STUDIES IN PHYLOGENY

I.

On the relation of Taxonomy, Phylogeny and Biogeography [1]

by

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> "Namentlich die Biogeographie ist ohne die "Geschichte der Organismen, die ja zugleich "die Geschichte ihrer Verbreitung ist, gar "nicht zu verstehen". (ADOLF MEYER, Logik der Morphologie, etc. 1926, p. 233).

Summary.

Taxonomy is static, its symbols are therefore two-dimensional, representing 1. differences or resemblances and 2. diversity (eventually are also area). Phylogeny is dynamic and its symbols are three-dimensional, representing 1. Time, 2. differences or resemblances and 3. diversity (eventually also migration). The term *"genorheithrum"* is proposed for a "stream of potentialities" as a phylogenetic unit in the Time. Taxonomic units are cross-sections through genorheithra, the boundaries of which are discontinuities of various kinds. A new discontinuity originates, as a rule, from a great number of potentialities (not from a single [pair of] parents). This implies the probability of polytopy as a common phenomenon, and also the supposition of a minimum of genetic property, below which a discontinuity is not viable. Natural extinction may be largely due to the loss of potentialities. — Corresponding reasonings may be applied to Biogeography, which may be static (floristics and faunistics) or dynamic (migrations). Taxonomic units are represented here by areas, the rate of extension of which may be a function of the number of potentialities. The forces, influencing the motion of any point of an area boundary are briefly summarized in a table, demonstrating the embarrassing complexity of WILLIS' statistical methods. In addition, the "law of BEYERINCK" is formulated anew on a broader basis. Disappearing of areas may be due to two causes: extinction of the units (loss of potentialities), or dissolution into new units (areas). The minimum of potentialities mentioned finds a geographic analogon in the law of the minimum area, established by PALMGREN.

As I have pointed out in a previous paper (lit. [2]) 16, p. 178 ss.),

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[1]) I have to express my sincere thanks to my friend Prof. L. G. M. BAAS BECKING fir kindly correcting the English.

[2]) At the end of Nr. II.

taxonomical and phylogenetical considerations, schemes and symbols have, in my opinion, to be sharply distinguished, and in symbols to every distance and angle a definite significance has to be attributed, if possible.

Taxonomy is the expression of momentary relations between concrete or abstract items which are found or brought together. It is nothing but classification. A classification, however, may be senseless or may have a certain leading idea as a basis or a frame and may, in the latter case, more or less claim the epithet "natural". As has recently been recalled in a clear and fascinating way by GILMOUR, a system is the more natural as a more important character has been chosen as a base for the classification; and a character is the more important, as it is more fundamentally connected with the origin or the (main) purpose of the unit in which it is incorporated. However, as GILMOUR states, there are no sharp boundaries and no essential differences between artificial and natural systems, no more than between taxonomy of inanimate and of animate, of concrete and of abstract things. A taxonomic scheme is the expression of relations at one moment and is therefore static; it is an instantaneous photograph of a moving object. It may therefore be symbolized by a two-dimensional figure. In Taxonomy we can never speak of kinship, but merely of resemblances or differences. The significance or the cause of these resemblances or differences cannot be stated by direct methods, as they cannot be concluded from data available in the system.

The mutual relations of taxonomic units may be indicated by a natural system, situated in a plane, which represents the moment of observation. Their relative diversity may be represented by the surface occupied by their symbols (delimited by circles which symbolize their discontinuity), their differences (or resemblances) may be represented by their mutual distances. However, such an arrangement cannot be but the product of intuition, as for each character incorporated in a system, another dimension is needed. It can therefore, as a rule, not be established on the basis of one of the exact methods. If one single character is taken to base the system upon, a linear arrangement is obtained. With two independent characters, the place of each object is defined by the coordinates in a plane. At the utmost three independent characters can be taken into account, viz. in a three-dimensional stereometric figure with three coordinates. As this method gives only small and relative advantage, and the third dimension, as will be shown below, is to be reserved for a special function, two-dimensional schemes are preferable for symbolizing static relations. However, as it is often desirable that more than 2 characters be incorporated in order to obtain a natural taxonomic arrangement, the only remaining method is that a certain, more or less arbitrarily chosen object be taken as a "standard object", around which all other objects may be arranged according to the number of characters they have or have not in common with it (cf. lit. 16, figs. 28b and 28c). The choice of the object can be based upon the sharing and participation of features (lit. 16, p. 183) or upon the importance of certain features.

It is, however, not my intention to discuss the nature of these taxonomic units here. Whatever they may be called and whatever their numerous definitions may be, for our present purpose it may be sufficient to state that they are delimited by discontinuities, i.e. by more or less sudden "gradient" of the greater number of their fundamental characters.

The distinguishing factor of Taxonomy towards Phylogeny is, as I see it, the factor Time. If taxonomical schemes are symbolized by two-dimensional figures in a plane, the Time factor must be thought perpendicular to that plane. Phylogenetic symbols must therefore make use of three dimensions, one of which is always Time. This Time Coordinate which is considered as constant, is crossed by innumerable Time Levels, in each of which a momentary taxonomic scheme may find its place. Phylogeny considers changes from Time Level to Time Level, from taxonomic scheme to taxonomic scheme, from one phase of a character to a next one, i.e. it considers kinship and is therefore dynamic. A relation along the Time Ordinate should mean a static condition (no evolutionary change), a line perpendicular to the Time Ordinate and therefore situated in a Time Level should represent a sudden change (at a certain time), e.g. a mutation; any angle with the Time Axis should indicate a resultant of Time and change and by its width the rate of evolution should be expressed (lit. 16, fig. 31).

Taxonomic schemes are therefore cross-sections through phylogenetic schemes. As the Time can never be eliminated from human interpretations of the Universe, Phylogeny is primary to Taxonomy and represents the more general case, while Taxonomy has to be considered as an interpretation of a temporal condition.

What has been said above concerning Taxonomic units, is also true for Phylogenetic ones. Whereas Taxonomy is based upon characters, Phylogeny is based upon changes of characters, i.e. upon evolutionary processes. As characters are, in some way, the materializations or functionalizations of genes or of combinations of genes, and these may be called potentialities in general, we can imagine the units of Phylogeny as "streams of potentialities", drifting by the power of Time. As we observe discontinuities in their cross-sections, they must be delimited by discontinuities also, and, as the term "*line* of evolution" does, I think, not satisfactorily fit the ideas, developed in this paper, I would, in accordance with the terms "mono-, bi- and polyrheithry" proposed by me in an earlier paper (lit. 16, p. 189), introduce here the term "genorheithrum" for such a stream of potentialities. As may already be stated in their cross-sections (the taxonomic units), their discontinuity may be sharp or vague. The discontinuity, which is based upon hybridization possibilities (lit. 5), though far from sharp in itself, may be considered as the most reliable and most comprehensive discontinuity to constitute genorheithra. I would, in this connection, recall the schematical "cross-section" through a genorheithrum by SHULL (quoted in lit. 16, p. 186, note). A genorheithrum might be considered as consisting of genes (or potentialities), which are more or less closely and indissolvably linked to each other. Whether this linkage shows any periodicity may remain undiscussed here, but it may be recalled that, in my opinion, *there is no essential difference between linked and unlinked genes.* Those genes which are not closely linked are constituting what has been named "Erbstock" (PLATE, quoted by LÜTJEHARMS, lit. 19, pp. 187—188) or "radicals" (VAVILOV, see lit. 16 and 19), but the differences in "linkage-power" and "dissolution-time" is, I think, showing a regular gradient or at least regular and small steps from the oldest and most solid "Erbstock" towards genes which are situated more near the "surface" of the genorheithrum, i.e. genes which are (still) more liable to participate partly or totally independently in hybridization. In a previous paper (lit. 14, p. 190) the same view has been put forward in regard to characters of subsequent rank, i.e. to materializations of genes.

I am inclined to consider this process also as a function of time and I might recall the attempt made by BLUM (quoted in lit. 16, p. 173) to gather both inorganic and organic evolution under the same explanation. Whether this explanation (the law of entropy) be correct or not, there is certainly a striking simile between atoms and genes, inasfar as both may be thought as "bodies" with a smaller or greater number of unsaturated affinities which strive for being occupied. We do not know whether there is more than an analogy in this resemblance and the gap between the animate and the inanimate is still insuperable.

As long as this gap is not bridged, we will not be able to say whether the origin of life was broadly or narrowly grounded, mono- or polyphyletic, restricted to one period or of all times. Yet, it may be supposed that Life is a special condition of matter which may be attained in various forms (of which we only know a single one) and in all those cases, when a certain "level" — the nature of which is still a mystery to us — is reached.

Whatever, for the rest, the internal factors may effectuate, concerning external or environmental ones (which are, perhaps, nothing else but complexes of *other* internal factors), *the rule of* BEYERINCK, running: "Everything is everywhere, but the environment selects", raised to the rank of a law by BAAS BECKING (lit. 1, p. 8, and 2, pp. 13—15; cf. also TAN, lit. 28, p. 116), *is possibly still more valid in regard to genes than to organisms.*

It might be suggested that sexual discontinuities should guard a genorheithrum against the escape of potentialities. Although there may be a certain protection in this sense, it becomes, I think, only more effective with age. *As I see it, a discontinuity — say a "species" — does not originate, as a rule, from a single parent or a couple of parents, but from a great number of potentialities.* This may be true if hybridization is the agent, but I see no reason why it would not be true also if the "new species" would originate as a mutant or as the product of poly- or heteroploidy. Whether induced by environmental conditions or not, I suggest that the origin of species is at least as much (if not more) a matter of time (or "maturity" or "periodicity" or "internal factors") as of anything else (external factors). I think — in contradistinction to the views of WILLIS — that most and perhaps all of the surviving new "species" (DANSER's comparia or commiscua, lit. 5) are disposing of a rich property of genes, *of which an arbitrary individual is only comprising a certain part.* I would also suggest that *the viability of a discontinuity is, in a way, proportional to the number (and also the quality?) of potentialities* ¹) *it has at its disposal. Consequently, it might be suggested that there is a certain critical minimum in this number, below which a new "species" either never arises, immediately disappears or is doomed to perish.* At any rate, a true sexual discon-

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¹) Cf. E. ANDERSON (Bot. Review 3, 1937, 335 and Amer. Naturalist 71, 1937, 223), who showed that the area of the tetraploid individuals of a species is often considerably larger than that of the diploid ones. According to the investigations of O. HAGERUP (Hereditas 16, 1932, 19, and 18, 1933, 122) polyploid species and individuals are, ecologically speaking, stronger than diploid ones.

tinuity, once in existence, cannot but become poorer in its genetic property, unless new genes are originating, of which, I think, we know nothing as far as an existing discontinuity is concerned (cf. DANSER, lit. 4, p. 34, and 5, pp. 409, 432). Apart from unknown causes, this impoverishment can be effected by catastrophal destruction of individuals (tectonic and volcanic processes and other sudden geological changes), but also by the escape of potentialities. In young discontinuities, there will be little chance for such an escape, but with age internal and external factors (isolation) may cooperate in severing parts of the genetic property. If similar combinations of genes are isolated at various places but in one and the same discontinuity, we speak of *polytopy*, which I think is very frequent but uneffective in young, ever less frequent and more effective (towards the origin of species) in older genorheithra. If the isolation of potentialities is taking place in two or more sexual discontinuities, we call it *bi-* or *polyrheithry*, which may be mono-, bi- or polytopic. Polyrheithry will, as a matter of course, be a more rare phenomenon than polytopy, as the chance that similar combinations of potentialities originate from two or more groups of potentialities is the smaller, the less potentialities these groups have in common. And they have, as a rule, the less potentialities in common, the longer they are sexually discontinuous. Of course polytopy and to a lesser degree also polyrheithry is not necessarily restricted to one and the same Time Level. If the time difference is large, this point may be of importance for the reliability of guide fossils.

According to the views mentioned above, it must be concluded that discontinuities may become so poor in genetic property that they are no longer viable. *The loss of potentialities (number and quality) may be one of the main causes of "natural" extinction.* This is, however, a matter which urgently requires a closer investigation, in which the palaeontologist may contribute a good deal of evidence. TAN (lit. 28, pp. 116—117) has shown that certain Foraminiferae are suddenly disappearing as soon as a certain final phase (even of a single feature) has been attained. The proportional influence of "number" and "quality" of genes on extinction is still entirely unknown. Age, furthermore, makes the discontinuities sharper, the distances between genorheithra greater. The chance for polytopy and polyrheithry is soon reduced to none and potentialities can no longer escape by this way.

Polytopy and polyrheithry are homologies. These may in some way persist for a long time. Analogies (which I consider as of genetic origin) are, in my opinion, merely unexplainable homologies. They may be found even between the most distant discontinuities. In most cases a genorheithrum which is doomed to perish, disappears soon, in a few cases it persists through astonishingly long times, such as *Ginkgo.* In some old genorheithra enough potentialities have apparently been preserved, so many that a new species explosion in a new area is possible (cf. lit. 18).

We have stated that there are both exact and intuitive methods in arranging taxonomic units and we have now to discuss the same theme concerning Phylogeny. The changes of characters, on which Phylogeny is based, may be investigated, as far as I can see, by means of three methods, (in addition to the methods of *morphology, ontogeny* and *teratology*), viz.:

1. *Genetical (and cytological) methods.* The advantage of these is that the phenomena are apparent and clear, but the great difficulty is to extrapolate the results into the past and relative to large differences.

2. *Palaeontological methods.* These are almost as exact as the genetic ones and they cover, moreover, the whole past. Unfortunately the gaps are large, and of large numbers of extinct creatures nothing is left. On the other hand, however, no other science yields so trustworthy and direct indications towards Phylogeny, since certain undisturbed beds in which certain groups of organisms were deposited in large numbers, with fairly constant rate and in horizontal layers, provide us with palaeontological evidence of the highest value. The palaeontologist is the only investigator who can directly interpret such fundamental data as the direction of an evolutionary tendency and changes in the evolutionary rate, as has been shown, for instance, by KAUFFMANN and by TAN; both of these authors are emphasizing the method of the phylogeny of single features in palaeontology. Environmental conditions, however, which may be studied both by method 1 and by method 3, are theory for the palaeontologist.

3. *Geographical methods.* These are less trustworthy as they are not direct but deductive. They are based upon the present distribution of succedaneous phases of characters (tendencies) (cf. lit. 14, 15 and 17).

With the last-named method Biogeography comes in. Also in this matter Time is a distinguishing factor; there is a biogeography of the moment and a biogeography in the time.

Taxonomy and Floristics (Faunistics) are static. The units are discontinuities in a taxonomic and a geographic sense respectively, i.e. species, etc. and areas. Floristics may study the distribution of species or of characters. An interesting analogy is found in the way in which taxonomic units (and areas) on one hand, and floristic regions on the other are delimited, viz. on the basis of sudden "gradients" of characters (taxonomic units and areas) and of specific areas (floristic regions).

Phylogeny and Historical Biogeography are dynamic. The latter considers migration of genorheithra (and dispersal of individuals). This is the field covered by WILLIS' theories of "Age and Area" and of "Size and Space". I need not recall the opposition and the criticism these theories have met with. Not only has WILLIS undoubtedly overestimated the bearing and the importance of his views and misused statistical methods, but the lecture of his reasonings made me often think of the story of the tall man who was asked why his legs were so long and who replied: "because short legs would not be long enough to reach as far down as the ground". I mean to say with this metaphor that WILLIS' reasonings are often sophisms, the invalidation of which is only obvious when they are pursued down to their very roots. While in many respects his book may have been a failure, one of its merits is certainly that it emphasizes the prime importance of the factor Time both for evolution and for migration. But, as has been repeatedly pointed out by several critics, every single case has to be separately considered, and the general rules, far from having the rank of the laws of Gravitation, of DARWIN's selection theory or of MENDEL's laws of hybridization, are too simple to require so extensive arguments.

The area of a taxonomic unit (as well as that of a feature and of a gene or of a group of genes), that has once come into existence and that is able to maintain itself, is subject to numerous forces, which are only partly known to us, but which may be classed into one of the following four categories (see Table I, p. 122).

The most ideal form of an area is a sphere. This is only very exceptionally realized for taxonomic units, though it is not uncommon in colonies (*Bacteria, Algae,* etc.). The most usual form is, as a matter of course, a surface, e.g. that of the earth, and its ideal form is a circle. However, the area of a taxonomic unit of living organisms is not static. Its boundary is incessantly moving, slowly or rapidly, on account of internal and external processes (among which migration and evolution are affecting all of the four categories mentioned), which processes are, in some way, a function of Time. The momentary movement of each point in the boundary of an area is a function of the rest of the positive and negative, internal and external factors, affecting that particular point at that particular moment.

TABLE I.

<table>
<tr><th></th><th>Positive</th><th>Negative</th></tr>
<tr><td>Internal,
(relative to taxonomical units, individuals or features [genes])</td><td>1. Eurybiotic
2. Large "viability" (genetic property?; polyploidy, fertility, etc.)
3. Well adapted to transport</td><td>1. Stenobiotic
2. Small "viability"
3. Not or not-well adapted to transport</td></tr>
<tr><td></td><td colspan="2">Regulation by Environment (selection) and Time (elimination of differences)</td></tr>
<tr><td>External
(environment)</td><td>1. Ecological gradient none or weak (no barriers; also: no parasites; man: growing, preservation of nature, etc.)
2. Competition none or weak
3. Accessibility large</td><td>1. Ecological gradient steep (strong barriers; also: parasites; man: devastation of natural vegetations)
2. Competition strong (inorganic nutrition: root competition; organic nutrition: shadow)
3. Accessibility small or none (climax)</td></tr>
</table>

These few and simple considerations comprise, I think, the whole theory of floristics and faunistics, in a nutshell. The above table hardly needs any comment. The terms *eury-* and *stenobiotic* are self-evident; they mean to comprise the action and reaction between the taxonomic unit, the individual, the feature or the gene or group of genes and the whole of the environment. What I mean with *"viability"* is discussed above. *"Ecological gradient"* is an expression to symbolize the measure of change in the constellation of ecological factors. *"Accessibility"* is a term, proposed by J. HEIMANS[1]) to comprise all those factors (such as chance, in the sense of PALMGREN), which cannot be classed with any current category of ecological factors (climatic, edaphic, biotic), but which nevertheless may be of the utmost importance. And I would add here a formulation of the "law of BEYERINCK" so as to comprise taxonomical units, as well as individuals, features and genes:

Diaspores (and therefore potentialities) are principally everywhere, but the environment selects potentialities and time eliminates differences in migrating velocity and the influence of chance. Furthermore factors thusfar unknown have to be taken into account, which are related to the number and the quality of the potentialities dispersed.

In this form the rule is based upon the principles of POTONIÉ ("Die Samen kommen im Prinzip überall hin"), BEYERINCK (principally for micro-organisms, cf. lit. 1 and 2) and PALMGREN (lit. 22).

In the above I have put forward the thesis that a new "species" may, as a rule, originate from a large group of potentialities. This implies the possibility, though not the necessity, that the specific area which comes into existence with the species, may be rather large, though of course smaller, and probably considerably smaller, than the parental area. In general, however, I think, a new area will not be very large and this is necessarily true in small islands and other regions which are ecologically isolated. What happens to an area of a new genorheithrum, depends upon innumerable factors, internal and external. In many cases the area may soon disappear, but if it succeeds in maintaining itself, it will try to extend and to occupy as much space as it can. In other words: in the last-named case it will increase with age. This is one of the simple truisms of WILLIS' theory. But as an area may start as a relatively large one, size cannot tell us, *in general*, something about age. Whether the new discontinuity enriches its genetic property at the expense of other discontinuities or whether latent genes are activated, it may be accepted that an explosion of diversity is following, possibly partly induced by environmental conditions (migration into new regions, etc.). In other words: its size increases with space. This is another one of WILLIS' truisms. But the development of an area has a very much complicated history, and what happens further to the genorheithrum and its area, depends upon specific and even individual conditions concerning affinities and linkage of genes, evolu-

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[1]) in "Nederl. Kruidkundig Archief" 44, 1934, 96 and in "Biologisch Jaarb." (Dodonaea) 4, 1937, 180.

tionary rate or periodicity, environmental factors met with during migration or changing factors while staying at the same spot, etc. *It may be suggested that it is again the number (and the quality?) of its potentialities, which is responsible for the rate of its extension, which rate is one of the manifestations of its viability.* All kinds of areas may be imagined, as there are all kinds of taxonomic units: rich and poor, large and small, long living and soon disappearing. At any rate, however, an increase must sooner or later be followed by a decrease. This decrease may have two causes; one is the loss of potentialities and the natural extinction, which may take a short or a long time. This is what happens, I think, to slowly changing old and relatively poor genorheithra with sharp discontinuities. It may be also found in such taxonomic units which (still) cover a large area but are very rare (reduced in number) either in a part of their area (regression; cf. Stud. in Phylog. II) or everywhere. The other way is a rejuvenation; the area is disappearing because the original definition of its taxonomic unit no longer fits, as it is evolving into one or dissolving into more new discontinuities. This is, I suppose, what happens to rapidly evolving and rich genorheithra. *The condition just mentioned, may be the main cause of the fact, that young (neo-) areas are apparently more frequent than old (relic) areas.* A remarkable example of coexistent small relic-areas, large areas and small neo-areas has been given as early as 1869 by KERNER.

An interesting floristic analogon with the idea of a "minimum number of potentialities" is found in the law of the minimum area, and of the proportional relation of the extensiveness of the region and the number of species, it may contain, established by PALMGREN (lit. 22, pp. 28, 76, 104, 120—125).

As the increase of area and of diversity are sometimes developing at about the same rate, viz. in well-delimited larger taxonomic groups and in well-delimited floristic regions, the same symbol may represent both items. This has been applied by me in a previous paper (cf. lit. 15); a new application may be found in the next "Study", in which some of the theses laid down in the present one, are illustrated.

The following scheme gives a survey of some of the ideas, mentioned above (Table II):

TABLE II.

General case		Special case	
Dynamic through the Time factor		*Static,* considering the conditions of one moment	
Symbols three-dimensional, comprising 1. Time; 2. difference or resemblance; 3. diversity (eventually also migration)		*Symbols* two-dimensional, comprising 1. difference or resemblance; 2. diversity (eventually also area)	
Historical Biogeography	**Phylogeny**	**Taxonomy**	**Floristics and Faunistics**
migration (dispersal)	genorheithra	taxonomic units	areas (distribution)
	kinship	resemblances (differences)	
migration of characters	changes in characters	characters (materializations or functionalizations of genes or combinations of genes)	distribution of characters
Analoga:		Analoga:	
minimum area (PALMGREN)	minimum genetic property	boundary of taxonomic units by "gradients" of character boundaries	boundary of floristic regions by "gradients" of areal boundaries