for special groups, as the *Ctenophores* and the *Diatoms,* but it is evident that a general nomenclature for all organisms is to be preferred.

1. *Axes.* According to a wide-spread custom the primary biological axis will be called here main axis. Other names as longitudinal axis, central axis or pervalvar axis (*Diatoms*) will not be used.

Secondary axes are called here sagittal axes, and tertiary axes transverse axes. Other names are apical for sagittal, and transapical for transverse axis, both used for *Pennate Diatoms.*

2. *Directions.* All lines parallel to the main axis will be called longitudinal, and if there are no other biological axes, all lines perpendicular to longitudinal lines will be called transverse. In classes with a sagittal axis the name transverse direction will be limited to the lines which are perpendicular to the sagittal plane.

3. *Sections.* The different planes in, or sections through organisms will be denominated as follows:

In the asymmetrical class local parts of sections which are perpendicular to the surface, are distinguished as such from other parts, and the same is to be said of local parts of sections which are parallel to the surface.

In the spheroidal symmetry class we have to distinguish between properly spherical and other bodies. In the former we have radial or median sections, all being symmetry planes, and lateral sections. In these lateral sections a small region is perpendicular to the radii and this part is called tangential.

In other spheroidal bodies there are local differentiations, and especially if these are large and few in number, those radial sections which pass through the middle of one or more of these differentiations have some special features, and may be indicated by special names, according to the case.

In all classes with biological axes there are longitudinal sections containing the main axis, or running parallel to it, and transverse sections, being perpendicular to the main axis.

If the main axis is isopolar, one of the transverse sections, in the middle of the axis, is a symmetry plane; it is called the equatorial plane.

The longitudinal sections are differently indicated according to the presence or absence of accessory axes.

If the latter are absent (discoidal and radial symmetry) the longitudinal sections are in all respects comparable to the sections through spherical organisms. There are radial or median sections, containing the axis, and lateral sections parallel to it. The latter have a tangential part which this time is a longitudinal strip, not a circular spot. If there are local differentiations, especially if large and few in number, radial sections passing through the middle of one or between two of these differentiations, have some special features, and both kinds often answer better to the idea of symmetry plane than other radial sections. They are often distinguished by the name radial and interradial sections.

If there is an isopolar sagittal axis and no transverse axis (trabel and bifrontal symmetry) only two of the longitudinal planes are symmetry planes, that which passes through main and sagittal axis is called sagittal plane, 1) the other, passing through the main axis in a transverse direction, is called frontal plane. All sections parallel to one of these symmetry

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1) Derived from the sutura sagittalis, the suture between the parietal bones of our skull (HAECKEL, 1866, p. 519) which winds along the symmetry plane, its original meaning is to indicate the symmetry plane of our body. It has been extended both in zoology and in botany to all classes with a sagittal axis, to indicate the plane through the latter and the main axis (KRUMBACH, 1923, p. 914; SCHÜTT, 1906, p. 44).

But at the same time the zoological anatomists had assumed the habit of applying the term sagittal to all sections parallel to the symmetry plane of dorsiventral animals. This custom, though clashing with the origin of the term as well as with the use in various departments of biology, is firmly established for the anatomy of the Vertebrates (ZIEGLER, 1903, p. 517; HIRSCH-SCHWEIGER, 1925, p. 475) and is not likely to be changed. However, as it is, neither to be adopted for other than dorsiventral organisms, a compromise has been tried here.

planes have special features and may be indicated as co-sagittal and co-frontal sections.

If a heteropolar transverse axis is added to the isopolar sagittal axis (unequal-sided trabal and unequal-sided bifrontal symmetry) the sagittal plane loses a larger or smaller part of its features as a symmetry plane; the difference between the sagittal and the co-sagittal sections may, however, be often kept up.

If there is a heteropolar sagittal axis and no transverse axis (pontal and dorsiventral symmetry), the sagittal plane is the only longitudinal symmetry plane. The frontal section, being no longer a symmetry plane, is often no longer to be distinguished from the cofrontal sections and accordingly the latter may be called frontal sections for simplicity's sake.

If a heteropolar transverse axis is added to the heteropolar sagittal axis (unequal-sided pontal and unequal-sided dorsiventral symmetry), the sagittal plane loses a larger or smaller part of its features as a symmetry plane; the difference between the sagittal and the co-sagittal sections may, however, be often kept up.

4. *Sides; external views.* In organisms of the asymmetrical and the spheroidal class no special terms are wanted for their different sides. In organisms with biological axes on the other hand it is always necessary to mention the spatial relations of the various regions to the biological axes which control the distribution of all differentiations.

In some cases such general designations as upper and lower, or light and shade side may do, as organisms generally assume definite positions in space in connection with gravity, light, a substratum or with other external influences.

Usually, however, a more concise indication is required, for instance if related organisms have different modes of life and turn their homologous parts in other directions, as in pendulous and erect flowers, in *Medusae* and polyps, or in star-fishes, sea-lilies and sea cucumbers. Here the mere mentioning of upper and undersides would frustrate a morphological comparison.

Accordingly in the majority of natural groups the sides of the organisms are indicated by designations derived from the position of the biological axes and their poles, such as apical and basal, oral and caudal, dorsal and ventral, and so on, and the same terms are used for indicating external views, as described in observations or represented in pictures.

These terms are, however, not only often different in different groups of organisms, but moreover they are sometimes morphologically unwarranted and misleading. A general system of reference might therefore be a gain, and though the present author is fully convinced of the extreme difficulties in eradicating even a notable imperfection in a once established nomenclature, a modest attempt will nevertheless be made.

a. Organisms with a single biological axis. If this axis is isopolar (discoidal symmetry class), the sides of the poles are called polar sides, and the sides midway between the poles are called lateral sides.

If the axis is heteropolar (radial symmetry class) the same terms are to be used, but as the poles are different they have to be distinguished by means of some addition. So we can speak of a sensitive and a generative pole (*Volvox*), an oral and an aboral pole (*Asteropecten*), an oral and a sessile pole (*Hydra*), an apical or free, and a basal or sessile pole (*Botrydium granulatum*), and so on.

Of course, in all cases in which the homology of the polar differentiation in different organisms has been established it is desirable that the same terms should be used, irrespective of the different adaptations which might have taken place.

Decidedly rejectable is the use of the terms dorsal and ventral for the poles of the main axis, as these two terms imply a comparison with the poles of the sagittal axis of *Vertebrates*. Yet it is a common practice in the case of the radiate *Echinoderms*. A few authors, it is true, such as CUÈNOT (1900), correctly speak of the oral and the aboral side, but in the use of such terms as *centrodorsal apparatus* the objectionable terminology is still preserved.

b. Organisms with two biological axes. As soon as a sagittal axis is added to the main axis, the use of the term lateral side is much restricted and is only applied to those two sides which are parallel to both the main and the sagittal axes. The sides at te ends of the sagittal axis are now called frontal sides.

If the sagittal axis is isopolar (trabal and bifrontal symmetry classes) no further designations are required. If, however, the sagittal axis is heteropolar (pontal and dorsiventral symmetry classes) we have to distinguish between its different poles. This may be done by mentioning some special feature of the two poles, such as attached and free, concave and convex, thick and slender side, and so on.

In the dorsiventral symmetry class we have two special terms at our disposal; dorsal and ventral. These are used in the first place for all higher animals, from the *Vermes* up to the *Vertebrates*. They need no explanation, and we may only add that in such cases in which an animal assumes an unusual attitude, different from its relatives, as in the *Heteropoda* or in *Pleuronectes* or in Man, they are applied to the homologous, not to the analogous sides.

In lower animals in which the heteropolarity of the sagittal axis is not related to that in higher animals, as in *Paramaecium*, there is no objection to the use of the same terms, if it is only borne in mind that it is a case of analogy, and the common practice is to use even the same terms for many dorsiventral plant organs.

We must, however, be aware that such extensions are only allowed after special definition, and that it causes confusion if different definitions are applied to related organisms or organs.

Two instances of such confusions may be given. In botany we have opposite definitions for foliage leaves and carpels: in the former it is usually the adaxial, in the latter the abaxial side which is called dorsal. And in dorsiventral *Echinoderms* two different definitions are in vogue for the regular *Echinoidea* and for the *Holothuria*. In both cases it might be therefore preferable to abstain altogether from the use of the terms dorsal and ventral.

The two lateral sides of all organisms with two biological axes are biologically equal, by want of a special differentiation. Yet the cases are not the same in all symmetry classes: in the trabal, pontal and bifrontal symmetry classes they are congruent, as far as biological formations may be, whereas in the dorsiventral symmetry class they are only mirror-images, with a different configuration of their parts as expounded above in § 13, B. In dorsiventral animals these sides are distinguished as right and left side. The extension of the use of these unparalleled terms to botanical objects lies on the surface; it is sufficient to determine which sides of the main and the sagittal axis are compared with the different poles of these axes in animals for the distinction between right and left to be established. 1)

c. Organisms with three biological axes. The addition of a (heteropolar) transverse axis hardly changes anything in the designation of the sides of the organism.

In the trabal, the pontal and the bifrontal symmetry classes the lateral sides, having lost their congruence, have to be distinguished by mentioning some special features of each of them, but in the dorsiventral symmetry class the right and left sides, however different, are already designated by these names, under which they have to be described separately.

It is of course impossible to elaborate this cursory general scheme for use in special groups of organisms. In some of these a wholly different nomenclature is in general use, as for instance in the Diatoms, where the polar, frontal and lateral view are generally called valve, short girdle and long girdle view.

All these special names, however clear and efficient they may be, have two important disadvantages. In the first place they stand in the way of

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1) It is most curious that in EICHLER's masterwork a definition of these terms is given which clashes with the conditions found in the Vertebrates. He writes (1875, p. 6): "Bei Seitenblüthen nennen wir die durch Blüthen- und Abstammungsaxe gelegte Ebene die Mediane der Blüthe, eine in der Blüthenaxe darauf senkrechte Ebene mag Transversale heissen. Oben oder hinten ist das, was von der Transversale aus gegen die Abstammungsaxe, vorn oder unten, was davon abgewendet liegt. Als rechts bezeichnen wir, was sich, die Blüthe von vorn betrachtet, auf der rechten Seite der Mediane befindet, links, was auf der linken Seite liegt." This would imply a comparison of the insertion of the pedicel with the cranial pole of Vertebrates, a comparison which the author will not have intended.

an easy understanding by the general biologist who is not sufficiently acquainted with the special features of the group, and secondly they impede even those who are, in making comparison between the symmetry relations in their special field and those in other group of organisms.

D. Description. A few remarks are finally to be made on the description proper of organic symmetry, to be made with the aid of the classification and the terminology developed above.

In the first place the investigator has to bear in mind (which is often disregarded) that the description has to serve biological, not mathematical purposes.

To quote an instance: in describing the symmetry of Diatoms OTTO MÜLLER enounced the view that the two valves on account of their difference in size can never be symmetrical to each other, but that the relation is only akin to symmetry. Accordingly he proposed the term consimility for this relation (1895, p. 224). Mathematically this is right, but biologically it is meaningless. 1) The small difference in size between the two valves is only due to the development of the younger valve inside the older, but if, as in most Diatoms, the two valves are otherwise equal, they are elaborated by the same set of morphogenetic factors, and the main axis is isopolar. In other genera, however, the two valves are markedly different by a true heteropolarity of the main axis, and this condition has to be distinguished clearly from the isopolarity.

In order to determine the symmetry of an organism our first task is to consider the distribution of equal parts, in the adult as well as in the developmental stages, and not only in normal, but also in abnormal specimens. From these facts we must try to understand the general course of the special morphogeny; the better this is known, the more correct our judgment.

Hence we may conclude to the absence or presence of biological axes, and of the latter we may determine the nature (differentiation-, growth-, segmentation axis; isopolarity of heteropolarity), the course (straight, curved, twisted), the order of importance (main, secondary, tertiary axes) and the distribution (mutual positions). If these data are known we are able to determine the symmetry class and at the same time we may come to a conclusion about the presence of symmetry planes, their number, their plane or curved nature and their distribution.

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1) It is worth while to remark that in literature on Diatoms this view has been avowed with the lips, but not with the heart, as it clashes with the sound judgment of the actual investigators.

SCHÜTT adopted the term consimility and even added (for unknown reasons) a second term, namely "Ähnlichkeits- oder Similisymmetrie" (1896, p. 45), but his conclusion was that it is still better to call it simply symmetry. And HUSTEDT, though adopting both new terms and recognizing that the main axis is theoretically heteropolar, writes nevertheless that he neglects the difference and calls the main axis isopolar, unless the two valves are of a different construction (1930, p. 14).

§ 15. Symmetry in organisms without biological axes.

A. Asymmetry. Organisms without biological axes may be subject to forces disturbing all regularity of form, even if it was originally present. Such forces are for instance amoeboid movements of a semi-fluid body, and heterogeneous growth. As an instance of the latter most plants may serve, which by their susceptibility to differences in external conditions grow differently in various directions. A dicotyledonous tree, grown in a virgin forest, as a rule will show this, as it fills up with its branches any gap between the crowns of foliage of neighbouring trees.

B. Spheroidal symmetry.

1. *Causes of spheroidal symmetry.* Various causes may tend to bring about spherical or circular forms: surface tension (cf. § 12); a homogeneous growth if this is limited to the superficial layers, and moreover such external conditions as are injurious to those parts which stick out from the body.

Spherical form by growth of the superficial layers is exhibited by colonies of bacteria growing inside a homogeneous medium; the circular form of colonies of aerobic bacteria, or of a fairy ring of toadstools, is the two-dimensional projection of such a form, the medium being this time flat. In these cases the resulting form is independent of the original shape, as the addition of equable layers to the surface always tends to draw the form nearer to the sphere.

Circumstances which are detrimental to the growth of protruding parts may be of various kinds; we see their effects in the well-known vegetable sheep, and in the spherical colonies of some fresh-water organisms living in shallow waters as *Ophrydium versatile, Nostoc pruniforme* and *Cladophora Aegagropila.* A non-living analogon is found in the spherical conglomerates of detritus from any kind of plant material, found on the shores of lakes.

2. *The forms themselves.* It is customary to distinguish between the spherical forms proper, and the polyhedral or allied forms as exhibited by some pollen grains (*Fumaria,* fig. 19) or by a Radiolarian as *Circogonia icosahedra,* pictured by HAECKEL (1862).

Biologically, however, there is little to be said in favour of such a distinction. As expounded in § 13 these mathematically highly remarkable forms are only incidental consequences of a distribution of differentiations, and a pollen grain with 8 or 12 places of exit has no other morphogenetic factors than another with 9 or 11.

The establishment of separate classes of organic symmetry for organisms showing, in a more or less pure form, the features, be it with convex or concave faces, of tetrahedron, cube, octahedron, pentagonal dodecahedron or icosahedron, as both HAECKEL and JAEGER suggest, is biologically not justified.

§ 16. Symmetry in organisms with an isopolar main axis.

A. The main axis. Isopolar main axes, being either differentiation or growth axes, are of a limited occurrence in nature.

This is not to be wondered at, as the only general biological advantage of such axes is the ordering of the fundamental plan, whereas the heteropolar main axes render the same service and are moreover of great importance for sessile as well as for motile organisms in attaining an efficient organization. Accordingly the isopolar main axis is only really adequate in floating organisms.

By its influence the general shape of the organisms is determined and the minor differentiations are localized in definite places, so that the fundamental plan can be adapted to various conditions of life.

Instances of organisms or organs with an isopolar main axis are many pollen grains (fig. 6), many planctontic *Algae* (Diatoms, Desmids), and, to give a zoological instance, the human red blood-globules.

B. The subordinate axes. The local activations which are dominated by the main axis being of any degree of importance, a few of them may in their turn develop a great influence on the still less important ones, and in such a way two equal or two unequal activations may form together a secondary axis, which as indicated in § 13, B, will be usually perpendicular to the main axis; of course the origin of tertiary axes is quite similar.

This mode of origin may account for the fact that subsidiary axes are generally differentiations axes. Theoretically they might be as well growth or differentiation axes, but it is uncertain whether such cases occur in nature. A somewhat dubious case is the growth axis of the *Pennate Diatoms*, which develops in the auxospore at right angles to the previously existing differentiation axis. But as here the leading rôle is taken over by the growth axis, the first axis remaining as the sagittal axis, we may just as well follow the common practice and call the growth axis main axis here.

C. Discoidal symmetry. The collection of forma united here in this symmetry class may seem at first sight to be rather heterogeneous.

First it contains such forms as *Bacterium*, in which there are no conspicous differantiations around the main axis; secondly we have such forms in which a large number of lateral differentiations are distributed more or less evenly, as in fig. 6, and in the third place we have those in which by a symmetrical distribution of three or more equal differentiations a radiate structure is realized, as in fig. 31. The reasons for drawing such broad lines may be illustrated with a few photographs.

In fig. 39 we see to the left a specimen of *Aulacodiscus Kilkellyanus* with a great number of radial rows of fine punctations and with three submarginal processes or moderate size. The latter differentiations are symmetrically arranged. Whereas the former only attain a lower degree of symmetry, the rows being discontinued towards the centre in an irregular way. We might therefore be inclined to attribute a triradiate symmetry to the object, and the same view seems even still more justified for the specimen of *Actinoptychus undulatus* at the right, with its six sectors in two alternating kinds.

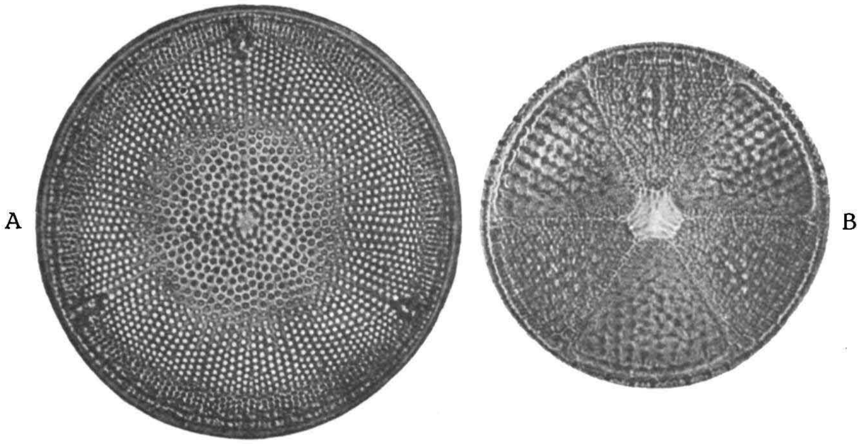

Fig. 39. A. *Aulacodiscus Kilkellyanus*, valve. B. *Actinoptychus undulatus*, valve. (Coll. KINKER).

Of course the distinction of a separate triradiate symmetry class would bring with it the necessity of the establishment of further classes for quadri-, quinque-, etc. radiate classes, so that the number of classes would increase indefinitely.

There are, however, serious objections. In the first place we may remark that a number of three equal differentiations is never constant. In the genus *Aulacodiscus* the number of processes varies from 1 to 45, according to KARSTEN (1928, p. 224) and in the genus *Actinoptychus* the sectors vary from 6 to 20 or more (HUSTEDT, 1930).

In the second place the three or more secondary axes which we should have to assume are always heteropolar if the number of equal differentiations is an odd one, as in fig. 30, B, but they are isopolar any time the number is even; any *Aulacodiscus* with 4 processes or *Actinoptychus* with 8 sectors shows this. Evidently the secondary "axes" in these objects have no biological character, the real situation being that in *Aulacodiscus* a varying number of processes are laid down which become equidistant, whereas in *Actinoptychus* in connection with the radial undulation of the valve the ornamentation develops differently in the raised and in the lowered sectors, the ornamentation being much more marked in the former sectors.

Of course the obvious objection against this reasoning is that if really all tri- and pluriradiate forms are to be included in the discoidal symmetry class, the same would hold true for the trabal symmetry class which only differs through the fact that its number of equal differentiations is two.

The reply to this objection is that the number 2 differs biologically from all higher numbers by its greater stability; a stability which is not absolute, but yet sufficient for the organization of a fundamental plan in which the single secondary axis may play a rôle.

Discoidal symmetry in the above sense is observed in a number of lower *Algae*, all having growth axes (many Bacteriaceae, and Oscillateriaceae, numerous Centric Diatoms, many *Conjugatae*); with a differentiation axis it occurs in the pollen grains of many Dicotyledons and in the red blood-corpuscules of Man.

The main axis is usually straight (*Bacterium*, *Melosira*, pollen grains) but it may be curved (*Closterium*), screw-shaped (*Spirillum*) or twisted (*Oscillatoria*).

D. Trabal symmetry. From what has been said above sub C about removing trabal symmetry from the discoidal class, it will be evident that the peculiar trabal symmetry is much more firmly established in some species than in others.

If we look at *Triceratium arcticum* forma *balaena* (fig. 40), a dimerous variation of an otherwise trigonous species, it is clear that the fundamental plan cannot be adapted to the special features of the trabal symmetry. In the genus *Auliscus* which normally has trabal symmetry by the presence of two "eyes" on every valve, the number of "eyes" may vary from 1 to 4 (fig. 41) and accordingly such adaptations are not to be expected either.

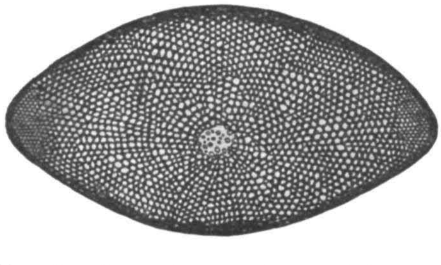

Fig. 40. *Triceratium arcticum* fa *baleana*. Valve. From HUSTEDT, Rabenhorst, VII, 1, p. 818.

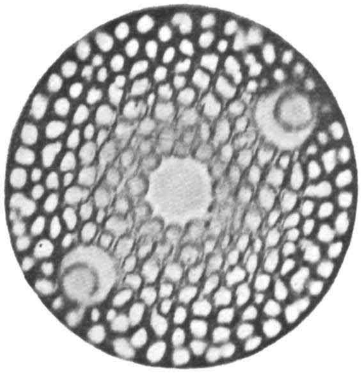

Fig. 41. *Auliscus Kinkeri*, valve with two "eyes". (Coll. KINKER).

In *Diatoma* or in *Fragilaria* on the other hand, where no other than trabal symmetry occurs, it is not to be wondered at that the sagittal axis, being the superseded main axis of the auxospore, is quite stable and may serve as a basis for further differentiations such as a locomotion organ in the raphe.

Moreover the forms of the next class, the unequal-sided trabal symmetry, may be considered as further differentiations which could be realized only by the well-established anchorage of the trabal symmetry in the fundamental plan.

Trabal symmetry occurs in some Desmids (*Eurastrum, Micrasterias*), in some Centric Diatoms (*Auliscus, Rutilaria*) and in a numerous Pennate Diatoms.

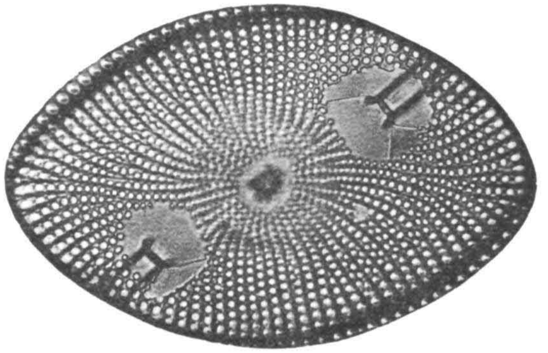

Fig. 42. *Kittonia elaborata,* valve. (Coll. KINKER).

The main axis as well as the sagittal axis are usually straight, but several marked exceptions are known: *Eucampia* (fig. 28) with a spirally curved, *Kittonia* (fig. 42) with a twisted main axis, *Campylodiscus* (fig. 43) with a curved, *Pleurosigma* with a *S*-shaped, *Surirella spiralis* and *Scoliopleura* (fig. 44) with a twisted sagittal axis.

Fig. 43. *Campylodiscus Echeneis,* surface view of valve. From ENGLER and PRANTL, 2nd ed., 1928, 2, p. 229, fig. 411a.

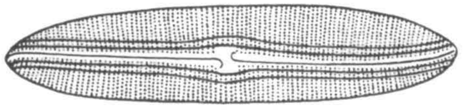

Fig. 44. *Scoliopleura* spec. Surface view of valve.

E. Unequal-sided trabal symmetry. The heteropolarity of the transverse axis enables the organisms of this group to develop a division of labour between the two lateral sides; usually one of these sides is flat or concave, and is attached by some means or other to a substratum so that the organism becomes sessile.

Amphora arceolata (fig. 35) is a good instance; the two different lateral views display the isopolarity of the main and sagittal axis, and the polar view exhibits the heteropolarity of the transverse axis.

Similar conditions are met in the genera *Campylosira* and *Ceratoneis* of the *Araphideae*, in *Eunotia* of the *Rhaphidoideae* and in *Toxonidea*, *Cymbella* and *Amphora* of the *Biraphideae*; to all appearance the heteropolar transverse axis has been developed polyphyletically amongst the *Pennate* Diatoms.

In literature the two lateral sides are usually designated as dorsal (the free) and ventral (the attached) side; against this custom the same objections are to be made as to the use of ventral and dorsal for the poles of a heteropolar main axis.

Curved axes are of frequent occurrence in this class, for the main axis as well as the sagittal axis are often curved towards the attached side. Obviously this is an adaptation to sessile life, which may be a direct consequenc of the heteropolar transverse axis.

F. Pontal symmetry. The organisms with this form of symmetry possess an isopolar main axis and a heteropolar sagittal axis. There is only one longitudinal symmetry plane, namely that through the main axis and the sagittal axis, the so-called sagittal plane. Of course the equatorial plane perpendicular to the main axis is also a symmetry plane.

Pontal symmetry occurs in some *Pennate* Diatoms such as *Gomphonema* (fig. 45) which are attached to the ventral side, and *Asterionella* (fig. 36).

We may recognize two cases: firstly that the sagittal axis is heteropolar from the beginning, and secondly that this axis begins as an isopolar one but afterwards becomes heteropolar. Therefore pontal symmetry may arise from discoidal symmetry if the isopolar sagittal axis becomes heteropolar. We may follow this process by regarding successively the figures 46—48. In *Anisodiscus* (fig. 46) the local activations at the two ends of the sagittal axis are somewhat different. In the genus *Asteromphalus* (fig. 47) one of the beams is smaller than the others. This is always the case with only one of them, no variation in number occurs. And in *Hemidiscus* (fig. 48) we see clearly a heteropolar sagittal axis, so we may consider this last object as a good instance of the pontal symmetry class.

G. Unequal-sided pontal symmetry. If a heteropolar transverse axis is added the unequal-sided pontal symmetry is derived from the pontal one. A good instance is *Gomphonema curvirostre*, where we come to the conclusion, that there have been unequal polar differentiations at the ends of the transverse axis.

In the second place, this symmetry may also be derived from the un-equal-sided trabal symmetry by a secondary alteration of the sagittal axis. Perfect instances are the genera *Nitzschia* and *Rhopalodia*. Some species of these genera possess an isopolar sagittal axis. The heteropolarity of this axis may increase gradually in other species, and so we may place the species in a row: at the beginning the species with an isopolar and at the end those with a heteropolar sagittal axis.

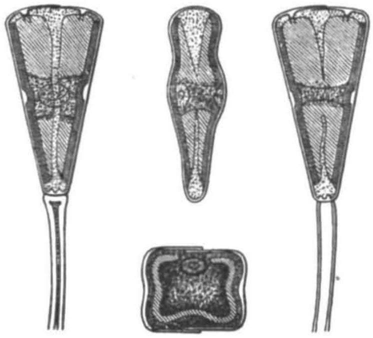

Fig. 45. *Gomphonema constrictum.* On both sides the different girdle-views; in the middle: above the valve and below a frontal section. From GOEBEL, Grundzüge, p. 21.

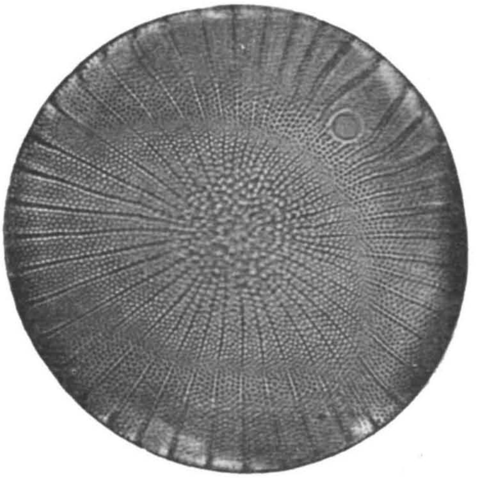

Fig. 46. *Anisodiscus*? Valve. (Coll. KINKER).

Fig. 47. *Asteromphalus Senectus.* Valve. (Coll. KINKER).

Fig. 48. *Hemidiscus cuneiformis.* Valve. (Coll. KINKER).

* § 17. Symmetry in organisms with a heteropolar main axis.

A. The main axis. In the following five classes the main axis is heteropolar, due to different growth localizations at the two ends. The classes 8—12 form a parallel with the classes 3—7, each of them may arise from the class represented in fig. 34 immediately above it, by an unequal differentiation of the poles. This may be due to the needs of locomotion, the front end having other qualities than the rear end. The second reason why the main axis may become heteropolar is a sessile habit; the free end having other qualities than the attached one. So the classes with a heteropolar main axis are of very great importance and therefore they are common both in plants and in the animal kingdom.

B. The subordinate axes. The local activations which are dominated by the main axis being of any degree of importance, a few of them may in their turn develop great influence on the less important ones, and in this way two equal or two unequal activations may form together a secondary axis which will usually be perpendicular to the main axis. Of course, the origin of tertiary axes is quite the same. Just as in the classes with an isopolar main axis, the subsidiary axes are nearly always differentiations axes.

C. Radial symmetry. This symmetry class is often realized in nature, especially by the orthotropic sessile forms, in plants as well as in the animal kingdom. At first sight the collection of forms contained in this class seems to be rather heterogeneous. Firstly, it contains such forms as *Botrydium granulatum*, in which there are no conspicuous differentiations around the main axis; secondly we find such forms as *Hydra vulgaris*, in which a large number of local differentiations is distributed more or less evenly and in the third place we have those in which by a symmetrical distribution of three or more equal differentiations a radiate structure is realized, as in *Echinodermata* (with the number 5) and in many vascular plants (with various numbers).

All these forms belong to one symmetry-class. A mathematical consideration, however, which would distinguish between triradiate and quadruradiate forms, has no biological sense.

A contort corolla of *Blumenbachia* with asymmetrical petals, as drawn in fig. 16, belongs to the same radial symmetry class even though there is no symmetry plane at all.

In literature we meet several names for this symmetry form, such as aktinomorphous and regular. These terms are rejected here in favour of the name radial in the broad sense mentioned above. The flower of the Cruciferian family is also an instance of this class, the two small filaments are of no importance.

D. Bifrontal symmetry. The bifrontal symmetry is removed from the class of the radial symmetry since the number of two differentiations is much more constant than that of three or more.

For instance we may consider the stem of *Fucus*, which is flattened with equal sides. In *Opuntia* the vegetation cone is round, but nevertheless the internodes of the stem are flattened. The genus *Campyloneis* of the *Monoraphideae* has two elliptical valves, one without and another with a raphe. The main axis is also heteropolar, but the sagittal axis is isopolar. This instance of bifrontal symmetry is due to a secondary differentiation, without the heteropolarity of the main axis it would be trabal symmetry. We cannot speak here of a right and a left side nor of a dorsal and a ventral one. Therefore in the case of *Fucus* we may say that the stem possesses two flattened sides and two rounded ribs (sides).

In the animal kingdom many *Ctenophora* belong to this symmetry class. In Diatoms the sagittal axis is sigmoid in *Cocconeis* and in *Achnanthes*.

E. Unequal-sided bifrontal symmetry. In this symmetry class there is an isopolar sagittal axis and moreover a heteropolar transverse axis; another Janus who possesses two unequal ears. A good instance of these forms is *Cocconeis notata*, one of the Monoraphideae (fig. 38). The comparison with fig. 49 of *Campyloneis* shows that here are also unequal differentiations at the ends of the transverse axis, whereas the sagittal axis is isopolar in both Diatoms. For the present I can give no more instances from nature: this class is not easy to distinguish because the sequence of the differentiations of the axes is decisive. Now we can very well determine this in the Diatoms in comparison with other species, but in other parts of the vegetable or animal kingdom this cannot be done.

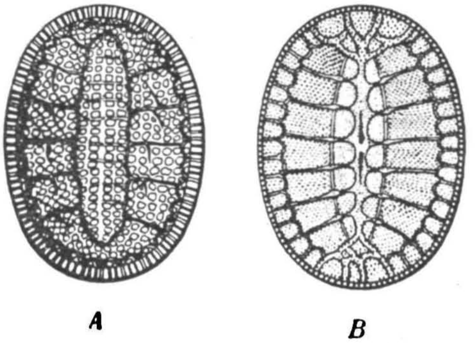

Fig. 49. *Campyloneis Grevillei*. A. Upper valve without raphe. B. Lower valve with raphe. From ENGLER and PRANTL 2nd ed., 2, 1928, p. 2/1, fig. 359, A and B.

If the heteropolar axis comes immediately after the main axis which of course has to be heteropolar also, the object belongs to the following symmetry class, that of the dorsiventral symmetry. It is evident that in future it may appear that some dorsiventral organisms are really unequal-sided bifrontal.

F. Dorsiventral symmetry. As already mentioned when discussing the preceding class the distinction between dorsiventral symmetry and unequal-sided bifrontal symmetry is not always easy. The body of Man for instance has from head to foot a very distinct main axis, which is heteropolar. Further there is another heteropolar axis, which we call sagittal axis. No reasons are to be found to distinguish a transverse axis, which would be isopolar: the two poles of the main axis and the two poles of the sagittal axis are sufficient to controll all the differentiations. But, as we do not know the sequence of the axes, we may also come to the conclusion that the secondary axis runs from left to right and is isopolar, while the ternary axis is heteropolar. This opinion cannot be proved, so it is simplest to say that the secondary axis is heteropolar. Then the human body is dorsiventral.

As already remarked, the dorsiventral symmetry is often realized in the animal kingdom as well as in plants. All *Vertebrates* are dorsiventral and so are the plagiotropic plants. Other instances are the flower of *Cassia* (fig. 50), the stem of *Marchantia*, the foliose Hepatics, some Diatoms as *Rhoicosphenia* (fig. 8) and many organs of plants.

G. Unequal-sided dorsiventral symmetry. Here we find three axes perpendicular to each other which are heteropolar. A good instance of this symmetry form is the flower of *Valeriana* (fig. 51) where the difference between front and back (fore and behind) (= ends of the sagittal axis) as in the flower of *Cassia* (fig. 50), is added a difference between left and right side if we mark the places of the three stamens.

Other instances are the leaf of *Begonia* and the contort corolla of many flowers if one side of the petals is much larger.

Fig. 50. *Cassia floribunda*. Flower. From BAILLON, p. 123.

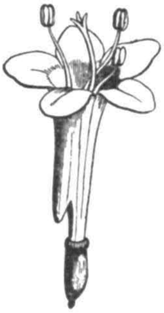

Fig. 51. *Valariana officinalis*. Section of flower. From BAILLON, p. 508.

* § 18. **Summary.**

1. Usually the organic symmetry is explained by means of idealistic suppositions. In this chapter an attempt will be made to replace this usual idealistic explanation by a causal one.

2. The meaning of the term symmetry has not always been the same. In modern sciences, especially in cristallography and in mathematics the following definition of symmetry is given: the quality of consisting of two or more equal parts, which are distributed in such a way that the spatial relations between the parts are the same for any part. This definition is also accepted in this paper for biology; the enlargement of the meaning of symmetry to all spatial relations in plants, as GOEBEL did, is rejected.

3. In zoological works the term symmetrical is often limited to the meaning dorsiventral; this meaning is also rejected here.

4. In mathematical figures with symmetry we meet symmetry axes, symmetry planes and often a symmetry centre. Symmetry axes are lines around which the equal parts are distributed in such a way that after certain movements of the figure around or along the axis the figure coincides with itself. A symmetry plane divide the figure into two parts which are each other's mirror-images. And a symmetry centre is such a point, that every line passing through it meets equal parts of the figure at equal distances.

5. There is a different way of symmetry in finite and in infinite figures. The symmetry axis present in figures with finite symmetry is a rotation axis the number n of which may vary from 2 to ∞, while the place of the axis is fixed. In figures with an infinite symmetry the number n of rotation axes which are perpendicular to an infinite plane, is limited to 2, 3, 4 or 6 and they have no determined position, only their direction is fixed.

Symmetry planes also lose their fixed positions in figures which extend infinitely in the dimension perpendicular to the plans. A symmetry centre has only a fixed position in finite figures.

6. As the occurrence of a symmetry element in nature is due to the previous action of natural causes, there must be an important difference between organic and methematical symmetry. This difference is only gradual, as the realization of the symmetry in organisms is more or less accurate.

7. The difference between the symmetry in crystals and in organisms is only due to the fact that the organic symmetry is generally that of finite figures, whereas the symmetry in crystals is always based on the features of infinite space-lattices.

The occurrence of infinite symmetry in organisms is limited to some local differentiations. A good instance is the symmetry of the alveoles on the valve of *Eupleurosigma* and *Gyrosigma*. The properties of this little realized form of organic symmetry are the same as those of crystals.

Generally speaking symmetry is realized to a much greater perfection in crystals than in organisms.

8. The symmetry in organisms is also compared with the symmetry in non-crystalline matter such as: a rain-drop, the chambers in a froth, and basaltic columns. The discussion of this point, giving in § 11, B, illustrate the fact that for the origin of a general symmetry in a large collection of elements a common cause ruling the distribution of the equal parts is required.

9. In literature the causal basis of organic symmetry is not often discussed. The biologists were mostly satisfied by assuming a tendency to symmetry in all living beings. Only THOMPSON and CHURCH endeavour to give an explanation by deriving it from the molecular structure of the protoplasm. THOMPSON further mentions the surface tension as the cause

of organic symmetry, not only in the cells with a spherical form but also as the cause of any outgrowth.

10. The distribution of the equal parts in organisms is due to their origin by growth and by differentiation, as it lies hidden in the ontogeny. Growth alone can never be the cause of symmetry, differentiation of growth is necessary. The cause of organic symmetry therefore lies hidden in the fundamental plan.

11. The symmetry in organisms without biological axes is demonstrated in the pollen grains of *Cucurbita* and *Alisma*. The researches of TAMMES on these pollen grains demonstrate that the symmetry is due to local formations in so far that the places of exit are at more or less equal distances. In such cases where it suits the size of the pollen grains this may give rise to forms with a high degree of symmetry. Therefore this symmetry is not a constant feature of the fundamental plan.

12. Even the structure of the valves of the Centric Diatoms is not due to physiological processes itself, but it is the combined action of all these processes which brings about the fundamental plan and the realized symmetry is always more or less approximate.

13. Biological axes can be curved or twisted or they can even be a screw line whereas mathematical axes are always straight. Even in other respects the biological axes are not identical with mathematical symmetry-axes. Thus the body of Man has two biological axes: a vertical axis and a horizontal one between the dorsal and the ventral side. The only mathematical axis on the other hand is the third line between the right and left, which is perpendicular to the two biological axes.

14. Any organism with an isopolar biological axis has a symmetry plane perpendicular to this axis, and both iso- and heteropolar biological axes bring about an infinite number of symmetry planes passing through the axis, if there are no other activations of morphogenetic factors.

15. The main features of organic symmetry are: 1) the imperfect character of it; 2) the frequent changes of symmetry in organisms; 3) the preponderantly finite character of the organic symmetry (only in a few cases a symmetry with an infinite character is realized); 4) the almost universal occurrence in organisms; 5) the predominance of a very few symmetry classes.

16. Two theses are put forth to explain the almost universal occurrence of symmetry in organisms: 1) symmetry is often nothing but a lack of differentiation; 2) organic symmetry may often be furthered by natural selection, due to the demands of locomotion and of statics.

17. Local symmetry may be due to a successive formation, starting from a certain centre, at equal distances from each other.

18. Three groups of causes bring about the symmetry: 1) surface tension; 2) the occurrence of biological axes, combined with a similarity by lack of differentiation of the minor activations controlled by these axes,

and 3) the biological advantages attained by an approach to symmetry, and which have been fixed by natural selection.

19. The predominance of radial and dorsiventral symmetry can be understood because these classes have great advantages for sessile and freely moving organisms, radial symmetry especially for orthotropic sessile organisms, and dorsiventral symmetry for plagiotropic sessile and freely moving organisms. Therefore dorsiventrality prevails in the animal kingdom and radial as well as dorsiventral symmetry is widespread in plants.

20. Two earlier classifications of organic symmetry have been discussed: 1) the classification of HAECKEL in his Generelle Morphologie (1866) which is a mixture of biology and mathematics, contains too many classes and, moreover, the names of the classes are difficult to memorize; 2) the classification of JAEGER (1917), which is too mathematical and which therefore pays no attention to causes and events, and, moreover, organic symmetry being only an approximation to symmetry, it cannot be described in a mathematical way.

21. The new classification of organic symmetry given here is based upon the essential biological features, such as the fundamental plan and the biological axes. It distinguishes twelve classes. Firstly two classes without biological axes: asymmetry with no regularity at all and spheroidal symmetry with a spherical form. Further five classes with an isopolar main axis: discoidal, trabal, unequal-sided trabal, pontal and unequal-sided pontal symmetry, and also five classes with a heteropolar main axis: radial, bifrontal, unequal-sided bifrontal, dorsiventral and unequal-sided dorsiventral symmetry. The distinction between these five classes in every group is that there are respectively only a main axis, a main axis with an isopolar sagittal axis only, an isopolar sagittal axis with a heteropolar transverse axis, a heteropolar sagittal axis only and a heteropolar sagittal axis with a heteropolar transverse axis.

All other names, commonly used in literature by zoologists and botanists are rejected.

22. For a further discussion and for instances of these various symmetry classes see the paragraphs 15—17.

LIST OF LITERATURE.

BOK, S. T. On the shape of froth chambers. Proceedings Nederl. Akad. Wet. **43**, 1940, p. 1180.

BOUILLENNE R. et F. WENT. Recherches experimentales sur la néoformation des racines dans les plantules et les boutures des plantes supérieures (substances formatrices de racines). Ann. du jardin botanique de Buitenzorg **63**, 1933, p. 1.

BOWER, F. O. Size and form in plants with special reference to the primary conducting tracts. London, 1930.

————. Botany of the living plant, 3rd ed. London, 1939.

BRAUN, AL. Über Symmetrie in der Pflanzenbildung. Flora, **25**, 1842, p. 729.

BRONN, H. G. Morphologische Studien über die Gestaltungsgesetze der Naturkörper. Leipzig, 1858.

CANDOLLE, A. P. DE. Théorie élémentaire de la botanique, etc. Paris, 1813.

CHURCH, A. H. On the relation of phyllotaxis to mechanical law. London, 1904.

————. On the interpretation of phenomena of phyllotaxis. Botanical memoirs No. 6. Oxford, 1920.

CLAUS, C., K. GROBBEN, A. KÜHN. Lehrbuch der Zoölogie. Berlin und Wien, 1932.

CLEVE, P. T. Synopsis of the naviculoid Diatoms. K. Sv. Vet. Ak. Handl., **26**, 2. 1894; **27**, 3. 1895.

CROW, W. B. Symmetry in organisms. Amer. Naturalist **62**, 1928, p. 207.

CUÉNOT, L. La Comatule, *Antedon bifida* (Pennant); in: L. BOUTAN, Zoölogie descriptive, Anatomie, Histologie et dissection des formes typiques d'Invertebrés, **1**, Paris, 1900.

DÖLL, J. CH. Bemerkungen über die Symmetrie in der organischen Natur, insbesondere über die Symmetrie der Blüthe, **25**er Jahresbericht d. Mannheimer Vereins für Naturkunde, Mannheim, 1859, p. 29.

EICHLER, A. W. Blüthendiagramme. Leipzig, 1875—1878.

ETTINGHAUSEN, C. RITTER VON. Die blattskelette der Apetalen. Eine Vorarbeit zur Interpretation der fossilen Pflanzenreste. Denkschr. math. naturw. Cl. K. Akad. d. Wiss. Wien, **15**, 1858.

FISCHER, H. Beiträge zur vergleichenden Morphologie der Pollenkörner, Breslau, 1890.

FREY, A. Geometrische Symmetriebetrachtung, Flora **120**, 1926, p. 87.

FREY—WYSSLING, A. Submikroskopische Morphologie des Protoplasmas und seiner Derivate. Protoplasma-Monographien **15**, Berlin, 1938.

FREYHOLD, E. VON. Über Symmetrieverhältnisse und Zygomorphismus der Blüthen, 1874er Herbstprogramm der höheren Bürgerschule zu Eupen, Eupen, 1874.

GIESENHAGEN, K. Untersuchungen über die Characeen. Flora **83**, 1897, p. 160.

GOEBEL, K. Organographie der Pflanzen, insbesondere der Archegoniaten und Samenpflanzen. Jena, 1898—1901. 2nd ed. Jena, 1913—1923. 3rd ed. Jena, 1928—1933.

————. Die Entfaltungsbewegungen der Pflanzen und deren teleologische Deutung, Ergänzungsband zur Organographie der Pflanzen, Jena, 1920; 2nd. ed. Jena 1924.

————. Blütenbildung und Sprossgestaltung (Anthokladien und Infloreszenzen), Ergänzungsband 2 zur Organographie der Pflanzen, Jena, 1931.

GRUNOW, A. Algae, in: Reise der Österr. Fregatte Novara um die Erde in den Jahren 1857, 1858, 1859 unter den Befehlen des Commodore B. von Willerstorf—Urfair, Botan. Theil, 1, Sporenpflanzen, Wien, 1870, p. 1.

————. Bemerkungen zu den Diatomeen von Finmark, dem Karischen Meere und vom Jenissey nebst Vorarbeiten für Monographien der Gattungen *Nitzschia,* *Achnanthes, Pleurosigma, Amphiprora, Plagiotropis, Hyalodiscus, Podosira,* und einiger *Navicula*-Gruppen; in P. T. CLEVE und A. GRUNOW. Beiträge zur Kenntniss der Arctischen Diatomeen. Kgl. Sv. Vetensk,-Akad. Handl. **17,** 2, 1880.

HAECKEL, E. Die Radiolarien (Rhizopoda Radiaria). Eine Monograhie, Atlas, Berlin, 1862.

————. Generelle Morphologie der Organismen, Berlin, 1866.

HERTWIG, R. Lehrbuch der Zoölogie. Jena, 1892.

HEYMANS, G. Einführung in die Metaphysik auf Grundlage der Erfahrung, Leipzig, 1905, 3rd ed., 1921.

HIRSCH—SCHWEIGGER, E. Zoölogiches Wörterbuch. Berlin und Leipzig, 1925.

HUSTEDT, FR. Die Kieselalgen Deutschlands, Oesterreichs und der Schweiz mit berücksichtigung der übrigen Länder Europas sowie der angrenzenden Meeresgebiete, in Rabenhorst's Kryptogamen-Flora von Deutschland, Oesterreich und der Schweiz, Band **7,** 1930.

JAEGER, F. M. Lectures on the principle of symmetry and its applications in all natural sciences, Amsterdam, 1917.

JAEGER. G. Über Symmetrie und Regularität als Eintheilungsprinzipien des Thierreichs. Sitz. ber. d. Kais. Ak. d. Wiss., Math.-natuurw. Cl., **24**, Wien, 1857, p. 338.

KARSTEN, G. Bacillariophyta (Diatomeae) in: Die natürlichen Pflanzenfamilien 2nd. ed., **2,** 1928.

KRUMBACH, TH. Ctenophora in W. Kükenthal — Th. Krumbach. Handbuch der Zoölogie. Bd. **1**. Berlin und Leipzig. 1923/1925, p. 405.

LEWIS, F. T. A note on symmetry as a factor in the evolution of plants and animals. Amer. Naturalist **57,** 1923, p. 5.

LUDWIG, W. Das Rechts-Links-Problem im Tierreich und beim Menschen mit einem Anhang Rechts-Links-Merkmale der Pflanzen, Berlin, 1932.

MEYER, E. Die Metamorphose der Pflanze und ihre Widersacher, Linnaea **7,** 1832, p. 401.

MOHL, H. Beiträge zur Anatomie und Physiologie der Gewächse, **1,** Über den Bau und die Formen der Pollenkörner, Bern, 1834. Reissued in shortened form and with less illustrations in Ann. d. sc. nat. Bot. 2nd ser. **3,** 1835, p. 148, 220, 304.

————. Über die Symmetrie der Pflanzen, see below under SCHNECKENBERGER.

MOLL, J. W. Phytography as a fine art. Leiden. 1934.

MÜLLER, FRITZ. Über die angebliche Bilateralsymmetrie der Rippenquallen, Archiv für Naturgesch. **27,** 1, 1861, p. 320.

MÜLLER, OTTO. Über Achsen, Orientirungs- und Symmetrieebenen bei den Bacillariaceae, Berichte d. D. bot. Ges. **13,** 1895, p. 222.

OLTMANNS, FR. Morphologie und Biologie der Algen, 2nd ed. Jena, 1923.

ORTHE, R. Zur Morphologie der Primärblätter einheimischer Farne. Flora **133,** 1938, p. 1.

PEYRITSCH, J. Untersuchungen über die Aetiologie pelorischer Blüthenbildungen, Denkschr. math. naturw. Cl. K. Akad. d. Wiss. Wien, **38,** 1878, p. 109.

RAIUS, J. Historia Plantarum species hactenus editas aliasque insuper multas noviter inventas & descriptas complectens. I. London 1686.

RASHEVSKY, N. Some remarks on the mathematical biophysics of organic assymmetry, Acta biotheoretica, Leiden, **4,** 1939, p. 197.

SACHS, J. Stoff und Form der Pflanzenorgane, Arbeiten des botan. Inst. Würzburg **2,** 1880. p. 452; reprinted in J. SACHS, Gesamm. Abh. **2,** Leipzig 1893.

SCHOUTE, J. C. Morphology in F. VERDOORN, Manual of Pteridophytology, 1938.

————. Whorled phyllotaxis. **4,** 1938.

SCHNECKENBERGER, T. CH. Über die Symmetrie der Pflanzen. Thesis Tübingen 1836, also published under the name of H. MOHL in Flora **20,** 1837, 2, p. 29 and in a revised form without the original authors name in: H. VON MOHL, Vermischte Schriften botanischen Inhalts, Tübingen 1845, p. 12.

SCHNUSSNIG, B. Vergleichende Morphologie der niederen Pflanzen. I. Formbildung. Berlin, 1938.

SCHÜTT, F. Bacillariaceae. Die natürlichen Pflanzenfamilien, I, **1**, b, 1906, p. 31.

SINNOTT, E. W. Morphology as a dynamic science. Science **85**, 1937, p. 61.

SPENGEL, J. W. Betrachtungen über die Architektonik der Tiere. Zoöl. Jahrb. Suppl. **8**, Jena, 1905 (Festschrift K. Möbius, p. 369).

TAMMES, P. M. On the origin of number and arrangement of the places of exit on the surface of pollen-grains. Rec. trav. bot. neérl. **28**, 1930, p. 1.

THOMPSON, D' A. W. On growth and form. Cambridge, 1917; 2nd. ed. 1942.

TROLL, W. Vergleichende Morphologie der höheren Pflanzen. Erster Band: Vegetationsorgane. Erster Teil. Berlin, 1937.

WILBRAND, J. B. Über die Natur der Blume, und über das gegenseitige Verhalten ihrer Theile; — insbesondere über den Kelch und die Krone bei den einsamenblättrigen Pflanzen. Flora **4**, 1821, p. 413.

ZIEGLER, H. E. Zoölogisches Wörterbuch. Jena, 1903.