

## THE HOMOLGY CONCEPT IN PHYTOMORPHOLOGY—SOME MOOT POINTS

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### ABSTRACT

1. Various aspects of the homology concept are critically discussed, including (a) the difference between the scholastic or 'classical' basis of the concept and the neomorphological (phylogenetic) or 'dynamic' approach, (b) the requisite of a reciprocity of the relationships among homologous elements belonging to the same conventional (i.e., a static and intranscendent) organ category, (c) the relativity of the homology concept in phylogenetic botany, and (d) the necessity of recognising categories of *ab initio* inhomologous objects other than those distinguished in static morphology (i.e., essentially, the postulation of *organa sui generis* — already silently practised in traditional morphological thought — along different lines).

2. Irrespective of the question whether the neological, i.e., evolutionary and hence 'dynamic', approach to the problem of homology is conceptually and methodologically different from the conventional, i.e., typological and 'static', phytomorphology, the conclusion must be drawn that the two are, in several respects, incompatible, the reasons underlying the differences in some fundamental acceptances and the ensuing interpretations being (a) the different delimitations of the intranscendent categories of morphological units (organs, etc.), (b) the invariable and 'all or none' equivalence of morphological entities in static phytomorphology *versus* the relativity of the homology relation in the 'dynamic' (semophyletic) morphology, and (c) the restriction of the old tenets of homotopy and homodynamy (serial homology) in the New Morphology by the additional requisite of constancy of organogenetic and histogenetic induction during the ontogenetic or morphogenetic differentiation and development of the organs and other structures involved.

3. A consequent application of the neomorphological principles leads to the rejection of several mainstays of the conventional interpretative morphology, such as the 'sporophyll' (foliar carpel and phylloic stamen) concept, and also to the emendation, or the dismissal, of several allegedly phylogenetic deductions and conclusions, especially of certain aspects of the Telome Theory (in the form developed by Zimmermann).

4. The application of the homology concept to organs belonging to the same individual, and to organs differentiating during diverse phases in the life cycle of an individual (such as the alternating gametophytic and sporophytic generations, or the vegetative shoot development and the state of flowering), also involving the concepts of homotopy and homodynamy, is discussed and the limitations in the application of the concept are outlined against the background of genetic potential, phenotypic expression, determination, induction and morphogenetic differentiation.

5. The comparatively insignificant contribution of teratology to interpretative morphology is explained.

### 1. STATEMENT OF THE PROBLEM

Recently a paper on the homology problem was published (ECKARDT, 1964) in which once more the statement is made (l.c., p. 81) that there is only one premise underlying all homology concepts, notwithstanding the rather dissentient views expressed by several other workers (see, e.g., SIMPSON, 1961, p. 78-79; BOCK, 1963). The controversy may appear to be rather trifling, but there are some fundamental questions which compel me to challenge the generalisation

in Professor Eckardt's paper. This criticism concerns what I hold to be the most essential differences between the so-called New Morphology (N.M.) and the conventional phytomorphology (Morphology 'Old Style', M.O.S.). Surprisingly, even most neologists failed to recognise these differences.

The principal bone of contention can be expressed in the form of the following question: – Is a homology concept which is based on the phylogenetic principle of 'common origin' (of 'propinquity of descent'), and is defined accordingly, different from the traditional (O.S.) homology concept which is based on the vague typological tenet of 'essential structural similarity'? Eckardt and others, such as BOYDEN (1947) and REMANE (1954), believe that the answer must be in the negative because the 'phylogenetic' definition of a homology relation is, in their opinion, primarily based on typology and, hence, only conventional morphology in disguise. However, I agree in so far with Simpson and Bock that there are certain differences between the two interpretations of the homology concept, if not in principles or philosophies, at least in a number of details and in certain applications, so that the alternative approach may lead to some altogether different deductions. It is, in my opinion, irrelevant whether this different outcome is attributable to a different insight into the proper method of approach to certain scientific problems, or rather to a different system of logic. P. SMIT (1964) has – most convincingly, I think – shown that the influence of the early nineteenth century school of 'natural philosophy' on German biological thought is still manifest, especially in the field of comparative morphology. There are also positive indications that in some continental 'schools' morphological thinking is still based on the 'idealistic' phytomorphology, sometimes interwoven with thomistic ideas. I may not be the most competent judge of trends in cognition theory and in phenomenology, but it strikes me that quite often the morphological and phylogenetic conclusions of one phytomorphological school are alleged to be deduced by a process of circular reasoning by protagonists of a different school of thought. Frequently this is a matter of the pot calling the kettle black, so that attempts to reconcile the different points of view will prove to be a thankless undertaking. The present paper is an effort to bring certain rather neglected aspects of the homology concept to the fore which may, I hope, clarify some points and thus contribute towards a better understanding of the controversy. It is up to the reader to decide whether the traditionalists' points of view concerning the theory of homology needs extension or modification, as I believe it does, in the light of neomorphological principles, but in any event the controversial issues must clearly be singled out as a starting point for future discussions before we may hope to gain a better understanding of this corner stone of biomorphology.

## 2. SOME SEMANTIC ASPECTS OF THE HOMOLOGY CONCEPT

Eckardt has again stressed the, in some circles at least, apparently still prevailing notion that morphology is the study of the unity of

diversity by referring certain forms (shapes) or structures to a common reference pattern or 'Gestalt': "*Morphologie ist also Bauplanforschung oder Typologie*" (ECKARDT, 1964, p. 79). He refers to the conventional ways of expressing homology, such as Owen's definition of homologous entities as objects exhibiting 'essential structural similarity', and Darwin's 'correspondence of the organisation plan' (see also BOYDEN, 1947), but like so many before him, does not touch upon – let alone concede – the largely subjective element in the selection of the common item of reference for a group of homologous objects (a so-called 'natural' group, or a specified organ occurring in such a natural group), i.e., of the structural pattern on the basis of which that group is supposed to be modelled (*casu quo*, to have been created). The delimitation of the 'natural' groups is completely aprioristic and not infrequently such a group is 'defined' as an assembly of organisms *having* the same basic pattern (the same 'essential' structure, also referred to as 'archetype', 'prototype', '*Bauplan*', 'structural plan', 'fundamental organisation', 'architecture', or by another term for what is essentially a kind of blueprint). It is quite clear that, at least theoretically, such a basic 'blueprint' or theme (idea!) can serve as a starting point for a number of 'expressions' or 'realisations' of that same structural organisation plan, so that all variations on this same theme have a common denominator of a sort and, as a group, are also automatically different from all assemblies of other (*essentially* dissimilar) objects whose structural qualities are modelled according to a different standard pattern. Conversely, a definition of a natural group as an assembly of entities or specimens whose morphology corresponds with the same essential *Bauplan* can be given. However, the crux of the matter is that the various categories of homologous objects (the 'natural' groups) are preconceived, either directly, or implicitly by their (postulated!) common standard of reference. It is often claimed that comparative morphology supplies the best proof of the existence of a common *Bauplan* by showing, within the natural groups, graded series of transitions 'linking' all variants of the same pattern semi-continuously. This is of course also a case of circularity of deduction (and of wishful thinking), because the group was already preconceived as an assembly of specimens 'belonging together' (on account of what else but an intuitively assessed structural similarity?). In phytomorphology O.S., the morphological organ categories (the 'natural' groups of homologous entities) have, in addition, a very strong bias on account of the M.O.S. being markedly 'Angiosperm-centred', so that not more than three organ categories are aprioristically recognised, viz., the, in the Angiosperms upon the whole rather conspicuously distinct, groups of 'stems', of 'roots' and of 'leaves'. All subsequent attempts to 'demonstrate' that these three types of organs (or two, if one is inclined to combine 'stems' and 'roots' and to distinguish them as 'axial' elements from the 'appendicular' phyllomes) are essentially and entirely diverse things are likewise examples of circularity of reasoning.

That a tendril is sometimes a modified leaf (or a part thereof),

but sometimes represents a modified stem-piece or a whole shoot, is universally accepted, and, similarly, the equivalence of the spines or thorns with different organs (leaves, leaflets, stipules, or axial organs) is clearly understood, although in these cases the phenetic resemblance between the inhomologous objects is particularly striking. This rather patently gives away the starting point of the morphological classification, viz., the aprioristic assumption that there *exists* a limited number of morphological organ classes, each category or group embracing homologous elements, and the different groups morphologically dissimilar or inhomologous elements. The recognition of this scholastic foundation of the conventional homology concept simplifies matters considerably. In Eckardt's recent paper under discussion its author devotes an appreciable amount of space to the presupposed similarity of essential structure, i.e., the community of the basic or intrinsic *Gestalt* of the morphological pattern (or *Bauplan*, etc.) of homologous objects, whilst completely evading the issue of *how to decide* (in any other way but by intuition, that is) if two morphological entities have the same 'essential' quality that renders them equivalent. This decision is always biased, the common point of reference alone being already preconceived! Once the, traditionally opposed and mutually exclusive, morphological categories have been postulated, one can only judge subjectively in which of these intransient groups a certain organ fits best. However, in a number of cases this has deteriorated into a conventionalism or even into complete hearsay. The literature on the interpretative morphology of what is called the angiospermous 'flower', especially of its gynoeceal ('carpellary') elements, keeps piling up, but if a worker *starts* from the assumption that all Angiosperms have flowers conformable to one and the same structural pattern (*Bauplan*, etc.) which represents a modified leafy shoot, and that all their genitalia are essentially modified leaves or aggregates of such leaves, all his subsequent deductions aiming at a confirmation of the 'classical' floral theory, i.e., of such *postulations* as the foliar nature of the carpels, are inconclusive because they follow from a process of circular reasoning. There is not much point in trying to 'prove' what has already been taken for granted and has in point of fact been the starting point of the discussion (see also UNRUH, 1939, and the forthcoming thesis by my collaborator Moeliono).

So ingrained had the recognition of the three traditional organ categories become in phytomorphological thinking that these concepts were 'extrapolated' into the morphology of the Lower Cormophyta by assessing and interpreting the nature of their organs in the rigid terminology of the Angiosperm-centred classification of organs as 'stems' and 'leaves' (as cauline *versus* foliar, or as axial *versus* appendicular). BREMEKAMP (1962, p. 28) criticised this unwarranted generalisation by saying, when referring to the 'sporophyll' doctrine, that outside a taxonomic group certain concepts may be completely meaningless and in any event require a relativation of their scope. Somewhat similar ideas were expressed by MASON (1957). It is, therefore, in the first place the static and intolerantly rigid classification in

P.O.S. that must be criticised. In this system there was scarcely any room for such important structures as thecae, ovules, integuments, funicles, arils, pseudoarils (arillodes), etc. Indeed, the thecae and the ovules (with their accessory organs) were rather generally considered to be merely portions of a fertile appendicular organ (a 'sporophyll', 'foliar carpel', etc.) and, phytomorphologically speaking, hardly of any consequence – so much so that EAMES (1961, p. 283–285) discusses the morphological nature of the ovule as if this so essential structure were only an 'emergence', an epidermal outgrowth of the 'carpel', which is of course totally absurd, the advent of the foliar element, in this train of thought, preceding the emergence of the ovule (in other words, prior to the phylogenetic appearance of the ovule sexual reproduction must have been non-existent!). The precursors of the essential ovular structures (called nucellus, integuments and funicle), i.e., the megasporangia and their stalks, are of course undeniably 'older' than the carpels (MEEUSE, 1963a, 1964).

Equally vexatious to traditionalists are the implications of the thrusting of this rigid morphological classification (O.S.) upon the telomic *Eocormophyta*.

Returning to the foundations of the homology concept, we must replace all previous attempts of a practical definition of 'homology' by beginning our analysis with the rather trivial and non-committal statement that homology, in the most general sense of the word, is a relation which provides a criterion that can serve to distinguish categories of living beings, or of parts of organisms, from dissimilar categories. In other words, two or more of these objects are associated in some way or another by something they have in common or by an equivalent relation of each of them to a common standard of reference, to a common denominator of a sort, and are thus different from all other objects with which they have none such characteristic features in common or do not share a common denominator. This is a prerequisite that is valid irrespective of all other aspects of the definition of homology. It does not make any difference either, if the objects are only *reputed* to be similar or dissimilar.

It should be noted at once that the relation between homologous entities, as here defined, is not necessarily, and quite often not by a long shot, in the nature of a perfect or 'true' identity. Here lies a possible cause of an adulteration of the concept. When EAMES (1961, p. 218) refers to "... the classical view that the carpel is a fertile lateral appendage of a determinate stem tip", and continues: "In details of position and origin on the stem, and of ontogeny and anatomy, it is like the leaf and is clearly of leaf rank. Comparative studies of the stamens ... show that this sporophyll ... is, like the carpel, basically leaflike in form, structure and ontogeny", it is not quite clear if he means that a carpel or a stamen is, strictly speaking, a leaf homologue in a classical sense. It all depends on a possible difference in *nuance* between the terms 'of leaf rank' or 'leaf like' and 'homologous with a leaf' ('a true leaf homologue'), i.e., the *equivalent* of a vegetative phyllome or trophophyll, or something more (or less) than that. Such a semantic vagueness and ambiguity is

most unsatisfactory and I shall discuss this point again later on.

If the above-mentioned first approximation of a circumscription of 'homology' (and inhomology!) applies to every form and to every notion of homology – as indeed it does in my opinion – one could maintain that conceptually there can only be one form of homology relation, which could be interpreted as meaning that there is no fundamental difference between a phylogenetically defined homology and one based on typology. However, and this is of vital importance, although its semantic basis seems to be sound the given definition is hopelessly inadequate in that it falls short of our goal, i.e., of what we really intend to convey, namely the correspondence of essential features and, more particularly, of *correlated* essential characters. Let us look at some examples. If two or more plants that are so different that they indubitably belong to different taxa bear flowers with red petals, they form for this reason a group of plants which is undoubtedly different and hence distinguishable from all other assemblies of angiosperms that have petals of a different colour. Although these forms share a 'common' character (the red petals) and are distinguishable as a group, presumably not a single phytomorphologist would, on this evidence alone, consider the flowers of these plants to be homologous entities as opposed to (and hence inhomologous with) all flowers that have petals of a different colour. This is not surprising, because the homology concept O.S. is concerned with structural features, not with 'non-essential' colours. However, if the red colour is brought about by the presence of a pigment of a rather unique chemical composition, the picture may change considerably – Bock (1963) and others, including the present author, extend the homology concept to include equivalence of other characters than the structural ones alone, such as a correspondence in chemical composition, in physiology, in behaviour, etc.

Let us now replace the colour character by a numerical difference in the spatial arrangement: if a flower is tetramerous, this does not mean that the flower is *per se* only homologous with tetramerous flowers and not with penta- or trimerous ones. Still, the consistent occurrence of tri- or pentamery is usually considered to be indicative of a 'natural' group (as opposed to other groups with a different number of members in each whorl, cf. Monocots and Dicots). Apparently there are borderline cases, and a homology relation can also be 'relative' in respect of other homology relations (see also Bock, 1963).

A second restriction is introduced by the assumption that a certain feature occurring in taxa which do not constitute a 'natural' group ("do not possess the same essential architecture", M.O.S.), or are phylogenetically unrelated (N.M.), is not necessarily homologous throughout these taxa, but may, on account of a 'superficial' structural resemblance, only simulate homology. Such cases are considered to be examples of analogy, homoplasy, convergence, parallelism, or (Bock, 1963) 'evolutionary homodynamy'. However, this reasoning is biased because the supposed degrees of relationship of the various taxa are, up to a point at least, also preconceived, and chiefly based

on the very same features that are supposed to be homologous (or inhomologous, as the case may be). From a theoretical point of view, at any rate, such instances (and forms) of inhomology can be assumed to exist (and there is indeed enough circumstantial evidence to corroborate this assumption in a number of examples). It follows that a close structural resemblance suggesting a morphological equivalence, or even an identity (compare the examples of the diverse morphological categories of tendrils and thorns), is not invariably indicative of homology.

On the other hand, there are examples of a relation which is more than a mere homology. The leaves of one branch of a tree are, for all practical purposes, identical objects (replicates, like the coins minted from the same mould) and it seems unduly formal to call them 'homologous', because they are all phenotypic expressions of the same genome. The same reasoning applies to all leaves of an individual tree and, generally speaking, also to the leaves of all individuals of the same botanical species (they having approximately the same genome), but is it still applicable to the trophophylls of all individual members of a natural taxon of a higher category? I think the answer to this last question must be in the negative, in the first place because phenotypic manifestations of the diverse genomes of not so closely allied species can hardly be expected to be identical replicates, and this applies *a fortiori* to taxa of a higher rank. In addition, the principle of serial homology is at issue, which, in the higher plants with their 'open' type of growth by means of vegetation points, is not necessarily of the same nature as serial homology in animal groups with an 'overall' development of the body (with a 'closed' type of growth). This point has been discussed by the author in a somewhat different context (see MEEUSE, 1963b) and will be dealt with again presently. It can be stated in anticipation that a distinction of homology *versus* inhomology is not just a matter of strictly opposed and mutually exclusive categories, but also depends on other relations which introduce a *relative* character into the homology concept (see also MASON, 1957).

When the conventional definition of homology is now reconsidered, the best provisional general circumscription seems to be: "*A relationship based on common characteristics or on a common item of reference, which relation must be restricted primarily to structural features and is used to refer an object to an aprioristically recognised group (or category) in a morphological classification; a second restriction to be made is that homology is not usually a more or less perfect identity, and, conversely, a striking structural similarity is not necessarily indicative of a high degree of morphological equivalence*".

### 3. THE SUI GENERIS CONCEPT, OR THE PRINCIPLE OF 'EITHER - OR'

In phytomorphology O.S. one starts from the assumption that there is a limited number of different and mutually exclusive, 'static' and 'rigid' categories of elements constituting the plant body. This is clearly a case of 'either - or', i.e., an organ is either a leaf, or a stem

or root, and it can not be both a leaf *and* a stem (or root). It is sometimes disguised as a 'bud', but since a bud is a prospective shoot one has, ultimately, to fall back on these same categories. According to BREMEKAMP (1962), the concept of *organa sui generis* has not been very popular in the classical plant morphology, but he, like so many others, overlooked the fact that the postulation of alternative and invariable categories implicitly presupposes the *sui generis* nature of each category in respect of the other ones. This oversight is understandable, because up to now nearly everybody only considered (and usually rejected) the possible *sui generis* origin of the fertile organs in respect of the vegetative ones, although most workers silently accepted the *sui generis* nature of the three 'fundamentally different' organ categories in respect of one another, or at least of two mutually exclusive and intransigent categories of 'axial' *versus* 'appendicular' elements.

In the conventional system of morphological classification there is no room for anything else but the recognised categories: an organ is either the one thing or the other. However, if – as is customary in the N.M. – the paleobotanic evidence is taken into account, one of the first fundamental results emanating from the neomorphological approach is the conclusion that the consequent application of the morphological tenets O.S. to fossil plants leads to inconsistencies, which demonstrates the inadequacy of at least some of the classical dicta in phylogenetic botany. The principle of 'either – or' fails when it is applied to the morphology of the Eocormophyta in the conventional way: the psilophytic rod-like vascularised pieces of differentiated thallus, called telomes (and mesomes) at the proposal of ZIMMERMANN (see his latest compilation of the Telome Theory, 1965), can not be referred to the stem or to the leaf category (or to the root class, for that matter) because they constitute, in all probability, the precursors of both the foliar and the cauline organs. The 'either – or' principle that seems to be so neatly applicable to the leaves and stems of higher plants (more precisely: of the Angiosperms!), is inadequate at the early phylogenetic level of the Psilophytes. In other words, the leaves and the stems of the spermatophytic forms, as having a common pattern of reference (a common origin), are not primarily *sui generis* in respect of each other. According to the general definition of homology given on p. 457, they must be homologous entities. Following in Zimmermann's footsteps, several protagonists of neological ideas have extended the 'classical' dicta by interpreting all organs as more or less modified syntelomes, i.e., as more or less derived aggregates of the same basic units, the telomes (including mesomes, as the case may be, but this is a mere technicality). This is essentially what STEWART (1964) dubbed the 'Upward Look' in phytomorphology. By postulating the equivalence (homology) of all telomes, irrespective of the presence or the absence of terminal sporangia, the Telome Theory supplied a tentative explanation of the 'long established' and reputedly fundamental homology of all foliar (phyllomic, lateral, or appendicular) organs: aggregates of telomes which underwent planation and webbing became phyllomes, whereas the remaining



telomes (and mesomes), after certain modifications, acquired an 'axial' (cauline) nature. However modern the Telome Theory may seem to be, in this respect very few essential changes took place in basic phytomorphological thought, the same three organ categories still being recognised as those distinguished in plant morphology O.S. The mainstay of the classical or ranelian floral theory, the postulate of the foliar or appendicular character of the genitalia of the Flowering Plants, was thus 'saved', notwithstanding the fact that seemingly the principle of 'either - or' was abandoned. However, the whole deduction hinges on one very fundamental premise, namely on the equivalence of the so-called 'sterile telomes' and their counterparts, the 'fertile telomes' in Zimmermann's terminology, and we are again confronted with the possible *sui generis* origin of certain elements. ZIMMERMANN (1964, 1965) has joined issue with the present author on account of the latter's opinion (MEEUSE, 1963a, p. 132-9) that the cormophytic sporangium is *sui generis* in respect of the vegetative organs of the sporophyte, so that the homology of a 'fertile telome' with a 'sterile' one is restricted to its vegetative portion or sporangiophore and does not include the terminal sporangium. This controversy is, properly speaking, intimately associated with the phylogenetic origin of the terrestrial plants (MEEUSE, 1966b). The connexion between this problem and the mutually *sui generis* nature of the sporangia and the sporangiophores (telomes) will be discussed presently. Suffice it to say that Bower's frequently quoted aphorism: "*The sporangium is older than the leaf*" can be modified into: "*The sporangium is older than the telome*". It goes without saying that something which is phylogenetically older than a different element can not possibly be a subordinate and integral part of that other element, because it had already originated before the second came into being. The fact that such 'ready-made' structures as sporangia and sporangial homologues (such as ovules) are not infrequently secondarily *incorporated* in a more complex organ also containing elements with some foliar characteristics (such as pteridospermous fronds) does not alter the fact that they are not of the same derivation as the elements with the phylloclimic nature and are beyond the homology relations of the *vegetative* associated elements. In other words, sporangia and derivatives of sporangia can not be discussed in terms of 'leaves' and 'stems', because they are antipodal, being *sui generis* in respect of the latter. Therefore, the deductions following from a phylogenetic approach to the homology concept do not seem to be very different from those obtaining in morphology O.S. in that the principle of 'either - or' (the *sui generis* nature of certain, mutually exclusive, categories) applies in both instances. The definition of homology requires the stipulation that homology is restricted to organs which are not mutually exclusive (*sui generis*) in respect of one another, organs (and other entities) of independent origin being inhomologous by definition. However, the dividing line between the principal groups of inhomologous categories must be drawn in a completely different place, the phylogenetic approach indicating the fundamental difference between the truly fertile organs and the

essentially vegetative parts of the sporophyte, instead of the semophyletically false, conventional categories of caulomes and phyllomes. In the conventional morphological classification of organs there was no 'room' for any other organ but a 'leaf', a 'stem', or a 'root', so that the interpretation of tegumentary envelopes of the megasporangium homologue did not usually go beyond an assumed equivalence of the integuments with indusia (epidermal outgrowths) or with parts (lobes) of a sporophyll, and the whole ovule was sometimes compared with a bud (i.e., with an incipient shoot).

The greater freedom of interpretation provided by the recognition of these *a priori* distinguished categories of vegetative *versus* fertile organs permits the conception of certain truly phylogenetic hypotheses such as Benson's explanation of the origin of one of the spermatophytic ovular integuments as a modified soral or synangial aggregate of megasporangia (see MEEUSE, 1963a, 1964).

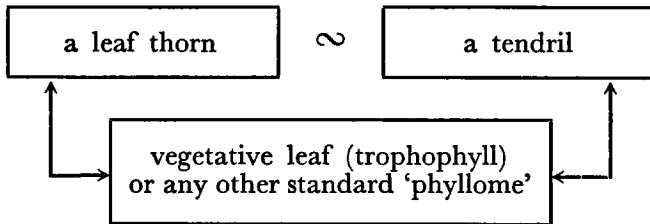
Another implication of the homology concept is the requisite of the reciprocity of the relation between homologous objects, to be discussed in the following chapter.

#### 4. THE RECIPROCITY OF THE HOMOLGY RELATION

The homology concept in the mathematical sense relates two homologous quantities through their connexions with a third. The homology of two quantities *a* and *b* can be expressed as follows:

$$a \sim b, \text{ but also as } b \sim a,$$

i.e., the relation is reciprocal. In phytomorphology, the reciprocity in the relation between homologous organs has not received sufficient attention, perhaps because one was wont to judge the various elements in an assembly of homologous entities by a common standard of reference (the 'essential structure', 'type', 'basic pattern', *Bauplan*, etc.) the mutual morphological equivalence of the elements of an assembly being underrated. The recognition of certain categories (leaf, stem, root) implies that homologues are reciprocally related, if only indirectly through the 'common standard of reference', thus, for instance:

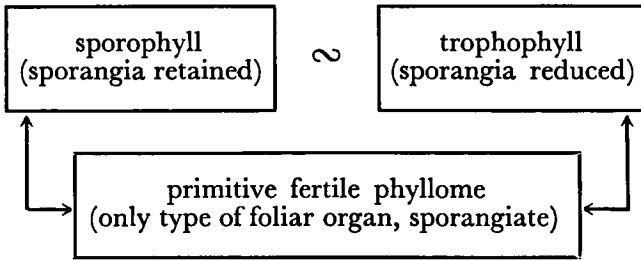


Apparently the requisite of reciprocity does not cause any difficulties in this case. The relation between thorn and phyllome being very much the same as that between the phyllome and the tendril, the equivalence of thorn and tendril is rather obvious. The general validity of this rule of reciprocity permits its application to all cases of

an assumed homology relation. However, if we symbolically render the traditional homology relation between vegetative leaves (trophophylls) and fertile floral appendages as follows:

$$\text{trophophyll} \sim \text{sporophyll},$$

this relation seems to be somewhat suspect if it is indeed reciprocal, although it is merely a different expression of the fundamental homology relation on which the whole 'classical' interpretation of the angiospermous flower rests. The logical conclusion was drawn by UNRUH (1939), who, by means of a purely conventional deduction, decided that the more 'primitive' and phylogenetically 'older' type of appendicular organ is the fertile phyllome or 'sporophyll', because the reciprocity implies that, within the limits of standard morphological thought, the trophophylls can conceivably only be derived from fertile appendicular organs by the loss of the sporogenous elements (the thecae or ovules) of the latter. Unruh expressed this unequivocally by calling the vegetative leaves *Vergrünungen* (virescences) of the fertile phyllomes, in other words, the trophophylls are supposed to be derived from (and phylogenetically younger than) the sporophylls. In diagram:



The reciprocity of a homology relation, properly speaking, only obtains in static systems and, therefore, has only a limited scope in the N.M. as we shall see. Still, it can be used to demonstrate certain inconsistencies. Apart from the example of an atavistic development of the fertile brachyblast of *Ginkgo biloba* I have already discussed elsewhere (see Fig. 1, adapted from MEEUSE, 1966a), the supposed morphological identity of a sterile telome and a fertile one advocated by ZIMMERMANN (e.g., 1959, 1964, 1965) is a case in point. The reciprocity of the homology of the two categories of telomes causes some complications. Quite apart from such questions as homotypy, morphogenesis, determination and differentiation to be discussed presently, the phylogenetic consideration that the sporangium is most probably 'older' than the intercalated vegetative sporophyte (the sporangiophore) and *sui generis* in respect of the latter (MEEUSE, 1966b), is already at variance with the reciprocity of the relation which implies that an organ bearing a terminal sporangium is, or was, equivalent to a similar structure devoid of such a sporuliferous extension. The so-called sterile telome can only be equivalent to as

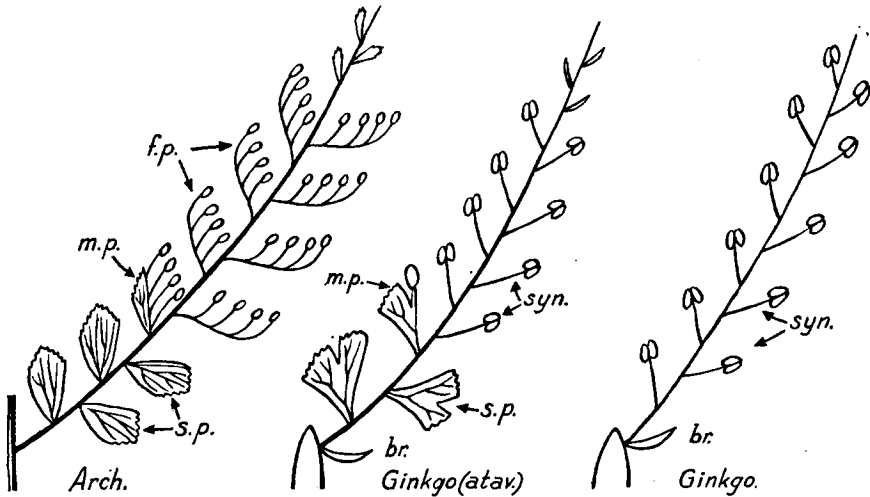


Fig. 1. Atavistically developed male brachyblast of *Ginkgo biloba* (centre) which is reminiscent of a putative progymnospermous archetype more or less closely corresponding with a fertile pinna of an *Archaeopteris* frond (*Arch.*, left). Right: a normal male brachyblast of *Ginkgo*. All figures diagrammatic; *s.p.*: sterile pinnule; *f.p.*: fertile pinnule; *m.p.*: mixed pinnule (an additive, not necessarily a partly substitutive aggregate of 'sterile' and 'fertile' telomes, and hence not unequivocally indicative of the equivalence = homology of adjacent fertile and sterile portions); *syn.*: stalked synangia; *br.*: axillant bract of brachyblast.

fertile one without its sporangium. Even if one assumes that a 'sterile' telome may conceivably be derived from a 'fertile' one by the loss of the sporangium, the homology is not 'complete' because the reciprocity is no longer 'complete' after the reduction of an essential integral part of one of the homologous subjects and can only extend as far as the limits of the 'retained' elements, thus excluding the (altogether dissimilar) reduced portion (in the case under discussion, the sporangium). It was on the ground of very similar, logical deductions that Unruh reached his paradoxical conclusion concerning the origin of the trophophylls as we have seen.

As a yardstick of morphological equivalence, the reciprocity is very important in various contexts. According to the telome theory, an aggregate of associated telomic elements, a syntelome, can evolve into an organ of the leaf class, or differentiate into an organ of cauline nature, depending on the morphogenetic processes operative during its semophylysis from a number of more or less independent telomes to an integrated organ of a more complex structure. It would follow from the postulated equivalence of fertile and sterile telomes that a syntelome compounded of sterile telomes that became a 'stem' must still be homologous with a derivative of a sporangiate syntelome of the phyllome class. Zimmermann only considered the cases of an aggregate of sterile telomes constituting a vegetative ('sterile') syntelome that became a trophophyll, and its counterpart, the mixed

syntelome built up of sterile and fertile telomes that he supposed to have become a leafy 'sporophyll'. However, the principal difference between such structures as the proto-coniferous fertile brachyblasts and the supposed fertile phyllomes or sporophylls of the Cycadopsid groups, usually considered to represent entities belonging to the mutually exclusive classes of cauline (or axial) and foliar (or appendicular) organs, respectively, is not at all attributable to the origin of the two fertile structures under discussion from aggregates of fertile and sterile telomes, but to different morphogenetic processes. The divergent, phenotypic modifications evolved gradually during the phylogeny and the semophylesis of each group and they had no bearing on the initial homology relation that existed between the elementary telomic elements incorporated in the syntelomes, i.e., on the primary equivalence of these elements. A coniferous female brachyblast originated as an aggregate of sterile and fertile telomes which eventually fused to form the ovuliferous cone scale that is subtended by the bract scale and can for that reason not be referred to the phyllome class, although it is the phylogenetic derivative of a mixed syntelome that underwent some webbing just like the cycadopsid fertile pterophyll or sporophyll is supposed to be in Zimmermann's interpretation of its semophylesis. In Zimmermann's own publications other derivatives of complexes of sterile and fertile telomes than the coniferous cone scales are referred to the category of the appendicular organs and named (appendicular) 'sporophylls'. Clearly the original morphological equivalence between the telomic and syntelomic precursors of fertile organs does not provide an adequate criterion to assess the homology of these organs at a much higher level of organisation. The evolutionary derivatives of identical archetypes acquired the 'special quality' of a phyllome or of a cauline organ, respectively, i.e., of one of two categories of traditionally antipodal elements. This is manifestly the result of the semophyletic advent of morphogenetic processes which progressively differentiated the appendicular organs from the axial ones. Somewhat surprisingly, this obvious conclusion still does not unequivocally explain why, at the present-day level, a certain type of fertile organ (viz., the ovuliferous cone scale), is, by a fairly general consensus of opinion, referred to as a fertile brachyblast, whereas the so-called megasporophylls of the Cycadopsid forms are supposed to be appendicular leaf homologues, although, according to the telome theory, the same elementary processes (in this case planation and webbing preceded or followed by some overtopping) are responsible for the semophyletic changes in shape and position. The supposition made by Zimmermann, and repeated by several other telomists, that, when an aggregate of fertile and sterile telomes (a mixed syntelome) and a corresponding vegetative syntelome evolved into a laminose structure, the fundamental identity of the telomes and the syntelomes is maintained, i.e., that the phylogenetic homology of sporophylls and trophophylls rests upon a morphological equivalence of the archetypes persisting during the series of evolutionary changes in morphogenesis (and organogenesis in the proper sense) to

which their derivatives were subjected, is clearly untenable. Irrespective of the answer to the question whether the so-called fertile telomes are complete homologues of the sterile ones, the morphological equivalence of the 'sporophylls' and the trophophylls of the Spermatophyta rests exclusively on the degree of similarity of the elementary determinative processes to which the supposedly identical archetypes were subjected during their evolution. The morphology of the fossil progymnosperms strongly suggests to me (see MEEUSE, 1963a) that the vegetative (and assimilatory) laminose organs of their descendants developed exclusively from 'sterile' syntelomes by the advent of morphogenetic processes which included planation and webbing, whereas the sporangiate complex syntelomes forming the complex, partly fertile and partly sterile ('mixed') frond-like structures of the proto-spermatophytes initially evolved without a previous association of the sterile and the fertile telomes into integrated units that subsequently behaved as single semophyletic entities, and without a process of webbing involving the fertile pinnules of these 'mixed' fronds. A subsequent *secondary* incorporation of derivatives of the fertile elements (such as ovules) in, or an adnation to, already laminose ('phyllomic') structures does not necessarily imply that the resulting laminose derivatives (so-called 'sporophylls' of, e.g., seedferns) are *per se* the morphological equivalents of the trophophylls. Their different mode of origin would rather preclude the unequivocal homology of the sterile assimilatory elements (leaves, trophophylls, vegetative fronds, etc.) and the fertile pseudo-sporophylls. The fact that the fertile phyllomes of many true (isosporous) ferns may well have originated in the fashion suggested in Zimmermann's Telome Theory (i.e., as a mixed syntelome during the semophytesis of which both the sterile and the fertile elements of the soma of the progenitor partook in the process of webbing) has no bearing on the problem under discussion, because there is sufficient evidence to accept an independent evolution of the fern and seed plant lineages. A secondary cladification of non-foliar elements during the phylogeny of an organ is equally irrelevant in this respect.

The principle of reciprocity obviously can not be applied to the ultimate stages of the dynamic semophyletic sequences belonging to divergent evolutionary lines, unless one relates the conformity of essential structure by a comparison at the phylogenetic level of the common prototype. The, at the onset of their evolution, reciprocally homologous entities have each acquired a special character determined neither by the morphology of the archetype (which is a telomic structure in any event), nor by the fundamental organogenetic processes operative at the telomic and post-telomic levels of organisation, but by the sequence, the interaction, and the relative time of initiation of these processes. These determinative changes have a considerable bearing on the relative degree of homology obtaining between originally equivalent and subsequently modified structures as shall be explained in the following chapter. For the time being it suffices to point out that the shifting degree of morphological

similarity is conceptually incongruous in the static phytomorphology Old Style.

##### 5. THE RELATIVITY OF THE PHYLOGENETIC HOMOLOGY CONCEPT

Definitions of homology, i.e., of a morphological equivalence, based on a common origin (on a propinquity of descent from a common prototype) as given by SIMPSON (1961) and by others, are inadequate as we have seen, because a divergent semophyletic evolution may mould originally identical structures into derivatives belonging to different morphological categories of organs (e.g., into axial elements or into phyllomes). The comparison of the secondarily inhomologous entities at various evolutionary levels yields different results depending on the semophyletic phase of differentiation, in other words, on the relative time factor. At the early phylogenetic stage of the dichotomously branched telomic Eocormophyta there was no clear distinction between 'axial' and 'appendicular' organs before the process of overtopping became manifest: every telome and every mesome occupied the same relative position in respect of its supporting mesome, viz., a 'semi-terminal' one. Leaving the sporangia out of consideration, we may accept that all telomes (and mesomes), and, accordingly, all vegetative syntelomes, are homologous structures. It was only after a process of overtopping that the 'lateral' position of some of the elements (viz., the overtopped ones) in respect of the overtopping ones became recognisable. Similarly, the processes of aggregation, planation, and webbing may each in their turn have caused a differentiation of the various elements, but normally two or more of these morphogenetic and determinative processes operated simultaneously. The same cumulative effect of the diverse morphogenetic processes on a number of homologous archetypes need not necessarily have altered the homology of the derivatives of the latter appreciably. However, a different sequence or intensity of these processes, but especially a different degree of interaction, may conceivably result in a progressively diminishing degree of morphological equivalence of the semophyletic derivatives of initially identical structures. The relation between morphological structures (or other organic entities, such as taxa, for that matter) is apparently dependent on various factors which – in phylogenetic botany at least – render the homology a *relative* quality. Thus a trophophyll is the homologue, by direct semophyletic derivation, of an aggregate of telomes, but a stem supporting the trophophyll, although also a derivative of a corresponding aggregate of telomes, is no longer the equivalent of the trophophyll even if their respective ancestral stages were fully homologous. At the present phylogenetic level of clearly distinct trophophylls and axes (caulomes) these organ categories are certainly not homologous if judged by the three criteria of the classical morphology again brought to the fore by ECKARDT (1964): they differ markedly in their mode of origin (in their ontogeny and morphogenesis), in their structural (anatomical) pattern, and in their 'special quality' (of an assimilatory appendicular organ and a supporting and trans-

locating cauline organ, respectively). Yet they had propinquity of descent and consequently a certain degree of homology must still be attributable to them on account of their common origin from telomic structures. The phylogenetic level of comparison and the common point of reference apparently matter a great deal in the assessment of the homology or inhomology of certain structures. The correspondence in the structural pattern and other indications of an initial morphological equivalence may ultimately diminish to such a low level that examples of inhomology rather than of homology seem to be present. This relativity of the homology relation is of far-reaching importance in connexion with the interpretative morphology of the reproductive structures of the Spermatophyta. After a clear differentiation of telomic aggregates into sporangiate (fertile) non-laminose structures and into overtopped laminose vegetative appendages of the rhachis of the compound (mixed) fronds of the progymnosperms (see, e.g., the latest reconstruction of *Archaeopteris* by BECK, 1962), the original homology of syntelomes had already been altered because they had attained semophyletic phases exhibiting a manifest lack of correspondence. The overtopped vegetative phyllome-like elements (the vegetative 'pinnules') are, at least functionally, already trophophylls and have acquired a lateral or appendicular position in respect of the supporting non-laminose organ which thus became promoted to the rank of a 'leaf-bearing' axis (and, in point of fact, soon assumed some of the characteristics of a spermatophytic cauline element, for instance a secondary growth in girth as observed in the 'petiolar' and main rhachidic axes of the progymnospermous 'fronds').

Insofar as the fossil records are trustworthy, we may assume that in the progymnosperms and in the seed ferns the sporangiophores (the sporangium-bearing telomes) did not *ab initio* become incorporated in a laminose overtopped appendage of a rhachidic axis (a so-called sterile pinnule) of the compound frond because they were during their early evolution apparently not subjected to a determinative morphogenetic induction process causing planation and webbing. On the contrary, the coalescence of the telomic elements of the so-called fertile pinnules of the progymnospermous and early pteridospermous fronds took the form of longitudinal mutual adnation of the sporangiophores which thus became a stalk-like synangiophore that did not exhibit a single singular characteristic of a phyllome (MEEUSE, 1963a). A subsequent coalescence and webbing of telomic axes to form a cupule around the ovule initiated *after* a clear differentiation into sterile pinnules (formed by a process of planation followed by webbing, semophyletically evident from various phases found in such forms as *Svalbardia* and *Archaeopteris*, see Fig. 2) and fertile pinnules (formed without a manifest process of planation followed by webbing, and apparently having lost their original assimilatory function) is a case of independent origin of the cupule as a third, i.e., neither strictly foliar nor manifestly cauline, category of sterile organs. The, phylogenetically speaking, still more recent incorporation of derivatives of the fertile pinnules (ovules and their stalks) in a



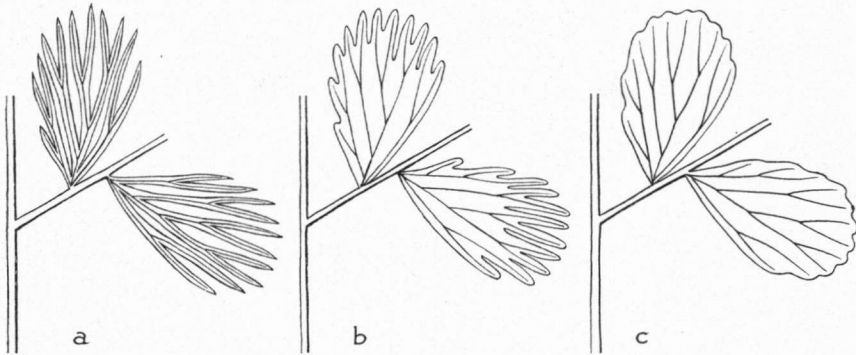


Fig. 2. Three stages of the semophytesis of a sterile progymnospermous pinnule, as illustrated by portions of the (sterile) fronds of different form species of *Archaeopteris*. A repeatedly bifurcate and assimilatory syntelome (protophyllome) *a*, already lateral in respect of the supporting protocaulome (rhachis), and also known from such fossils as *Svalbardia*, evolves into a 'simple' leaflet or pinnule *c* (also known from the fronds of, e.g., sphenopterid Pteridosperms) by a process of 'webbing', *b* representing an intermediate stage. It is assumed that the planation had already occurred before the initial phase *a*.

laminostructure as a result of the progressive increase of the surface area of the laminae of the assimilatory leaflets of 'mixed' pteridospermous fronds (the derivatives of the vegetative pinnae of their archetypes) does not make the already cupule-borne ovules leaf-borne after the event (see Fig. 3).

The various structures under discussion – the vegetative leaflets of phyllomic nature, the stems and other 'axes' such as the petiolar frond stalk and the rhachis, the ovular stalks, cupules and male synangiophores – all originated as syntelomes, but soon evolved along different and divergent lines. The homology of the various organs was, (if we disregard the sporangia and the sporangial homologues) reciprocal and absolute at the level of the undifferentiated syntelome, but the relation became progressively more obscure as each category of organ evolved along its own semophyletic pathway of evolution. The relative degree of homology is best illustrated by the interpretation of the nature of the cupule. After its initiation as a branched, more or less 'cage-like' syntelome a process of webbing occurred which transformed its rather loosely associated component parts into a close-knit and continuous, cup-shaped or campanulate to urceolate structure and in this respect it differs from stems and from synangiophores (which were not subjected to a process of webbing), so that one might consider a cupule to be more leaf-like than a truly cauline organ such as a stem, a root, or a pteridospermous petiole or frond rhachis. On the other hand, a cupule is undoubtedly less leaf-like, i.e., of a more cauline nature, than a trophophyll. This reasoning involves the 'special quality' of each organ category and, therefore, can not altogether be separated from the respective functions of the organ. Soon the cupule followed its own evolutionary pathway and

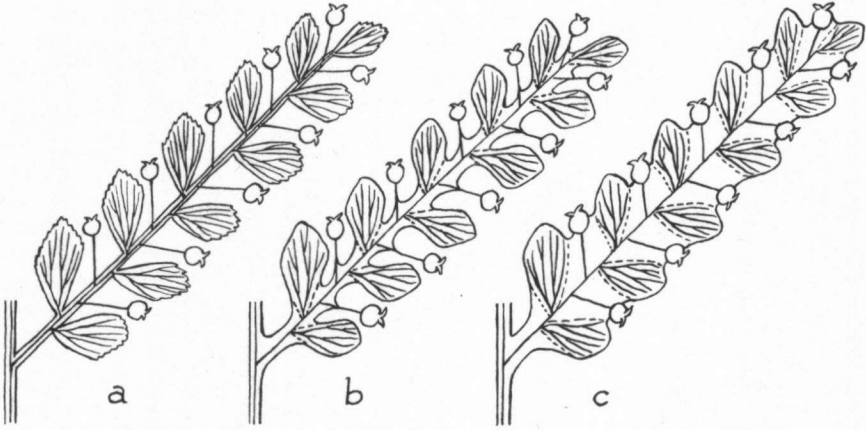


Fig. 3. The 'simplification' of a fertile pinna of a pteridospermous frond, diagrammatic. In the initial phase (a) the sterile pinnules are still primitive in that they have a cuneate base (compare also Fig. 1a and Fig. 2). By the lateral extension of the assimilatory (phyllomic) leaflets (b, c.) the 'laminae' of these pinnules join to form the assimilatory portions of a single simple pinna which has incorporated the stalks of the coaxial fertile organs (e.g., ovules, cupules). The resulting leaf-like structure bearing 'marginal' ovules (or cupules, etc.) is not a true 'sporophyll', but a secondarily originated aggregate formed by coalescence and adnation *after* the initial segregation of telomic archetypes into laminose protophyllomic structures (the vegetative pinnules) and non-laminose, non-photosynthetic (protocauline) elements (syngangiophores, rhachides of fertile pinnules) had been completed.

its interpretation as a cauline (axial) or a foliar (appendicular) organ becomes inane – it is neither stem nor leaf but a derivative of a syntelome that independently developed its own 'special qualities'. The ovules of the cycadopsid groups, primarily inserted on organs of cupular derivation, can not be considered to be axis-borne (and the *Cycadopsida*, accordingly, not truly stachyosporous), but they are not really leaf-borne (and the *Cycadopsida*, therefore, not phyllosporous) either.

The relativity of the homology relation was previously sensed and had already been expressed in several different ways. Bremekamp was quoted before as saying that 'outside' a certain group (or taxon) the relation called homology has only a limited scope and that it may lose its original meaning if one extends its application to other groups than the one it was established in originally. At an earlier date, MASON (1947) had discussed a relativity within and between morphological classes of organs such as exists among elements of the floral envelopes (perianth lobes, tepals, sepals, petals), prophylls, bracteoles, bracts, trophophylls, phyllomes, etc., and their respective derivatives such as foliar thorns and tendrils, elements reduced to glands, bud scales, etc. The degree of morphological equivalence (or homology) between elements *within* each subordinate group (in the example given, belonging to the phyllome class) need not necessarily equal the degree of correspondence existing between elements be-

longing to *different* groups. As Mason clearly points out, the assessment of morphological equivalence depends to a large extent upon the relation of the entities to be compared (or assessed) with other entities or groups of entities: a sepal corresponds better with another sepal of the same whorl than with a petal of the same flower, although they both belong to the phyllome class of floral appendages; in other words, the similarity, and hence homology, is relative. Bock (1963), as we have seen, attributes a great deal of importance to the various forms and degrees of inhomology and pseudo-homology, a subject dealt with by the present author in a somewhat different fashion under the heading '*Lines and Levels*' (MEEUSE, 1966b, Ch. 8). The assessment of degrees of homology, of homoplasy, of parallelisms, of 'evolutionary homodynamy', etc., is largely decided by 'relative' yardsticks such as the geological time factor and the comparison in the semo-phyletic sequence (in a 'line') as opposed to a comparison of different 'lines' at the same time 'level'. The shorter the time interval, the closer the correspondence between the elements of the 'lines' and the 'levels' in a group showing radiating evolution, so that Bock has rightly pleaded for a restricted assessment of morphological relationships by applying our standards of judgment only to smaller 'natural' groups of taxa (Bock, 1963, p. 283: "*Homology is not an absolute quality but varies just as much as monophyly.*"). This does not imply that one could not pursue semophyletic studies, but one should not base one's deductions on the Angiosperm-centred terminology and semantics of the classical morphology (In Bock's terminology: One should beware of silently accepting a transcendence outside the categories!). In several recent text-books and in other publications the anatomical features of, e.g., a pteridospermous frond rhachis are used as if they were indicative of the nature of the organ involved by being assessed at the 'level' of the higher cycadopsids. The once-pinnate and simple leaf-types of the higher cycadopsid groups are the semophyletic derivatives of the complex fronds of protogymnospermous and pteridospermous archetypes. The principal rhachidic axes of these complex fronds were structures which can perhaps best be called 'protocauline', but in the cycadopsid line of descent they eventually became subordinate elements (the principal veins) of a discrete entity, the simple bennettitalean, chlamydospermous and angiospermous 'leaf'. The 'same' protocauline organs developed, in another evolutionary lineage, into the axial portion of the ginkgopsid and coniferopsid 'leafy shoots' and they assumed all the characteristics of a stem including radial symmetry and secondary growth. The assimilatory appendages of these coniferopsid shoots and of the twigs of *Ginkgo* are functionally trophophylls, hence 'leaves' of a sort, but they are not the homologues of an angiospermous simple leaf which incorporates in its lamina a number of elements each of which is the homologue of a coniferopsid trophophyll. This is another demonstration of the relativity of the homology concept when applied in a phylogenetic sense.

Summarising the arguments, I believe one can safely assume that the

relativity of the homology relation is the most essential difference between phytomorphology O.S. and the N.M. as regards the interpretation and the semantics of the concept of homology.

#### 6. MORPHOLOGICAL RELATIONS BETWEEN ORGANS OF A SINGLE INDIVIDUAL AND RELATED CASES

The morphological relationships between different portions of the same organism, of topologically corresponding parts of individuals belonging to the same taxon of lower rank, and of the two generations of the same taxon (gametophyte and sporophyte), have been discussed in terms of 'determination', 'differentiation', 'morphogenesis (histogenesis)', 'correspondence in development (in ontogeny)', 'serial homology', 'equivalence through homotopy', etc. These terms are sometimes more or less contradictory and in any event the whole picture is rather confusing, because frequently only one aspect is emphasised in a series of deductions and the other aspects are conveniently left unconsidered (see also MEEUSE, 1963). ZIMMERMANN (1964, 1965) among others, defends the complete morphological equivalence (hence: homology) of the fertile and sterile telomes, by basing their equivalence on their common origin from the same single element. For example, an apex of a telome axis may divide longitudinally to produce two prospective daughter telomes. If one of these division products develops into a sterile telome and its twin counterpart into a sporangiophore topped by a sporangium (a so-called fertile telome), the reasoning followed by Zimmermann is that the two elements originate in the same way, viz., as perfectly identical ('twin') derivatives of a single entity and retain this identity (apparently irrespective of any subsequent differences in ontogenetic and histogenetic development). This train of thought is not so easily applicable to the more complicated situations found in, e.g., the shoot apex of a spermatophytic plant which in its most apical part is undoubtedly a single and self-perpetuating entity, but whose tunica differentiates in the somewhat older regions into entirely different things, viz., into the future stem cortex and the leaf primordia. Obviously a different organisation is induced by some morphogenetically active principle or by a gradient of such a determinant. I fail to see why this is not the *general* case when organs develop, and prefer to explain the process of a different ontogenetic and histogenetic organisation in initially identical structures as the resultants of different morphogenetic inductions acting upon the same substratum. This explanation still holds if this supposition is applied to the extreme case of the single fertilised egg cell: out of a single entity, the zygote, a complicated organism develops comprising several types of organs, tissues, cells, etc., although in principle the genetic constitution (and hence the genetic potential) is retained in the nuclei of all derivative cells of that fertilised egg cell. Apparently the genetic factors responsible for the changes and the differences can only express themselves in certain preconditioned regions or zones and

sometimes, as in the case of sporulation or flowering, only after an initial period of growth and development of some duration and not infrequently after an additional induction. There must be a remarkable interaction between the genetic code and the responding regions of the organism which moulds seemingly equivalent things, such as groups of practically identical cells, into diverse structures that are by general consensus of opinion nominally inhomologous after their maturation. The assessment of homology exclusively based on a common origin from morphologically equivalent ontogenetic (precursory) stages is, therefore, often manifestly false. In an earlier paper (MEEUSE, 1963) I have already suggested that only if organs (or other, comparable structures), develop in the 'same' (i.e., corresponding or homotopic) places in the same sequence and histogenetically in exactly the same way can there be a morphological identity. If the histogenetic (or 'ontogenetic') development of more or less clearly homotopic organs (e.g., serially originating elements) does not follow the same pattern and, as can frequently experimentally be ascertained, it is regulated by other morphogenetic forces than those previously operative, e.g., by the introduction or translocation of various quantities of biochemically active substances (which are usually restricted in their action to certain areas, zones or 'fields', or produce gradients to which the substratum responds only locally), there is not necessarily a high degree of morphological correspondence between these organs of unequal ontogeny (and of unequal 'Gestalt' and anatomy in the mature stage). The genetic potential is essentially present in all nucleate cells, even among higher plants the 'latently' omnipotent somatic cells often betraying their potentialities in cases of regeneration (also in tissue cultures!), of adventitious bud formation (e.g., along the leaf margins of species of *Kalanchoë*, etc.), of wound healing and of artificially induced abnormalities. Out of cells of an organ belonging to a fixed category, say, a phyllome (such as epidermal cells of a *Begonia* leaf), an entire shoot (bud) may develop which contains an axial organ belonging to an altogether different class of organs. Nevertheless we maintain the distinction between cauline and appendicular organs because of the manifest differences in *Gestalt*, in structure, in histogenesis, in function, etc. in their mature state. In other words, one of the old criteria of homology, a corresponding ontogenetic development, should be emended to read (in addition to other requisites of homology): "*and a conformity of morphogenetic determination*". The principle of serial homology, and also of some other forms of homotopy, is only applicable with this restriction. The traditional, alleged equivalence of all floral appendages, of the sterile as well as the fertile ones, is chiefly based on this principle of serial homology (i.e., of homotopy combined with a supposed similarity in development). However, the mere fact that in several cases the change-over from the vegetative phase of the shoot apex to the reproductive condition only initiates after some florigenic stimulus (for instance, an appropriate sequence of photoperiods) has acted upon that apex, knocks the bottom out of the argument, the induction

causing a different determination associated with differences in the histogenetic development resulting in a different adult structure and 'Gestalt'. Similarly, sporulation and gametogenesis in lower cormophytic forms only set in at a certain developmental stage. Presumably such processes are also governed by the interplay of genetic potential, various morphogenetic inductions and the structure, symmetry and polarity of the somatic substratum or the growing parts thereof. The fact that a gametophytic generation succeeds a sporophytic one, and *vice versa*, is genetically determined it is true, but regulated by the interaction of a number of factors. The homology (*casu quo*, inhomology) of the gametophytic and the sporophytic generations of the same species is pertinent to the question of the origin of the early terrestrial plants (for a discussion, see MEEUSE, 1966b). In the 'homologous' theory concerning the advent of the eocormophytes, the two alternating generations are supposed to be isomorphic, whereas in the alternative 'intercalation theory' the gametophyte and the sporophyte are supposed to be *ab initio* different ('antithetic'). Being an adherent to the second hypothesis, I believe that also in this example one should attempt to distinguish between genetic potential, phenetic 'Gestalt' (i.e., the phenotypic expression of these potentials) and determinative morphogenetic processes as much as possible. There is a certain plasticity, which is also a demonstration of the genotypic potential. The well-known experiments with mosses in which vegetatively propagated sporophytic tissue develops into a diploid gametophyte and other examples of the 'transcendence' (or 'spilling-over') of sporophytic characteristics to the gametophyte, such as the occasional occurrence of tracheids in the prothalli of *Psilotum*, show that there is a certain amount of flexibility. The incidental transcendence of features of one stage may become phylogenetically stabilised, as has, for instance, happened in the primary xylem of certain Dicotyledons which contains pitted tracheary elements reminiscent of secondary xylem cells and quite unlike the typical tracheids of the primary xylem (which have ring-shaped, reticulate, or helical wall thickenings). This is an example of 'adult' features having become precocious, but the opposite, viz., the persistence of characteristics of the younger developmental stages (in other words: proterogenesis or neoteny) is presumably also of frequent occurrence. The importance of neoteny during the evolution of the higher Spermatophyta has for instance repeatedly been advocated in the writings of the Armeno-Russian botanist TAKHTAJAN (1959a, 1959b).

In bryophytic and pteridophytic forms, the different gross morphology, anatomy and ecology (physiology) of the gametophytic and the corresponding sporophytic generation is clearly the result of a different morphogenetic determination. In accordance with my previous conclusion concerning serial homology, the different histogenetic induction in the prothallus and in the sporophyte points to the inhomology rather than to the homology of the haplontic and diplontic phases. The postulation of isomorphic alternating generations in the progenitors of the archeogoniate land plants is clearly incon-

gruous in respect of the conditions in the living cormophytic forms, but even if this is left aside it is not pertinent to the question of homology or inhomology of certain structures. Organs that were identical at an early phylogenetic stage may have undergone so many changes during a subsequent divergent semophyletic evolution that they are no longer equivalent as we have seen, so that initially isomorphic haplontic and diplontic generations (or parts thereof) need not remain homologous after a divergent evolution. The early hemicormophytes transitional between green algae and archegoniate plants did, in my opinion, not have an alternation of independent isomorphic generations and the vegetative parts of the sporophyte presumably arose *de novo* (i.e., *sui generis* in respect of the gametophyte and of the sporangia). There is, accordingly, and irrespective of their ontogenetic and histogenetic origin, no homology between the gametophytic soma and the sporophyte, nor is there an equivalence between a sterile telome (a part of the vegetative sporophytic soma) and a so-called fertile telome (a part of the vegetative soma plus the inhomologous sporangium). As we have seen in one of the previous chapters, such simple and clear-cut assumptions pave the way towards a neological approach to the dynamic phytomorphology of the higher Cormophyta and to the phylogenetic ('relative') homology concept.

## 7. TERATOLOGICAL ASPECTS

Teratology had always been considered to be indicative of the morphological nature of the malformations, or at least to have some bearing on their interpretative morphology, until HESLOP-HARRISON (1952) made it very clear, in my opinion, that one should distinguish two forms of abnormal development, viz., (a) the truly atavistic terata which are manifestations of the genetic constitution of ancestral forms by a recombination of genetic factors through which certain retained 'ancient' genes (alleles) which normally are not phenotypically expressed, regain their capacity of a phenotypic expression, and (b) the various deformations resulting from abnormalities in the rate of growth and differentiation during development caused by an interfering (stimulating, inhibiting, selectively distorting, etc.) influence throwing the processes of histogenesis and organogenesis out of gear. Examples of the first group are such phenomena as the development of a fertile fifth median stamen in quadristaminate zygomorphic flowers of *Scrophulariaceae* and *Labiatae*, the presence of an additional stamen (or of two) in the flowers of *Orchis* and *Dactylorchis*, and the occasional development of a pistil instead of the pistillode in (secondarily) unisexual flowers, the occurrence of three or more microsporangia in a stalked synangium in the male *Ginkgo* instead of two, etc. Upon the whole such cases are clear and unequivocal. Examples of the second category are again of two kinds, the one being only an abnormal development of the vegetative soma, and the other being more complicated by an abnormal sex expression. Sex determination and sex expression have been the subject of several papers by HESLOP-

HARRISON (e.g., 1957). Aberrant forms of sex expression are almost invariably a substitution of one sex by the other, i.e., a 'reversal' of the sex expression in equivalent (homologous) structures (see also MEEUSE, 1965, Ch. IX, p. 95-111). Atavistic abnormalities are, generally speaking, so clear-cut that they are anything but exciting, and, accordingly, the morphological interpretation is in most instances evident from a comparative analysis (see, e.g., the 'series' *Verbascum*, with 5 stamens → *Celsia*, with 4 and a staminode → *Scrophularia*, with 4 → *Veronica*, with only two developed stamens: the homotopy of a staminode or nectary with a 'missing' stamen already betrays its nature). Deformities caused by an aberrant growth rate and/or an irregular differentiation do not usually have much demonstrative force in the interpretative morphology of the floral region: a phylloclid 'degeneration' of a pistil, even if concomitant with virescence, is not an unequivocal proof of the foliar (appendicular) character of a 'carpel' (MEEUSE, 1963b). Sex reversal must be interpreted as an interchange of male and female (micro- and megasporangiate) structures and this may be a guide in the analysis, whilst it may serve as an aid in avoiding errors of judgment. The partial difference in sex expression in, e.g., a female coniferous cone (a so-called androgynous one) or in an amentiferous 'catkin' should not be morphologically assessed on the basis of an equivalence of 'sporophylls' (micro- and megasporophylls, 'carpels' and 'stamens'), but of syngangial aggregates, i.e., of anthers and bitegmic ovules. Even such 'problematical' cases as the development of polliniferous, stamen-like structures on the placenta inside an angiospermous ovary (observed, for instance, in *Petunia hybrida* by my Amsterdam colleague, Dr. F. Bianchi) become quite clear if the rules of the interchangeability of the sexes and of the homology of the basic category of fertile organs (the sporangia) are applied: an ovule on its funicle is practically the equivalent of a stamen (of the anther and its stalk, the filament). It is exactly these simplifications which render the analysis rather simple and unambiguous, but at the same time demonstrate the poor value of 'monstrosities' in interpretative morphology. Incidentally, they appear to be more compatible with neological concepts than with the classical tenets.

## 8. THE CLASSICAL AND THE NEOMORPHOLOGICAL HOMOLGY CONCEPTS

My starting point was the question whether the conventional homology concept and the pertaining classical doctrines of essential phenetic similarity (homoiomorphy), of correspondence in origin and in development (homotopy, homodynamy, etc.), and of the identity of 'special quality', are not appreciably different from the concepts and the criteria to be applied in dynamic phytomorphology and phylogenetic botany. Protagonists of phytomorphology O.S. have repeatedly accused neologists of assessing relationships between organisms and their integral parts (organs and associated organ complexes) by the same standards as those used in the classical



morphology (and conventional taxonomy), followed by a phylogenetic interpretation, or, in other words, of circularity of reasoning. I do not think this can possibly be true, because the basic postulates and the deductions following from these assumptions are not identical with those of the classical phytomorphology. Phylogeny and semophyletic morphology are based on the doctrine of evolution and the first difference between the two concepts of homology is the static classical (and in point of fact scholastic) postulation of fixed and mutually exclusive categories versus the dynamic neomorphology of relative and changing degrees of homology. Bock (1963) clearly appreciates the consequences of the acceptance of the static groups in scholastic thought: *As in the taxonomic tenet of the constancy (non-mutability) of species, morphological categories have absolute boundaries that cannot be transgressed.* Owen's formulations of homology and analogy are based on the philosophy of typological anatomy, i.e., on the postulation of clear-cut 'natural' groups of organisms, each group with a specific and 'ideal' pattern, on the basis of which the morphology of all its members was constructed (or created). Bock also made it very clear that the postulation of homology on a phylogenetic basis rests upon the phylogenetic relationships, i.e., on the relation between various and diverse aspects of organisms and their constituting parts (organs) – including 'Gestalt' (form), structure (anatomy), function, genetics, karyogenetics, behaviour, ecology, physiology and biochemistry – and that it is something quite different from the working criteria by means of which the (chiefly phenotypic) features are assessed in *practice*, in very much the same way as the theoretical species concept differs altogether from the methods by means of which the practical or 'applied' taxonomist strives at distinguishing ('recognising'!) formal species in his museum or herbarium. The working criteria of applied taxonomy are often inadequate, in my opinion, in that they do not necessarily result in the delimitation and subdivision of a taxon or in the recognition of a semophyletic homology relation which are the only possible ones according to the (admittedly, frequently unknown) evolutionary history of the taxon involved. The standard counter-argument that this distinction is of no practical value whatsoever because the 'theoretical' concept of propinquity of descent cannot be put to the test for the lack of other tangible evidence than the criteria provided by the typological method, is crucial, but, to my mind, not so pertinent as several workers seem to think. If we compare, for instance, the so-called cytotaxonomic approach to the delimitation of species by means of non-conventional (and, in fact, evolutionary) criteria, there is no *a priori* reason to reject a phylogenetic approach of phytomorphology and markedly less so if we consider that the palaeobotanic evidence gathered from numerous fossil records is not meaningless and may be quite consistent. I shall leave it at that as I have discussed this particular point exhaustively elsewhere (MEEUSE, 1966a, Ch. II–VI), but I may add that even if one disregards the issue of fundamental method, the neological postulation of intranscendent categories must be altogether different from the

conventional one. The gametophyte, the vegetative parts of the sporophyte, and the sporangia are the three basic categories of *sui generis* elements to be distinguished in phylogenetic botany instead of the Angiosperm-centred notions of 'stem', 'root' and 'leaf'. The third difference, apart from the dynamic instead of the static approach and the different delimitation of the fundamental organ categories already mentioned, is the restriction of the criterion of homotopy and serial homology (of the similarity in origin and development) by adding the proviso that this is a reliable yardstick only if the morphogenetic and histogenetic induction is invariable during the various developmental stages or approximately so. These three differences between the Old interpretative Phytomorphology and the N.M. account for quite a few unorthodox interpretations of the organs of the higher *Spermatophyta* and their homology relations given by neologists such as Lam, Melville and the present author (see MEEUSE, 1966a). To sum up, I believe that there are indeed some very fundamental differences, both conceptually and semantically, between the Old Morphology and the New centred around the problem of homology, which inevitably lead to a greater freedom of thought and of interpretation.

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