A DURIAN BY ANY OTHER NAME:
TAXONOMY AND NOMENCLATURE OF THE CORE MALVALES[1]

DAVID A. BAUM,[2,3] WILLIAM S. ALVERSON,[2,3] AND RETO NYFFELER[3]

Abstract. The phylogeny of core Malvales (the traditional families Bombacaceae, Malvaceae, Sterculiaceae, and Tiliaceae) has been greatly clarified by recent molecular systematic studies. In this paper we explore the options available for incorporating this phylogenetic information into a classification for the group. We first discuss a range of options within the traditional system of nomenclature with the added constraint of only recognizing monophyletic groups. These schemes differ in the ranks applied and in the degree to which currently used names continue to apply to familiar groups. We then propose an alternative set of unranked names within the framework of phylogenetic nomenclature. The taxon names we propose are very similar to those used in a forthcoming classification scheme using the traditional nomenclatural system. However, in the phylogenetic system these names refer to unranked taxa with explicit phylogenetic definitions. Each of these phylogenetic names is distinguishable from traditional, ranked names by a "clademark." We note some advantages of phylogenetic nomenclature: monophyly of taxa can be assumed, a greater number of nested clades can be named with less difficulty, and classifications are stable so long as phylogenetic knowledge does not change. Furthermore, it will be easy to establish useful, Web-based data sources of phylogenetic names. The traditional and phylogenetic classifications of the core Malvales are almost identical, given current knowledge of phylogeny. Therefore, this group provides a controlled experiment with which to see how the two nomenclatural codes perform in practice as phylogenetic knowledge increases.

Keywords: phylogenetic taxonomy, classification, monophyly, Phylocode.

Knowledge of broad-scale plant phylogeny has increased greatly in recent years, primarily as a result of improved techniques for obtaining and analyzing DNA sequence data. However, no consensus exists as to how such phylogenetic information should be incorporated into taxonomy and whether it can be done without major changes to the traditional taxonomic and nomenclatural systems. Two points of controversy are pertinent: (1) Should formal classifications be restricted to monophyletic taxa? and (2) If we require monophyly, can we continue to use the traditional system of nomenclature or must we develop a new framework such as the phylogenetic system of nomenclature developed by de Queiroz and Gauthier (1990, 1992, 1994)? We subscribe to the view that only monophyletic groups (clades) are individuated parts of the tree of life (e.g., Hennig, 1966; Griffiths, 1976; Wiley, 1981; Donoghue and Cantino, 1988), and therefore we answer question (1) in the affirmative. Question (2), in contrast, remains unanswered.

The choice between a monophyletic version of the traditional nomenclatural system and the new phylogenetic system depends in part on theoretical issues, such as the status of ancestral taxa (Lidén, 1997; van Welzen, 1997). These issues warrant further exploration, but at this time we believe that they are not decisive. It is clear that the traditional system cannot include all living and extinct organisms into monophyletic groups at every rank without breaking two rules in the current codes (Brummitt, 1996, 1997; Brummitt and Sosef, 1998; Knox, 1998; Sosef, 1997): (1) the principle of exhaustive subsidiary ranks, which holds that if a taxon is split into subgroups, all species in that taxon must be assigned to one of those subgroups; and (2) the principle of mandatory ranks, under which every plant is assigned to at least the ranks of species, genus, family, and order. However, it seems to be the case that these problems would not apply if we were trying only to classify taxa at the tips of the tree of life (Lidén, 1997; Sosef, 1997). Since it is difficult

to show that organisms are located at internal branches, we think that users will choose between the nomenclatural systems primarily on the basis of practical issues, such as nomenclatural stability, ease of communication, and operational flexibility. Many of these issues have been discussed before in the abstract (e.g., de Queiroz and Gauthier, 1992; Bryant, 1994; Schander and Thollesson, 1995; de Queiroz, 1997; Lidén et al., 1997; Moore, 1998; Stevens, 1998). Here we revisit them in the context of a worked example, the core Malvales (for other examples see Kron, 1997; Cantino et al., 1997; Hibbett and Donoghue, 1998).

PHYLOGENY OF MALVALES

Recent molecular studies (Alverson et al., 1998; Fay et al., 1998; Bayer et al., in press) have confirmed the monophyly of the core Malvales, which contains species traditionally included in the families Bombacaceae, Malvaceae, Sterculiaceae, and Tiliaceae. Recent studies based on chloroplast DNA sequences have suggested that the core Malvales fall into a clade, the expanded Malvales (= Malvales sensu APG, 1998), along with the traditional families Bixaceae, Cistaceae, Cochlospermaceae, Diegodendraceae, Dipterocarpaceae, Sarcolaenaceae, Sphaerosepalaceae, and Thymelaeaceae, but not Elaeocarpaceae (Alverson et al., 1998; Fay et al., 1998; Bayer et al., in press). In addition, the expanded Malvales also includes Neurada (and probably its relatives Grielum and Neuradopsis, formerly included in Rosaceae) and four genera that have historically moved among Tiliaceae, Elaeocarpaceae, and Flacourtiaceae: Dicraspidia, Muntingia, Neotessmannia, and Petenaea (Alverson et al., 1998; Bayer et al., 1998; in press). Expanded Malvales appear to be most closely related to Sapindales and Capparales (Chase et al., 1993; Rodman et al., 1993; Gadek et al., 1996; Alverson et al., 1998; Nandi et al., 1998). The compositions of the expanded and core Malvales are largely consistent with morphological and phytochemical data (Alverson et al., 1998; Nandi et al., 1998; Bayer et al., in press).

Relationships within the core Malvales have been greatly clarified by analyses of sequences of ndhF (Alverson et al., in press; Nyffeler et al., in preparation; Whitlock et al., in preparation), atpB and rbcL (Bayer et al., in press), and ITS (Nyffeler et al., in preparation).

Combining these data with insights from morphology it is possible to project with some confidence the placement of almost every genus in core Malvales (see Bayer et al., in press). Although the only morphological cladistic analysis of the core Malvales shows little resolution (Judd and Manchester, 1997), the morphological data at hand correspond reasonably well with the molecularly derived hypotheses of relationships. That is to say, the clades suggested by molecular data are not strongly rejected and in some cases gain weak support, especially from wood anatomical, palynological, and embryological data (e.g., the sister-group relationship of Craigia and Tilia, the placement of Fremontodendron near traditional Malvaceae and Bombacaceae, and the placement of Pterospermum closer to Dombeya than to Helicteres). Collaborative studies are underway to further refine knowledge of the group's phylogeny using additional molecular and morphological data and by conducting combined analysis of different data sets (collaborators on this joint effort include W. Alverson, D. Baum, C. Bayer, F. Blattner, M. Chase, R. Nyffeler, and B. Whitlock).

A hypothetical phylogeny of core Malvales is shown in Fig. 1. This is informed by both published and unpublished data but does not represent the outcome of any explicit analysis and therefore does not provide standard measures of support (e.g., bootstraps, decay indices). None of the clades shown were meaningfully contradicted by any of the explicit analyses. We have indicated with a thicker line the branches that we consider strong, by which we mean either that they appeared in the most parsimonious trees of all relevant molecular data sets, or they have high bootstraps (>90%) with one data set, or they are supported by distinctive characters (e.g., unique indels in DNA sequences).

This phylogenetic hypothesis for the core Malvales suggests that Sterculiaceae and Tiliaceae, as traditionally circumscribed, are not monophyletic but rather composed of several distinct evolutionary lineages. Bombacaceae as traditionally delimited (Fig. 1) are also nonmonophyletic, but a majority of the traditional genera (excluding Durio and its allies in clade 8) form a paraphyletic grade (within clade 3). Malvaceae appears to be monophyletic (clade 14).
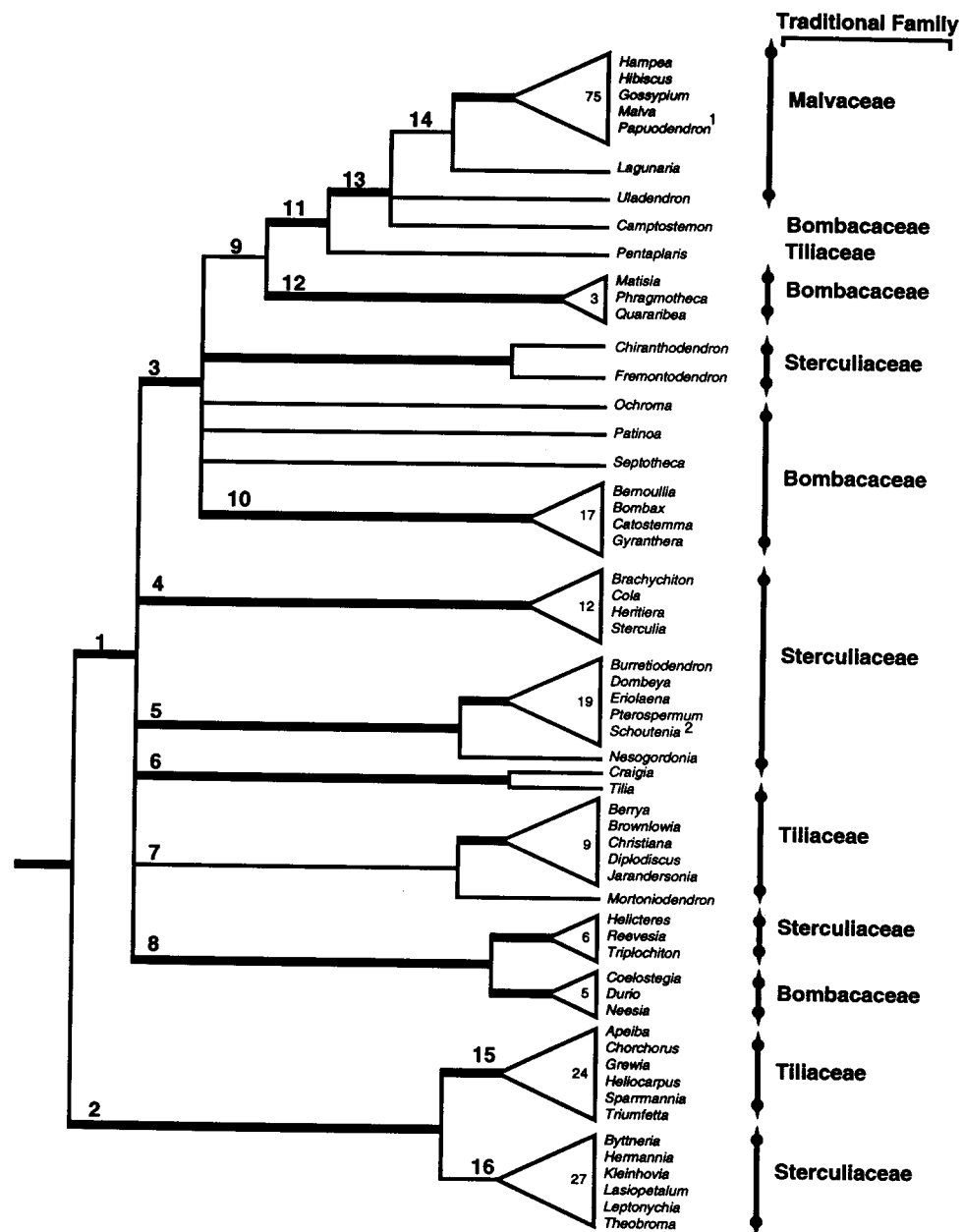
FIGURE 1. Phylogenetic hypothesis for core Malvales. This phylogeny is compiled from diverse sources of information. In particular, we have drawn heavily on the analyses of Alverson et al. (in press), Bayer et al. (in press), and unpublished *ndhF* and ITS data generated at the Harvard University Herbaria by W. Alverson, R. Nyffeler, and B. Whitlock. Branches shown with a thick line are well supported, being present in multiple data sets and/or being strongly supported by a single analysis (see text). Noteworthy clades are numbered 1–15 on the branch leading to the clade. Clades comprising multiple traditional genera are shown as triangles, with the estimated number of included genera shown inside (based on Hutchinson, 1967; Cronquist, 1981; and Bayer et al., in press). Selected genera are listed because they feature in the phylogenetic definitions or in the text, or because they will be familiar to readers. For information on the other taxa falling in these clades, consult Alverson et al. (in press) and Bayer et al. (in press). Traditional family assignments are based on Takhtajan (1997). [1] *Papuodendron* is usually placed in Bombacaceae. [2] *Schoutenia* is traditionally Tiliaceae.

One of the most notable features of the molecular studies (Alverson et al., in press; Bayer et al., in press) is the division of the core Malvales into two large clades, clades 1 and 2 (Fig. 1). Clade 1 is robust, on the basis of its decay and bootstrap values (+5, 88%, for *ndh*F) and the presence of a unique and unreversed 21-base-pair deletion in the 3' half of *ndh*F. The monophyly of clade 2 has only moderate support (decay = +4, bootstrap = 84% for *ndh*F) but is marked by a unique but later reversed 6-base-pair insertion in *ndh*F (Alverson et al., in press).

Clade 2 is divided into two clades containing taxa usually placed in Tiliaceae (clade 15) or Sterculiaceae (clade 16). Within clade 1, six lineages can be identified (clades 3–8). Clade 4 is well supported (bootstrap = 99% for *ndh*F; Alverson et al., in press) and includes traditional Sterculieae, all of which are apetalous. Clade 5 comprises a large proportion of the traditional Sterculiaceae and includes most representatives of traditional tribes Dombeyeae, Eriolaeneae, and Helmiopsideae. This clade is well supported by molecular data (bootstrap = 96% for *ndh*F) and is consistent with morphological data (Barnett, 1987). Clade 6 comprises *Tilia* and *Craigia*. It is well supported by molecular data (bootstrap = 98% for *ndh*F; Alverson et al., in press) and consistent with the morphological data (Judd and Manchester, 1997). Clade 7 is similar to the traditional subfamily Brownlowioideae of Tiliaceae, including mainly the tribes Brownlowieae and Berryeae. The association of these tribes is well established, based on, among other things, a campanulate calyx with fused lobes (Burret, 1926). Data from genes *atp*B and *rbc*L place *Mortoniodendron* at the base of this clade, but with only moderate support (74% after successive weighting; Bayer et al., in press). *Mortoniodendron* was not sampled for *ndh*F, but the remaining exemplars formed a well-supported clade (bootstrap = 100%). Clade 8 comprises *Helicteres* and allies (*Reevesia, Ungeria, Triplochiton,* and probably also *Neoregnellia* and *Mansonia,* but not *Kleinhovia*), and *Durio* and its allies (*Neesia, Cullenia, Kostermansia,* and *Coelostegia).* The clade as a whole gains strong support from *ndh*F (bootstrap = 95%; Alverson et al., in press) and also appears on the *atp*B/*rbc*L trees (Bayer et al., in press). As yet, however, there is no strong morphological evidence in favor of this hypothesis. Clade 3 includes all traditional Malvaceae and all traditional Bombacaceae except *Durio* and its allies, plus *Pentaplaris* (traditionally placed in Tiliaceae; but see Bayer and Dorr, in press) and *Fremontodendron* and *Chiranthodendron* (both traditionally placed in Sterculiaceae). Members of this clade share anthers that are usually interpreted as monothecate or monothecate-derived, but the polysporangiate condition of several potentially basal members of the clade suggests that monothecy might not be the ancestral condition for clade 3 (Endress and Stumpf, 1990; Alverson et al., in press). Clade 3 appears in all molecular analyses and has moderate bootstrap support in the *ndh*F analysis (82%). A clade of similar composition, but including *Durio* and relatives, was weakly supported by an analysis of morphological data alone (Judd and Manchester, 1997).

The base of clade 3 is poorly resolved in all analyses because of the uncertain placement of three traditional Bombacaceae genera *(Ochroma, Patinoa,* and *Septotheca),* and *Fremontodendron* + *Chiranthodendron.* However, two nested clades are notable. Clade 10 includes the palmately leaved taxa traditionally put in Bombacaceae. It is only weakly supported by molecular data but is morphologically cohesive. Clade 14 includes all of the taxa that have traditionally been included in the family Malvaceae. *Papuodendron,* usually recognized in Bombacaceae, tribe Durioneae, is nested within this clade close to *Hibiscus,* with a bootstrap support of 96% (Nyffeler et al., in preparation). The placement of *Papuodendron* in Bombacaceae is known to be problematic (Sosef et al., 1998), and a position within Malvaceae close to *Hibiscus* was already suggested by White (1946) and Kostermans (1960). Likewise, *Hampea,* previously placed in Bombacaceae, is nested within Malvaceae s. str., as suggested by recent classifications (e.g., Fryxell, 1968, 1988). On the basis of *ndh*F, clade 14 is weakly supported, with a bootstrap of 64%, and *Lagunaria* appears to be sister to the remainder of this clade (Alverson et al., unpubl.). Clade 14 (traditional Malvaceae) falls into a series of larger, nested clades (9, 11, and 13) that include *Camptostemon* (traditionally Bombacaceae-Durioneae), *Uladendron* (a recently discovered genus, tentatively placed in Malvaceae), *Pentaplaris,* and Bombacaceae tribe Matisieae *(Matisia, Quararibea,* and *Phragmotheca).*

Taxonomy of the Core Malvales Based on Traditional Nomenclature

The traditional system, as codified in the current International Code of Botanical Nomenclature (Greuter et al., 1994), is relatively permissive in terms of how the names of higher taxa are applied. To use a particular name for a group of organisms, it is necessary that (1) the taxon contain the type associated with the name, (2) the taxon not contain the type of another name having priority at that rank (below the rank of class), (3) the taxon not be included within any other taxon of equal or lower rank, and (4) the taxon not include any taxa of equal or higher rank. Beyond these, there is no requirement that the content of a taxon approximate prior usage or that the group should be monophyletic. One is not required to use or cite any published taxonomic scheme nor to specify the exact content of a named group. Thus, the stability of the traditional system depends largely on taxonomists choosing to agree on the general membership of named groups.

Insofar as one wishes to name only monophyletic groups, changes in our understanding of plant phylogeny can make it difficult to retain continuity in the use of familiar names. The problems faced are well illustrated by core Malvales. Because of the logical problems of a strictly monophyletic classification within the traditional system of nomenclature when ancestral organisms are included (Brummitt, 1996; 1997; Sosef, 1997), we will assume here that we are trying to classify only living organisms and those extinct organisms that reside on tips rather than internal branches of the phylogeny.

Of the four traditionally recognized families, only Malvaceae appears to be monophyletic on the basis of the current phylogeny (Fig. 1). To maintain a concept of this family similar to traditional usage, one must decide whether to restrict the concept of Malvaceae to its traditional limits (approximately clade 14) or expand the family to equal clades 9, 11, or 13. Equating Malvaceae with clade 9 would expand the family to include five genera that have not usually been placed in Malvaceae (*Camptostemon*, *Pentaplaris*, *Matisia*, *Quararibea*, and *Phragmotheca)*, while adding only one that has been included in the family

(Uladendron). Nonetheless, normal practice would probably favor such an inclusion because if clade 14 were equated with Malvaceae, the convention of exhaustive subsidiary taxa would require that these sister-lineages be treated at the family rank. For example, one might recognize Pentaplaraceae, Camptostemonaceae, and Matisiaceae. An intermediate decision would be to expand Malvaceae to include *Pentaplaris, Camptostemon,* and *Uladendron* (i.e., clade 11) but not the three genera of clade 12, on the grounds that the resulting version of Malvaceae could be diagnosed by the occurrence of spiny pollen. (Note, however, that it is possible that this character is plesiomorphic for clade 3.) There are no firm rules for deciding among these three delimitations of Malvaceae, but we will assume here that unless the concept of Malvaceae is expanded to include all of the core Malvales (see below), it would be equated with clade 9.

Because the phylogenetic data allow for the maintenance of Malvaceae with almost unchanged limits, one might have thought that this option would be perfectly acceptable. However, when the traditional system is used, the fact that a familiar taxon is found to be monophyletic may be trumped if maintaining that taxon leads to a proliferation of, say, families, especially if those new families are difficult to diagnose using morphological data (Cantino et al., 1997; Stevens, 1998). The topology of the core Malvales means that whatever rank is applied to clade 9 should also apply to several other clades. The minimum number of families that would have to be recognized depends on aspects of the phylogeny that are as yet undetermined, but one possible classification system, shown in Fig. 2A, recognizes nine, rather than the traditional four, families of core Malvales. Alternatively, to avoid the recognition of these additional families, one could expand the limits of Malvaceae to include the entirety of the core Malvales (Judd and Manchester, 1997; APG, 1998; Bayer et al., in press). Either Malvaceae or Tiliaceae may be chosen as the correct name for this family, since they were published simultaneously (de Jussieu, 1789) and are both conserved names. However, the name Malvaceae has now been proposed as the correct name for this large clade (Judd and Manchester, 1997; Bayer et al.,
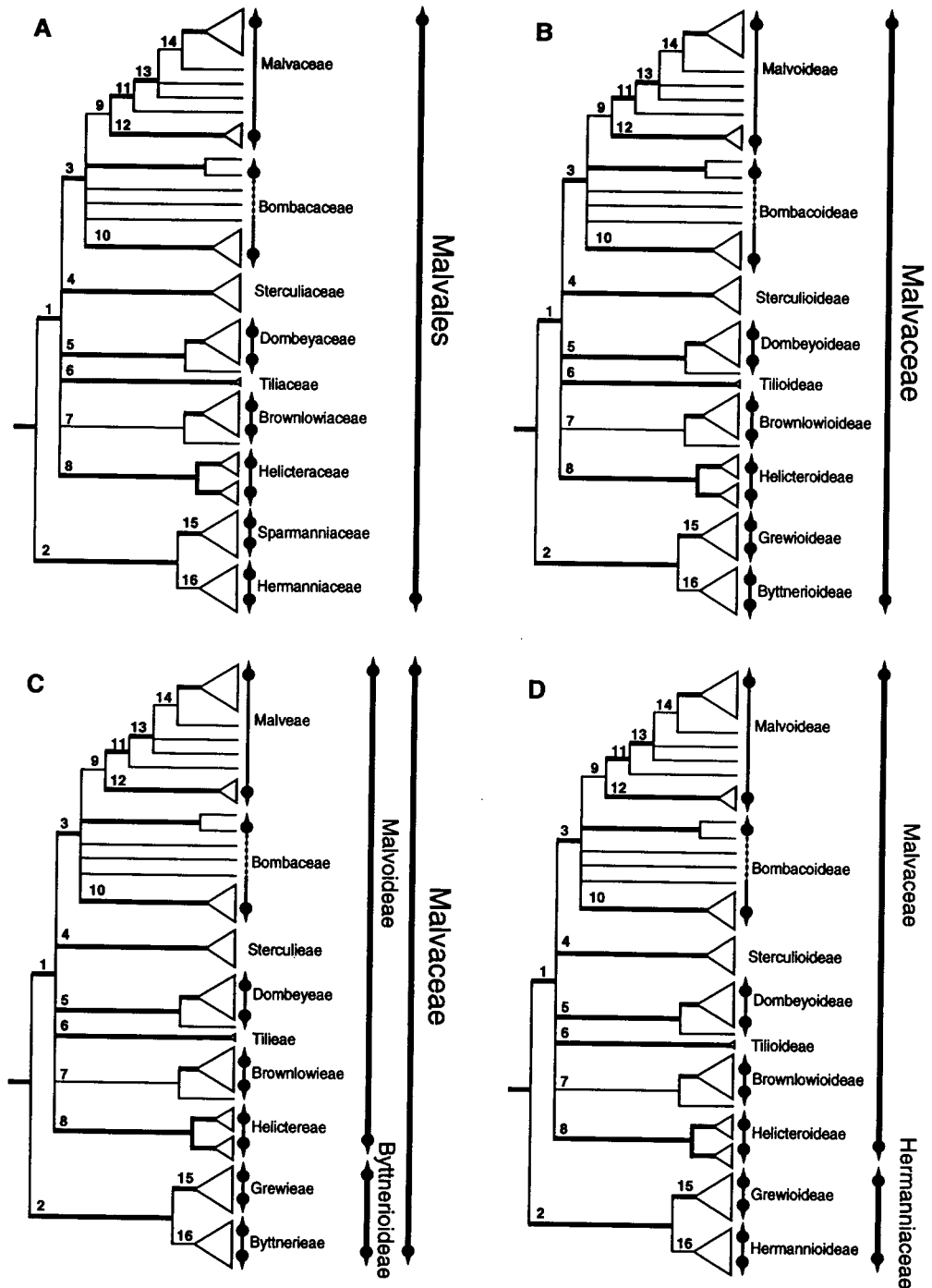
FIGURE 2. Alternative ranked nomenclatural schemes for core Malvales. The phylogenetic structure is taken from Fig. 1, with clade numbers indicated on the relevant internal branches. In all trees we have assumed that unresolved lineages at the base of clade 3 are in the same taxon as clade 10. The scheme shown in Fig. 2B is similar to that of Bayer et al. (in press), except that we place *Pentaplaris* and Matisieae in Malvoideae and *Kleinhovia* in Byttnerioideae.

in press), as illustrated in Fig. 2B. This scheme is nearly identical to that proposed by Bayer et al. (in press), except that they recognized a paraphyletic Bombacoideae and were noncommittal as to the placement of several taxa. Another scheme, which also treats the core Malvales at the family rank, is shown in Fig. 2C. This scheme differs in that tribal ranks are given to clades 4–10, 15, and 16, leaving the subfamilial rank for clades 1 and 2. A fourth alternative within the traditional nomenclatural system would recognize clades 1 and 2 at family rank (Fig. 2D). The name of the former could be selected from Malvaceae and Tiliaceae (see above), and the correct family name for the latter should be Hermanniaceae if one considers Durande (1782) to have validly published this family name (see Reveal, at www.inform.umd.edu/PBIO/fam/revfam.html). If, instead, one contends that valid publication of the name Hermanniaceae occurred later, by Schultz-Schultzenstein in 1832 (*fide* Takhtajan 1987: 130), then Byttneriaceae R. Brown (1814) would have priority. (Note that Art. 19.4 of the International Code of Botanical Nomenclature requires that clade 16 be called Byttnerioideae or Byttnerieae when nested within Byttneriaceae, but otherwise it is called Hermannioideae. Likewise, the principle of priority at rank means that clade 15 is called Sparmanniaceae when recognized at the family rank, but otherwise it is Grewieae or Grewioideae.)

The four taxonomic schemes summarized in Fig. 2 are but a sample of the choices available under the traditional system. There are no absolute criteria for choosing among these alternatives. Instead we have to be guided by authority, tradition, and our subjective sense of the appropriate rank for particular clades. The option shown in Fig. 2A would probably be preferable if one wanted to retain a familiar usage of the name Malvaceae, because it entails adding only five genera to the large and well-known "mallow family." This choice would maintain continuity of the extensive literature on this economically important and well-studied clade. The other three ranked schemes (Fig. 2B–D) substantially alter the content and characters of the taxon named "Malvaceae" but reduce the number of families that must be created.

TAXONOMY OF THE CORE MALVALES BASED ON PHYLOGENETIC NOMENCLATURE

Guiding Principles

In contrast to the traditional systems, the phylogenetic code of nomenclature proposed by de Queiroz and Gauthier (1990, 1992, 1994) anchors a taxon name by reference not to a rank but to the relationships among taxa on a phylogeny. A formal version of this code of nomenclature (the Phylocode) is in preparation by a group of interested systematists. Once completed, the Phylocode will allow for the registration of phylogenetic names. Until that time, phylogenetic definitions cannot be validly published. Nonetheless, it is valuable to attempt to develop a phylogenetic systematization of Malvales and other groups so as to explore the practical issues that will need to be addressed.

Within phylogenetic taxonomy, taxon names can be defined in one of three ways (de Queiroz and Gauthier, 1994). A node-based definition indicates two or more internal "types" and serves to indicate to the most inclusive clade that includes all those types. A type (or "specifier") refers to a species with a designated type specimen that serves to anchor the meaning of a name, much as a type in the traditional system. A stem-based definition indicates at least one internal and one external type and refers to the most inclusive clade that includes the internal but not the external types. An apomorphy-based definition applies to all species bearing a given apomorphy in its original or modified form. However, because application of apomorphy-based names entails homology assessment, which can be highly problematic in some cases (Schander and Thollesson, 1995), we believe that apomorphy-based definitions should be avoided and will not discuss them further.

Node-based or stem-based definitions mean that taxon names will refer only to monophyletic taxa, and given a phylogeny that contains the relevant types, there will be no ambiguity over the clade to which a phylogenetic name applies. In cases where two validly published names apply to the same clade, the correct name is the one that was published first.

A node-based definition refers to one clade on any possible resolved phylogeny that includes the relevant types. For stem-based definitions,

this is only true if one internal type is used (Schander and Thollesson, 1995) and if the internal and external types are specimens, not phylogenetically defined taxa. That is to say, if a stem-based definition refers to more than one internal type, then there are some trees on which the name cannot be attached to any clade. We think it is important that names will refer to a clade on any tree to avoid familiar names becoming unusable if knowledge of phylogeny changes. Therefore, it is important when using stem-based definitions to list only species (with associated specimens) as types and only to include single internal types.

As a basis for comparison of traditional and phylogenetic nomenclature, we have developed two alternative phylogenetic systematizations of Malvales as shown in Fig. 3. These schemes are not exhaustive and deal with higher-level relationships only. For the second, favored (see below) system we provide a set of phylogenetic definitions in the Appendix. In naming taxa, we have generally coopted currently accepted names with rank endings (cf. Cantino et al., 1997). We feel it is valuable to maintain these familiar names while marking them to indicate that they are unranked taxa whose names have explicit phylogenetic definitions. In our treatment, all phylogenetic taxa are proceeded by a forward slash, which we have termed a "clademark," as in /Malvaceae. Other clademark conventions that could be used are Malvaceaeᴾ, Malvaceaeφ, φ-Malvaceae, and so on, depending on the forthcoming Phylocode. The forward slash holds some appeal, since it is on every keyboard in the world and is familiar to Internet users as a symbol implying hierarchical relationships (e.g., a series of nested clades can be written /Malvoideae/Eumalvoideae/Malva).

All phylogenetic names need to be anchored ultimately by reference to particular type specimens (or perhaps illustrations), rather than to species. This applies because changes in species limits or doubts about species validity can cause confusion over the correct clade to which a name applies. Thus, even though we list species as types in the Appendix, we imply that the correct anchor is the type specimen of that species as determined under the traditional code. Determining correct type specimens was beyond the scope of this paper but will be done when the Phylocode is in place. To maintain maximal continuity with traditional usage of names, the species we have selected as internal

or external types of phylogenetic names are the type species of the relevant traditional genera, primarily ascertained by reference to Farr et al. (1979). In the event that we have selected the wrong type species as judged by the traditional code, our choice of type species should remain unchanged so as to avoid instability in the definitions of taxon names.

In some node-based definitions, we have cited phylogenetic taxa as internal types (e.g., /Malvaceae based on /Malvadendrina and /Byttneriina). These definitions are just indirect ways to refer to species as types. If the type has a node-based definition, then the type species of the internal type become the internal types of the more-inclusive taxon. For example, if X is defined on the basis of internal types a and b, and Y is defined on the basis of X and c, then the definition of Y is effectively a node-based definition based on internal types a, b, and c. If the type has a stem-based definition, the conversion would be more complex. For example, imagine that X was defined on the basis of the internal type a and the external type b, and Y had a node-based definition based on X and c. In this case, the definition of Y could be rewritten as the least-inclusive clade including a and c or the least-inclusive clade including a but not b, whichever is bigger. Note that in such a case the more-inclusive taxon cannot be seen as having a node-based definition despite appearing to do so. Therefore, one should refer to a taxon as a type only when it has been provided with a node-based definition.

A Phylogenetic Systematization of the Core Malvales

In developing phylogenetic classifications we have attempted to give clade names that are in line with tradition. To minimize the possibility of changes in phylogeny disrupting the traditional concept of the taxa, we have selected types carefully so as to avoid lineages whose placement is uncertain (Cantino et al., 1997; Hibbett and Donoghue, 1998). Furthermore, when we have used a traditional name, we have included its traditional type as an internal type in the phylogenetic definition. For example, /Byttnerioideae is defined as a node-based taxon based on the type specimens of *Byttneria scabra* L., *Hermannia hyssopifolia* L., and *Theobroma cacao* L. This simple measure ensures that, regardless of phylogeny, /Byttnerioideae will always include *Byttneria scabra*, the type of the

traditional genus *Byttneria*. Similarly, in cases where the traditional names for which we have provided definitions form a nested series with different rank-endings but the same root (e.g., /Malvales/Malvaceae/Malvoideae), we preferred to enforce the correct nesting. For example, because both the internal and external types of /Malvoideae are internal types of /Malvaceae (indirectly via /Malvadendrina), the clade /Malvoideae must be nested within /Malvaceae regardless of phylogeny. Although we recommend this strategy for maintaining conventional nesting of coopted traditional names, it cannot be carried out fully unless one proposes an exhaustive system of classification. For example, we would have preferred that the clade given the name /Bombax was listed as a type of /Bombaceae, and that /Bombaceae was listed as a type of /Bombacoideae. However, because we are not yet in a position to define either /Bombax or /Bombaceae and do not want to use as types taxa that are undefined, we have simply listed species, including *Bombax ceiba* L., as types of /Bombacoideae.

In deciding on a system of phylogenetic names for the major clades of the core Malvales, we found ourselves debating the merits of the two schemes summarized in Fig. 3. These two classifications have much in common, especially the application of the same traditional names with subfamilial endings to most of the lower-level clades. The primary difference between these systems is in how the names "Malvaceae" and "Bombacaceae" are coopted. In the first system, /Malvaceae maintains boundaries that are identical to the traditional limits of the family Malvaceae, and, likewise, /Bombacaceae is a slightly contracted version of the traditional family Bombacaceae. Since /Malvales is now taken to refer to the expanded Malvales clade, we coined a new name, /Eumalvales, for the core Malvales. The second system, in contrast, equates /Malvaceae with the core Malvales (Judd and Manchester 1997; APG, 1998), and clades 4–10, 15, and 16 are treated with subfamilial endings. In each system we coined new names for several clades. When new names are based on taxa with rank endings (/Eumalvales, /Eumalvoideae, /Metamalvoideae) we retained those rank endings. In the other cases, we used the endings -ina (proposed by Kron, 1997, as a general rankless ending) or simply -a.

The choice between these two systems of phylogenetic nomenclature is difficult. The first system has the desirable feature of maintaining the traditional usage of the name "Malvaceae." Given the extensive literature associated with this name and its general familiarity to amateur and professional botanists, it would be highly desirable to maintain its current limits. On the other hand, the second system has the advantage of using the same clade names as APG (1998) and the forthcoming ranked treatment of the core Malvales (Bayer et al., in press). Furthermore, this set of names (with their traditional, not phylogenetic, connotations) will be used in the forthcoming treatment in the *Families and Genera of Vascular Plants* (C. Bayer, pers. comm.). We decided in favor of the second system because, like it or not, we think that this set of names will prevail in systematic circles by the time the Phylocode is operational. In addition, we think it will be useful if the clades named under the phylogenetic and traditional codes have the same names at this moment in time (but are distinguishable by the clademark). Then we can see what happens to the application of these names over the next few years as phylogenetic knowledge advances. Starting from such parity of meaning, we will be able to see more clearly which set of nomenclatural rules promotes greater taxonomic stability while recognizing only groups believed to be monophyletic.

The phylogenetic systematization of core Malvales we are advocating is summarized in Fig. 3B, and definitions are provided in the Appendix. By looking at Fig. 1 and referring to Alverson et al. (in press) and Bayer et al. (in press), one can determine the probable membership of these taxa. Note, however, that because of points of uncertainty in the phylogeny of /Malvaceae, the limits of some taxa remain undetermined. For example, we do not yet know if *Ochroma pyramidale* and *Patinoa almirajo* are members of /Bombacoideae or /Malvoideae (they might be neither). For the time being, however, such uncertain lineages can be specified as members of the next larger clade named without specific assignment to less inclusive taxa (cf. Cantino et al., 1997). Thus, *Ochroma pyramidale* and *Patinoa almirajo* can be referred to /Malvatheca until their affinities become clearer.
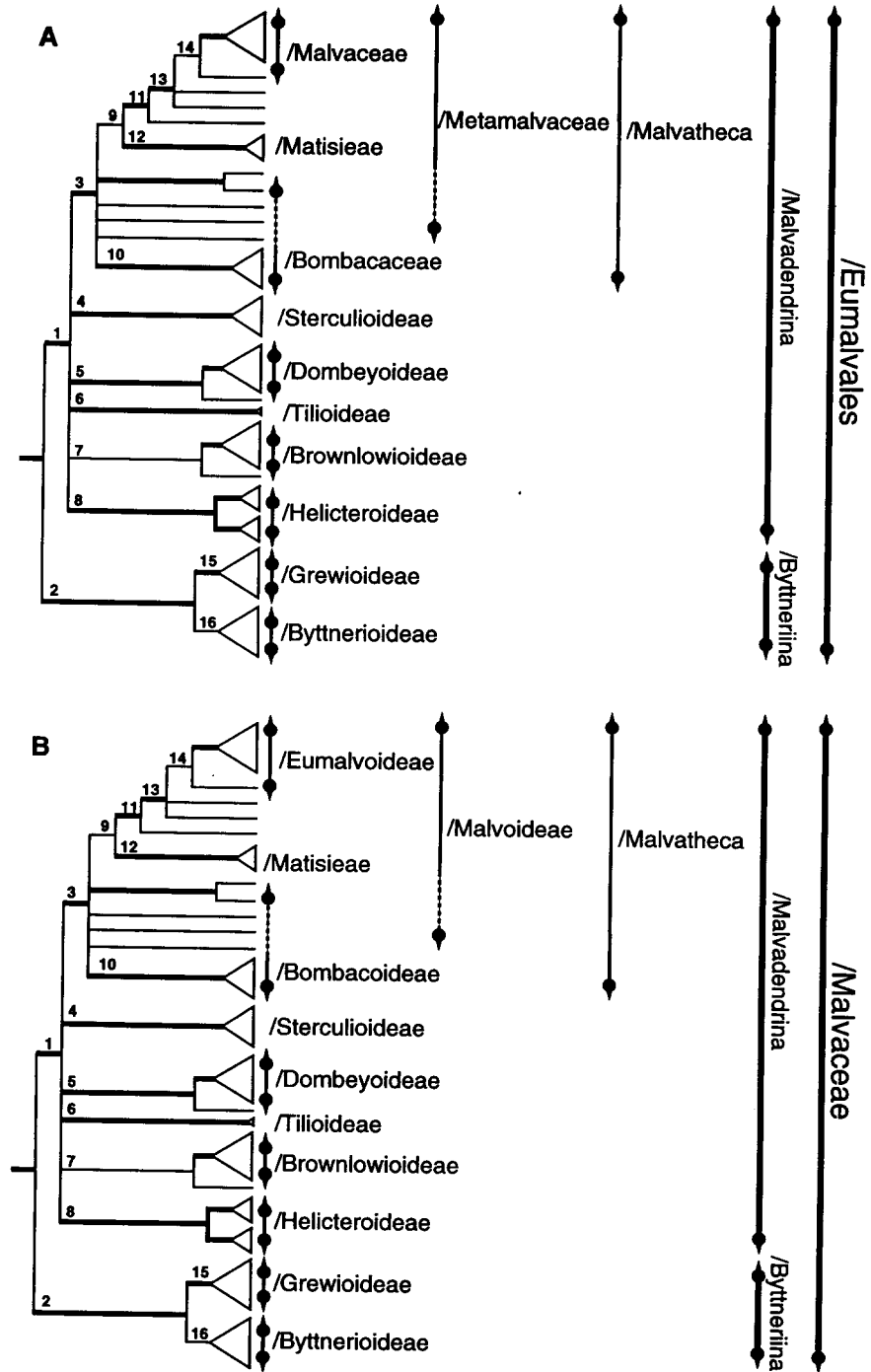
FIGURE 3. Two alternative rankless nomenclatural schemes for core Malvales. The phylogenetic structure is taken from Fig. 1, with clade numbers indicated on the relevant internal branches. A, classification in which /Malvaceae and /Bombacaceae have similar limits to traditional Malvaceae and Bombacaceae; B, our favored classification (see text), based on the ranked scheme of the APG (1988) and of Bayer et al. (in press), as modified in our Fig. 2B. See Appendix for taxon definitions under the favored scheme.

COMPARISON OF THE LINNAEAN AND PHYLOGENETIC NOMENCLATURAL SYSTEMS

It is our view that phylogenetic and traditional schemes for Malvales can and should coexist side-by-side for a period of time that allows a careful evaluation of the merits and problems of each system. Just as it is normal practice to use special formatting to distinguish scientific names from common names, so should we distinguish between traditional and phylogenetic taxon names (indicated by the "/" convention or some other clademark). The issue should not be seen as asking whether we should immediately set aside 250 years of systematic practice in favor of the phylogenetic system. Rather, we wish to undertake a comparative trial of the two systems so that systematists and the broader community of users can choose the system that is optimal for representing genealogical relationships in a useful and memorable way (similar sentiments may be found in Brummitt, 1997; Cantino et al., 1997; and Moore, 1998). The following represents our preliminary observations on the applicability of the two systems to the Malvales and closely parallel comments in the few recent papers also dealing with rankless names for angiosperms (Cantino et al., 1997; Crane and Kenrick, 1997; Kron, 1997).

Stability

As can be seen here, when a new phylogenetic nomenclature is developed for a group, it is quite feasible to maintain consistency with current usage. Thus, at the time that a phylogenetic classification is proposed, users may not even notice that anything significant has happened. Thus, at the moment, Malvaceae (sensu Judd and Manchester, 1997) and /Malvaceae refer to the same group of organisms. Over time, however, this equivalence may break down. The two names may diverge because of (1) changes in phylogenetic knowledge or (2) changes in classification that are independent of phylogeny.

If knowledge of phylogeny changes, then one expects changes in both systems, but these changes are unlikely to be the same. The changes induced under the phylogenetic code can be determined algorithmically by knowing how the tree has changed. The degree of change will generally reflect the extent to which knowledge of phylogeny has changed.

However, some particular changes, such as a jump in the perceived location of some types, could greatly modify the content of taxa (see Moore [1998] and Stevens [1998] for examples of such phylogenetic "bombs"). The traditional system of nomenclature is flexible, and thus there is no way to predict how taxonomists will change classification when phylogenetic knowledge changes.

If there is no change in knowledge of phylogeny, then the phylogenetic classification cannot change. The two systems can diverge in such a circumstance, however, because under the traditional system there is no obligation to use any previously suggested taxonomy provided the rules of priority are obeyed. For example, the various schemes depicted in Fig. 2 are all valid. Because there is no criterion based on priority that would allow one to make an objective choice between these options, it is possible and perhaps likely that more than one would come into use in parallel. The resulting nomenclatural instability is unnecessary in the sense that it would not entail changed knowledge of phylogenetic relationships, but it nonetheless cannot be prevented under the traditional system. This is an important weakness, which has been highlighted by previous authors (especially, de Queiroz and Gauthier, 1992, 1994; de Queiroz, 1997).

Because there are various sources of instability in the content of any given taxon with a particular name, we do not know at the moment which system will actually be less stable in practice. It is for this reason that we have provided here a phylogenetic nomenclature of core Malvales that is in very close accord with a forthcoming systematization using traditional nomenclature (Bayer et al., in press). We will thereby be able to see in a few years the extent to which the two classifications diverge and the degree to which this divergence arises from instability in the phylogenetic or traditional classifications.

Ranks and Nameless Clades

Ranks are an unavoidable part of the traditional system, but they have no objective meaning. For example, within the order Malvales (sensu APG, 1998), there is little objective basis on which to compare the family Malvaceae (ca. 3000 species) with family Muntingiaceae (three monotypic genera; Bayer

et al., 1998). This leads to invalid comparative studies of biogeography, adaptation, and so on. Such misunderstanding might be dealt with in the traditional system by further education to the effect that ranks are not real (Stevens, 1998), but we suspect that this educational effort will take a long time.

The need to attach a rank to every formal taxon name can make it difficult to name all the clades of interest. For example, under all four of the traditional classifications shown in Fig. 2, some major clades were left without names. For example clade 3 is not named in any of the classifications shown in Fig. 2, and clades 1 and 2 are unnamed in Fig. 2A–B. In principle, under the traditional system they could be given names because there are an unlimited number of available ranks, but one would have to employ unconventional ranks. For example, clade 3 in Fig. 2B could be called a supersubfamily. However, although permitted, the use of these unconventional ranks would be problematic because many rank endings would need to be invented and would not be familiar (Cantino et al., 1997; Hibbett and Donoghue, 1998).

An alternative to using unconventional ranks would be to slide the ranks of other clades up or down so as to maintain a familiar rank for those clades of interest in a given context. Thus, one author who wanted to emphasize the characters of clade 1 might call it Malvaceae, whereas another interested in the origin of the "monothecate" condition might call clade 3 Malvaceae. However, although such taxonomic gerrymandering may facilitate communication in a particular, narrow context, names will accumulate multiple meanings as alternative schemes are proposed, leading to confusion.

Unlike the traditional system, the phylogenetic system allows one to give a unique formal name to any clade and leaves it to the community of users to decide by convention which names are put into common use. Do we need to name every clade? We think that a full exposition of the tree of life is facilitated if we have the ability to provide formal names for any recognized clade, even if we do not always choose to exercise that ability. In view of our rapidly expanding knowledge of the phylogeny of life, it is clear that there exist many more interesting clades than can be handled easily by the traditional system. One can easily think of many well-supported clades at higher levels which

have yet to receive formal taxonomic names. Furthermore, in any group, there are new clades at lower hierarchical levels that specialists want to name formally. In view of these considerations, we think it is unfortunate to be constrained by a system that facilitates formal naming of only a subset of the well-supported clades.

One response within the traditional system is to give clades between conventional ranks informal names that are not governed by any rules of nomenclature (e.g., APG, 1998). The idea is that the usage of such names would become established by convention so that there would be a general understanding as to their meaning. In the short term we can see the appeal of this approach, but over the long term we think the extensive use of informal names undermines the purpose of taxonomy—namely, providing stable units for communicating knowledge of organismic diversity. Informal names are often quite unstable. For example, "paleoherb" was initially used for a putative clade that includes monocotyledons and some other herbaceous lineages near the base of the angiosperms (Donoghue and Doyle, 1989). It now appears that the paleoherbs as originally circumscribed are not a clade, but the term remains in common usage with diverse and often ambiguous meaning. It is noteworthy that the informal name "eudicot" (Doyle and Hotton, 1991) has fared better because of its atttachment to a particular apomorphy (triaperturate pollen). This observation suggests to us that if informal names are used it would be wise to provide rigorous definitions along the lines required under the phylogenetic code of nomenclature.

Peter Stevens (1998; pers. comm.) is concerned that the proliferation of formally named clades under the phylogenetic system will cause problems in the memorization of relationships. Further, he postulates that if different people learn different subsets of those groups, then communication will be hindered. We believe, instead, that even if many clades were named, taxonomists and other users would continue to focus on the same few that are easy to recognize, maximally explanatory about the path of evolution, or otherwise interesting or useful. However, although we are skeptical that the ability to name every clade will cause practical problems, we recognize that it would be valuable to observe what happens in groups

such as /Malvaceae, where names are provided for clades that are not given ranks in traditional classifications. By observing the extent to which names such as /Malvatheca and /Malvadendrina are used, we will be able to evaluate empirically the utility of this aspect of the phylogenetic system.

Nesting

In the traditional system, the endings of names convey information on the nesting of taxa that are based on the same type (e.g., Malveae, Malvoideae, Malvaceae, Malvales). If one names clades in the phylogenetic system by coopting traditional names and enforces the traditional nesting pattern as we have done here, then the same advantage can apply. However, this does not work in cases where taxa have different types. For example, in the unlikely event that *Heritiera* turns out to be sister to the rest of the core Malvales, /Sterculioideae would come to contain /Malvaceae. Thus, within the phylogenetic system one cannot make inferences about nesting relationships solely by reference to the suffix attached to the name. Within the traditional system, in contrast, given two family names, one knows that neither should be nested in the other (assuming monophyly has been enforced), and one knows that a family can never be nested within a tribe (and so on). This is a valuable feature of the traditional system (Hibbett and Donoghue, 1998; Moore, 1998; Stevens, 1998).

Representing History

Within the traditional system we can choose to develop a strictly monophyletic classification. However, there is nothing in the code that requires that a name refer only to a monophyletic group. Therefore, working within the traditional system, one can never assume that a name applies to a monophyletic group of organisms. In contrast, under the phylogenetic system, names apply only to monophyletic groups (de Queiroz and Gauthier 1990, 1992, 1994). When genealogies are divergent (tree-like), monophyletic groups, unlike paraphyletic groups, carry explicit and easily interpretable information about history. Therefore, the strict monophyly of taxa under the phylogenetic system is, to us, an important advantage of that system.

Registration and Data Resource Issues

One concern with the phylogenetic system is that the correct naming of groups is entirely contingent on a phylogenetic hypothesis, and this is external to the names themselves. Therefore, in order to determine the nested set of taxon names containing, for example, *Oceanopapaver*, one would need to have access to a phylogenetic hypothesis for flowering plants. By virtue of being proposed during the late 20th century, the phylogenetic taxonomic system can utilize powerful information technologies to solve this potential problem. The draft Phylocode demands that all taxon definitions be registered. This can result in the formation of a data system containing all valid phylogenetic names with unambiguous registration dates. A model for such a system might be the International Plant Name Index, a data source of angiosperm binomials (Croft et al., in press; also http://pnp.huh.harvard.edu). Such a data system of phylogenetic names could be wedded with current and future repositories of phylogenetic information, such as TreeBASE (www.herbaria.harvard.edu/treebase/index. html) and the Tree of Life (phylogeny.arizona. edu/tree/phylogeny.html). This would allow one to obtain phylogenetic hypotheses and then use these to query the phylogenetic names data system so as to obtain the phylogenetic name with priority for a given clade. This is something that one cannot do with traditional names, because the correct name of a clade depends on its rank, which is a subjective decision guided by authority and convention rather than phylogenetic information.

Such a data source of rankless names would have another significant advantage over data sources of traditional, ranked names. Despite the fact that the International Plant Names Index will contain 99% or more of the angiosperm names that have been validly published, some of these names will remain unstable, given the possibility that older names, bearing priority, will be rediscovered. Because the registration of phylogenetic names will apply from the outset, such a source of nomenclatural instability will be avoided. Although this is a potential benefit of the phylogenetic system, it is one that would disappear if the traditional code of nomenclature required registration and developed a system whereby overlooked names would be unable to overturn names in current use.

Conclusions

In sum, it remains unclear whether the phylogenetic system or the traditional system of nomenclature is better suited to regulate the formal naming of taxa. The phylogenetic system has some obvious strengths, such as the fact that it only includes monophyletic taxa and that the correct name of a clade does not depend on subjective rank assessments. However, it also has some potential disadvantages, such as the inability to infer local nesting relationships from names in isolation. Thus, it seems most prudent to conduct a long-term test of the properties of the phylogenetic system in practice before thinking about discarding the current system of taxonomy. By setting up parallel sets of names under the two systems, as we have done here for the core Malvales, we believe that it will soon become clear whether the phylogenetic system can live up to its promise of providing a unified and stable system for communicating knowledge of biodiversity.

Literature Cited

Alverson, W. S., K. G. Karol, D. A. Baum, M. W. Chase, S. M. Swensen, R. McCourt, and K. J. Sytsma. 1998. Circumscription of the Malvales and relationships to other Rosidae: Evidence from *rbcL* sequence data. Amer. J. Bot. 85: 876–887.

Alverson, W. S., B. A. Whitlock, R. Nyffeler, and D. A. Baum. In press. Phylogeny of core Malvales: Evidence from *ndhF* sequence data. Amer. J. Bot.

Angiosperm Phylogeny Group (APG). 1998. An ordinal classification for the families of flowering plants. Ann. Missouri Bot. Gard. 85: 531–543.

Barnett, L. C. 1987. Tribal realignment of certain paleotropical Sterculiaceae. Amer. J. Bot. 74(5, supplement): 724.

Bayer, C., M. W. Chase, and M. F. Fay. 1998. Muntingiaceae: A new family of dicotyledons with malvalean affinities. Taxon 47: 37–42.

Bayer, C., and L. J. Dorr. In press. A synopsis of the neotropical genus *Pentaplaris*, with remarks on its systematic position in core Malvales. Brittonia.

Bayer, C., M. F. Fay, A. Y. de Bruijn, V. Savolainen, C. M. Morton, K. Kubitzki, W. S. Alverson, and M. W. Chase. In press. Support for an expanded family concept of Malvaceae within a recircumscribed order Malvales: A combined analysis of plastid *atpB* and *rbcL* DNA sequences. Bot. J. Linn. Soc.

Brown, R. 1814. Buttneriaceae (sic). Pages 540–541 in M. Flinders, *A Voyage to Terra Australis*. Vol. 2. G. & W. Nicol, London.

Brummitt, R. K. 1996. In defense of paraphyletic taxa. Pages 371–384 in L.J.G. van der Maesen et al., eds., *The Biodiversity of African Plants*. Kluwer Academic Publishers, Netherlands.

————. 1997. Taxonomy versus cladonomy, a fundamental controversy in biological systematics. Taxon 46: 723–734.

Brummitt, R. K., and M. S. M. Sosef. 1998. Paraphyletic taxa are inherent in Linnaean classifications—a reply to Freudenstein. Taxon 47: 411–412.

Bryant, H. 1994. Comments on the phylogenetic definition of taxon names and conventions regarding the naming of crown clades. Syst. Biol. 43: 124–130.

Burret, M. 1926. Beiträge zur Kenntnis der Tiliaceen. Notizbl. Bot. Gart. Berlin-Dahlem 88: 592–605.

Cantino, P. D., R. G. Olmstead, and S. J. Wagstaff. 1997. A comparison of phylogenetic nomenclature with the current system: A botanical case study. Syst. Biol. 46: 313–331.

Chase, M. W., et al. [47 co-authors] 1993. Phylogenetics of seed plants: An analysis of nucleotide sequences from the plastid gene *rbcL*. Ann. Missouri Bot. Gard. 80: 528–580.

Crane, P. R., and P. Kenrick. 1997. Problems in cladistic classification: Higher-level relationships in the land plants. Aliso 15: 87–104.

Croft, J., N. Cross, S. Hinchcliffe, E. Nic Lughadha, P. F. Stevens, J. G. West, and G. Whitbread. In press. Plant names for the 21st century: The International Plant Names Index, a distributed data source of general accessibility. Taxon.

Cronquist, A. 1981. *An Integrated System of Classification of Flowering Plants*. Columbia University Press, New York.

de Jussieu, A. 1789. *Genera Plantarum*. Paris.

de Queiroz, K. 1997. The Linnaean hierarchy and the evolutionization of taxonomy, with emphasis on the problem of nomenclature. Aliso 15: 125–144.

de Queiroz, K., and J. Gauthier. 1990. Phylogeny as a central principle in taxonomy: Phylogenetic definitions of taxon names. Syst. Zool. 39: 307–322.

————. 1992. Phylogenetic taxonomy. Annual Rev. Ecol. Syst. 23: 449–480.

————. 1994. Toward a phylogenetic system of biological nomenclature. Trends Ecol. Evol. 9: 27–31.

Donoghue, M. J., and P. D. Cantino. 1988. Paraphyly, ancestors, and the goals of taxonomy: A botanical defense of cladism. Bot. Rev. (Lancaster) 54: 107–128.

Donoghue, M. J., and J. A. Doyle. 1989. Phylogenetic analysis of angiosperms and the relationships of Hamamelidae. Pages 17–45 in P. R.

Crane and S. Blackmore, eds., *Evolution, Systematics, and Fossil History of the Hamamelidae*. Clarendon Press, Oxford.

DOYLE, J. A., AND C. L. HOTTON. 1991. Diversification of early angiosperm pollen in a cladistic context. Pages 169–195 in S. Blackmore and S. H. Barnes, eds., *Pollen and Spores*. Clarendon Press, Oxford.

DURANDE, J. F. 1782. *Notions élémentaires de botanique*. Dijon.

ENDRESS, P. E., AND S. STUMPF. 1990. Non-tetrasporangiate stamens in the angiosperms; structure, systematic distribution, and evolutionary aspects. Bot. Jahrb. Syst. 112: 193–240.

FARR, E. R., J. A. LEUSSINK, AND F. A. STAFLEU. 1979. *Index Nominum Genericorum*. Bohn, Scheltema and Holkema, Utrecht.

FAY, M. F., C. BAYER, W. S. ALVERSON, A. Y. DE BRUIJN, AND M. CHASE. 1998. Plastid *rbcL* sequence data indicate a close affinity between *Diegodendron* and *Bixa*. Taxon 47: 43–50.

FRYXELL, P. A. 1968. A redefinition of the tribe Gossypieae. Bot. Gaz. 129: 296–308.

——. 1988. Malvaceae of Mexico. Syst. Bot. Monogr. 25: 1–522.

GADEK, P. A., E. S. FERNANDO, C. J. QUINN, S. B. HOOT, T. TERRAZAS, M. C. SHEAHAN, AND M. W. CHASE. 1996. Sapindales: Molecular delimitation and infraordinal groups. Amer. J. Bot. 83: 802–811.

GREUTER, W., F. R. BARRIE, H. M. BURDET, W. G. CHALONER, V. DEMOULIN, D. L. HAWKSWORTH, P. M. JORGENSEN, D. H. NICOLSON, P. C. SILVA, P. TREHANE, AND J. MCNEILL. 1994. *The International Code of Botanical Nomenclature (Tokyo Code)*. Koeltz Scientific Books, Königstein.

GRIFFITHS, G. C. D. 1976. The future of Linnaean nomenclature. Syst. Zool. 25: 168–173.

HENNIG, W. 1966. *Phylogenetic Systematics*. University of Illinois Press, Urbana.

HIBBETT, D. S., AND M. J. DONOGHUE. 1998. Integrating phylogenetic analysis and classification in fungi. Mycologia 90: 347–356.

HUTCHINSON, J. 1967. *The Genera of Flowering Plants. Dicotyledons*, vol. 2. Clarendon Press, Oxford.

JUDD, W. S., AND S. R. MANCHESTER. 1997. Circumscription of Malvaceae (Malvales) as determined by a preliminary cladistic analysis of morphological, anatomical, palynological, and chemical characters. Brittonia 49: 384–405.

KNOX, E. 1998. The use of hierarchies as organiza-

tional models in systematics. Biol. J. Linn. Soc. 63: 1–49.

KOSTERMANS, A. J. G. H. 1960. Miscellaneous botanical notes. Reinwardtia 5(3): 233–254.

KRON, K. 1997. Exploring alternative systems of classification. Aliso 15: 105–112.

LIDÉN, M. 1997. Process and pattern again. In response to Sosef. Taxon 46: 527–528.

LIDÉN, M., B. OXELMAN, A. BACKLUND, L. ANDERSSON, B. BREMER, R. ERIKSSON, R. MOBERG, I. NORDAL, K. PERSSON, M. THULIN, AND B. ZIMMER. 1997. Charlie is our darling. Taxon 46: 735–738.

MOORE, G. 1998. A comparison of traditional and phylogenetic nomenclature. Taxon 47: 561–579.

NANDI, O. I., M. W. CHASE, AND P. K. ENDRESS. 1998. A combined cladistic analysis of angiosperms using *rbcL* and non-molecular data sets. Ann. Missouri Bot. Gard. 85: 137–212.

RODMAN, J., R. A. PRICE, K. KAROL, E. CONTI, K. J. SYTSMA, AND J. D. PALMER. 1993. Nucleotide sequences of the *rbcL* gene indicate monophyly of mustard oil plants. Ann. Missouri Bot. Gard. 80: 686–699.

SCHANDER, C., AND M. THOLLESSON. 1995. Phylogenetic taxonomy—some comments. Zool. Scripta 24: 263–268.

SOSEF, M. S. M. 1997. Hierarchical models, reticulate evolution, and the inevitability of paraphyletic supraspecific taxa. Taxon 46: 75–85.

SOSEF, M. S. M., L. T. HONG, AND S. PRAWIROHATMODJO, EDS. 1998. *Timber Trees: Lesser Known Timbers*. Plant Resources of Southeast Asia 5(3). Backhuys, Leiden.

STEVENS, P. F. 1998. What kind of classification should the practising taxonomist use to be saved? Pages 295–319 in J. Dransfield, M. J. E. Coode, and D. A. Simpson, eds., *Plant Diversity in Malesia III*. Royal Botanic Gardens, Kew.

TAKHTAJAN, A. L. 1987. *Systema Magnoliophytorum*. Nauka, Lenningrad.

——. 1997. *Diversity and Classification of Flowering Plants*. Columbia University Press, New York.

VAN WELZEN, P. C. 1997. Paraphyletic groups or what should a classification entail. Taxon 46: 99–103.

WHITE, C. T. 1946. *Papuodendron*, a new genus of arborescent Malvaceae from New Guinea. J. Arnold Arbor. 27: 272–274.

WILEY, E. O. 1981. *Phylogenetics. The Theory and Practice of Phylogenetic Systematics*. John Wiley and Sons, New York.

APPENDIX
DEFINITIONS OF PHYLOGENETIC NAMES AS
ILLUSTRATED IN FIG. 3B

All phylogenetic names are preceeded by a clademark ("/"). When we use species as types, the correct type is implied to be the type specimen of that species (using the traditional system). Taxon membership of these clades can be inferred by reference to Figs. 1 and 3B and to Alverson et al. (in press) and Bayer et al. (in press).

/Bombacoideae. Stem-based: internal type = *Bombax ceiba* L.; external type = *Malva sylvestris* L. The clade comprises mostly traditional Bombacaceae (minus Durioneae and perhaps some other genera). The relationships of /Fremontodendreae, /Matisieae, *Ochroma, Patinoa,* and *Septotheca* to /Bombacoideae and /Malvoideae remain uncertain.

/Brownlowioideae. Stem-based: internal type = *Brownlowia elata* Roxb.; external types: *Dombeya palmata* Cav., *Malva sylvestris* L., *Sterculia foetida* L., *Helicteres isora* L., *Tilia europaea* L. Note: We have chosen a stem-based name because of the uncertain position of *Mortoniodendron.* The stem-based definition specifies as external types representatives of all the major clades of /Malvadendrina.

/Byttneriina. Node-based: internal types = /Byttnerioideae, /Grewioideae.

/Byttnerioideae. Node-based: internal types = *Byttneria scabra* L., *Hermannia hyssopifolia* L., *Theobroma cacao* L.

/Dombeyoideae. Node-based: internal types = *Dombeya palmata* Cav., *Nesogordonia bernierii* Baill., *Pterospermum suberifolium* (L.) Willd. We have selected a node-based definition because we think that the basal position of *Nesogordonia* is quite robust.

/Eumalvoideae. Node-based: internal types = *Gossypium arboreum* L., *Hibiscus syriacus* L., *Lagunaria patersonii* G. Don., *Malva sylvestris* L.

/Fremontodendreae. Node-based: internal types = *Chiranthodendron pentadactylon* Larreategui, *Fremontodendron californicum* (Torrey) Coville.

/Grewioideae. Node-based: internal types = *Grewia occidentalis* L., *Heliocarpus americanus* L., *Sparrmannia africana* L.

/Helicteroideae. Node-based: internal types = *Durio zibethinus* L., *Helicteres isora* L.

/Malvaceae. Node-based: internal types = /Byttneriina, /Malvadendrina.

/Malvadendrina. Node-based: internal types = *Malva sylvestris* L., *Bombax ceiba* L., *Brownlowia elata* Roxb., *Dombeya palmata* Cav., *Helicteres isora* L., *Sterculia foetida* L., *Tilia europaea* L. We coined this name to refer to traditional Malvaceae and their primarily tropical, woody relatives.

/Malvales. Node-based: internal types = /Malvaceae, *Bixa orellana* L., *Dipterocarpus costatus* C. F. Gaertner, *Muntingia calabura* L., *Neurada procumbens* L., *Petenaea cordata* C. L. Lundell, *Thymelaea sanamunda* Allioni.

/Malvatheca. Node-based: internal types = /Bombacoideae, /Malvoideae, /Fremontodendreae, /Matisieae, *Ochroma pyramidale* (Cav. ex Lam.) Urb., *Patinoa almirajo* Cuatrecasas, *Septotheca tessmannii* Ulbrich. In the absence of any traditional name for this taxon, we propose this new name, which refers to the modified staminal thecae seen in this clade.

/Malvoideae. Stem-based: internal type = *Malva sylvestris* L.; external type = *Bombax ceiba* L. The clade is made up of traditional Malvaceae (/Eumalvoideae) plus associated lineages of /Malvatheca.

/Matisieae. Node-based: internal types = *Matisia cordata* Humbolt et Bonpland, *Phragmotheca siderosa* Cuatrecasas, *Quararibea guianensis* Aublet.

/Sterculioideae. Node-based: internal types = *Brachychiton paradoxum* H. W. Schott et Endlicher, *Cola acuminata* (Palisot de Beauvois) H. W. Schott et Endlicher, *Heritiera littoralis* W. Aiton, *Sterculia foetida* L.

/Tilioideae. Node-based: internal types = *Craigia yunnanensis* W. W. Smith et W. E. Evans, *Tilia europaea* L.