



Kaplan's Principles of Plant Morphology: A Critical Review

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Published online: 8 June 2022

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“We should not confuse our favourite metaphors (including concepts such as root, shoot, leaf and flower) with reality, which is more complex” (Kirchoff et al., 2008).

Kaplan's Principles of Plant Morphology (2022) by Donald R. Kaplan, edited by Chelsea D. Specht, is a monumental work of 1305 pages in a large format. It presents a wealth of well-organized morphological data that are relevant not only to plant morphology but also to many other fields such as plant genetics, molecular biology, evolution, systematics, biodiversity, crop science, etc. The interpretations of the data are in terms of classical plant morphology, a rigid typological framework that Kaplan adopted from Troll (1937-1943). Before I discuss this typological framework of classical plant morphology, a few comments on the fundamental importance and relevance of plant morphology in general.

Plant Morphology Remains Important

For centuries, plant morphology, besides plant physiology, genetics, ecology, and systematics, has been one of the basic disciplines of plant biology or botany. Hence, universities offered courses in plant morphology. But nowadays this is no longer the case. Plant morphology has been absorbed into Evolutionary Developmental Biology (Evo-Devo). This does, however, not diminish the importance and relevance of plant morphology. Besides molecular genetics, morphology remains an integral part of evo-devo. To emphasize the importance of morphology, Wanninger (2015) referred to MorphoEvoDevo. Minelli's comprehensive book on plant evo-devo has as its subtitle “The evolvability of the phenotype” (Minelli, 2018).

Kaplan emphasized that plant morphology is more fundamental than plant anatomy, which deals with tissues, cells, and subcellular components. He devoted a whole chapter of his book to this topic where he pointed out that “organ differentiation is independent of the arrangement of cell and tissue types and even multicellularity itself. For example, the various siphonous greens, such as *Bryopsis* and *Caulerpa*,

exhibit organ differentiation that converges with that of higher plants without being cut up into cells at all” (Kaplan, 2022, p. 62).

Sattler and Rutishauser (1997) emphasized that in most botanical disciplines, including molecular genetics, morphological concepts are used or implied. Thus, morphology plays a fundamental role in these disciplines. And therefore new empirical findings, conceptual and foundational innovations such as continuum and process morphology are fundamentally relevant not only in morphology but also in many other fields of plant biology.

Classical Morphology

As stated above, Kaplan’s morphological principles are based on classical morphology. According to classical morphology, there is a trinity of three fundamental organ categories: root, stem (caulome), and leaf (phyllome), and all lateral appendages, including those of flowers, are considered homologous. The three organ categories are considered mutually exclusive. Hence, classical morphology implies Aristotelian either/or logic: any organ is either a root or a stem (caulome) or a leaf (phyllome). Troll (1937–1943) defended this logic of the trinitarian view. It is called classical because Goethe, the classical and romantic German poet and scientist, expounded this view in his classic *Metamorphosis of Plants* (Goethe, 1790). But although he referred to root, stem, and leaf, he also saw the shoot composed of units that comprise a leaf and its subtending stem segment, units which are called phytomers or metamers (Rutishauser & Sattler, 1985). According to this view, the plant does not consist of roots, stems, and leaves, but only of roots and phytomers. Kaplan referred to decurrent leaf bases. As I shall point out below, Goethe also embraced yet other views. But Troll and Kaplan, as many other contemporary morphologists, remained locked in the root-stem-leaf trinity of classical morphology that Goethe envisaged in 1790, over 200 years ago. Other morphologists could see beyond this trinity of classical morphology (see below).

Since classical morphology implies a discontinuity between the organ categories, one could also refer to it as a discontinuum view. Contrary to this discontinuum view, much evidence has been accumulated in support of a continuum view, which implies that the organ categories are bridged through intermediate forms (see below). Therefore, a continuum view, which includes the intermediate forms that don’t fit into the categories, appears more comprehensive than the discontinuum view. However, this does not mean that the discontinuum view of classical plant morphology is useless. One cannot deny that classical morphology is useful in many instances, but as an overarching theory it is contradicted by many morphological findings, by molecular genetics and mathematical analyses (see below). Nonetheless, Kaplan claimed: “All vascular plants ... appear to be built on the same fundamental organizational theme or ground plan” (Kaplan, 2022, p. 1) comprising a root system and a shoot system, which consists of stem(s) and leaves. Kaplan noted that the stem and leaves cannot be clearly delimited from one another and that “they only have meaning in their spatial relations to one another, not as separate elements” (Kaplan, 2022, p. 159). Nonetheless, he

upheld the trinitarian view of three major organ categories and maintained that the diversity of plant organs can be reduced to these organ categories. This view appears rather static. Change may occur within the categories, but the categories are fixed as are positional relationships within the ground plan: “the leaf component of the shoot always occupies a set position as a lateral outgrowth from the stem” (Kaplan, 2022, p. 6). In contrast, process morphology is profoundly dynamic: plant structures are seen as process combinations that may change during ontogeny and phylogeny (Sattler, 1992, 1994, 1998, 2019; see below). Heterotopy refers to positional changes.

How do classical morphology, continuum and process morphology relate to typology? Typology can have two very different meanings depending on which type concept is implied. There are two type concepts: the classificatory type and the extreme type (see Sattler, 1996). Classificatory types are mutually exclusive, following either/or logic. They represent the discontinuum view of classical plant morphology, the rigid typological framework of Troll's and Kaplan's morphology I referred to above. In contrast, extreme types are continuous, implying fuzzy logic (see Rutishauser and Isler, 2001). They are compatible with the continuum and process view of plant morphology.

Homology

Homology is a central concept in morphology. According to Kaplan, it means “morphological correspondence to one of the major organ categories, i.e. leaf, stem, or root” (Kaplan, 2022, p. 5). To determine homologies, Kaplan refers to three criteria that have been explicated by Remane (1952): 1. Equivalent positions (position criterion), 2. Equivalent special quality (quality criterion), 3. Intermediate transitional forms (transition criterion). Like Troll, Kaplan considered the position criterion the most fundamental. Its general validity has been undermined, however, by the phenomenon of homeosis. Homeosis means replacement of one structure or a trait of one structure by another one. In other words, “at the site of one part another part or feature(s) of another part are expressed” (Sattler, 1986). In cases where an organ of one category is replaced by an organ of another category, the position criterion leads to absurd conclusions. For example, in *Nasturtium officinale*, axillary shoots may be replaced by roots (Champagnat & Blatteron, 1966). According to the position criterion, this would mean that the roots are shoots. Evidently, we recognize a root or a shoot by its special quality, not by its position. Therefore, the quality criterion appears more fundamental than the position criterion. Yet Kaplan emphasized that “organs in plants are defined principally by their topographic-positional relationships” (Kaplan, 2022, p. 265). Besides the position criterion, the transition criterion can also lead to absurd conclusions. In cases of a transition from an organ of one category to an organ of another category, it would mean that they are homologous because they are linked through transitional forms. But what the transition criterion shows is a continuum, not necessarily a homology (Sattler, 2018, expanded version).

Consider the following series of transitional forms, each of which exhibits three of the properties a,b,c,d,f:

1. abc
2. bcd
3. cde
4. def

1 and 4 share none of their properties, yet they are connected through transitional forms. To conclude that there is a correspondence or homology between 1 and 4 appears absurd. Even the first three forms, although they could be defined by property c (as a category, for example), show only a partial correspondence; they are not the same; they are only partially homologous. Deducing identity, 1:1 correspondence or homology from a continuum of forms appears to be fallacious reasoning.

Kaplan did not sufficiently envisage the problems with the position and transition criteria. Furthermore, at least in the first chapter in which he dealt with the concept of homology, he did not refer to the enormous literature on homology since the publication of Remane's book. He did not cite and discuss important articles and books such as *Homology* (edited by Hall, 1994). He ignored the concepts of partial homology (Sattler, 1994), factorial and combinatorial homology (Minelli, 1998, 2018; Minelli & Fusco, 2013), which do not fit into the Aristotelian either/or logic of classical morphology.

Morphological Principles

Kaplan's principles are the principles of classical plant morphology. In a book on principles, it would have been helpful for the reader to have a list where the principles are explicitly stated. No such list is in Kaplan's book. Therefore, we cannot even tell exactly how many principles there are. In contrast, Ganong (1901), the Canadian-American botanist (not cited by Kaplan), stated explicitly seven cardinal principles. The seventh principle, which he considered the most important one, is the principle of gradation in morphological membership, which means that "difference of degree passes over gradually into difference of kind." As a result, categories become linked through a continuum. Evidently, this principle surpasses the principles of classical plant morphology.

Axioms and Principles of Plant Construction (edited by Sattler, 1982) (not cited by Kaplan), contains an article by Cusset (1982) in which he listed explicitly 37 principles. Kaplan's principles represent only a small subset of these principles, mainly the ones that imply typology. Hence, Kaplan's morphology seems a rather impoverished version of the many insights morphologists have gained since the time of Goethe and by Goethe himself who could see far beyond the tenets of classical morphology that he expounded in his *Metamorphosis of Plants* (1790) and subsequently surpassed (see below and Sattler, 2018). Excluding so much does not benefit plant morphology and plant biology (see below).

Shoot Morphology

Besides a chapter on roots, Kaplan's book contains several instructive chapters on various aspects of shoot morphology and phyllotaxis. But Kaplan's interpretation of phylloclades shows once again that he remained locked in Troll's typological framework and the position criterion for homology (Kaplan, 2022, pp. 258–266). According to this typological way of thinking, since phylloclades are formed in an axillary position, they must be homologous to a shoot as a shoot normally arises in the axil of a leaf. However, as we pointed out above, the validity of the position criterion has been undermined by the phenomenon of homeosis, which in this case means that leaf traits are expressed in a position where normally shoots are formed. Since phylloclades, for example, in the Asparagaceae (Ruscaceae s.l.), show the whole range from more shoot-like to less shoot-like to leaf-like, they show a gradation in the integration of leaf traits into axillary shoots (Cooney-Sovetts & Sattler, 1987). This homeotic interpretation of phylloclades has been supported by molecular genetic analysis. For example, during the development of the phylloclades of *Ruscus aculeatus* genes are expressed that are normally expressed in the shoot apex and in leaves (Hirayama et al., 2007). Hence, these authors concluded that “the phylloclade is not homologous to either the shoot or the leaf, but that it has a double identity” (ibid.). This shows clearly that the either/or logic of Troll, Kaplan, and other morphologists is inappropriate and needs to be replaced by a both/and logic.

As leaf traits may be integrated into axillary positions, so shoot traits may be integrated into the subtending positions of leaves. For example, the so-called “leaves” of *Chisocheton* integrated traits of shoots such as indeterminate growth and bud formation in the axil of the so-called leaflets. As a result, they show a combination of leaf and shoot traits (Fisher & Rutishauser, 1990, 1990). Nonetheless, Kaplan and DeMason (in a review at the end of Chapter 14) homologize them with leaves using all three homology criteria (Kaplan, 2022, pp. 348 and 366). First of all, they claim that they are leaves because they occupy the position of leaves. But they ignore that the position criterion has been undermined by homeosis. Second, they use the quality criterion to emphasize that they are dorsiventral like typical leaves. But dorsiventrality occurs also in some shoots and even roots. Third, using the transition criterion, they point out that there is a transition from determinate leaves at the base of the shoot to the indeterminate “leaves” higher up. But as pointed out above, a transition does not indicate identity, a 1:1 correspondence or homology. It just shows a continuum whose endpoints are different. Yet, as pointed out by Kaplan and DeMason, I agree that these so-called “leaves” occupy typical leaf positions, are dorsiventral, and are preceded by typical leaves, but they show an integration of shoot features, which means that there is an expression of shoot traits in leaf positions, which is a case of homeosis, “the assumption of one part [of an organism] of likeness to another part” (Holmes, 1979). One cannot deny that the indeterminate “leaves” of *Chisocheton* combine leaf and shoot traits.

One widespread problem in plant morphology – and many other fields, including everyday life—is that one author selects one feature and declares it essential or

fundamental. Then another author selects another feature and declares it essential or fundamental. And then we have the conflict and controversy. Solution: consider all features, the total picture, and avoid essentialism and fundamentalism. For example, in the case of the indeterminate *Chisocheton* “leaves,” Kaplan and DeMason selected the position and symmetry as the essential or fundamental features and therefore concluded that they are essentially leaves, preserving their “fundamental leaf nature” (DeMason in Kaplan, 2022, p. 366). Schacht and Curry (1854) selected indeterminate growth as the essential feature and therefore concluded that these structures are essentially shoots. But if all features are considered without declaring one or the other as essential or fundamental, then I can see that there is a combination of leaf and shoot features. Hence, we can conclude that the *Chisocheton* “leaves” are partially homologous to leaves and shoots.

In general, classical morphology works well for the typical forms. But for intermediates between the typical forms it led to almost endless futile debates whether they belong to one or the other category, and at times these debates degenerated into hostility and nastiness. But recognizing that the intermediate forms belong neither to this category, nor to that category and that therefore the categorical either/or approach of classical morphology is inappropriate, would have been highly beneficial for morphology (Sattler 2022a).

Leaf Morphology

Kaplan’s book includes five lengthy chapters on leaf morphology. Kaplan made many detailed contributions to a clarification of leaf morphology. He upheld the classical view also for leaf morphology. According to this view, the leaf category has three subcategories: leaf base, petiole, and blade (lamina), which are considered mutually exclusive. Hence, leaf morphologies we observe must be reducible to these categories. Kaplan stressed, however, that the primary subdivisions of the leaf are the lower and upper leaf zones.

Another assumption of classical morphology with regard to leaf morphology is the homology of simple and compound leaves. However, this assumption has become increasingly rejected. Already Goethe realized that compound leaves cannot be placed into the leaf category because they resemble branches. Contrary to his *Metamorphosis of Plants* (1790) where he claimed that all lateral appendages are essentially the same (“one and the same organ”), in other morphological writings (that are not cited by Kaplan) he wrote: “When leaves divide, or rather when they advance from their original state to diversity, they are striving toward greater perfection, in the sense that each leaf has the intention of becoming a branch” (quoted by C. J. Engard in Mueller, 1989, p. 10). In another statement, Goethe considered compound leaves as “in reality branches, the buds of which cannot develop, since the common stalk is too frail” (Goethe, quoted by Arber, 1946, p. 78). Other morphologists such as Casimir De Candolle (1868), Arber (1950), Sattler and Rutishauser (1992), Rutishauser and Sattler (1997), and Lacroix et al. (2003) concluded that compound leaves combine leaf and shoot properties. On the basis of molecular genetics, Eckardt and Baum (2010) concluded that “it is now generally accepted that

compound leaves express both leaf and shoot properties.” In more general terms, James (2009, p. 17) stated that “it is now widely accepted that...radiality and dorsiventrality are but extremes of a continuous spectrum. In fact, it is simply the timing of the KNOX gene expression!”.

On morphological grounds, Sattler and Jeune (1992), Jeune and Sattler (1992) and Cusset (1994), using multivariate analysis, demonstrated a continuum between leaf and shoot and all other morphological categories. This continuum is a dynamic continuum according to process morphology that recognizes plant structures as process combinations (Sattler, 1992, 1994, 1998, 2019). Thus, process morphology and continuum morphology supersede the trinitarian categorical view of classical plant morphology, but the latter remains useful. For this reason, the trinitarian categorical view and the dynamic continuum view can be seen as complementary (Rutishauser & Sattler, 1985; Rutishauser & Isler, 2001, Kirchoff et al., 2008). The principle of complementarity can be widely used in morphology and other sciences. In physics, it has been used since Niels Bohr introduced it. As far as I can see, Kaplan failed to use this principle. His thinking was based on Aristotelian either/or logic. But the principle of complementarity implies both/and logic. Thus, both categorical and continuum morphology can be used, although the latter is more comprehensive than the former.

Besides compound leaves, there are other structures that cannot be fitted into the leaf category, although Kaplan insists that they are leaves. For example, in *Utricularia*, stolons or runners show a combination of leaf, shoot, and root properties (see, for example, Rutishauser & Sattler, 1989; Rutishauser & Isler, 2001; Rutishauser, 2020; Reut & Plachno, 2020). Depending on which of these properties is considered fundamental, different authors homologized the stolons with leaves, shoots, or roots (Kaplan, 2022, p. 566). Kaplan homologized them with leaves because they are dorsiventral, but shoots and even roots can also be dorsiventral (see, for example, Fisher, 1973; Kaplan, 2022, p. 251, 1222). Kaplan also used the questionable position and transition criteria to support his leaf homology. He pointed out that “in embryos of many species of *Utricularia*, the first two leaves of the shoot will be a laminate leaf and a runner” (Kaplan, 2022, p. 568). If this is so, then we could see the runner as a case of homeosis, the integration of shoot and root properties into the leaf. A leaf that has integrated shoot and root properties is no longer a pure leaf but a combination of leaf, shoot, and root properties. Recognizing such a combination contradicts and transcends classical morphology, which operates in terms of either/or logic: either a leaf, or a shoot, or a root.

Sattler and Rutishauser (1990) analyzed two species of *Utricularia* in terms of process morphology that also transcends morphological categories because structures are understood as process combinations that have changed during ontogeny and phylogeny. This approach is dynamic and not constrained by the categories of classical morphology that often have led to nearly endless futile debates on whether a structure that does not fit the categories is homologous to a root, a stem, or a leaf. Rutishauser and Isler (2001) concluded: “The orthodox distinction of ‘root’, ‘stem’ and ‘leaf’ is transcended throughout the genus *Utricularia*.”

Genomic analyses of *U. gibba*, and *U. vulgaris* revealed the presence of a considerable number of root-specific genes in their vegetative structures” (for references see Rutishauser, 2016). “Various Utricularias (e.g., *U. longifolia*, *U. livida*, *U. sandersonii*) have straight stolon tips which look (including anatomy) similar to cap-less root tips of *Pinguicula*. When *U. longifolia* is cultivated in a hanging pot, the root-like stolons breaking through the bottom show positive geotropism” (Rutishauser, 2020).

Besides *Utricularia*, there are other taxa such as, for example, Podostemaceae, whose morphology does not fit into the classical root-stem-leaf trinity (Rutishauser, 2016; Minelli, 2018).

Flower Morphology

Besides two chapters on the reproductive shoots in Pteridophytes and Gymnosperms, Kaplan’s book contains two chapters on flowers and one chapter on inflorescences. Like Troll and other morphologists, he defined a flower as “a reproductive short shoot bearing microsporophylls (stamens)... and megasporophylls (carpels) as its appendages or leaf homologues. In addition, it bears sterile appendages” (Kaplan, 2022, p. 1169). He did not point out that this definition has been contested by many plant morphologists based on many contradictory facts. Stamens in at least some taxa have been homologized with caulomes or branchlets. Sattler (1988) demonstrated a heterogeneous continuum from phyllomic stamens to caulomic stamens and branchlets. Gynoecia of various taxa are acarpellate, that is, they don’t have appendages that bear ovule(s) because the ovule(s) are born on the floral axis. For example, Macdonald and Sattler (1973) and Sattler and Lacroix (1988) demonstrated how the floral apex becomes gradually transformed into the ovule. Instead of declaring these gynoecia acarpellate, one could redefine the carpel as an appendage that encloses the ovule(s) and may or may not bear them, as proposed by Sattler and Perlin (1982) Greyson (1994), and Leins and Erbar (2010, in their glossary only). In any case, it is important to acknowledge that during evolution the position of the placenta or ovules has changed within the gynoecia (Sattler, 1974, 2022b). This is an example of heterotopy. Molecular geneticists refer to ectopic gene expression.

Since Goethe, who expounded the classical concept of the flower in his *Metamorphosis of Plants* (1790), almost endless debates about the nature of flowers have ensued. Many of these debates have been in terms of morphological categories such as caulome and phyllome. However, some authors took a more process-oriented approach. According to anaphytosis, the theory of anaphytes, proposed by Schultz (1843), who was also known as Schultz-Schultzenstein (1867), plant form is the result of branching and articulation that produces articles (anaphytes). These anaphytes can be understood as process combinations according to process morphology (Sattler, 2018, 2019). Thus, stamens and carpels can be seen as articles (anaphytes) or systems of articles, that represent unique process combinations not found in the vegetative region. Consequently, the questions whether stamens and carpels are leaf homologues and whether the flower is a

modified monaxial shoot are superseded. Toward the end of his life, Adriance S. Foster, Kaplan's thesis director, accepted that "a theory, in some way analogous to that of anaphytes, was most valuable" (quoted by Cusset, 1982, p. 46). It can be updated in terms of process morphology (Sattler, 2018, 2019).

Although not referring to the theory of anaphytes, Claßen-Bockhoff (2016) also went beyond the classical interpretation of the flower when she concluded: "Flowers are sporangia bearing units rather than short shoots with floral organs." These sporangia bearing units can be understood as branching systems with unique articles (process combinations).

A Broader and More Comprehensive View of Plant Morphology

To better understand the present situation of plant morphology, a knowledge of its historical development is very helpful. Kaplan was interested in the history of plant morphology, but his view was one-sided and incomplete. He wrote: "Plant morphology is largely a German science" (Kaplan, 2001). He ignored that French plant morphologists contributed as much or more to plant morphology than their German counterparts (see Cusset, 1982). And plant morphologists in other countries such as England, Russia, India, Japan, North and South America have also made very important contributions. Therefore, plant morphology cannot be considered largely a German science.

Kaplan noted that "the origin of plant morphology as a discipline can be dated by the appearance of his [Goethe's] pivotal publication [in 1790]" (ibid.). Goethe coined the term "morphology," and in 1790 postulated the identity of all lateral appendages, including those of flowers. However, Wolff (1768) came to a similar conclusion 22 years before Goethe. And A. P. De Candolle, a contemporary of Goethe, elaborated more comprehensive treatises on plant morphology than Goethe (see Cusset, 1982).

About German plant morphology, Kaplan wrote: "Despite its history of over two centuries, German plant morphology has had only four principal figures who were significant in its development: Johann Wolfgang von Goethe, Wilhelm Hofmeister, Karl von Goebel, and Wilhelm Troll." Although these botanists have made extensive contributions to plant morphology, others such as Walter Zimmermann have also made highly significant contributions that were not in line with Troll's typology favoured by Kaplan. Schultz (1843), also known as Schultz-Schultzenstein (1867), elaborated his theory of anaphytes (anaphytosis) that transcends morphological categories because plants are described in terms of the processes of branching and articulation (see Sattler, 2018, 2019). Schultz-Schultzenstein (1867) was highly critical of Goethe's theory of metamorphosis. But Goethe himself also expressed doubts about the type concept that was so central to his morphology. He wrote that "this idea [of the type] which I prize so much, can be considered as a conducting thread facilitating discoveries, but that it is of no help in determining particular cases, and in fact is a hindrance" (quoted by Cusset, 1982, p. 27). Goethe also anticipated Arber's Partial-Shoot Theory of the Leaf when he wrote: "When leaves divide, or rather when they

advance from their original state to diversity, they are striving toward greater perfection, in the sense that each leaf has the intention of becoming a branch” (quoted by C. J. Engard in Mueller, 1989, p. 10). Most of all, Goethe emphasized that “the researcher should not confine himself within one uniform mode of explanation” (quoted by Cusset, 1982, p. 27). But his followers such as Troll and Kaplan have narrowed him down to one mode of explanation in terms of the type concept of classical morphology, according to which plants consist of roots, stems, and leaves in prescribed positions. French morphologists such as Casimir De Candolle, Baillon, Clos, and others provided evidence for alternative views of plant form, emphasizing a continuum between the categories (see Cusset, 1982). Ganong (1901), a Canadian-American botanist, who was president of the Botanical Society of America, expressed a principle of gradation between morphological categories that superseded the constraints of classical morphology. Laevitt (1909), an American Harvard-educated botanist, introduced the principle of homeosis to plant morphology and thus demonstrated that positional relationships are not necessarily fixed. And the list goes on (see Cusset, 1982). This shows that the views of Kaplan were very narrow and one-sided. Yes, they illuminate one aspect of plant morphology but ignore so many others. Rutishauser and Sattler (1985) underlined the complementarity of different, even contradictory views.

Claßen-Bockoff (2001) presented an exposition of three very different views of morphology in the twentieth century: those of Wilhelm Troll, Walter Zimmermann, and Agnes Arber. Kaplan almost completely ignored those of Zimmermann and Arber and considered them unimportant. Zimmermann (1959) is mainly known as the founder of his telome theory (for an extension see Sattler, 1998). But more generally, he advocated a dynamic morphology that emphasized the importance of heteromorphy, heterotopy, and heterochrony for the evolution of novel plant forms. Furthermore, he emphasized hologeny, which means that phylogeny is a succession of modified ontogenies. In this sense, Zimmermann can be considered a forerunner of modern evolutionary developmental plant biology (plant evo-devo). Arber (1950) went beyond the limitations of the categorical approach of classical plant morphology (see Rutishauser & Isler, 2001).

Besides Arber, there were other important plant morphologists in England such as E. J. H. Corner and C. W. Wardlaw. In Russia Takhtajan and Meyen made very important contributions to our understanding of the evolution of plant form. Takhtajan (1972) distinguished the following three processes for the evolution of morphological novelty: prolongation, abbreviation, and deviation. Neoteny is the combination of terminal abbreviation and deviation. Meyen (1987) presented many original insights into plant morphology and its methodology. In India V. Puri, B. G. L. Swamy and others made important contributions to our understanding of plant form, and so did F. Maekawa, H. Tsukaya, and others in Japan and L. Croizat in Caracas, Venezuela, through his *Principia Botanica* (1960) and other publications. Hence Kaplan’s characterization of plant morphology as “largely a German science” seems indeed one-sided and incomplete.

Conclusions

Kaplan's monumental book presents a wealth of well-organized morphological data. These data are interpreted in terms of classical morphology, which postulated a trinity of mutually exclusive categories (root, stem (caulome), and leaf (phyllome)) and the phylloclad homology of all lateral appendages, including those of flowers. For classical morphology Kaplan's book is a milestone of enormous significance that needs to be celebrated.

Classical morphology has one of its roots in Goethe's *Metamorphosis of Plants* (1790), which postulated the essential similarity of all lateral appendages and the fixity of positional relationships within a static ground plan. Many innovations in the way we view and interpret plant form have been made since the publication of Goethe's *Metamorphosis of Plants*. Even Goethe himself surpassed his *Metamorphosis of Plants* (see Arber, 1946; Sattler, 2018). However, Troll, Kaplan, and many other morphologists remained locked in the conceptual framework of the *Metamorphosis of Plants*. Although this framework is useful, there are many plants that do not fit into it, for which we need a more comprehensive framework of continuum and process morphology that is supported by morphological, mathematical, and molecular genetic analyses.

Acknowledgements I am very grateful to Rolf Rutishauser for his many critical comments and helpful suggestions.

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References

- Arber, A. 1946. Goethe's Botany. *Chronica Botanica* 10: 63-126.
- Arber, A. 1950. *The Natural Philosophy of Plant Form*. Cambridge University Press.
- Champagnat, M. & S. Blatteron. 1966. Ontogénie des organes axillaires du cresson (*Nasturtium officinale* R. Br.). *Revue Générale de Botanique* 73: 85-102.
- Claßen-Bockhoff, R. 2001. Plant Morphology: The historic concepts of Wilhelm Troll, Walter Zimmermann and Agnes Arber. *Annals of Botany* 88: 1153-1172.
- Claßen-Bockhoff, R. 2016. The shoot concept of the flower: Still up to date? *Flora* 221: 46-53.
- Cooney-Sovetts, C. & R. Sattler. 1987. Phylloclade development in the Asparagaceae: an example of homoeosis. *Botanical Journal of the Linnean Society* 94: 327-371.
- Croizat, L. 1960. *Principia Botanica*. Caracas.
- Cusset, G. 1982. The conceptual bases of plant morphology. Pp. 8-86. In: R. Sattler (ed.), *Axioms and Principles of Plant Construction*. The Hague/Boston/London, Martinus Nijhoff/ Dr. W Junk Publishers; also published in *Acta Biotheoretica*, Volume 31A.
- Cusset, G. 1994. A simple classification of the complex parts of vascular plants. *Botanical Journal of the Linnean Society* 114: 229- 242.

- De Candolle, C. 1868. Théorie de la feuille. Arch. Sc. Phys. Nat. Genève, 5th series, 32: 32–67.
- Eckardt, N. A. and Baum, D. 2010. The Podostemad puzzle: The evolution of unusual morphology in the Podostemaceae. The Plant Cell 22: 2104.
- Fisher, J. B. 1973. Unusual branch development in the palm *Chrysalidocarpus*. Botanical Journal of the Linnean Society 66: 83–95.
- Fisher, J. B. & R. Rutishauser. 1990. Leaves and epiphyllous shoots in *Chisohton* (Meliaceae). A continuum of woody leaf and stem axes. Canadian Journal of Botany 68(11): 2316–2328. <https://doi.org/10.1139/b90-296>.
- Ganong, W. F. 1901. The cardinal principles of morphology. Botanical Gazette 31: 426–434; <https://www.journals.uchicago.edu/doi/epdf/10.1086/328124>
- Goethe, J. W. von. 1790. Versuch die Metamorphose der Pflanzen zu erklären. Gotha, C. W. Ettinger (translated into English as *Metamorphosis of Plants* by Arber, 1946)
- Greyson, R. I. 1994. *The Development of Flowers*. New York/Oxford: Oxford University Press.
- Hall, B. K. (ed.) 1994. *Homology: The Hierarchical Basis of Comparative Biology*. New York: Academic Press.
- Hirayama, Y., T. Yamada, Y. Oya, M. Ito, M. Kato & R. Imaichi. 2007. Expression of patterns of class I Knox and Yabby genes in *Ruscus aculeatus* (Asparagaceae) with implications for cladode homology. Development, Genes and Evolution 217(5): 363–372.
- Holmes, S. 1979. *Henderson's dictionary of biological terms*. New York, Van Nostrand Reinhold.
- James, P. J. 2009. 'Tree and Leaf': A different angle. The Linnean 25: 13–19.
- Jeune, B. & R. Sattler. 1992. Multivariate analysis in process morphology. Journal of Theoretical Biology 156: 147–167.
- Kaplan, D. R. 2001. The science of plant morphology: definition, history, and role in modern biology. American Journal of Botany 88: 1711–1741.
- Kaplan, D. R. 2022. *Kaplan's principles of plant morphology*. Edited by C. D. Specht. New York, CRC Press.
- Kirchoff, B. K., E. Pfeifer & R. Rutishauser. 2008. Plant structure ontology: How should we label plant structures with doubtful or mixed identities? Zootaxa 1950: 108–122. <https://www.mapress.com/zt/article/view/zootaxa.1950.1.10>
- Lacroix, C., B. Jeune & S. Purcell-Macdonald. 2003. Shoot and compound leaf comparisons in eudicots: dynamic morphology as an alternative approach. Botanical Journal of the Linnean Society 143: 219–230.
- Laevitt, R. G. 1909. A vegetative mutant, and the principle of homeosis in plants. Botanical Gazette 47: 30–68.
- Leins, P. & C. Erbar. 2010. *Flower and Fruit*. Stuttgart: Schweizerbart Science Publishers.
- Macdonald, A.D. and Sattler, R. 1973. Floral development of *Myrica gale* and the controversy over floral theories. Canadian Journal of Botany 51: 1965–1975.
- Meyen, S. V. 1987. *Fundamentals of Palaeobotany*. London: Chapman & Hall.
- Minelli, A. 1998. Molecules, developmental modules and phenotypes: A combinatorial approach to homology. Molecular Phylogenetics and Evolution 9: 340–347.
- Minelli, A. 2018. *Plant Evolutionary Biology. The Evolvability of the Phenotype*. New York: Cambridge University Press.
- Minelli, A. & G. Fusco. 2013. Homology. Pp. 289–322. In: K. Kampourakis (ed.), *The Philosophy of Biology: A Companion for Educators, History, Philosophy and Theory of the Life Sciences*. Dordrecht, Springer.
- Mueller, B. 1989 (translator) *Goethe's Botanical Writings*. Woodbridge, CT: Ox Bow Press.
- Remane, A. 1952. *Die Grundlagen des natürlichen Systems, der vergleichenden Anatomie und der Phylogenetik*. Geest & Prtig: Leipzig.
- Reut, M. S. & B. J. Plachno. 2020. Unusual development and anatomy of vegetative organs in *Utricularia dichotoma* – leaf, shoot and root dynamics. Protoplasma 257: 371–390. <https://doi.org/10.1007/s00709-019-01443-6>
- Rutishauser, R. 2016. Evolution of unusual morphologies in Lentibulariaceae (bladderworts and allies) and Podostemaceae (river-weeds): a pictorial report on the interphase of developmental biology and morphological diversification. Annals of Botany 117: 811–832. <https://doi.org/10.1093/aob/mcv172>
- Rutishauser, R. 2020. Past and future of continuum and process plant morphology. *Philosophies*, 5(4), 41. <https://doi.org/10.3390/philosophies5040041>
- Rutishauser, R. & B. Isler. 2001. Developmental genetics and morphological evolution of flowering plants, especially bladderworts (*Utricularia*): Fuzzy Arberian Morphology complements Classical

- Morphology. *Annals of Botany* 88: 1173–1201. http://www.systbot.uzh.ch/static/personen/rolf_rutishauser_assets/Rut_Isl_AnnBot_2001.pdf
- Rutishauser, R. & R. Sattler. 1985. Complementarity and heuristic value of contrasting models in structural botany. I. General considerations. *Botanische Jahrbücher für Systematik* 107: 415–455.
- Rutishauser, R. & R. Sattler. 1989. Complementarity and heuristic value of contrasting models in structural botany. III. Case study on shoot-like "leaves" and leaf-like "shoots" in *Utricularia macrorhiza* and *U. purpurea* (Lentibulariaceae). *Botanische Jahrbücher für Systematik* 111: 121–137.
- Rutishauser, R. & R. Sattler. 1997. Expression of shoot processes in leaf development of *Polemonium caeruleum*. *Botanische Jahrbücher für Systematik* 119: 563–582.
- Sattler, R. 1974. A new approach to gynoeical morphology. *Phytomorphology* 24: 22–34.
- Sattler, R. (ed.). 1982. *Axioms and Principles of Plant Construction*. The Hague/Boston/London, Martinus Nijhoff/ Dr. W Junk Publishers.
- Sattler, R. 1986. Homeosis in plants. *American Journal of Botany* 75(10), 1606–1617.
- Sattler, R. 1988. A dynamic multidimensional approach to floral morphology. Pp. 1–6. In: P. Leins, S. C. Tucker, & P. Endress (eds.), *Aspects of Floral Development*. Berlin/Stuttgart, J. Cramer.
- Sattler, R. 1992. Process morphology: structural dynamics in development and evolution. *Canadian Journal of Botany* 70: 708–714. <https://cdnsiencepub.com/doi/abs/10.1139/b92-091>
- Sattler, R. 1994. Homology, homeosis and process morphology in plants. Pp. 775–793. In: B. K. Hall (ed.), *Homology: The hierarchical basis of comparative biology*. New York, Academic Press.
- Sattler, R. 1996. Classical morphology and continuum morphology: opposition and continuum. *Annals of Botany* 78: 577–581. <http://aob.oxfordjournals.org/content/78/5/577.full.pdf>
- Sattler, R. 1998. On the origin of symmetry, branching and phyllotaxis in land plants. Pp. 775–793. In: R. V. Jean & D. Barabé (eds.), *Symmetry in Plants*. Singapore, World Scientific.
- Sattler, R. 2018. Philosophy of Plant Morphology. *Elemente der Naturwissenschaft* 108: 55–79, 2018 (for an expanded version see www.beyondwilber.ca/about/plant-morphology/philosophy-of-plant-morphology.html).
- Sattler, R. 2019. Structural and dynamic approaches to the development and evolution of plant form. Chapter 6, pp. 57–70. In: G. Fusco (ed.), *Perspectives on evolutionary and developmental biology. Essays for Alessandro Minelli*. Padova, Padova University Press. https://www.padovauniversitypress.it/system/files/attachments_field/9788869381409-0a.pdf
- Sattler, R. 2022a, March 6. Plant morphology. Retrieved April 14, 2022a, from https://www.beyondwilber.ca/about/plantmorphology/plant_morphology.html
- Sattler, R. 2022b, March 7. Morphological development of flowers. Retrieved April 14, 2022b, from <https://beyondwilber.ca/about/flower/floral-development.html>
- Sattler, R. & L. Perlin. 1982. Floral development of *Bougainvillea spectabilis* Willd., *Boerhaavia diffusa* L. and *Mirabilis jalapa* L. (Nyctaginaceae). *Botanical Journal of the Linnean Society* 84: 161–182.
- Sattler, R. & B. Jeune. 1992. Multivariate analysis confirms the continuum view of plant form. *Annals of Botany* 69: 249–262. <https://www.semanticscholar.org/paper/Multivariate-Analysis-Confirms-the-Continuum-View-Sattler-Jeune/891f934e517534fe12fefc43ec5e5af8ebb2c520>
- Sattler, R. & C. Lacroix. 1988. Development and evolution of basal cauline placement: *Basella rubra*. *American Journal of Botany* 75: 918–927. <https://www.semanticscholar.org/paper/Development-and-evolution-of-basal-cauline-Basella-Sattler-Lacroix/a361a3b4f3ba1816cc7e7351237062a2ecf14ec0>
- Sattler R. & R. Rutishauser. 1990. Structural and dynamic descriptions of the development of *Utricularia foliosa* and *U. australis*. *Canadian Journal of Botany* 68: 1989–2003. <https://cdnsiencepub.com/doi/abs/10.1139/b90-261>
- Sattler, R. & R. Rutishauser. 1997. The fundamental relevance of plant morphology and morphogenesis to plant research. *Annals of Botany* 80: 571–582. <https://www.semanticscholar.org/paper/The-Fundamental-Relevance-of-Morphology-and-to-Sattler-Rutishauser/f31f5666f7d12cf277abc0f399083024ae7745d1>
- Sattler, R. & R. Rutishauser. 1992. Partial homology of pinnate leaves and shoots. Orientation of leaflet inception. *Botanische Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie* 114: 61–79.
- Schultz, C. H. 1843. *Die Anaphytose oder Verjüngung der Pflanzen. Ein Schlüssel zur Erklärung des Wachsens, Blühens und Fruchtragens, mit praktischen Rücksichten auf die Kultur der Pflanzen*. Berlin: Julius Sittenfeld.
- Schacht, H. & F. Curry. 1854. Reviews: The microscope in its special application to vegetable anatomy and physiology. *Journal of Cell Science* 1(5): 45–47.

- Schultz-Schultzenstein, C. H. 1867. De la différence qui existe entre la théorie de l'anaphytose des plantes et la théorie de la métamorphose. Actes du Congrès International de Botanique Paris: 100–117.
- Takhtajan, A. 1972. Patterns of ontogenetic alterations in the evolution of higher plants. *Phytomorphology* 22: 164–170.
- Troll, W. 1937–1943. *Vergleichende Morphologie der höheren Pflanzen*. Berlin: Bornträger.
- Wanninger, A. 2015. Morphology is dead - long live morphology! Integrating MorphoEvoDevo into molecular EvoDevo and phylogenomics. *Frontiers in Ecology and Evolution* 3, Article 54.
- Wolff, C. F. 1768. De formatione intestinorum. *Novi Commentarii Acad. Sci. Imperialis Petropolitanae* 12: 403–507.
- Zimmermann, W. 1959. *Die Phylogenie der Pflanzen*. 2nd edition. Stuttgart: Gustav Fischer Verlag (1st edition 1930).