

What to do with *Hibiscus*? A proposed nomenclatural resolution for a large and well known genus of Malvaceae and comments on paraphyly

B. E. Pfeil^{A,B,C} and M. D. Crisp^A

^AAustralian National University, School of Botany and Zoology, Canberra, ACT 0200, Australia.

^BCSIRO Plant Industry, GPO Box 1600, Canberra, ACT 2601, Australia.

^CPresent address: 228 Plant Science Bld, Cornell University, Ithaca NY 14853, USA.

Corresponding author. Email: bep27@cornell.edu

Abstract. The generic classification of Hibisceae has long been unstable. A new understanding of the phylogeny of Hibisceae has found that genera from three tribes (Decaschistieae, Hibisceae and Malvaceae) are nested within *Hibiscus*. We discuss issues that impinge upon the classification of *Hibiscus* in a general sense, including the genus concept, monophyletic and paraphyletic taxa, the use of characters and phylogenies to define taxa, and the current ranked system (based on the International Code of Botanical Nomenclature) v. a rank free alternative (the PhyloCode). We conclude that genera are subjective constructs that are only real in the sense of their phylogenetic origins (i.e. the taxa they denote may be real discoverable monophyletic groups), that paraphyletic taxa are not necessary in classification, that overemphasis of ‘distinctive’ characters in preference to phylogenies leads to recognition of paraphyletic taxa, and that there is no objective fixed and discoverable rank for any taxon. While the PhyloCode avoids some of these problems, it fails to adequately provide an alternative to the mnemonically powerful and information rich Linnean binomial and its advantages do not, in our opinion, outweigh the utility of the ICBN system when the latter employs only monophyletic taxa. With these conclusions in mind, we offer a brief set of guidelines for higher level classification and apply this to *Hibiscus*. The severe paraphyly in *Hibiscus* means that no classification using the ICBN system with exclusively monophyletic taxa will be free of major nomenclatural changes. We argue that including over 200 species from several genera within a broadly defined *Hibiscus* causes fewer nomenclatural changes overall than do alternative schemes, while promoting stability and attempting to minimise change to well known species. A hybrid formal ranked and informal rank free system is discussed and proposed for this group. A series of rank free names that are nested within *Hibiscus s.l.* are proposed to convey information about membership of distinctive clades within *Hibiscus s.l.* in lieu of a complete ranked subgeneric classification that awaits more investigation.

Introduction

Hibiscus L. as traditionally delimited is a large and mostly tropically distributed genus that includes many species that are widely used in horticulture (e.g. *H. rosa-sinensis* L., China rose; *H. syriacus* L., Rose of Sharon; *H. mutabilis* L., Confederate rose; *H. moscheutos* L., swamp mallow) as well as for food (*H. sabdariffa* L., roselle) and fibre (*H. cannabinus* L., kenaf). A widely distributed Old World and Australasian weed (*H. trionum* L., flower-of-an-hour, bladder ketmia) and a common littoral plant in the tropics and sub-tropics (*H. tiliaceus* L., beach hibiscus) rounds out a subjective list of the most familiar members of this well known taxon.

Hibiscus was last revised on a world-wide basis over a century ago (Hochreutiner 1900) and contained almost 200 species at that time. More recent revisions

of selected parts of the genus [e.g. section *Azanzae*, Fryxell (2001); section *Bombicella*, Fryxell (1980); section *Furcaria*, Wilson (1999); Malaysian species, Borssum Waalkes 1966; Mexican species, Fryxell (1988)] combined with recent estimates have pushed the approximate number of species to between 300 and 350.

Hibiscus has usually been placed in tribe Hibisceae [authorities for higher taxa covered in the classification (below) will not be mentioned in text] in the family Malvaceae *s.s.*, but there has been considerable debate as to the best classification at all taxonomic levels. At the familial level, it has been advocated recently that Malvaceae should be expanded to include Tiliaceae, Sterculiaceae, and Bombacaceae (Bayer *et al.* 1999). Under that broader conception, *Hibiscus* is recognised as a member of Malvaceae subfamily Malvoideae (Bayer and Kubitzki 2002). The

composition (and by implication the monophyly) of *Hibiscus* has been regularly questioned, with numerous genera segregated or included in various treatments. For example, *Fioria* is recognised as a distinct genus by Sivarajan and Pradeep (1996) but not by Borssum Waalkes (1966) or Thulin (1999). *Hibiscus* section *Azanzae*, while generally recognised as a section (Hochreutiner 1955; Borssum Waalkes 1966), has been (at least in part) raised to generic rank as *Talipariti* (Fryxell 2001). Further, the infrageneric classification of *Hibiscus* has been unstable despite the existence of some cohesive groups. The composition of some sections has been debated as illustrated by actions such as the splitting of *H.* section *Trionum* into sections *Clypeati*, *Muenchhusia*, *Striati*, *Trionum s.s.*, and *Venusti* (Blanchard 1991, but the names published in Fryxell 1988), and the decision to subsume *H.* section *Trichospermum* within *H.* section *Ketmia* (Borssum Waalkes 1966). Similarly, most of the commonly recognised sections of *Hibiscus* have been recognised as separate genera at some time. This taxonomic fluidity in part stems from the lack of clear morphological discontinuities among most of these groups, but is mainly due to the lack of characters to define *Hibiscus*, whether broadly or narrowly conceived, as clearly distinct from other malvaceous genera. Consequently no single interpretation of the morphological variation has been widely accepted, although a broader circumscription has perhaps predominated in the last 100 years.

This paper provides a summary of the nomenclatural problems that have arisen as molecular data have begun to resolve the phylogenetic structure of *Hibiscus s.l.* We discuss some controversies in taxonomy and nomenclature that directly relate to our wish to produce a revised classification for *Hibiscus* in its subfamilial context that uses only monophyletic taxa. These controversies include paraphyly, character-based *v.* tree-based taxonomy, and ranked *v.* rank-free nomenclature. We then sketch two alternative solutions to the challenge of developing a useful, stable, and evolutionarily meaningful classification for *Hibiscus s.l.* and show that one of these is preferable on the basis of some guidelines that we propose.

Data

Our research, and that of other Malvaceae researchers, has focused on the production of a robust hypothesis of evolutionary relationships using multiple sources of character information. The summary of current phylogenetic estimates shown here (Fig. 1) is based mainly on chloroplast (*rpL16* intron, *ndhF*, *matK*) and nuclear (*rpb2*) DNA sequences in the context of our current understanding of the morphological variation, including chromosome numbers (some subgroups show patterns consistent with recent polyploidy). Details of the analyses will be found in Pfeil *et al.* (2002, 2004), B Pfeil (unpubl. data), Baum *et al.* (2004), and DA Baum and M Koopman (unpubl. data). Broad agreement among

these sources of data has been found at multiple levels, and, while not all relationships have been adequately resolved, two clear conclusions can be drawn: both *Hibiscus* and Hibisceae are not monophyletic since the smallest clade including all '*Hibiscus*' also includes other traditionally recognised genera of Hibisceae and tribes Decaschistieae and Malvaceae (Fig. 1). Below we review some of the broader philosophical and conceptual issues that bear on the problem of translating our improved understanding of the evolutionary relationships within Malvaceae into a better taxonomic circumscription of *Hibiscus* and Hibisceae. How these new data are translated into a circumscription depends very much on the classification principles applied, particularly in regard to cladistic topologies.

Conceptual overview

Is a genus real, and if so, in what sense?

Genera have two components: they are higher taxa (here we mean groups of organisms more inclusive than a single species); and they have rank. We assume the existence of higher taxa and intend to argue only whether genera have any objective reality beyond that of being a higher taxon. Some authors see genera as real and objectively recognisable natural units of biological variation, on the basis of their member species sharing character similarity (Kornet 1994). This idea has been expressed in terms of multivariate (phenetic) analyses of species character information (the species themselves being multivariate clusters of individuals), with genera emerging as species clusters of varying distinctness (Clayton 1983). Jeffrey (1987) made the argument that higher taxa will possess characters that have become fixed within the group and, therefore, serve to diagnose the group. However, the fact that species of the same genus share characters can be explained by the existence of a hierarchical pattern of relationships among species (such as could be produced by a generally divergent phylogeny). This indicates only that a taxon can be recognised, not of a taxon with a particular rank (as any higher taxon could possess this property), and thus provides no basis for the application of a particular rank. Because there is no objective way to measure the degree of character similarity within a group of species, there is no phenetic criterion by which to decide whether to recognise a group of similar organisms as a genus, family, or any other rank. Thus an objective, fixed and discoverable category of the genus cannot be defended on phenetic grounds.

A further outcome of defining genera based on character similarity (rather than phylogeny) is that it would not preclude paraphyletic genera from being recognised where there is sufficient divergence of monophyletic subgroups. While this is clearly allowable under the ICBN (Greuter *et al.* 2000), it would obscure the information content that monophyletic groups provide, particularly because monophyly predicts the

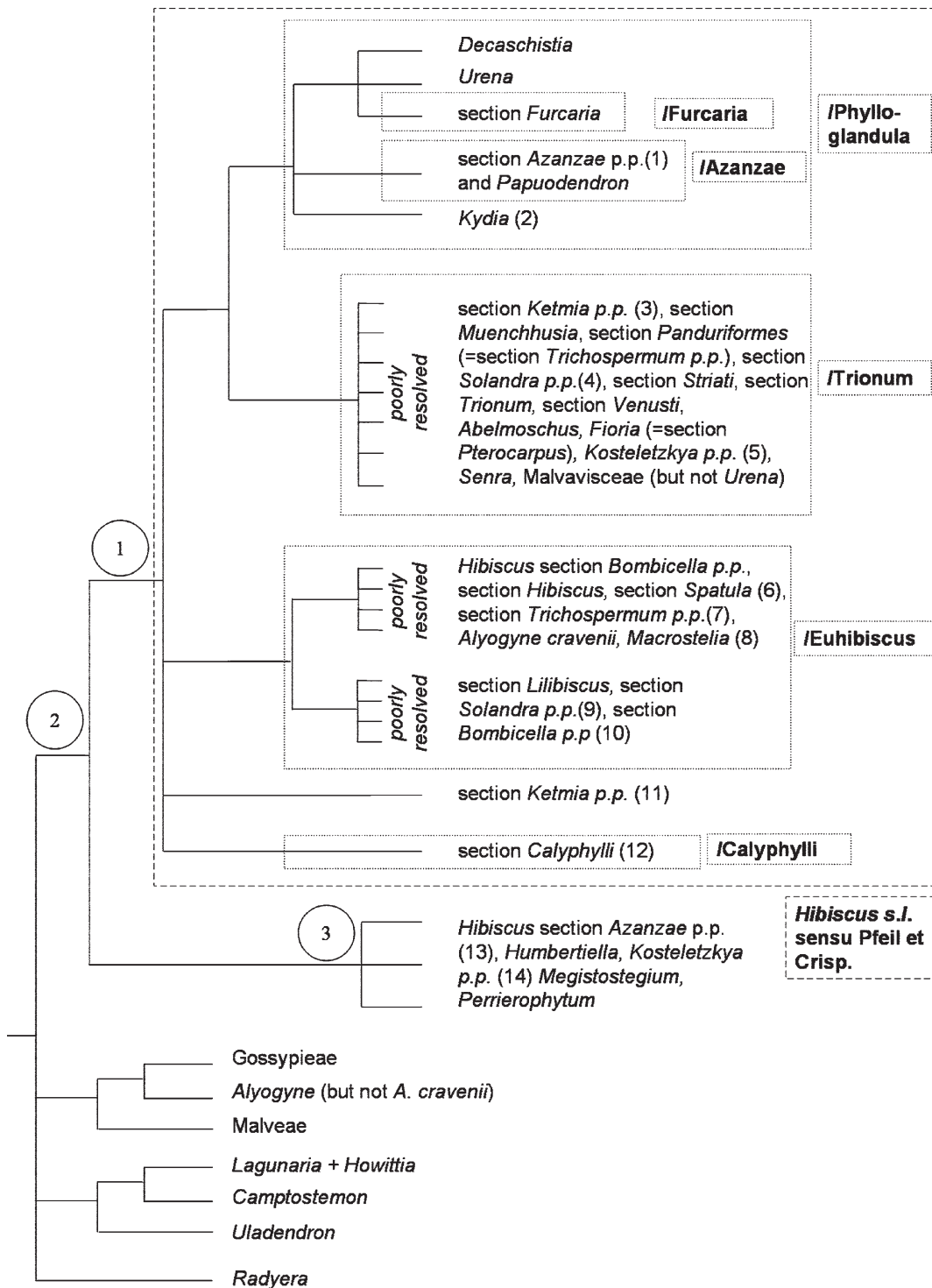


Fig. 1. Summary relationships in Malvoaceae subfamily Malvoideae based on chloroplast *rpl16* intron, *ndhF*, *matK*, and nuclear *rpb2*. Parsimony bootstrap support for node 1 *ndhF/matK* (85%) *rpl16* (<50%, but not contradicted) *rpb2* (node 3 taxa not sampled) copy1 (99%) copy2 (77%), node 2 *ndhF/matK* (100%) *rpl16* (59%), node 3 *ndhF/matK* (83%) *rpl16* (<50%, but not contradicted). Major clades are boxed and named. (1) Malesian members of section *Azanzae*, (2) may include *Dicellostyles*, *Julostylis*, *Nayariophyton*, (3) *H. physaloides*, (4) *H. schinzii* group, (5) excluding *Kosteletzkya* section *Azanzoides*, (6) *H. normanii*, (7) *H. aethiopicus*, (8) Madagascan and Australian members of *Macrostelia* may not be monophyletic, (9) *H. lobatus* group, (10) *H. peralbus* group, (11) *H. pentaphyllus*, (12) may include *H. dongolensis*, (13) Madagascan section *Azanzae*, (14) *K.* section *Azanzaoides*, (15) *Wercklea* placement based only on *ndhF*. Unknown (unsampled) groups: *Hibiscus* sections *Aristivalva*, *Bombycidendron*, *Clypeati*, *Gigantocalyx*, *Parapavonia*, *Trionastrum*; *Symphiochlamys erlangeri*.

existence of further synapomorphies among characters that have not yet been examined, while paraphyly does not.

That taxa should be monophyletic has been argued by many (and we agree), based most commonly on the claim that such units of biological organisation contain the greatest information content and are thus best able to predict the attributes of uncharacterised or undiscovered members of the group (Hennig 1966; Stevens 1985, 1987; Oberwinkler 1994; Parmasto 1994; Singer 1994). Implicit in this statement is the assumption that characters evolve relatively slowly such that traits show phylogenetic correlation (closely related individuals should share more character states than more distantly related individuals). Therefore, excluding characters that vary at population level, we consider that most heritable characters do show phylogenetic correlation at some scale, and where they do not, it is hard to imagine any criterion besides phylogenetic relatedness providing generally greater predictive power. Furthermore, even if one decided that classification were not intended to be predictive, the theoretical and practical developments of phylogenetic analysis (coincident with and fueled by the increased availability of molecular data) mean that determination of monophyly has become a much more objective and scientific enterprise than attempts to decide which characters are of sufficient importance to segregate a derived clade from (and raise to the same rank as) its paraphyletic remainder. Therefore, we argue that any systematisation of *Hibiscus s.l.* should recognise only monophyletic groups in order to maximise the utility of the resulting classification.

Generic definition using characters and character differences

The problem of paraphyly

Genera (and other higher ranked groups) are often maintained by an argument which one might characterise as the ‘but it’s so different’ (BISD) argument. This argument results in the erection of paraphyletic taxa, when a set of supposedly distinctive characters are used to diagnose a monophyletic taxon, leaving a more inclusive taxon at the same rank as a paraphyletic residual. *Hibiscus* illustrates this phenomenon well. For example, *Malvaviscus*, which was diagnosed by 10 style branches, a 2 : 1 style to carpel ratio, and fleshy indehiscent fruit, is nested within a paraphyletic *Hibiscus* (with five style arms, a 1 : 1 style to carpel ratio, and capsular fruit). There is nothing to stop this under the ICBN system, but the maintenance of these genera with their current circumscriptions perpetuates a classification that obscures information and reduces predictive power.

An alternative might be to split the more inclusive genus into several smaller monophyletic genera. However, each monophyletic minor branch of the non-monophyletic genus may lack ‘distinctive’ features, meaning that one is left with several genera that cannot be readily diagnosed by visible

characters. Thus, the understandable desire to have all named taxa diagnosable by morphological characters can be at odds with the aim of only recognising monophyletic groups. Brummitt (2002) has taken this logic one step further, arguing that it is impossible to develop an exhaustive, hierarchically ranked classification of an entire clade while only recognising monophyletic groups. We contend that Brummitt’s logic is flawed and based on the recognition of taxa by character differences rather than by their phylogenetic relationships. As we disagree and wish to create a monophyletic classification for *Hibiscus*, we address his contentions in some detail below.

Our Fig. 2 is a modified version of Brummitt’s (2002) fig. 1. Suppose that one wanted to classify organisms *a–h* on the phylogeny as species and genera (the ICBN requires that all species be placed in a genus), assuming that the existence of these organisms and their phylogenetic relationships were uncontroversial. In Brummitt’s example, species *b* and *c* are assigned to a genus on the basis of their shared characters, but the paraphyletic remainder are classified as a single genus ‘[i]f I call all the dark circles one genus defined by the characters at 1, then the open circles must be a different genus’. However, this is not the only way to ‘chop up’ (sic) this tree. Extant species *a*, *b* and *c* could easily be placed in a monophyletic genus that does not overlap with a monophyletic genus comprising *d* and *e*. These genera might not be easily recognised by convenient features, but as taxa are defined by their shared ancestry rather than their conspicuous characters, that is, they should be monophyletic. Brummitt’s segregation of higher taxa on the basis of selected distinctive features rather than ancestry creates the conflict between paraphyletic and monophyletic classifications that he presents. This is not to say that he cannot do this—of course he can—but that a classification that allows paraphyletic taxa

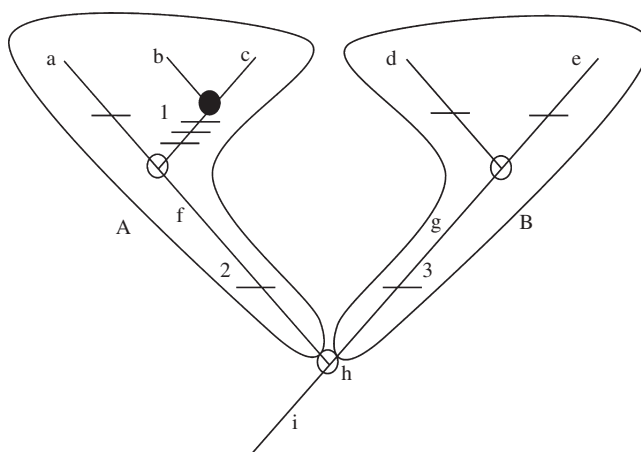


Fig. 2. Hypothetical phylogeny based on Brummitt’s fig. 1 (2002). Bars indicate character change, *a–e* are extant species, circles are hypothetical most recent common ancestors at nodes, *A* and *B* are two possible monophyletic genera that could be erected.

will be unnecessarily less useful because it is based on artificial groupings of species.

This needless conflict becomes more apparent when we consider the placement of ancestral taxa into the same classification as extant taxa (again we assume for the purposes of this argument, as Brummitt does, that their existence is uncontroversial, though this may not be the case). The placement of ancestors within a contemporary classification is problematic because the most recent common ancestor (*h*) of e.g. a pair of genera (*A* and *B*), should not logically belong in either descendent genus (Fig. 2). The extinct organism gave rise to the two daughter lineages, but was not a member of either: it cannot be both parent and offspring at the same time—even if some of its descendants appear little changed from the ancestor [This summary of speciation is an over simplification and does not adequately acknowledge speciation processes that could produce monophyletic daughter lineages that are most closely related to only a part of a larger remnant paraphyletic species (e.g. Crisp and Chandler 1996). Also, an explosive radiation might result in a polytomous species tree, with the underlying gene trees having different but unsupported resolutions (Orthia *et al.* 2005). However, we expect that processes, such as allele birth and death coupled with breeding within rather than between species (even if not exclusive), occurring over macro-evolutionary time, will produce taxa that have the properties of an idealised monophyletic taxon *sensu* Hennig (1966). Given these assumptions, which do not appear to be contradicted by Brummitt, we can proceed to address the other arguments of his thesis]. Also, the ancestor does not share that part of the offspring lineage's history from the earlier cladogenesis (at *h*) to the next (e.g. where *d* and *e* diverge), and therefore it does not have any synapomorphies that *d* and *e* (and undiscovered members of this clade) might possess that *a–c* do not. In many cases a fossil specimen that might represent an ancestor (e.g. because of its antiquity), but displayed no character differences between it and extant species (e.g. *h* in relation to *d* and *e*) would for practical purposes probably be placed in the same higher taxon as *d* and *e* (but not necessarily *a–c*). The phylogeny as known at this point would be a polytomy with a clade containing *a–c*, as well as lineages containing the individual species *d*, *e* and *h*, all radiating from a common point. When character information is found that produces the phylogenetic hypothesis in Fig. 2, *h* is now distinguishable from *d* and *e*, and no longer needs to be maintained in the same higher taxon exclusive of *a–c*, if monophyly of taxa is to be preserved. Brummitt's (2002) assertion that 'every monophyletic genus we recognise in the tree of life must have arisen from a single species in a different genus, which must be paraphyletic' conflates the rank of taxa solely comprising extant species (modern higher taxa) with that of wholly extinct taxa. The modern genera, the rank of which is a human construct, did not exist at that time (although its constituent taxon may

have), so clearly the ancestral organism cannot have been a member of either modern genus (contrary to Brummitt's proposition). A theoretical ancient classification could have included a genus containing the ancestral species, but again this genus is not comparable to modern genera, although it could be a member of a modern taxon of a higher rank than genus. Humans have invented the rank of genus—it is clades that have objective reality separate from human existence, not ranked taxa. Brummitt's statement could thus be amended to read: every monophyletic higher taxon we recognise in the tree of life must have arisen from a single species in a more inclusive taxon, which must be paraphyletic if we choose to recognise both taxa at the same rank. We do not need to do this.

By including all open circle taxa and extant species *a*, *d* and *e* in the same genus based on their lack of the apomorphies at 1 (Fig. 2), Brummitt is implicitly defining these taxa using symplesiomorphies. Hennig (1966) anticipated that this kind of grouping would lead to the recognition of paraphyletic taxa, and proposed grouping by synapomorphies only. Brummitt charged that 'Hennig fatally ignored Darwin's observation ... that evolutionary classification depends on two factors, descent and modification. Hennig ignored modification and thought classification could be based on phylogeny irrespective of characters'. This position seems to ignore Hennig's reliance on characters as evidence for phylogeny, but more importantly appears intended to reverse the correctly assigned primacy of an hypothesis of phylogeny over any subset of the characters (Hennig 1966).

Despite the acceptance that phylogenies can be reconstructed, and that monophyletic groups can be recognised, Brummitt (2002) would have us return to a kind of essentialism, where an arbitrarily selected sub-set of characters ('major character change') is used to define taxa (admittedly producing some paraphyletic ones), thereby sacrificing the predictive power that a wholly monophyletic system has to offer. He appears to do this solely because he asserts that paraphyletic taxa cannot be avoided. As we have shown, his logical basis for this is flawed. If we return to the quote above '[i]f I call all the dark circles one genus defined by the characters at 1, then the open circles must be a different genus', an obvious question arises: why must the open circles be a different (single) genus? These organisms belong to different clades. They have, after a certain point, independent histories. It is a trivial matter to designate from either one to five monophyletic genera in Fig. 2.

The solution to Brummitt's conundrum is to use phylogenetic trees to define higher taxa – not an arbitrary subset of the characters that produced the trees.

Problems with distinctiveness as a guide to rank

While there are several reasonable approaches to applying rank, such as sister groups (that are the same age), or clades of similar age that are not sister, being given the same rank, at

best these approaches offer a guide to *relative* rank and cannot be an objective means to the application of absolute rank. In the lack of any such objective criterion authors commonly fall back on the BISD argument. For example when a large genus such as *Hibiscus* is found to be paraphyletic, encompassing several smaller clades, one could choose to enlarge the genus to include all the nested clades or to split the genus into smaller, monophyletic groups, only one of which retains the original genus name. In such a situation, the inclusion of one or a few small genera that are 'distinctive' can become the justification for splitting of the entire group into numerous small genera, even if many of the genera generated are not easily defined. Furthermore, we reject the idea that some kind of objective level of character difference or distinctiveness is an appropriate guiding principle for circumscription of the generic (or any other) rank.

Procedure for recognising genera in Hibisceae

Given that we prefer to keep classification within the traditional ranked system, we suggest the following guidelines for deciding on the circumscription of genera.

- (a) Define monophyletic genera.
- (b) Since the genus plays a special role in ICBN nomenclature (by virtue of its inclusion in every species' name, e.g. Articles 23.1, 43.1, Greuter *et al.* 2000), genera should be defined by robust clades in order to minimise nomenclatural instability caused by enforcing monophyly if more information becomes available. Although long-term stability cannot be guaranteed, the aim is to choose a node that maximises the chance of stability.
- (c) Choose a clade that requires the fewest nomenclatural changes while still achieving monophyly. There may be argument as to what constitutes 'fewest nomenclatural changes'—we mean here that one should maximise the use of previously applied names rather than coin new ones and maximise the number of species that remain in the genus within which they have traditionally been placed. In databased collections, it should be easier to find specimens and taxa using an older (resurrected) name than it would be to enter many new generic names.

The recognition of only age-equivalent genera, while a reasonable aim [e.g. to improve the accuracy of diversity comparisons (Orthia *et al.* 2005)], is not feasible at this time within the tribes of Malvaceae subfamily Malvoideae since it conflicts with aims (b) and (c) above. Indeed, given the historical context of ranked classifications, we cannot hope to reconcile the current higher taxon circumscriptions with complete equivalence of any rank across all organisms, although this may be achieved locally. While the tribe Gossypieae is reasonably well understood phylogenetically, the tribe Malveae (which contains many more genera and species than Hibisceae) is not. The application of phylogenetic data to inform a monophyletic classification

is likely to result in nomenclatural realignment within Malveae, some minor (e.g. within *Malva* L. and *Lavatera* L.; Ray 1995, 1998) and some potentially more major (e.g. *Sida* L., with about 150 species, is probably not monophyletic as *S. hookeriana* and *S. acuta* Burman f. are distantly related; Pfeil *et al.* 2002). It is difficult to predict how great this realignment is likely to be, but it may not be trivial. As in Hibisceae, small genera in Malveae have been segregated from larger genera on the basis of one or a few distinctive features [e.g. *Meximalva* Fryxell (2 spp.) and *Rhynchosida* Fryxell (2 spp.) from *Sida*, further details in Fryxell (1988)]. The generic classification in Malveae is, therefore, not yet at a point where it could be usefully compared with that in Hibisceae. Perhaps the reverse situation might be worth pursuing when more phylogenetic data in Malveae become available.

ICBN or PhyloCode?

The phylogenetic system of classification and nomenclature (PhyloCode) that has been developed in recent years (Donoghue and Gauthier 2004) needs to be assessed with regard to the ICBN system. This is relevant to our discussion as the PhyloCode is explicitly monophyletic. We will briefly summarise some of the pros and cons of both systems before arguing that the ICBN (with monophyly enforced) meets our utilitarian aims much better than does the PhyloCode. However, a hybrid version can be used successfully as an interim measure in *Hibiscus*, in lieu of more complete information regarding subdivision of the genus.

We point out that the ICBN system, while primarily a nomenclatural system, is also a system of classification because of the mandatory rank of genus. By enforcing monophyly of the genus, the link between nomenclature and classification is increased. The PhyloCode is primarily a system of classification based upon the recognition of monophyletic higher taxa that impinges upon nomenclature in different ways depending upon how species names are handled.

The greatest strength of the ICBN system lies in the information that is conveyed by the use of rank. Any two taxa of the same rank (when monophyly is enforced) cannot be nested within one another. A phylogenetic system requires a phylogenetic hypothesis (presented as a tree, an indented list of names, etc) or the ranking of clades in order to convey this information. The ICBN system provides for the latter by having standardised name endings denoting rank. This provides information about nesting of taxa, e.g. that Malvaceae includes Malveae, rather than the reverse. By contrast, phylogenetic nomenclature does not provide such information because it is deemed more important to connect names to clades rather than to ranked Linnean binomials [It has been pointed out in review that names governed by the ICBN are attached to groups through types but that names are not connected to ranks. This is a fallacy, as taxa above

(at least to family, Article 7.1) and at or below (Article 10.1) the rank of genus require reference to a type species, which in turn requires type material (i.e. a specimen or rarely an illustration). As Article 23.1 makes it clear that species names include the genus name in a binomial combination, all names governed by the ICBN are attached to a ranked genus-species combination. Allowing paraphyletic genera makes this a weak (information poor) application of rank, but these names are ranked nonetheless.]. Also, the mnemonic power of the Linnean generic and specific binomial should not be understated. Without binomials, a phylogenetic system will have difficulty finding the millions of memorable names needed for species (see below).

Doing away with the mandatory rank of genus, the phylogenetic system has much more flexibility in cases such as *Hibiscus*, where traditionally recognised genera are found to be monophyletic but nested within a paraphyletic taxon of the same rank. Under the PhyloCode, one could retain the names of all the nested genera (although unranked) and their species without any requirement (contra the ICBN) to place the remaining species into a paraphyletic genus or genera. For example, *Malvaviscus* (in Malvaceae) has several distinctive features that allow it to be easily recognised, but we now know that it is nested within Hibiscaceae (and *Hibiscus s.l.*). In a rank free system, the name *Malvaviscus* can become the valid name of that nested clade even if *Hibiscus* is the name of a clade that includes *Malvaviscus*. With the PhyloCode one can take a phylogeny and provide individual species with a ‘clade address’. For example, *Malvaviscus arboreus* could be referenced as: Malvoideae/Hibiscaceae/Hibiscus/Trionum/Malvaceae/Malvaviscus/arboreus, indicating its membership of an unranked clade ‘Malvaviscus’ that is nested within another unranked clade ‘Trionum’ etc. The clade address could include the traditional names needed for referencing the historical literature (unless alternative names were chosen for these clades)—one would find little under *Hibiscus malvaviscus* L. (the name with priority in *Hibiscus*) and none under *Trionum malvaviscus* (not a combination that we are aware of) but there is much relevant literature accessible through *Malvaviscus arboreus*. Telescoping this information into an enforced Linnean binomial, e.g. *Hibiscus malvaviscus*, increases the difficulty of maintaining connections to the relevant literature, although current nomenclatural databases can allow one to obtain access to alternative valid names, no matter whether a current or earlier name was initially used in a search.

Additionally, because the PhyloCode does away with the need to classify exhaustively at the mandatory rank of genus required by the ICBN, one can ‘cherry-pick’ when building a classification: one can formalise names only in cases where clades are both robust and diagnosable, leaving the less-resolved parts of the tree with less deep hierarchies of names. For example one could recognise ‘Trionum’,

‘Malvaceae’, and ‘Malvaviscus’ clades, giving former species of *Malvaviscus* deep clade addresses, while leaving *Hibiscus pentaphyllus* unassigned to any named clades within the broader clade Hibiscaceae.

In our opinion, the PhyloCode suffers from a lack of utility in two main areas: clade circumscription (defining clade content) and species names. In the PhyloCode a named taxon is attached to a clade circumscription: a list of two or more specifiers (basically equivalent to types) that can be used to ‘point to’ a clade. What this means is that the correct composition of a named taxon is dictated only by the structure of the phylogeny, which one hopes is an objective piece of reality that can be studied empirically. This system avoids subjective arguments over the correct rank of a taxon—issues that can have significant nomenclatural ramifications due to issues of priority-at-rank and homonymy. While phylogenetic nomenclature provides an unambiguous definition of clade/taxon composition, this rule can cause practical difficulties when competing phylogenetic hypotheses exist, as well as changing with each update of an existing single phylogeny (e.g. by the addition of taxa). In contrast, the ICBN system requires only the type as content of a taxon, and makes no rules about the inclusion of other species. This definition of a taxon does not automatically change with each new phylogenetic hypothesis (reducing instability) and the content can be changed by recircumscription. In the PhyloCode recircumscription is more or less automated (appeals for conservation or redefinition while possible, will probably be rare and difficult). While the ICBN system is obviously subjective in this regard, this subjectivity allows systematists flexibility to critically assess new phylogenetic hypotheses and decide whether they are convincing enough to warrant the modification of taxon definitions. Such flexibility is highly desirable (perhaps inevitable) in the ICBN system, when circumscribing genera (where the nomenclatural impact is greatest). Flexibility should also be part of a rank free system to mitigate the effects of poorly executed analyses on named taxa. At genus level in *Hibiscus*, the stability conferred by the use of traditional definitions of taxon content (rather than node-pointing approaches) is preferred and will be used here.

The PhyloCode community has, until recently, been divided regarding the best way to accommodate species names. At the first International Phylogenetic Nomenclature Meeting a consensus emerged (DA Baum pers. obs.) that species names should be converted from species epithets referenced fully by reference to the Author, year, publication, and page number as proposed by Dayrat (abstract at the first IPNM). While the formatting details have not yet been established, *Malvaviscus arboreus* could become *arboreus* Cav. Diss. iii. t. 48. f. 1. It is now recommended, however, that species usually be written with the name of at least one including clade, preferably that which would provide maximal continuity of

information with the traditional literature. Thus *Malvaviscus arboreus* Cav. Diss. iii. t. 48. f. 1 would be preferable to *Hibiscus arboreus* Cav. Diss. iii. t. 48. f. 1. Further, it will probably be permitted to simplify such names by removal of the publication information, resulting in the familiar construction, *Malvaviscus arboreus*. It is not clear how a name such as this, being at a glance indistinguishable from an ICBN name, will not add to confusion if the two systems are in parallel operation.

Within *Hibiscus*, we will use rank free taxa (clades) to convey our current understanding of relationships in the group without needing to name all clades, nor to burden nomenclature with additional (and likely soon to be modified) infra-generic ranked names. This approach sets a boundary (the genus *Hibiscus*) on any unranked names. Each species must conform to the ICBN requirements (e.g. *Hibiscus exemplum-unus*), but may be placed within unranked clades within the genus (e.g. *H. exemplum-unus*/clade A/subclade 1). Additional information about other species' relationships can be quickly gained when clade addresses are shown, but these need not be. For example, *H. exemplum-duos*/clade A/subclade 2 would be more closely related to *H. exemplum-unus* than to *H. exemplum-tres*/clade B (the entire clade address needs to be shown, if at all, to avoid reference to a phylogeny to understand the unranked names). The convention of forwards slashes (/) to denote unranked names follows Baum *et al.* (1998).

A new hybrid classification for *Hibiscus*

We propose here a new classification of Malvaceae subfamily Malvoideae that follows a conventional ranked system above the generic level but uses unranked higher taxon names within a broadly construed genus, *Hibiscus*.

The most important decision we faced in developing this system was where to delimit *Hibiscus*. This genus has the largest number of species of those affected by our results (approximately 350 v. the next largest, *Pavonia*, with somewhat over 200), and therefore drives the changes we are proposing to the classification. Two primary questions needed to be answered in order to best delimit *Hibiscus*: which nodes are likely to be stable (to minimise future changes), and which stable node will maximise continuity with historical usage and minimise the amount of immediate nomenclatural change?

First, the current generic delimitation needs to be considered. It would be difficult to maintain the genera of Malvaceae and Hibisceae that fall within /*Trionum* (see below) because to do so would produce many new genera to accommodate other clades of Hibisceae and would force us to apply *Hibiscus* to a small clade, for example /*Euhibiscus*. As a result, maintaining genera such as *Pavonia* and *Malvaviscus* would require that around 200 or so species traditionally placed in *Hibiscus* would need to be accommodated in new genera, or genera that have rarely been

used for over a century (/Furcaria [approximately 150 spp.], /Azanzae [Malesian taxa only, approximately 20 spp.], /*Trionum* [approximately 20+ spp.], /*Calyphylli* [5+ spp.]).

On the other hand, this splitting approach would allow several (approximately 16) traditionally recognised genera (not including those that have been part of *Hibiscus*) to be maintained, including the genera of Malvaceae, and species-rich *Pavonia* in particular. However, the monophyly of *Pavonia* is not firmly established—the boundaries between it and the other Malvaceae genera are not entirely clear (Fryxell 1999), so the overall species number of that genus should not carry quite as much weight. A further disadvantage would be that many new (for *H.* sections *Striati* and *Venusti*) or out-of-circulation (*Furcaria*, *Muenchhusia*) generic names would be needed for plants traditionally recognised as *Hibiscus* (10+), some of which will delimit very small groups. However, the greatest disadvantage is that many well known and/or widely cultivated plants (including most listed at the outset of this paper) would be moved out of *Hibiscus* to other genera (e.g. *H. moscheutos*, *H. sabdariffa*, *H. cannabinus*, *H. trionum*, and *H. tiliaceus*).

Conversely, the inclusion of Malvaceae genera in an expanded *Hibiscus* would mean changing the generic status of some well known plants. However, perhaps the most well known of these has already been treated under *Hibiscus* (*Malvaviscus arboreus* Cav. from 1787 = *Hibiscus malvaviscus* L. from 1753). On balance, we consider that a narrowly delimited *Hibiscus* does not best serve the interests of the botanical, horticultural and agricultural communities and other users of these names.

If *Hibiscus* is to be defined broadly, then the question now concerns how broadly. If most or all species currently treated in *Hibiscus* are to be included in the genus as broadly defined, then the stability of only a few nodes needs to be discussed.

An intermediate option, namely including the genera of Malvaceae into genus *Trionum* and segregating *Hibiscus* more or less along major sectional lines (*H.* sections *Furcaria*, *Azanzae*, *Trionum*, *Hibiscus* [including *Bombicella*], *Lilibiscus* and *Calyphylli*), is not worth pursuing, because it sinks most of the Malvaceae genera while also dismembering *Hibiscus* for no clear gain in information. The characteristic features of most of these groups do not appear to be synapomorphies (e.g. the raised calyx veins in *H.* section *Furcaria* are also found in *Decaschistia*, the long seed hairs in *H.* section *Bombicella* are lost many times and are shared with *H.* section *Calyphylli*, the inflated calyx of *H.* section *Trionum* is present in few species of that clade).

Unfortunately, neither node 1 nor 2 (Fig. 1) has unambiguous support from all data sources, but we conclude that both clades probably exist. Strong support for these clades is provided by *ndhF* and *matK* data (DA Baum, M Koopman pers. comm.). The *rp16* intron data do not robustly support these nodes, but node 2 is present in the

strict consensus of most parsimonious trees and no analysis of this data contradicts these nodes (including Bayesian and maximum likelihood analyses; BE Pfeil unpubl. data). The nuclear *rpb2* data do not contain samples of species grouped by node 3, but also support the monophyly of the remaining taxa (node 1). Delimiting *Hibiscus s.l.* at node 2 would result in an additional four genera containing 33 species (*Humbertiella* [inc. *Neohumbertiella*], 5 spp.; *Megistostegium*, 3 spp.; the remainder of *Kosteletzkya*, namely *K.* section *Azanzoides*, 3 spp.; *Perrierophytum*, 9 spp.; *Wercklea*, 13 spp.) being included in *Hibiscus*, while an uncertain but smaller number of endemic Malagasy species misplaced in *Hibiscus* section *Azanzae* would be 'saved' from generic transfer. On the other hand, the majority of this clade is endemic to Madagascar (except *Wercklea*, for which preliminary data are ambiguous), and transferring these species out of *Hibiscus* would not require alterations to many floristic treatments. Therefore, we propose that *Hibiscus* be circumscribed broadly to include all embedded genera, but exclude the Malagasy clade so long as the phylogenetic data continue to suggest that this clade is sister to *Hibiscus*. We are not yet proposing new names for the Malagasy members of *Hibiscus* section *Azanzae* nor of *Kosteletzkya* section *Azanzoides* because this work is ongoing, and anticipated new collections will provide critical sampling to test the robustness of the Malagasy clade (M Koopman and DA Baum unpubl. data).

elsewhere in this treatment (e.g. Hutchinson places *Radyera* in synonymy with *Hibiscus*, but

Classification of Malvaceae subfamily Malvoideae and *Hibiscus*

Malvaceae subfamily **Malvoideae** Burnett

Gossypieae Alefeld (treatment as in Bayer and Kubitzki [2002]).

Hibisceae Reichenbach Conspect. Reg. Veg. 202 (1828). Type: *Hibiscus* L. Decaschistieae Fryxell Amer. J. Bot (1975). Type: *Decaschistia* Wight & Arnott Kosteletzkyeae Alefeld Österr. Bot. Zeitschr. (1862). Type: *Kosteletzkya* K. Presl. Kydieae Edlin New Phytologist (1935). Type: *Kydia* Roxb. Malvavisceae K. Presl. Reliq. Haenk. (1835). Type: *Malvaviscus* Fabricius Pavonieae Alefeld Österr. Bot. Zeitschr. (1862). Type: *Pavonia* Cav. Ureneae Bentham & Hooker (1862). Type: *Urena* L.

Included genera:

Hibiscus sensu lato (except for some Madagascan members of *Hibiscus* section *Azanzae* which are yet to be placed in a genus), *Humbertiella*, *Megistostegium*, *Perrierophytum*

Hibiscus L. Sp. Pl. 2: 693 (1753). Type: *Hibiscus syriacus* L. [Except for some Madagascan members of *Hibiscus* section *Azanzae* and *Kosteletzkya* section *Azanzoides* that are yet to be placed in a genus. Generic synonyms listed in Borssum Waalkes (1966), Hutchinson (1967), and Fryxell (1988) are accepted, unless contradicted

Table 1. Sampled species of Hibisceae and the clades to which they belong

Species	Clade	Subordinate Clade
<i>Hibiscus ellipticifolius</i> Borssum Waalkes	Phylloglandula	Azanzae
<i>Hibiscus macrophyllus</i> Roxb.	Phylloglandula	Azanzae
<i>Hibiscus tiliaceus</i> L.	Phylloglandula	Azanzae
<i>Papuodendron lepidotum</i> C.T.White	Phylloglandula	Azanzae
<i>Kydia calycina</i> Roxb.	Phylloglandula	Kydia
<i>Hibiscus acetosella</i> Welw. ex Fic.	Phylloglandula	Furcaria
<i>Hibiscus arnhemensis</i> F.D.Wilson	Phylloglandula	Furcaria
<i>Hibiscus asper</i> Hoek. f.	Phylloglandula	Furcaria
<i>Hibiscus cannabinus</i> L.	Phylloglandula	Furcaria
<i>Hibiscus costatus</i> A.Rich.	Phylloglandula	Furcaria
<i>Hibiscus divaricatus</i> Graham	Phylloglandula	Furcaria
<i>Hibiscus fryxellii</i> D.J.Mabberley	Phylloglandula	Furcaria
<i>Hibiscus forsteri</i> F.D.Wilson	Phylloglandula	Furcaria
<i>Hibiscus furcellatus</i> Lam.	Phylloglandula	Furcaria
<i>Hibiscus greenwayi</i> Baker f.	Phylloglandula	Furcaria
<i>Hibiscus heterophyllus</i> Vent.	Phylloglandula	Furcaria
<i>Hibiscus hiernianus</i> Exell & Mendonca	Phylloglandula	Furcaria
<i>Hibiscus mastersianus</i> Hiern	Phylloglandula	Furcaria
<i>Hibiscus mechowii</i> Garcke	Phylloglandula	Furcaria
<i>Hibiscus meeusii</i> Exell	Phylloglandula	Furcaria
<i>Hibiscus meraukensis</i> Hochr.	Phylloglandula	Furcaria
<i>Hibiscus nigricaulis</i> Baker f.	Phylloglandula	Furcaria
<i>Hibiscus radiatus</i> Cav.	Phylloglandula	Furcaria
<i>Hibiscus rostellatus</i> Guill. & Perr.	Phylloglandula	Furcaria
<i>Hibiscus sabdariffa</i> L.	Phylloglandula	Furcaria
<i>Hibiscus saponarius</i> Craven	Phylloglandula	Furcaria
<i>Hibiscus splendens</i> Fras. ex Graham	Phylloglandula	Furcaria
<i>Hibiscus sudanensis</i> Hochr.	Phylloglandula	Furcaria
<i>Hibiscus surattensis</i> L.	Phylloglandula	Furcaria
<i>Hibiscus zonatus</i> F. Muell.	Phylloglandula	Furcaria
<i>Decaschistia byrnesii</i> Fryxell	Phylloglandula	Decaschistia
<i>Decaschistia occidentalis</i> A.S.Mitch. ex Craven & Fryxell	Phylloglandula	Decaschistia
<i>Urena lobata</i> L.	Phylloglandula	Urena
<i>Hibiscus apodus</i> in ed.	Trionum	
<i>Hibiscus engleri</i> K.Schum.	Trionum	
<i>Hibiscus incanus</i> J.C.Wendl.	Trionum	
<i>Hibiscus lasiocarpus</i> Cav.	Trionum	
<i>Hibiscus moscheutos</i> L.	Trionum	
<i>Hibiscus mutabilis</i> L.	Trionum	
<i>Hibiscus palustris</i> L.	Trionum	
<i>Hibiscus physaloides</i> Guill. & Perr.	Trionum	
<i>Hibiscus schinzii</i> Hochr.	Trionum	
<i>Hibiscus striatus</i> Cav.	Trionum	
<i>Hibiscus trionum</i> L.	Trionum	
<i>Ablemoschus ficulneus</i> (L.) Wight & Arn.	Trionum	Abelmoschus
<i>Abelmoschus manihot</i> (L.) Medik.	Trionum	Abelmoschus
<i>Fioria vitifolia</i> (L.) Mattei	Trionum	
<i>Kosteletzkya adoensis</i> Mast.	Trionum	
<i>Kosteletzkya grantii</i> Garcke	Trionum	
<i>Senra incana</i> Cav.	Trionum	
<i>Anotea flavida</i> (DC.) Ulbr.	Trionum	
<i>Malachra fasciata</i> Jacq.	Trionum	
<i>Malvaviscus arboreus</i> Cav. [<i>H. malvaviscus</i> L.]	Trionum	Malvaviscus
<i>Pavonia hastata</i> Cav.	Trionum	Pavonia
<i>Alyogyne cravenii</i> Fryxell [<i>H. cravenii</i> (Fyxell) B.E.Pfeil and Craven]	Euhibiscus	
<i>Hibiscus aethiopicus</i> L.	Euhibiscus	

Table 1. continued

Species	Clade	Subordinate Clade
<i>Hibiscus brachysiphonius</i> F.Muell.	Euhibiscus	
<i>Hibiscus burtonii</i> F.M.Bailey	Euhibiscus	
<i>Hibiscus coatesii</i> F.Muell.	Euhibiscus	
<i>Hibiscus coulteri</i> Harv. ex A.Gray	Euhibiscus	
<i>Hibiscus drummondii</i> Turcz.	Euhibiscus	
<i>Hibiscus ferrugineus</i> Cav.	Euhibiscus	
<i>Hibiscus hirtus</i> Buch.-Ham. ex Roxb.	Euhibiscus	
<i>Hibiscus insularis</i> Endl.	Euhibiscus	
<i>Hibiscus lobatus</i> (Murr.) O.K.	Euhibiscus	
<i>Hibiscus longifilus</i> Fryxell	Euhibiscus	
<i>Hibiscus microchlaenus</i> F.Muell.	Euhibiscus	
<i>Hibiscus normanii</i> F.Muell.	Euhibiscus	
<i>Hibiscus pedunculatus</i> L.f.	Euhibiscus	
<i>Hibiscus peralbus</i> Fryxell	Euhibiscus	
<i>Hibiscus rosa-sinensis</i> L.	Euhibiscus	
<i>Hibiscus setulosus</i> F.Muell.	Euhibiscus	
<i>Hibiscus sidaeformis</i> H. Bn.	Euhibiscus	
<i>Hibiscus sturtii</i> Hook.	Euhibiscus	
<i>Hibiscus syriacus</i> L.	Euhibiscus	
<i>Hibiscus waimeae</i> A.Heller	Euhibiscus	
<i>Macrostelia grandifolia</i> Fryxell	Euhibiscus	
<i>Macrostelia laurina</i> (Baill.) Hochr. & Humbert	Euhibiscus	
<i>Hibiscus calyphyllus</i> Cav.	Calyphylli	
<i>Hibiscus dongolensis</i> Caill. ex Delile	Calyphylli	
<i>Hibiscus ludwigii</i> Eckl. ex Zeyh.	Calyphylli	
<i>Hibiscus pentaphyllus</i> F.Muell.		
<i>Hibiscus bojeranus</i> H. Bn.	Not in Hibiscus s.l.	
<i>Kosteletzkya diplocater</i> Hochr.	Not in Hibiscus s.l.	
<i>Hibiscus mandrarenensis</i> Humbert et Hochr.	Not in Hibiscus s.l.	

Perrierophytum Hochr. Anns. Cons. Jard. Bot. Genève, xviii 229 (1915). Type: *P. viridifloru* Hochr.

Perrieranthus Hochr.

Malveae J. Presl (treatment as in Bayer and Kubitzki [2002]).

Genera incertae sedis

Jumelleanthus Hochr. Candollea, ii 79 (1924). Type: *J. perrieri* Hochr. (may be related to Gossypieae – not sampled)

Helicteropsis Hochr. Candollea, ii 156 (1925). Type: *H. microsiphon* (H. Bn.) Hochr. (may be related to *Hibiscus s.l.* – not sampled)

Hibiscadelphus Rock Hawaii, Board Agric. Div. For. Bot. Bull. 1, 8 (1911). Type: (may be related to *Hibiscus s.l.* – not sampled)

Humbertianthus Hochr. Bull. Mus. Hist. Nat. Paris, Ser. 2, xx, 476 (1948). Type: *H. cardiostegius* Hochr. (may be related to *Hibiscus s.l.* – not sampled)

Symphychlamys Gürke in Engl. Jahrb. xxxiii (1903) 379 (may be related to *Hibiscus s.l.* – not sampled)

Wercklea Pittier & Standl. Contrib. USA Nat. Herb., xviii 112 (1916) (may be related to *Hibiscus s.l.* – not sampled)

Genera in tribu non dispositis

Alyogyne Alefeld Oestr. Bot. Zeitschr., xiii 12 (1863). Type: *A. hakeifolia* Alefeld (may be added to Gossypieae)

Camptostemon Mast. in Hook. Ic. Pl. xii 18 (1872). Type: *C. schultzii* Mast

Cumingia Vidal

Howittia F. Muell. Trans. Vic. Inst., i 116 (1855). Type: *H. trilocularis* F. Muell

Lagunaria (DC.) Reichenbach Conspect. Reg. Veg. 202 (1828). Type: *L. patersonia* (Andr.) G. Don

Radyera Bullock Kew Bull. 454 (1956). Type: *R. urens* (L.f.) Bullock

Allenia Phill

Acknowledgments

BEP thanks Curt Brubaker and Lyn Craven for their excellent and generous supervision during his PhD study as well as for helpful comments on an early draft of this paper. We thank David Baum for many helpful comments on final drafts, and he and Maggie Koopman for access to unpublished *ndhF* and *matK* results. BEP was supported by an APA (1999–2002); other funding from ABRIS and CSIRO was also invaluable during this time and is gratefully acknowledged. Two anonymous reviews helped improve the manuscript.

References

- Baum DA, Alverson WS, Nyffeler R (1998) A durian by any other name: taxonomy and nomenclature of the core Malvales. *Harvard Papers in Botany* **3**, 315–330.
- Baum DA, Smith SD, Yen A, Alverson WS, Nyffeler R, Whitlock BA, Oldham RL (2004) Phylogenetic relationships of Malvaceae (Bombacoideae and Malvoideae; Malvaceae *sensu lato*) as inferred from plastid DNA. *American Journal of Botany* **91**, 1863–1871.
- Bayer C, Fay MF, De Bruijn AY, Savolainen V, Morton CM, Kubitzki K, Alverson WS, Chase MW (1999) Support for an expanded family concept of Malvaceae within a circumscribed order Malvales: a combined analysis of plastid *atpB* and *rbcL* DNA sequences. *Botanical Journal of the Linnean Society* **129**, 267–303. doi: 10.1006/boj.1998.0226
- Bayer C, Kubitzki K (2002) Malvaceae. In 'The families and genera of vascular plants'. (Eds K Kubitzki, C Bayer) pp. 225–311. (Springer: Berlin)
- Blanchard OJ (1991) 'A revision of species segregated from *Hibiscus* sect. *Trionum* (Medicus) De Candolle *sensu lato* (Malvaceae).' PhD thesis. (Cornell University: Ithaca, NY)
- Borssum Waalkes J (1966) Malesian Malvaceae revised. *Blumea* **14**, 1–213.
- Brummitt RK (2002) How to chop up a tree. *Taxon* **51**, 31–41.
- Clayton WD (1983) The genus concept in practice. *Kew Bulletin* **38**, 149–153.
- Crisp MD, Chandler G (1996) Paraphyletic species. *Telopea* **6**, 813–844.
- Donoghue MJ, Gauthier JA (2004) Implementing the Phylocode. *Trends in Ecology and Evolution* **19**, 281–282. doi: 10.1016/j.tree.2004.04.004
- Fryxell PA (1980) A revision of the American species of *Hibiscus* section *Bombicella* (Malvaceae). *USDA Technical Bulletin* **1624**, 1–53.
- Fryxell PA (1988) Malvaceae of Mexico. *Systematic Botany Monographs* **25**, 1–522.
- Fryxell PA (1999) *Pavonia Cavanilles* (Malvaceae). *Flora Neotropica Monograph* **76**, 1–285.
- Fryxell PA (2001) *Talipariti* (Malvaceae), a segregate from *Hibiscus*. *Contributions from the University of Michigan Herbarium* **23**, 225–270.
- Greuter W, McNeill J, Barrie FR, Burdet H-M, Demoulin V, *et al.* (2000) International Code of Botanical Nomenclature (St Louis Code). *Regnum Vegetabile* **138**, 1–474.
- Hennig W (1966) 'Phylogenetic systematics.' (Illinois Natural History Survey: Urbana)
- Hochreutiner BPG (1900) Revision du genre *Hibiscus*. *Conservatoire et Jardin Botaniques Genève. Annuaire* **4**, 23–191.
- Hochreutiner BPG (1955) Malvacées. In 'Flore de Madagascar et des Comores.' (Ed. H Humbert) pp. 1–170. (Firmin-Didot: Paris)
- Hutchinson J (1967) 'The genera of flowering plants.' (Clarendon: Oxford)
- Jeffrey C (1987) The concept of the genus. *Australian Systematic Botany Society Newsletter* **53**, 27–31.
- Kornet DJ (1994) The existence of genera. *Mycologia Helvetica* **6**, 5–7.
- Oberwinkler F (1994) Genera in a monophyletic group: the Dacrymycetales. *Mycologia Helvetica* **6**, 35–72.
- Orthia LA, Cook LG, Crisp MD (2005) Generic delimitation and phylogenetic uncertainty: an example from a group that has undergone an explosive radiation. *Australian Systematic Botany* **18**, 41–47.
- Parmasto E (1994) Limits of splitting. (On schizotaxia). *Mycologia Helvetica* **6**, 8–34.
- Pfeil BE, Brubaker CL, Craven LA, Crisp MD (2002) Phylogeny of *Hibiscus* and the tribe Hibisceae (Malvaceae) using chloroplast DNA sequences of *ndhF* and the *rpl16* intron. *Systematic Botany* **27**, 333–350.
- Pfeil BE, Brubaker CL, Craven LA, Crisp MD (2004) Paralogy and orthology in the Malvaceae *rpb2* gene family: investigation of gene duplication in *Hibiscus*. *Molecular Biology and Evolution* **21**, 1428–1437.
- Ray MF (1995) Systematics of *Lavatera* and *Malva* (Malvaceae, Malveae)—a new perspective. *Plant Systematics and Evolution* **198**, 29–53. doi: 10.1007/BF00985106
- Ray MF (1998) New combinations in *Malva* (Malvaceae: Malveae). *Novon* **8**, 288–295.
- Singer R (1994) Toward a definition of the genus in mycological taxonomy. *Mycologia Helvetica* **6**, 92–94.
- Sivarajan VV, Pradeep AK (1996) 'Malvaceae of southern peninsular India: a taxonomic monograph.' (Daya Publishing House: Delhi)
- Stevens PF (1985) The genus concept in practice—but for what practice? *Kew Bulletin* **40**, 457–465.
- Stevens PF (1987) Genera, what and why—some thoughts. *Australian Systematic Botany Society Newsletter* **53**, 31–38.
- Thulin M (1999) Malvaceae. In 'Flora of Somalia'. (Ed. M Thulin) pp. 40–83. (Royal Botanic Gardens: Kew)
- Wilson FD (1999) Revision of *Hibiscus* section *Furcaria* (Malvaceae) in Africa and Asia. *Bulletin of the Natural History Museum, London (Botany)* **29**, 47–79.

Manuscript received 16 July 2004, accepted 24 January 2005