



Character Description in Phylogenetic Analysis: Insights from Agnes Arber's Concept of the Plant

BRUCE K. KIRCHOFF*

Department of Biology, P.O. Box 26174, University of North Carolina at Greensboro, Greensboro, NC 27402-6174, USA

Received: 21 September 2000 Returned for revision: 5 November 2000 Accepted: 26 March 2001

Throughout her work Agnes Arber argues for an inclusive, synthetic concept of the vascular plant as 'consisting of a unification of every phase of its existence'. Her view of the leaf as a partial-shoot reflects this unification by relating the part (leaf) to the whole (shoot). According to Arber's view of the plant, the part can be fully understood only in the context of the whole. Morphological character description as it is currently practiced in systematics is in sharp contrast with this holistic view of plant structure. Systematic characters are removed from their context when they are described. This problem is greatest when characters are expressed verbally. Verbal descriptions convey little of the content of the character. A shift from verbal to visual characters allows systematists to capture more information, including some of the context in which the character occurs. By using a photograph, the fringe on a labellum of *Alpinia* spp. (Zingiberaceae) can be viewed in the context of the labellum in a way that the word 'fringe' cannot convey. The use of pictorial characters also allows reliable data storage and retrieval from databases, much as DNA sequences are currently being stored and retrieved. © 2001 Annals of Botany Company

Key words: Agnes Arber, character concept, character state, cladistics, database, holism, partial-shoot theory, phylogeny, phylogenetic systematics, plant morphology, process morphology, typology.

INTRODUCTION

Agnes Arber's (1950) partial-shoot theory of the leaf is one of the best known alternatives to the classical model of the leaf, based as it is on the division of the plant into the mutually exclusive categories of root, stem and leaf (de Candolle, 1827/1841; Eames, 1936 p. 380). Unlike this categorical model, the partial-shoot theory breaks down the hard and fast distinction between the stem and leaf. The leaf is seen as having some shoot characteristics, and the shoot as having some characteristics of leaves. Since most morphological characters currently used in systematics are based on the classical model, it is useful to review Arber's (1950) disagreement with this model to see what can be learned about character definitions from the principles implicit in her work.

THE PARTIAL-SHOOT THEORY OF THE LEAF

In the first few chapters of her book, *The natural philosophy of plant form*, Arber (1950) accepts the stem-leaf model of the plant implicit in much of the botanical work since Goethe (Miller, 1988). According to this model, the plant body can be divided up into the mutually exclusive categories of stem and leaf. Although she adopts this model as her starting point, Arber soon begins to question it by pointing out that there is a second, equally ancient way of viewing vascular plant structure. This second way gives

primary importance to the shoot, a complex of stem and leaf (Sachs, 1875). In this model the shoot exists in its own right, apart from its constituent stems and leaves. The concepts of stem and leaf refer only to the relationship between parts within the context of the shoot, the larger whole. By contrasting the stem-leaf and shoot models of plant structure, Arber (1950) sets up an opposition between two seemingly irreconcilable theories of plant construction, an opposition she immediately works to destroy.

After acknowledging that both models embody truth, Arber (1950) goes on to point out that neither is completely adequate. Her task is then to find a new, more adequate, model that transcends the limitation of both older models.

'We should aim at including and transcending both in a synthesis, which, while treating the shoot as a primary unit, will yet have absorbed into itself such truth as is to be found in the concept of the antithesis of stem and leaf.' (Arber, 1950 p. 72)

This new model is her partial-shoot theory of the leaf.

Before I present the evidence for this theory, I want to emphasize that Arber did not believe that the partial-shoot theory solved all of the problems of plant construction. She did think that it was better than the existing alternatives, but she recognized its limitations and emphasized that other scientists would extend or replace it in the future. She saw all models as partial, as embodying some aspects of plant structure, but never capturing all aspects of the plant. It is important to remember this, not because her attitude is so different from that of other botanists, but because the decline of morphology as a vital science has resulted in the acceptance of rather simplistic models as the final word on

* Fax 001 336 334 5839, e-mail kirchoff@uncg.edu

plant structure. It seems clear that Arber did not realize how hard it would be to transcend a concept of the plant as consisting of relatively few fundamental parts (leaf, stem, root, flower, etc.). This view of the plant has persisted to the present day and forms the basis for most systematic work.

The evidence for the partial-shoot theory of the leaf can be divided into two sections, ontogenetic and structural. Arber (1950) begins her summary of the ontogenetic evidence with a review of the early stages of leaf growth. The initial growth of the leaf is terminal, similar to the terminal growth that occurs in the shoot. However, in the leaf, terminal growth is of limited duration. In almost all cases, terminal leaf growth ceases after a short period. Linking this observation to her theory, Arber (1950 p. 79) speculates that the limited growth of the leaf may be due to the imperfect nature of the leaf as a partial-shoot.

The lamina begins to form during the later stages of leaf initiation. Lamina development in dicotyledons is primarily pleuroplastic: the blade forms from the lateral margins of the leaf primordium. Marginal, lamellar meristems form in the leaf margins and produce the blade. Although this process seems distinctly unlike that which produces the shoot, Arber reminds us that tunica growth is lamellar and that folds resulting from this growth produce the leaf primordia (Arber, 1950 p. 79). In this way, she finds a similarity between shoot and leaf growth. Of course, she does not deny that there are differences. She is well aware of the differences, but attributes them to the observation that the shoot is radial while the leaf is dorsiventral.

Turning from development to mature form, Arber (1950) suggests that the leaf can be seen as consisting of both axial and foliar elements. The axial elements include the petiole, median portion of the leaf base, midrib, non-winged leaf apex (where it occurs), and any leaf tendrils that are present. The foliar elements include the stipules, lamina, and lateral wings of any sheathing leaf bases. Continuing these comparisons, Arber (1950) refers to the leaflets of a compound leaf and the leaves of a shoot. The primary difference between these two forms is the presence of axillary buds on the shoot. The likenesses include their overall similarity in form and the repetition of the abscission layer at the base of the petiolule, which is present in *Aesculus hippocastanum* (Arber, 1950 p. 80). Finally, Arber (1950) draws a parallel between stipules (leaf elements) and various modified phyllomes such as cotyledons, prophylls and bracteoles (shoot elements). For instance, stipules often differ morphologically from the lamina, just as cotyledons differ from the succeeding leaves of a seedling, or prophylls from the mature leaves of a shoot.

The last line of evidence that I will summarize concerns phyllomes that bear foliar outgrowths. These phyllomes range from cabbage leaves that bear miniature leaf forms (enations), to the honey-leaves of *Ranunculus* that bear nectary scales, to the perianth of *Narcissus* that bears a corona. In all of these cases, the vasculature of the lateral member bears the same relationship to the parent phyllome as the vasculature of a leaf bears to its parent shoot: the xylem-poles of the bundles face the parent. The parent phyllomes thus function as axes in that they bear lateral members with vasculature oriented as it is in a leaf. Through

comparisons like these, Arber (1950) searches for the 'intrinsic relation of parts' (p. 84) that is expressed in the various forms of the leaf and shoot. She sees this intrinsic relation not as a static form, but as a dynamic relationship between the part and the whole. She is not searching for a better way to describe plant form, but for a better way to see what is already visible. She is not interested in just having a method by which to describe plant form. If she were, she would be content with the classical leaf-stem theory of plant form. This conceptualization is as good as any other if we only want to create categories on which to hang our sense impressions. What Arber is seeking is a way to look into the dynamic movements that form the plant. She is not interested in static categories. The evidence she presents shows that these movements cut across traditional morphological categories. Although she speaks of the 'theory' of the partial-shoot, this is merely a convention that she is forced to by scientific language and methodology. She is not really proposing or testing a theory, certainly not in any modern sense of how theories are tested. Rather, she wants to draw our attention to the interrelation among a number of phenomena to help us see the plant with fresh eyes. To speak about the results of this 'seeing', and to place her results in the context of botanical thought, Arber needs a way to summarize her work. Only in this sense, as a summary of empirical observations, can we understand her partial-shoot theory of the leaf. Arber is much closer to the original Greek meaning of theory (*theoria*, to behold) than to the current scientific meaning of this term.

PRINCIPLES IMPLICIT IN ARBER'S ANALYSIS

The analytic and holistic principles Arber (1950) employs in explaining her partial-shoot theory of the leaf are applicable far beyond the confines of her work. It is worthwhile summarizing these principles so that they can inform other aspects of our work as systematists.

One of the primary characteristics of Arber's analysis is her propensity to break down fixed categories. This propensity is clearly visible in her partial-shoot theory where her intent is to show that leaf and shoot are not mutually exclusive categories. We also find this propensity in her earlier book, *Monocotyledons* (Arber, 1925). Here, she first describes the root, axis and leaf as independent organs, but then turns to Saunder's (1922) leaf-skin theory and discusses the structure of the axis as composed of decurrent leaf bases. Although the content of this theory differs from that of her later partial-shoot theory, her method of analysis is similar.

Arber's ability to look beyond pre-established categories helps us see the plant in ways that are not confined to the well-trodden paths of traditional morphology. The plant becomes something real in and of itself, real in the sense that it exists beyond our categorical interpretations of it. While most botanists would agree that the plant exists in this sense, few put this theory into practice by continually returning to the plant and looking at it again and again with fresh eyes, as Arber does. To her, the plant is not something fixed, something that we have understood and

now merely have to place within a classification scheme. The plant is something that we are continually in the process of understanding. The concepts and categories that we apply to the study of morphology help us to understand the being of the plant as it exists beyond all categories. Thus, our current concepts should not constrain us from seeing the plant in new ways. At any one time we may work within the framework of a prevailing concept of the plant, but with each new conceptualization the plant comes to a new expression in our experience (Rutishauser and Sattler, 1985, 1987, 1989). We never have all aspects of the plant before us at once, and Arber (1950) never loses sight of this fact. She is aware that she is continually trying to describe something that remains out of our reach. She is aware that the plant is beyond all categorical interpretations of it. A plant is not merely a collection of characters. It can never be finally and completely known.

This brings us to the second principle implicit in Arber's (1950) analysis: the realization that knowing a plant is not simply a matter of conglomerating characters and summarizing them in a description. On the first page of her book, Arber (1950) makes it clear that she understands the difference between parts that are merely placed together, and those that have an intrinsic relationship to each other.

'The different branches [of biology] should not, indeed, be regarded as so many fragments which, pieced together, make up a mosaic called biology, but as so many microcosms, each of which, in its own individual way, reflects the macrocosm of the whole subject.' (Arber, 1950 p. 1)

To Arber, the plant is not a collection of parts, but rather a 'unification of every phase of its existence' (Arber, 1950). Hidden within this phrase is the relationship between part and whole in the plant. To understand what she means by it, we need to subject it to the same type of analysis that she applies to the plant itself. We need to consider this phrase from several points of view to bring out a meaning that cannot be captured in any one view.

In this phrase, both the word 'unification' and the phrase 'every phase of its existence' are significant and must be considered separately before we recombine them in the whole. The phrase 'every phase of its existence' is significant because it draws our attention to the characteristics of the plant, without actually enumerating them. Any enumeration would necessarily be incomplete, especially given Arber's propensity to think across traditional categories. Saying that a plant consists of the unification of root, stem, leaf and flower is not at all what Arber means. These divisions of the plant are arbitrary and do not capture the full diversity of ways in which we can conceive of the plant. By using a somewhat vague phrase for a plant's characteristics, Arber is able to suggest an analytic division of the plant into morphological categories, without tying herself to any one categorization.

Understanding what Arber (1950) means by the word 'unification' is more difficult. To Arber, the plant cannot be conceived of as a *collection* of characters. It is not a 'unification' in the sense of separate characters that are placed together. If plants could be described in this way, then it would be possible to have one correct enumeration

of the characteristics of a plant. Clearly, Arber (1950) does not support this view. A plant does not arise from the aggregation of characters. Each plant is an intrinsic unity, a unity that exists prior to our process of analysis. This unity can be conceptually dismembered into characters, but it can never be fully represented by any single characterization.

Bortoft's (1996) explanation of Goethe's scientific method (Miller, 1988) helps clarify the difference between 'unification' in the sense that Arber (1950) uses this term, and the unity that arises from the apposition of separate characters. Bortoft (1996) points out that wholes that are created from the aggregation of separate characters are always artificial. The relationship between the parts is external, they are not part of an intrinsic whole. For instance, relationships among items sitting on a desk are not intrinsic to the items, or to the desk. There is no necessary relationship between a coffee cup and a pen that sits beside it. They are only in proximity because someone has placed them together. Their relationship is created. Bortoft (1996) calls this type of relationship a 'counterfeit whole'. It is created by bringing unrelated objects into relationship.

The unity that Arber (1950) speaks about is of a different sort. It is a unity that is not dependent on human activity in bringing it about. Goethe, who was an important influence on Arber (Arber, 1946), speaks of this type of unity when he says:

'Hence we conceive of the individual animal as a small world, existing for its own sake, by its own means. Every creature is its own reason to be. All its parts have a direct effect on one another, a relationship to one another, thereby constantly renewing the circle of life; thus we are justified in considering every animal physiologically perfect. Viewed from within, no part of the animal is a useless or arbitrary product of the formative impulse (as so often thought). Externally, some parts may seem useless because the inner coherence of animal nature has given them this form without regard to outer circumstance.' (Goethe, 1820/1988 p. 121)

When Arber (1950) speaks of the plant as the 'unification of every phase of its existence', she is referring to the unity that exists prior to analysis. Both Goethe (1817/1988) and Bortoft (1996) claim that this type of unity is directly perceptible.

Within the intrinsic unity of the organism there is a special relationship between the parts and the whole (Kirchoff, in press). Like any object that is authentically whole, the parts are intrinsically related to the whole that they create (Bortoft, 1996; Kirchoff, in press). The whole is built up of the parts in such a way that each part bears something of the whole within it (Sattler, 2001). The structure of each part reflects the whole, and the whole is created out of parts that have an intrinsic relationship to each other and to the whole itself.

Returning to our previous example, a cup sitting on a desk has no intrinsic relationship to the desk. The cup-desk unity is not an authentic whole. The cup can be removed without disturbing either the unity of the desk or the cup. The two items only come into relationship because someone placed the cup on the desk. The relationship is functional, not intrinsic or structural.

The relationship between a leaf and stem is of a different sort. Although, in one sense, a shoot is created out of leaves

and a stem, in another sense a shoot has a reality that goes beyond the separate categories of leaf and stem. Arber (1950 p. 70) recognizes this when she says ‘The possibility of grafting buds on to an alien stock was one of the points that led botanists long ago to the realization of the *individuality* of the bud, and hence of the shoot into which it developed’. In any authentic whole, the parts enter into a mutually supportive relationship that produces the whole. Neither the parts nor the whole can exist without the other. In this sense, individual characters (leaf and stem) do not exist outside the whole (shoot) to which they belong. The parts create the whole, while the whole gives meaning to the parts. The shoot is created from leaves and stems, but leaf and stem are not mutually exclusive categories. Each is intrinsically related to the other. We see this when we follow Arber (1950) in her analysis of the leaf as a partial shoot. The leaf has both ‘leaf-like’ and ‘shoot-like’ characteristics.

Another way of understanding the difference between counterfeit and authentic wholes is to think about how our ability to conceptually dismember the whole differs in these two types. There are relatively few ways in which to dismember counterfeit wholes, while authentic wholes can be conceptualized in many different ways, perhaps in infinitely many ways. Our cup-desk whole can be separated into the parts ‘cup’ and ‘desk’, but not in many other ways. At the molecular level we may be able to separate the organic from inorganic components of the cup-desk, in which case we would see a kind of patchwork that looks nothing like a desk or cup. However, with the disappearance of these objects we would also move beyond concepts that have specific reference to the cup-desk whole. Any object can be dismembered into organic and inorganic components. These concepts can be applied to many other systems besides a cup sitting on a desk. On the other hand, an authentic whole such as a shoot can be conceptualized in many different ways, all of which have relevance to the whole (Rutishauser and Sattler, 1985). Arber (1925, 1950) demonstrates this in her discussions of the leaf-skin, partial-shoot, and leaf/stem theories, all of which conceptually divide the plant in different ways.

Recognizing the relationship between part and whole in authentic wholes is important because it helps explain why Arber (1950) continually moves back and forth between part and whole in her analysis of the plant. Doing so enables her to approach the unity of the plant with analytical tools. We can follow her as systematists by learning to create characters that retain something of their context, characters that retain the relationship between part and whole that Arber tries to include in her theories.

The final principle of Arber’s (1950) analysis is the dynamic way in which she views plant structure. By ‘dynamic’ I do not mean that Arber uses developmental evidence to support her views, but that she sees plant structure in a continual process of becoming. For Arber, there are no primary morphological categories. All organs have the same potential. They differ only in their ability to actualize this potential.

‘. . . in the shoot radiality is actual, or explicit, while dorsiventrality is potential or implicit; for the leaf, on the other hand, the reverse is true.’ (Arber, 1950 p. 87).

This point of view allows Arber to see individual leaves not as static structures, but as incomplete shoots: organs that embody some, but not all, of the features of the whole shoot. The features that are not embodied are present in potential. Their lack is accidental, not essential. If conditions change, for instance in cases of teratology, these characteristics may appear. When they do, they show another aspect of the dynamic nature of the leaf, which can take many forms.

TAXONOMIC CHARACTERS

Character descriptions

Given the importance of characters to the process of reconstructing phylogeny, the description of characters should be one of the most intensely studied issues in systematics. Unfortunately, until recently, this has not been the case. Stevens (1991) and Gift and Stevens (1997) do much to deconstruct the concept of a character by showing that there is little validity to character states of quantitative (continuous) characters. Thiele (1993) takes a different approach by stressing that cladistic characters are features of taxa, and as such cannot overlap. Weston (2000) discusses Sattler’s (1992) process morphology in the context of creating cladistic characters, and Wagner (2001) assembles a wide range of papers addressing many aspect of the creation and use of characters in evolutionary studies.

The modern age of character analysis began when Hennig (1950, 1966) recognized that characters differ in their usefulness in predicting evolutionary relationships. Hennig understood that to reconstruct phylogeny it is not enough for organisms to be similar. Similarity alone is not a guarantee of evolutionary relationship. For this, a special type of similarity is needed. Only organisms that share derived characters (synapomorphies) also share a common ancestor (Hennig, 1950, 1966). Because of the central role of Hennig’s (1950, 1966) work in reformulating systematics, I will primarily refer to his work in the remainder of this section.

Although Hennig was undoubtedly the first to formulate the methods of phylogenetic systematics, it is worth noting that in the 1950s W. H. Wagner elaborated methods nearly identical to Hennig’s for use in his plant systematics classes at the University of Michigan, USA (Hardin, 1957; Wagner, 1961). As far as I know, Hardin (1957) was the first to publish a phylogenetic analysis using Wagner’s ‘Ground plan-divergence’ method (W. H. Wagner, pers. comm.). Still, neither of these authors was able to develop their work in a way that allowed it to spread throughout the larger systematic community. Wagner’s methods did, however, receive wider recognition through Farris’ (1970) formalization of them as computational methods. This formalization became the basis for modern numerical cladistics.

From Hennig (1950, 1966) and Wagner (1961) we learned that choosing the right characters and determining the derived states are two of the most important steps in phylogenetic analysis. Hennig’s full method for reconstructing phylogeny using morphological characters consists

of: (1) identifying characters and character states; (2) determining the derived character state for each character (Stevens, 1980); and (3) constructing a phylogenetic tree based on some model of character evolution (parsimony is the most commonly used model). This process is now widely thought to give the best estimate of the true phylogeny.

The part of Hennig's (1950, 1966) method that concerns us here is the treatment of characters. Although not original with him, Hennig (1950, 1966) gives such a clear description of the process that it is worth review. There is a clear contrast between the methods of Hennig and Arber.

The unit of systematic analysis for Hennig (1950, 1966) is not the individual, but the semaphoront. The Greek roots of this word give us a clue to its meaning. The root 'sema' means mark, sign, or signal, and 'phor' means to carry or bear. A semaphoront is the organism conceived of as a 'character bearer'. Hennig (1966) gives a more precise definition:

'the individual at a particular point of time, or even better, during a certain, theoretically infinitely small, period of its life' (Hennig, 1966 p. 6)

By considering the taxonomic entity as an organism at one instant of its life, Hennig (1966) is able to isolate variable parts of an organism's life history. This can be important when working with holometabolous insects (insects with complete metamorphosis), as Hennig did in his work on Diptera.

Like most taxonomists, Hennig (1966) does not give a precise definition of 'character'. He merely acknowledges that semaphoronts possess features that distinguish them from other semaphoronts.

'We will call those peculiarities that distinguish a semaphoront (or group of semaphoronts) from other semaphoronts "characters".' (Hennig, 1966 p. 7)

This definition is similar to many others proposed by taxonomists over the years. I have chosen two additional definitions as typical. Other definitions can be found in Stuessy (1990).

Davis and Heywood (1973 p. 113) define a character as 'any attribute (or descriptive phrase) referring to form, structure or behavior which the taxonomist separates from the whole organism for a particular purpose such as comparison or interpretation'. Stuessy (1990 p. 27) proposes the definition 'a feature of an organism that is divisible into at least two conditions (or states) and that is used for constructing classifications and associated activities'.

Neither of these definitions, nor any other that I have seen, gives any indication of how to recognize characters, or how they relate to the form of the organism as a whole. At first glance, Stuessy's (1990) phrase 'divisible into at least two conditions' does seem to give some guidance, but this impression quickly evaporates when we realize that describing any attribute of a plant (presence of chlorophyll, for instance) immediately implies the existence of at least two conditions. The presence of chlorophyll implies its absence, living implies non-living, etc. All characters have at least two states. However, not all characters are

informative in resolving taxonomic relationships. Those that are homogeneous in the study group (Ingroup) can be excluded from studies designed to elucidate the relationships among taxa in this group. Although these characters satisfy Stuessy's (1990) definition in that they have two states (one in the Ingroup, one or more in the Outgroup), they are not useful in phylogenetic analyses.

After discussing semaphoronts and characters, Hennig (1966) moves on to describe how characters can be combined to form the totality of the form, or holomorphy, of the organism.

'We will call the totality of all these characters simply the total form (or the holomorphy) of the semaphoront, which thus is to be regarded as a multidimensional construct.' (Hennig, 1966 p. 7)

Although he speaks of the holomorphy as a 'multi-dimensional construct', it is unlikely that Hennig mistook this construct for the organism itself. In this sense he is close to Arber. For both, the organism in its full reality remains unknown. Still there is a difference between the two approaches. For Arber, the organism continually discloses itself through our various theories. While none of these theories is completely adequate to describe the organism, each captures part of the whole. Hennig (1966), on the other hand, is not interested in the organism that exists behind our theories. He focuses his efforts on creating a 'general reference classification' not on understanding the organism. In fact, a large portion of the first part of his book is devoted to showing that a phylogenetic classification is better suited for this purpose than any other classification scheme (Hennig, 1966). Hennig's methods of character analysis make sense in light of this goal. They are focused on giving us tools (synapomorphies) with which we can discover evolutionary relationships. A method that dismembers the individual into semaphoronts, dismembers the semaphoront into characters, and then combines the characters to form the holomorphy can never provide an adequate description of organismal form. Arber's work shows this clearly, but Hennig has focused our attention on another goal. The task now is to find a way of applying Arber's insights to the process of creating characters for use in phylogenetic systematics.

The context of character descriptions

Character description is always done in a specific context by specific investigators. All that is absolutely necessary to create a character is variability in the Ingroup and the ability to categorize this variability into characters and character states. The ability to partition the variability depends on the taxonomic context in which the characters are to be defined. This context includes the taxa under study (the Ingroup), the morphological theory under which the characters are created, and the training of the investigator, which influences his choice of characters and his description of these characters in specific ways.

The selection of an Ingroup determines which characters are chosen by partitioning morphological variability in ways that are unique to the taxa under study. For instance, a phylogenetic study of the Cannaceae will contain few

characters dealing with inflorescence branching, while a study of the Marantaceae will produce several. There is relatively little variability in the degree of branching in the Cannaceae compared with the Marantaceae (Andersson, 1976; Sell and Cremers, 1994).

The morphological theory under which the characters are defined is a major part of the conceptual context of character description. As currently used, morphological characters are abstractions, conceptually separated from the plant as a whole. They are a view of the plant through a particular conceptual lens. This is one reason why different scientists studying the same taxon describe different characters. The whole can be broken up in many different ways.

As discussed above, the most commonly used morphological theory divides the plant into leaf, stem and root. This method of conceptualizing plant structure is well established, but as Rutishauser and Sattler (1985, 1987, 1989) demonstrate, these divisions are only one way of viewing the plant. The choice of this model focuses our attention on specific characters and character combinations to the exclusion of others. If, instead, we adopt Arber's (1950) partial-shoot theory we will look for characters that cross the boundaries of leaf and stem. Using this theory as our basis we might define characters that emphasize the axial nature of the leaf or the foliar nature of the shoot.

As an example we can consider the shoots of the Zingiberales, which are supported by sheathing leaf bases that provide much of the stem's rigidity. The degree to which the shoot receives support from sheathing leaf bases varies throughout the order. Familiarity with Arber's partial-shoot theory might lead us to define characters that describe the extent to which the shoot is supported in this way. For example, except at flowering, the stem of the Musaceae is completely composed of overlapping leaf sheaths; the stems of most members of the Strelitziaceae are woody and arborescent and receive no support from the leaves; the Lowiaceae have short stems that receive little or no support from the leaf sheaths; while those of the Zingiberaceae, Cannaceae, Heliconiaceae and Marantaceae are intermediate in structure in ways that have never been fully described. Characters based on shoot structure in the Musaceae and Strelitziaceae have been used in phylogenetic analyses, but the intermediate structure of the shoot in the other families has not (Dahlgren and Rasmussen 1983; Kirchoff, 1988; Kress 1990, 1995). One possible explanation for this is that our conceptual dissection of the plant into leaf, stem and root impedes our identifying characteristics of these shoots that are strongly supported by, but not solely composed of, leaf sheaths.

In addition to the taxonomic and conceptual contexts, the social context of the scientist also plays an important role in how he describes characters. A scientist's training influences how he will approach his work at least as much as does his choice of taxa. At the grossest level, scientists acculturated as molecular biologists (which includes many molecular systematists) are less likely to include extensive morphological analyses, or to appreciate the relevance of theoretical morphology in creating characters. On the other hand, morphologists are less likely to include genetic

analyses in their studies. Even within morphological analyses, the choice of characters is influenced by the approaches the scientist was exposed to as a student. For instance, if his or her main influence was from Eames (1936) and his followers, the characters he or she chooses will probably be based on the concept of the plant as divisible into leaf, stem, root and flower. Exposure to the work of Arber (1950) and Rutishauser and Sattler (1985, 1987, 1989) will probably lead to less traditionally defined characters (Weston, 2000). Of course, all of these shortcomings can be ameliorated by selecting co-workers who bring complementary skills to the analysis. My point is only that each of us brings his or her training with them to any task. This training is part of our social context because in it we are exposed not only to specific theories, but to what Keller (1985) calls an 'aesthetic' of science. We use our scientific aesthetic to tell us what is important, what can be ignored, and to establish the preferred methods for carrying out our day-to-day scientific work. The vehicles for conveying this aesthetic are our social interactions with our teachers and colleagues.

Alternatives to traditional character descriptions

Process morphology. Sattler's (1992) and Jeune and Sattler's (1992) use of process morphology is an alternative to the conceptual division of the plant into mutually exclusive, static categories (leaf, stem, root, etc.) (Weston, 2000). Adopting this framework allows the description of characters that cut across traditional boundaries between organ classes. Describing characters based on processes instead of structural categories will yield a completely different set of characters and may influence the final form of the phylogeny. A brief summary of the principles of process morphology will make this clear.

Process morphology is an attempt to break down the fixed categories of plant construction that have influenced much of plant morphology since de Candolle (1827/1841). The concepts of process morphology follow on (though are not dependent on) Sattler's (1966) earlier work on partial homology, in which he suggests that strict one-to-one homology is inadequate to deal with the full range of plant form. Sattler (1966, 1996) sees strict homology as forcing variation into mutually exclusive morphological categories. One remedy to this situation is to consider the plant dynamically rather than statically. To do this, Jeune and Sattler (1992) identify a number of process-categories that describe plant structure. For instance, they use the two pairs of processes growth/decay and differentiation/differentiation to analyse the structural dynamics of plants. Within the growth category, they define the subcategories (1) growth rate, (2) growth duration, and (3) growth distribution (Jeune and Sattler, 1992; Sattler, 1992). The structures themselves disappear in this analysis. What remains are 'process combinations' that can be placed into at least partial equivalence with traditional morphological categories (Jeune and Sattler, 1992). These 'process combinations' are dynamic systems that exist through their constituent processes, but which are not endowed with an essential nature (Sattler, 1993).

The processes [Jeune and Sattler \(1992\)](#) use to create their combinations cut across traditional morphological organ descriptions ([Jeune and Sattler, 1992](#); [Sattler, 1993](#)). As shown above, their growth characters are defined without reference to any specific organ or organ system. To take another example, a single character state of their character ‘branching’ occurs in both stems and compound leaves ([Jeune and Sattler, 1992](#)). In both organs the ‘branches’ form acropetally. In stems the ‘branches’ are shoots. In compound leaves they are phyllomes. Thus, the character states of the character ‘branching’ are not confined to a single organ category. The lack of correspondence between process-characters and organs means that there will be little overlap between process-characters and traditional characters.

The move from traditional characters to process-characters is similar to [Arber’s \(1950\)](#) move from traditional morphological description to her partial-shoot theory. Both transitions break down static categories and replace them with dynamic alternatives. The effect of process-characters on the form of a phylogeny remains to be investigated.

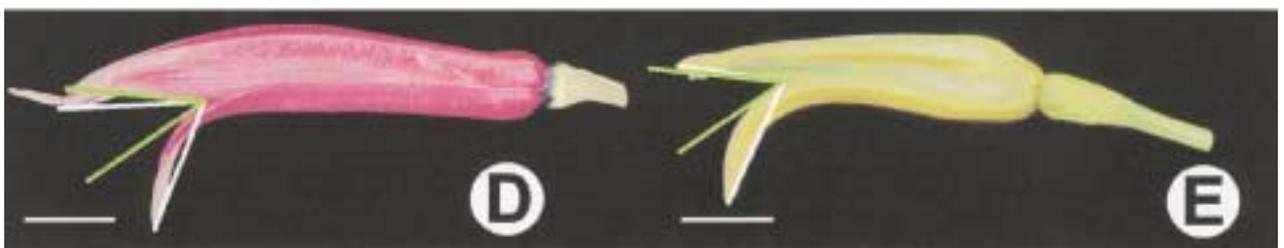
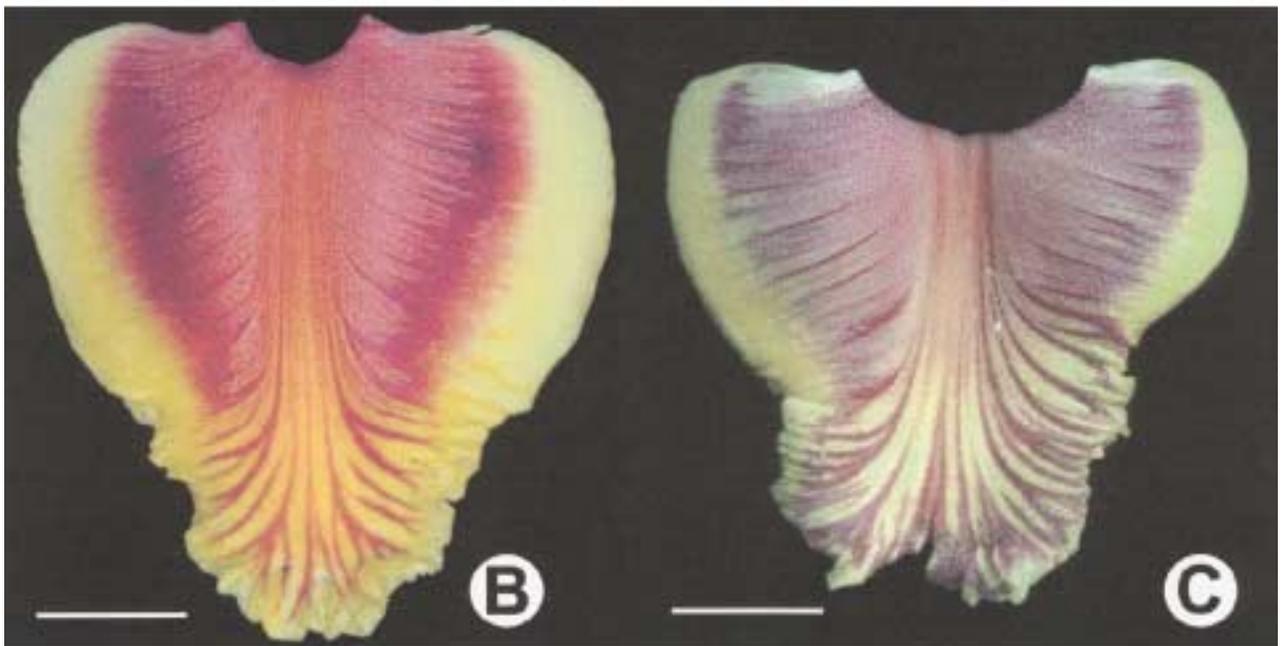
Other holistic approaches. Underlying [Arber’s \(1950\)](#) partial-shoot theory of the leaf is her consistent attempt to think holistically. The shift from defining characters based on theories of plant construction to a more holistic approach involves a change in the way we conceive of the plant ([Bortoft, 1996](#); [Kirchoff, in press](#)). For [Arber \(1950\)](#) this conception is expressed in her partial-shoot theory, but it is clear that her methods are applicable far beyond this theory. The potential to move beyond this theory is inherent in her method from the start. In essence, her method involves a shift in the way we ‘see’ plants. Her work suggests the need to shift from seeing the plant as composed of parts, to seeing the plant as a whole that can be decomposed into parts. [Bortoft \(1996\)](#) has characterized this change in conceptual framework as a shift from seeing disconnected parts (isolated characters) to seeing the parts intrinsically related to the whole. An illustration from art will clarify how we can make this conceptual shift.

In [Ando Hiroshige’s *View of Mt. Akira, Kakegawa* \(Fig. 1A\)](#), the artist uses several compositional principles to create the composition. The main action of the picture takes place in the space created by two curving lines, one formed by the kite string and the other by the curve of the bridge. These two movements are echoed and reinforced by similar lines throughout the picture. The curve of the kite string is echoed in the string of the balloon, the slopes of the mountain and several other subsidiary curves ([Fig. 1A](#), red lines). The arch of the bridge is reflected in the backs of the bowing figures, the upraised arm of the child, the backs of the peasants planting rice, and the bent stalks of weeds ([Fig. 1A](#), blue lines). The composition is stabilized by the vertical and horizontal lines, some of which are broken (bridge support and official’s walking stick) ([Fig. 1A](#), white lines). In addition to reinforcing the vertical stability of the composition, the mountain provides a strong stop to our eye’s movement across the page.

All of these compositional principles are built up by a number of seemingly independent parts that cooperate to create the work of art ([Fig. 1A](#), lines). The composition is constructed through the harmonious interaction of these parts, much as the form of an organism is built up through the interaction of its individual characteristics. Each element of the composition both plays a role in creating the whole, and has its own specific form because of the role it plays. The vertical lines stabilize the picture only in relationship to the strong implied movements of the central curves. In the same way, the curved backs of the peasants provide a counter to the strong left to right movement of the official crossing the bridge, not just by their central position on the page, but through the similarity of their forms. As in all great works of art, the parts reflect the whole, which they help create. Our goal is to describe systematic characters that reflect the integrity of the plant much as compositional element reflects the composition as a whole.

A simple step in this direction can be taken by moving from verbal descriptions of characters, to pictorial ones. Typically, morphological characters originate from studies of plant structure, and are then converted to verbal descriptions for use in phylogenetic analyses. In describing characters we make decisions on similarities between observations to place them into classes (character states), which are then grouped into characters ([Stevens, 2000](#)). In this process, we drastically reduce the amount of information available to future investigators. For instance, the character ‘labellum fringed’ captures only a small amount of the information available from observing the labellum of *Alpinia* spp. (*Zingiberaceae*) ([Fig. 1B and C](#)). Several of the differences that are not captured are (1) the presence or absence of a split at the tip of the labellum; (2) the degree to which the margin of the labellum is recurved; and (3) the symmetry of the labellum. Of course we can include these characters, and others, in our analysis, but even including them does not do justice to the structure of the labellum. The character ‘labellum symmetry’ does not take into account the handedness of the symmetry. The larger portion can be either on the left or right side. Although these problems can be partially dealt with by creating finer and finer verbal descriptions, verbal descriptions will never fully capture the structure of the labellum. They will never capture it even at the level of detail that is present in a photograph ([Fig. 1B and C](#)). The use of visual characters (photographs or drawings) obviates the need for complex verbal descriptions. ‘A picture is worth a thousand words’ was never more true than in systematics. The use of pictorial characters unifies features that would otherwise be separated into distinct characters. This allows us to summarize complex information in a form that is easy to assimilate and understand.

An example of the pictorial description of characters can be found in [Thiele and Ladiges’ \(1996\)](#) cladistic analysis of *Banksia* (*Proteaceae*). I will use their analysis of cotyledon shape as an example of this process. [Thiele and Ladiges \(1996\)](#) published outlines of the cotyledons of all species in the genus *Banksia*. They presented their two-state character, based on these shapes, by drawing a line to separate the



shapes into groups. This partitioned diagram represents the character. Their description of the two states as flabellate and spatulate refers to this diagram. Although I do not know how they proceeded in practice, the terms could have been applied after the division, as a way of drawing attention to the different shapes in the two groups. This method would be consistent with a pictorial approach to creating characters. It is possible to use terms to draw attention to a partition that has been made on other grounds. Shape terms do not have to be used as criteria for separating the shapes into groups. Ribeiro *et al.* (1999) also used a pictorial approach, but this time to create a flora, the keys of which are mainly based on pictures of plant characteristics.

An additional advantage to the use of pictorial characters is that they are amenable to storage and retrieval from databases. Although verbal characters can be stored, the information they contain cannot easily be retrieved. The representation of organismal features in verbal descriptions does not provide sufficient information for subsequent investigators to recreate these features. This is because the process of creating verbal characters emphasizes one feature of the organism over another. The features that are emphasized will vary from study to study, with the result that comparisons across studies will be almost impossible. For instance, in describing a labellum we can emphasize the outline of the organ and can create the character 'labellum shape' with states 'obdeltoid' (Fig. 1B) and 'obdeltoid/irregular' (Fig. 1C). In labelling the shapes in this manner we emphasize the shape of the labellum of *Alpinia zerumbet* (Fig. 1B) and give less attention to that of *Alpinia henryi* (Fig. 1C). The larger attachment site of the latter and the way that its sides slope steeply toward the irregular fringe suggest the term 'cordate/irregular' instead of 'obdeltoid/irregular' for this species (Fig. 1C). Giving emphasis to the attachment site and steeply sloping sides results in the character states 'cordate' (Fig. 1B) and 'cordate/irregular' (Fig. 1C). The choice of which pairs of terms to apply is arbitrary. Both pairs describe an aspect of labellum shape. Neither captures the shape as well as do the photographs. Someone who only had access to the verbal descriptions from a database of characters would have a very difficult time determining the shape of the labellums, let alone incorporating the labellum of a third species into this character. Stevens (1991) and Gift and Stevens (1997) have discussed similar problems in relation to quantitative characters. The situation is similar to that which would occur were there no standardization for the representation of the identity of the bases in DNA. Each laboratory would have to develop its own scheme, which would have to be

decided before the sequences could be used or evaluated by other investigators.

Quantifying organ shape does not help solve this problem. Although it appears accurate, morphometric quantification depends upon qualitative assessments of shapes, which are subjective. For instance, to measure the degree to which the petal is reflexed in *Heliconia* spp. (Fig. 1D and E) we must establish the procedures for defining the angle we will measure. This can be done based on landmarks (Fig. 1D and E white lines) (Bookstein, 1998), or based on any of several measures of the apparent angle (Fig. 1D and E, green lines). The use of landmarks allows comparable measurements to be made easily across species, but the apparent angle may be biologically more relevant as it is related to the opening that pollinators perceive when approaching the flower (Fig. 1D and E, green lines). Both methods will give precise answers, but neither will be accurate in the sense that neither will yield the 'true' angle of sepal reflexion. Though not completely free of these problems, photographs are a much more accurate way of representing not only this angle, but all aspects of flower shape.

A related approach to character descriptions builds on the work of the European typological school of plant morphology (Troll, 1964; Weberling, 1989; among many others). Through comparisons of the form and position of the various organs, the scientists of this school have described inflorescence structure in many groups of plants. These descriptions and their summary in diagrams are representations of the morphology of the inflorescence as a whole (Fig. 2A–E). Although positional information is given primacy in these studies, other types of information can also be included. Presence or absence of organs and aspects of organ form and development can be included in diagrams only slightly more complex than those published in typological studies (Fig. 2F). For instance, internode length can be shown by varying the length of the lines connecting the phyllomes or by using dashed lines (Fig. 2F–H), and the presence of organ rudiments can be shown by using broken lines to draw the organ (Fig. 2F). Flower symmetry and more complex aspects of inflorescence morphology can be illustrated with other conventions (Fig. 2G and H).

An additional benefit of adding information to a single diagram is that it helps clarify the morphological relationships between the parts. For instance, in the Cannaceae, the flowers of a cincinnus always have the same symmetry, but within a florescence (i.e. between cincinnati) the flowers may be mirror images (Fig. 2G). In the Marantaceae flowers occur in pairs and have mirror image symmetry (Fig. 2H). The relationship between the two arrangements of flowers is clearly seen in diagrams that include floral symmetry

FIG. 1. Ando Hiroshige's *View of Mt. Akira, Kakegawa* from the series *Fifty-Three Stations of the Tokaido Road* (1833–34). Wood block print. Bar = 2 cm. Original size 16.3 cm by 22.1 cm. The composition is built up through the use of repetitive forms and movements, some of which are structured from several unconnected elements (e.g. bridge pillar and official's walking stick, white lines). Compositional principles are illustrated by the coloured lines. B, Labellum of *Alpinia zerumbet* (Zingiberaceae). Bar = 1 cm. C, Labellum of *Alpinia henryi* (Zingiberaceae). Bar = 1 cm. D, E, Flowers of *Heliconia* spp. The degree of reflexion of the free sepal can be measured in at least two ways either by determining the angle between landmarks such as the tip of the petals and the tip of the free sepal (white angle) or by situating the vertex at the point where the free sepal meets the remaining corolla members and measuring the angle between the tangents to the sepal and other members (green angle). D, *Heliconia metallica*, lateral view. Bar = 1 cm. E, *Heliconia lingulata* lateral view. Bar = 1 cm.

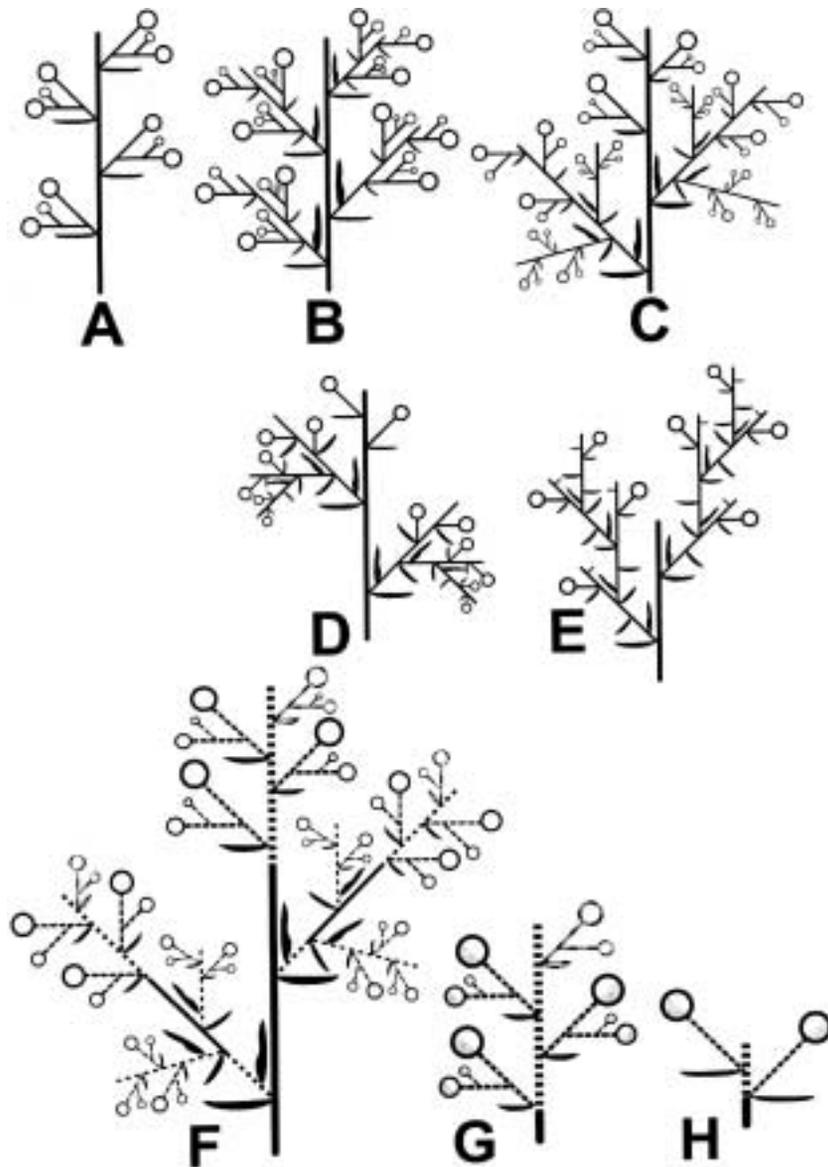


FIG. 2. A–E, Inflorescence structure in the Zingiberales showing positional relationships between the organs (after Kunze, 1996). Flowers are represented by circles. A, Zingiberaceae, Costaceae, Musaceae, Heliconiaceae, Strelitziaceae (*Phenakospermum*). B, Strelitziaceae (*Ravenala, Strelitzia*). C, Cannaceae, Zingiberaceae (*Alpinia* spp.). D, Marantaceae. E, Lowiaceae. F, Modified diagram of inflorescence structure in the Cannaceae. Short internodes are represented by dashed (---) lines. Organs that are initiated but do not complete development are drawn with broken (- · · -) lines. G, Diagram of inflorescence structure in the Cannaceae. Internode length and flower development are represented as in F. Shaded circles indicate flower symmetry. Flowers on opposite sides of the main axis are represented as having mirror image symmetry. H, Diagram of inflorescence structure in the Marantaceae. In this family the inflorescence is represented by a pair of flowers connected by very short internodes (dashed lines). Flower symmetry is represented as in G.

(Fig. 2G and H). Insights gleaned from these diagrams support Kunze's (1984) interpretation of the flower pair of the Marantaceae as equivalent to a reduced florescence of the Cannaceae. It only became apparent that observations of flower symmetry were relevant to this issue when I added symmetry to Kunze's (1984) diagrams of inflorescence morphology.

I see two possibilities for the use of photographs or diagrams like these in phylogenetic analyses. The first is to include as much information as possible in each diagram, and to use the whole diagram as the character state for a

taxon. This approach has the advantage of placing different aspects of the inflorescence in their context. For instance, the relationship between the position of the flowers and the length of the subtending internode can easily be seen in these diagrams (Fig. 2F). However, using only a few elaborate characters has the disadvantage of reducing the total number of characters in the analysis. This could cause a loss of resolution in the resulting phylogenetic tree, but might also increase the reliability of the resolution that remains because of the broadened context for establishing homologies (Weston, pers. comm.). Weighting the complex

characters could help resolve this problem in studies that use both complex and traditional characters. The traditional characters would provide the resolution, while the complex characters would increase the accuracy.

A second possibility is to create a number of diagrams, each focused on a specific aspect of organ structure. Each set of diagrams would express an aspect of the organ's structure but in a larger context than is usually possible when using verbal characters. For instance, one set of diagrams could be used to express symmetry relationships between flowers (Fig. 2G and H), one to express positional relationships (Fig. 2A–E), another to represent size relationships (foliage leaves vs. bracts, etc.), and another to show internode length (Fig. 2F), etc. The advantage of this approach is that it allows the creation of a number of characters while at the same time retaining some information from the whole inflorescence. Each character would be placed in at least part of its context.

The use of visual methods of representing characters raises two problems that need to be addressed before these methods can be used in phylogenetic analyses: standardization of the images and the taxonomic level at which the characters are described. The problem of standardization is one that will have to be dealt with no matter what methods of character description are used. To a certain extent, the problems of using verbal characters can be seen as a problem of standardization. There is no standard way in which shape terms can be applied. The application of the terms 'acute', 'obtuse' and 'rounded' to leaf form cannot be standardized. It will always involve judgements on the part of the investigator. Considered against this background, the use of photographs is easy to standardize. All that is needed is a repeatable method of photographing a particular part of a plant. The procedures are so basic that they hardly need to be specified. The major plane of the organ should be parallel to the film plane. An accurate scale should be included in each photograph. The image should, as much as possible, fill the frame, etc. It is even possible to begin to standardize colour by specifying the brand (and consequently the colour characteristics) of the film to be used and the colour temperature of the illumination. If the photographs are to be stored in a database it will also be necessary to standardize the type of scanner to be used and the colour space definition (RGB, CMYK, LAB, etc.) in which the images are stored. This is because scanner type and quality influence the colour rendition of the scans, and colour space definitions do not completely overlap. Converting from one colour space to another can change colours. These problems are real, and not minor. Still, we can begin to define reasonable standards for photographic characters.

The problem of the proper taxonomic level at which to describe characters has already been solved by molecular systematics. DNA sequences are usually only reported for a single specimen representing a species level taxon. When a study involves taxa of higher rank, several species are included from each taxon. For instance, when Caddick *et al.* (2000) carried out their phylogenetic analysis of the Dioscoreales they included sequences from 182 species. They did not attempt to combine any of this data and create characters that typify genera or families, as is commonly

done for morphological characters. Although Caddick *et al.* (2000) collected some of the data themselves, much of it was available from the literature, and is stored in electronic databases. Contrasting with this surfeit of molecular data, their morphological data set consists of only six characters for 31 species. They collected the greater part of these data themselves. Their morphological analysis would probably have included many more characters if databases of morphological characters had been available.

Describing morphological characters at the species level begins to address one of the problems of using morphological characters in phylogenetic analyses, the problem of variability. Any taxon at a rank higher than species will show more variability than can be conveniently represented in a single term, photograph or diagram. Diagrams of inflorescence structure prepared at the family level serve as convenient introductions to inflorescence structure, but they do not adequately represent the variability that is present. Variability in inflorescence structure of the Marantaceae is so great that no single diagram can do it justice (Sell and Cremers, 1994). Rather than try to reduce this variation to a single type, it will be more beneficial to standardize methods of data collection and report inflorescence structure on a species by species basis. If the species is polymorphic, a set of diagrams can be used, much as Andersson (1985) uses several diagrams to describe floral variation in *Heliconia*. If this process can be combined with the creation of an on-line database of visually based characters, we will have solved one of the major problems in sharing morphological data between investigators.

ACKNOWLEDGMENTS

I thank the many people who helped me develop and refine the ideas presented here including Andrea Shapiro, Peter Weston, and my art history professors at the University of Michigan. I also thank Rolf Sattler, Rolf Rutishauser, Reginae Classen-Bockhoff and Paula Rudall for comments that improved the manuscript. Portions of this research were supported by a grant from the Future Value Fund of the Rudolf Steiner Foundation. I retain all responsibility for the views expressed here.

LITERATURE CITED

- Andersson L. 1976. The synflorescence of the Marantaceae: Organization and descriptive terminology. *Botaniska Notiser* 129: 39–48.
- Andersson L. 1985. Revision of *Heliconia* subgen. *Stenochlamys* (Musaceae-Heliconioideae). *Opera Botanica* 82: 1–124.
- Arber A. 1925. *Monocotyledons*. Cambridge: Cambridge University Press.
- Arber A. 1946. Goethe's botany. *Chronica Botanica* 10: 63–126.
- Arber A. 1950. *The natural philosophy of plant form*. Cambridge: Cambridge University Press.
- Bookstein F. 1998. *Morphometric tools for landmark data: geometry and biology*. Cambridge: Cambridge University Press.
- Bortoft H. 1996. *The wholeness of nature: Goethe's way toward a science of conscious participation in nature*. Hudson, New York: Lindisfarne Press.
- Caddick LR, Rudall PJ, Wilkin P, Chase MW. 2000. Yams and their allies: systematics of Dioscoreales. In: Wilson KL, Morrison DA, eds. *Monocots: systematics and evolution*. Melbourne: CSIRO, 475–487.

- Dahlgren RMT, Rasmussen FN. 1983.** Monocotyledon evolution: characters and phylogenetic estimation. *Evolutionary Biology* **16**: 255–395.
- Davis PH, Heywood V. 1973.** *Principles of Angiosperm taxonomy*. Huntington, NY: Robert Kreiger.
- de Candolle AP. 1827/1941.** *Vegetable organography*. Kingdon B, translator. London: Houlston & Stoneman.
- Eames AJ. 1936.** *Morphology of vascular plants. Lower groups*. New York: McGraw-Hill.
- Farris JS. 1970.** Methods for computing Wagner trees. *Systematic Zoology* **19**: 83–92.
- Gift N, Stevens PF. 1997.** Vagaries in the delimitation of character states in quantitative variation—an experimental study. *Systematic Biology* **46**: 112–125.
- Goethe JW von. 1817/1988.** Fortunate encounter. In: Miller D, ed. *Goethe, scientific studies*. New York: Suhrkamp Publishers, 18–21.
- Goethe JW von. 1820/1988.** Outline for a general introduction to comparative anatomy, commencing with osteology. In: Miller D, ed. *Goethe, scientific studies*. New York: Suhrkamp Publishers, 121.
- Hardin JW. 1957.** A revision of the American Hippocastanaceae. *Brittonia* **9**: 145–195.
- Hennig W. 1950.** *Grundzüge einer Theorie der phylogenetischen Systematik*. Berlin: Deutscher Zentralverlag.
- Hennig W. 1966.** *Phylogenetic systematics*. Urbana: University of Illinois Press.
- Jeune B, Sattler R. 1992.** Multivariate analysis in process morphology of plants. *Journal of Theoretical Biology* **156**: 147–167.
- Keller EF. 1985.** *Reflections on gender and science*. New Haven: Yale University Press.
- Kirchoff BK. 1988.** Floral ontogeny and evolution in the ginger group of the Zingiberales. In: Leins P, Tucker SC, Endress PK, eds. *Aspects of floral development*. Berlin: J. Cramer, 45–56.
- Kirchoff BK. (in press).** Aspects of a Goethean science: complexity and holism in science and art. In: Rowlan H, ed. *Goethe, chaos, and complexity*. Amsterdam: Editions Rodopi, 79–89.
- Kress WJ. 1990.** The phylogeny and classification of the Zingiberales. *Annals of the Missouri Botanical Garden* **77**: 698–721.
- Kress WJ. 1995.** Phylogeny of the Zingiberanae: morphology and molecules. In: Rudall PJ, Cribb PJ, Cutler DF, Humphries CJ, eds. *Monocotyledons: systematics and evolution*. Kew: Royal Botanic Gardens, 443–460.
- Kunze H. 1996.** Infloreszenz- und Blütenmorphologie von *Orchidantha maxillarioides* (Ridl.) K. Schum. (Lowiaceae). *Beiträge Biologie der Pflanzen* **61**: 221–234.
- Kunze H. 1984.** Vergleichende Studien an Cannaceen- und Marantaceen-Blüten. *Flora* **175**: 301–318.
- Miller D. 1988.** *Goethe, scientific studies*. New York: Suhrkamp Publishers.
- Ribeiro JEL da S, Hopkins MJG, Vicentini A, Sothers CA, Costa MA da S, Brito JM, de Souza MAD, de Martins LHP, Lohmann LG, Assunção PACL, Pereira E da C, Silva CF da, Mesquita MR, Procópio LC. 1999.** *Flora da Reserva Ducke*. Manaus: INPA-DFID.
- Rutishauser R, Sattler R. 1985.** Complementarity and heuristic value of contrasting models in structural botany. I. General considerations. *Botanische Jahrbücher* **107**: 415–455.
- Rutishauser R, Sattler R. 1987.** Complementarity and heuristic value of contrasting models in structural botany: II. Case study on leaf whorls: *Equisetum* and *Ceratophyllum*. *Botanische Jahrbücher* **109**: 227–256.
- Rutishauser R, Sattler R. 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 *Utricularia purpurea*, Lentibulariaceae. *Botanische Jahrbücher* **111**: 121–138.
- Sachs J von. 1875.** *Text-book of botany*. Translated by Bennet AW and Thistelton Dyer WT. Oxford: Oxford University Press.
- Sattler R. 1966.** Towards a more adequate approach to comparative morphology. *Phytomorphology* **16**: 417–529.
- Sattler R. 1992.** Process morphology: Structural dynamics in development and evolution. *Canadian Journal of Botany* **70**: 708–716.
- Sattler R. 1993.** Why do we need a more dynamic study of morphogenesis? Descriptive and comparative aspects. In: Barabé D, Brunet R, eds. *Morphogénèse et Dynamique*. Frelighsburg: Editions Orbis, 139–152.
- Sattler R. 1996.** Classical morphology and continuum morphology: opposition and continuum. *Annals of Botany* **78**: 577–581.
- Sattler R. 2001.** Some comments on the morphological, scientific, philosophical and spiritual significance of Agnes Arber’s life and work. *Annals of Botany* **88**: 1215–1217.
- Saunders ER. 1922.** The leaf-skin theory of the stem. *Annals of Botany* **36**: 135–165.
- Sell Y, Cremers G. 1994.** Identification de l’unité de floraison des Marantacées. *Beitrage zur Biologie der Pflanzen* **68**: 27–49.
- Stevens PF. 1980.** Evolutionary polarity of character states. *Annual Review of Ecology and Systematics* **11**: 333–358.
- Stevens PF. 1991.** Character states, morphological variation, and phylogenetic analysis: A review. *Systematic Botany* **16**: 553–583.
- Stevens PF. 2000.** On characters and character states: Do overlapping and non-overlapping variation, morphology and molecules, all yield data of the same value. In: Scotland R, Pennington VF, eds. *Homology and systematics: coding characters for phylogenetic analysis*. London: Taylor & Francis, 124–144.
- Stuessy TF. 1990.** *Plant taxonomy: the systematic evaluation of comparative data*. New York: Columbia University Press.
- Thiele K. 1993.** The Holy Grail of the perfect character: The cladistic treatment of morphometric data. *Cladistics* **9**: 275–304.
- Thiele K, Ladiges PY. 1996.** A cladistic analysis of *Banksia* (Proteaceae). *Australian Systematic Botany* **9**: 661–733.
- Troll W. 1964.** Die Infloreszenzen, Typologie und Stellung im Aufbau des Vegetationskörpers, Vol. 1. Stuttgart: Fischer.
- Wagner GP. 2001.** *The character concept in evolutionary biology*. San Diego: Academic Press.
- Wagner WH. 1961.** Problems in the classification of ferns. In: Bailey DL, ed. *Recent advances in botany*. Toronto: University of Toronto Press, 841–844.
- Weberling F. 1989.** *Morphology of flowers and inflorescences*. Cambridge: Cambridge University Press.
- Weston P. 2000.** Process morphology from a cladistic perspective. In: Scotland R, Pennington VF, eds. *Homology and systematics: coding characters for phylogenetic analysis*. London: Taylor & Francis, 124–144.