



Classical Morphology and Continuum Morphology: Opposition and Continuum

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Classical plant morphology still provides the conceptual framework for most phytomorphological investigations and highly relevant concepts and data for other botanical disciplines such as plant morphogenesis, molecular genetics, ecology, systematics, evolutionary plant biology, etc. Typical classical morphology is categorical, i.e. the diversity of plant form is reduced to mutually exclusive morphological categories such as root, shoot, stem (caulome), leaf (phyllome), and trichome. In contrast, continuum morphology established a morphological continuum between all these categories. As a consequence, homology becomes a matter of degree. Hence, the difference between continuum morphology and classical morphology is striking. Nonetheless, the two approaches and views need not be seen as opposed to each other. They can be considered complementary: classical morphology emphasizing the difference between typical representatives of morphological categories and continuum morphology stressing the continuum between these fuzzy categories. Furthermore, if the morphological categories are interpreted as extreme types, which by definition are fuzzy and continuous with each other, then classical morphology becomes continuum morphology. If such reinterpretation occurs only to some extent, intermediate positions between typical classical morphology and continuum morphology result. Examples of various intermediate positions indicate that a continuum exists between typical classical morphology and continuum morphology. Hence, there is not only a continuum between morphological categories but also between approaches to and views of the field of plant morphology. Consequences of this reconciliation are briefly discussed.

Key words: Classical plant morphology, morphological categories, continuum morphology, complementarity, classificatory type, extreme type, categorical world view, relational world view, fuzzy logic, fuzzy morphology, open morphology, typology, evolutionary biology, cladistics.

INTRODUCTION

Classical morphology and continuum morphology are two major approaches to, and views of, plant form (Sattler and Jeune, 1992). At the present time, classical morphology still provides the conceptual framework for most phytomorphological investigations and highly relevant concepts and data for other botanical disciplines such as plant morphogenesis, molecular genetics, ecology, systematics, evolutionary plant biology, etc. Because of this strong influence that often is not noticed, it is important to reassess its relation to continuum morphology—another approach to, and view of, plant form that at first sight appears completely opposed to classical morphology. This paper begins with a brief characterization of classical morphology and continuum morphology.

Typical classical morphology is categorical. The diversity of plant form is reduced to mutually exclusive morphological categories. In the case of flowering plants and some other taxa, the basic structural categories are root, shoot, stem (caulome), leaf (phyllome) and trichome. Thus, any structure encountered must be either a root, a shoot, a caulome, a phyllome or a trichome (or a combination of any of these): *either-or*, as in Aristotelian logic which is an *either-or* logic according to which the world is seen as either this or that, black or white, etc. Aristotle also appreciated gradations, a philosophy of the 'more or less' (Gotthelf and Lennox, 1987). However, his logic, which fundamentally influenced

Western thinking including the foundations of classical plant morphology, was strictly categorical. It also provided the basis for almost all homology concepts which are qualitative, and thus based on *either-or* thinking (see, e.g. Sattler, 1994). Accordingly, in typical classical morphology homology is *either-or*: an organ is homologous to *either* a root, *or* a caulome, *or* a phyllome. This view has been rigidly defended by Troll (1937–43, 1944, 1954) and many of his followers, typologists, evolutionary biologists as well as cladists (Sattler, 1994). Troll built on a long tradition of classical morphology. He fully endorsed the views of Braun (1851) to whom the sharp distinction of the basic structural categories was the foundation of morphology.

In contrast to this categorical view of typical classical plant morphology, continuum morphology acknowledges gradations between typical structures. Thus, for example, fertile phylloclades are seen as phyllome-shoot intermediates because they combine features of both categories to various degrees (Cooney-Sovetts and Sattler, 1987). Sattler and Jeune (1992), Jeune and Sattler (1992) and Cusset (1994) presented quantitative evidence of many other intermediates between typical representatives of structural categories. Thus, a continuum of structures became established. From this point of view, homology is a matter of degree (Sattler, 1974, 1994). Intermediates are partially homologous to typical representatives of structural categories. For example, a fertile phylloclade is partially homologous to a phyllome and a shoot. The logic implied in this homologization is

fuzzy logic which is a logic of degrees instead of *either-or* (Kosko, 1993). Morphology based on this type of logic has been called ‘fuzzy morphology’ (Rutishauser, 1995) which is an English translation of the French expression ‘morphologie floue’ (Cusset and Ferrand, 1988). A synonym of ‘fuzzy morphology’ is ‘open morphology’ (Cusset, 1982) which indicates that the structural categories are open to each other through intermediates that link the typical representatives of categories into a morphological continuum.

It is important to note that the continuum is heterogeneous, which means that some areas (namely those of the typical structures) are denser than others (i.e. those of intermediate structures) (Sattler and Jeune, 1992). Furthermore, it should be recognized that the continuum is dynamic (Sattler, 1990, 1992, 1994; Sattler and Rutishauser, 1990; Jeune and Sattler, 1992; Hay and Mabblerley, 1994; Mabblerley and Hay, 1994). This means that each structure can be seen as a process combination and thus the structural continuum is a continuum of process combinations.

Since typical classical morphology and continuum morphology are based on a different logic and way of thinking, they seem to be opposed to each other. In other words, there appears to be a deep gulf between the two different morphological approaches and views. This gulf, however, can be bridged in at least two ways: (1) through the general principle of complementarity, and (2) through the concept of the ‘extreme type’ (Hempel, 1965).

COMPLEMENTARITY

The principle of complementarity can be understood in a narrow and a wide sense. In the narrow sense, it refers to the complementarity of the particle and wave view of electrons and light. In the wide sense, complementarity goes beyond physics and implies perspectivism (Bertalanffy, 1975). Accordingly, contrasting or even contradictory views represent different perspectives of the unnamable truth of reality (Rutishauser and Sattler 1985, 1987, 1989; Sattler, 1986). Since each view is relative to a view point, different views illuminate reality from different perspectives and therefore all views together provide a richer and more comprehensive picture of reality than only one. It also follows that all views are limited. This does not mean, however, that all views are equally limited. It is possible that some views are much more comprehensive than others. The following mountain analogy may be helpful to illustrate this. Imagine a mountain with a steep slope on one side and a gentle slope on the other side. Asking in terms of *either-or* logic whether this mountain is *either* steep *or* gently sloping is a hindrance to our understanding. Depending on the viewpoint, the mountain is steep or gently sloping. Hence, it is *both* steep *and* gently sloping. Thus, a *both-and* logic is more appropriate than an *either-or* logic.

A synthesis of different perspectives may be possible, but only to a limited extent. With regard to the mountain analogy, an aerial view of the mountain would give us a more comprehensive picture including both the steep and gently sloping aspects. Nonetheless, even this view will not show everything. For example, it will not reveal the details

of a gorge that can be better seen from the ground. Therefore, although some perspectives may be more encompassing, other more restrictive perspectives retain a certain validity and usefulness.

Now I want to propose that we look at the relation between typical classical morphology and continuum morphology in terms of perspectives. Thus, typical classical morphology shows the striking differences between typical representatives of different morphological categories. Continuum morphology reveals the continuum between these categories. Since the latter encompasses both intermediate and typical representatives, it is more comprehensive than typical classical morphology which deals satisfactorily only with the typical representatives of categories. However, since the majority of structures are typical, classical morphology is adequate and useful to a great extent (Sattler, 1974, 1994), especially if complemented by continuum morphology.

EXTREME TYPES

The notion of the extreme type provides yet another way to bridge the apparent gulf between typical classical morphology and continuum morphology. Hempel and Oppenheim (1936) and Hempel (1965) distinguished three type concepts, two of which are especially pertinent to the present discussion, namely, the ‘classificatory type’ and the ‘extreme type’. The ‘classificatory type’ obeys *either-or* logic. Therefore, any particular form such as, for example, a stamen belongs *either* to the phyllome type *or* it does not. *Tertium non datur*. This means the classificatory type has sharp boundaries as indicated in Fig. 1A. In contrast, the extreme type has no boundaries. Thus, different extreme types flow into each other as indicated in Fig. 1B, C. Consequently, we cannot define these types by a property or a set of properties as in the case of classificatory types. We can, however, define the centre of each type that in Fig. 1B, C is indicated by a dashed line. To use a simple example, we could define the centres of the two extreme types of Fig. 1B by the properties *abcd* and *efgh* respectively. Intermediates that link the centre of the two extreme types would have the following combinations of properties (the property combination of the centre of the extreme types are added in bold):

abcd
bcde
cdef
defg
efgh

A morphological illustration of this formal example was given by Sattler (1990, Fig. 1): *abcd* present four properties of a typical phyllome, whereas *efgh* are four properties of a typical shoot. The intermediate property combinations represent intermediate structures such as the so-called indeterminate leaves of *Chisocheton* (Fisher and Rutishauser, 1990) and phylloclades of the Asparagaceae (Cooney-Sovetts and Sattler, 1987). A still simpler representation of this situation was given by Sattler (1994, Table 1). Because of the continuity between the centres of

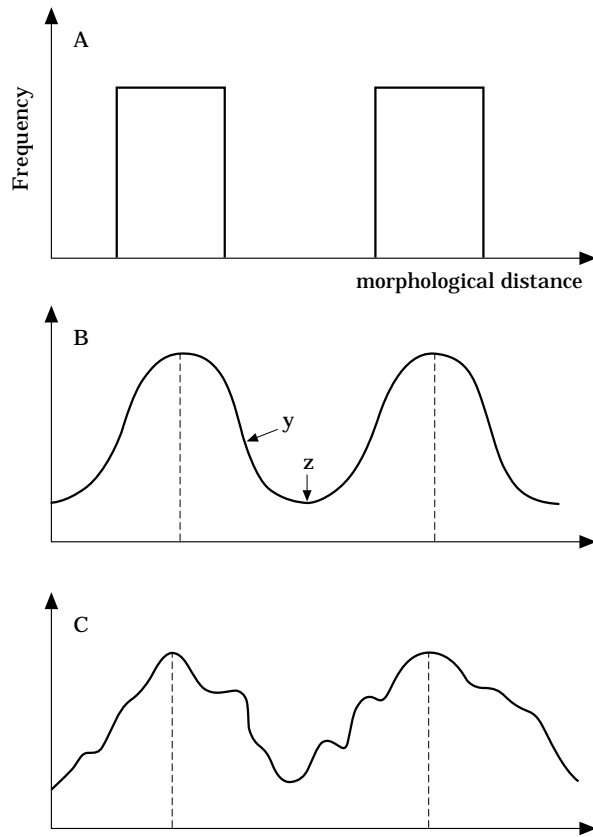


FIG. 1. Schematic representations of the concepts of the classificatory type (A) and the extreme type (B, C). One coordinate represents morphological distance, whereas the other indicates the frequency of structures. The two classificatory types (A) are completely separate, i.e. mutually exclusive. The extreme types (B, C) are continuous with each other. Structure *y* is closer to the centre of one type than to that of the other. Structure *z* is equally distant from the centres of the two types, i.e. it is exactly intermediate between the two centres. The centres are indicated by dashed lines. The frequency distribution in (B) follows Gaussian curves, whereas that in (C) has secondary peaks.

the extreme types, one can also refer to a morphocline. In such a morphocline the plant structures representing the centres of the extreme types, however, are more frequent than the intermediates. Because of this difference in frequency, it makes sense to refer to two extreme types in addition to the morphocline. The notion of morphocline underlines the continuity, whereas the notion of extreme type emphasizes in addition the relative frequency of the centre and the central region of the extreme types. Hence, the notion of the extreme type contains more information than that of the morphocline.

The intermediate forms can be related to the centres of the extreme types comparatively or quantitatively. In a comparative relation it is simply stated that a particular form is closer to one centre than to another. For example, the so-called indeterminate leaves of *Chisocheton* are closer to the leaf centre than to the shoot centre. If a structure is exactly intermediate between two centres (i.e. *z* in Fig. 1B), it is equally distant from both centres. In comparing two intermediate forms, one can say that one is closer to a centre than another one. In Fig. 1B, for example, *y* is more closely related to the centre of the extreme type to the left than to

the other one. From this point of view, relationships are a matter of 'more or less', as already recognized by Aristotle in at least certain cases (Gotthelf and Lennox, 1987). In contrast, relationships can also be quantified. In this case, the distance of a particular structure from the centres of the extreme types is determined quantitatively (Sattler and Jeune, 1992; Jeune and Sattler, 1992; Sattler, 1994).

How does the notion of the extreme type affect typology that plays a central role in classical morphology (e.g. Troll, 1937–43, 1944, 1954; Hagemann, 1973)? It is rarely stated which of the two type concepts is used. However, from the questions asked, it is evident that in most cases the classificatory type concept is implied. Even when no reference to types is made, as in evolutionary morphology or in cladistics, the same kind of thinking is involved as is obvious from the questions asked concerning homology. These questions are almost always based on the assumption that a structure must be homologous to *either this or that* (Sattler, 1994).

In spite of this strong tendency toward *either-or* thinking as exemplified by the classificatory type, there are also morphologists who think in terms of a morphological continuum and extreme types (for references see Sattler and Jeune, 1992). It seems that the notion of the extreme type is increasingly implied, although the term 'extreme type' is not used. Froebe (1987) emphasized that the centres of the types are well defined but that their boundaries are fuzzy. He compared types to Gaussian curves that are continuous at their base as illustrated in Fig. 1B. Thus he described the model of the extreme type without using this term.

Now to the relation of classical morphology and continuum morphology. As pointed out already, the type concept is central to classical morphology. If, either explicitly or implicitly, it is understood as extreme type, then classical morphology becomes continuum morphology because structural categories are no longer seen as mutually exclusive but as centres of continuous types. If, in classical morphology, the notion of the extreme type is used only occasionally, the general orientation remains largely classical, but with a small degree of continuum thinking. As the notion of the extreme type is implied more and more, continuum morphology is increasingly approached. Consequently, the boundary between typical classical morphology (in which only the classificatory type concept is involved) and continuum morphology becomes fuzzy and disappears. Thus, the schemes of Fig. 1B, C apply not only to plant structures but also to approaches and views of plant morphologists. Just as it is too simplistic to insist that all organs of flowering plants and some related taxa must be either roots, caulomes (stems and their homologues) or phyllomes (leaves and their homologues), so it is inappropriate to conclude that all plant morphologists are either classical morphologists or continuum morphologists. Both classical and continuum morphologists are more adequately seen as extreme types. Troll (1937–43, 1944, 1954) and some of his followers represent the centre of the extreme type of classical morphology. I referred to them as typical classical morphologists because of their insistence on classificatory typology. Others are more or less intermediate between the centre of classical morphology and that of

continuum morphology. For example, Rohweder and Endress (1983) drew attention to unusual structures such as radial leaves that combine features of a typical leaf and stem. Although they recognized such intermediate structures in a descriptive sense, they felt compelled to interpret them in terms of classical morphology which means placing them into mutually exclusive classificatory types. They added, however, that it depends on our aim whether we insist on mutually exclusive categories or recognize a continuum. This statement could be interpreted as a recognition of some sort of complementarity. Bell (1991) went one important step further. In his discussion of morphological 'misfits', he underlined that these forms do not fit into the categorical framework of classical morphology. Therefore, the problem is not with the 'misfits' but rather with the rigidity of typical classical morphology. Klotz (1985), in a discussion of the typology of the leaf, drew attention to intermediate forms between typical leaves and stems. He concluded that the leaf 'is not, neither typologically nor phylogenetically, clearly separated from the stem' (Klotz, 1985).

CONCLUSIONS

The recognition of the continuum between typical plant structures such as roots, caulomes and phyllomes is important because it has many consequences for plant morphology and other biological disciplines (Sattler and Jeune, 1992; Sattler, 1994). The recognition of the continuum between typical classical morphology and continuum morphology is equally important because it also has far-reaching implications.

Classical morphology and continuum morphology are not two sharply circumscribed approaches and views. As they merge with each other, opposition dissolves because there are no longer two separate fields that could be opposed. One can, of course, isolate two centres within the continuum of the two extreme types of classical and continuum morphology. But even then typical classical morphology and continuum morphology need not be in opposition but can also be seen as complementary to each other, the former emphasizing the difference of typical forms and the latter stressing the continuity between these forms. Continuum morphology, however, offers a more comprehensive perspective since it comprises the whole spectrum of forms, i.e. intermediate as well as typical forms.

Both typical classical morphology and continuum morphology with their associated type concepts can be seen as the expression of different world views. Typical classical morphology and the classificatory type concept exemplify a categorical or even an essentialistic world view: everything has to be accommodated in mutually exclusive categories (see, e.g. Sattler, 1986, Chapter 10). Intermediates that do not fit are ignored or forced into one or the other category. It is not surprising that this may lead to violence. The categorical world view itself has streaks of violence: cutting up the whole into categories is a destructive act; forcing intermediate forms into categories creates conflict in a violent manner. Unfortunately, conflict and violence can be found almost everywhere in our society that has been shaped by a predominantly categorical world view. Different

'schools' within academia, ideologies and dogmatic religions are often perceived as mutually exclusive which creates the dynamite for potential conflict, violence and war.

Continuum morphology can be seen as the expression of a fuzzy and relational world view with its underlying fuzzy logic (see Kosko, 1993). In this view, the questions are no longer: Is it this or that? Do I belong here or there? The questions are rather: How is it related to this and that? How am I related to this and that? Since I and anything else can be related to many points or centres of extreme types, multidimensional relations may result that extend far beyond simplistic *either-or* thinking and its behavioural and political consequences.

To conclude, I want to suggest that world views can also be seen as extreme types. Thus, the categorical world view and its adherents need not be fundamentally opposed to the fuzzy and relational world view with its supporters. They are linked through an actual and potential continuum. Furthermore, extreme positions can be seen as complementary to each other. Therefore, instead of fighting each other, we could realize that we complement each other. We could recognize that a position apparently opposed to ours, may be enriching our understanding and our life. Co-operation may then ensue, leading to more peace within the scientific community, nations, ideological, religious and other groups.

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