To be or not to be – principles of classification and monotypic plant families

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Introduction

The primary principle of phylogenetic classification is that of monophyly: taxa should be clades, monophyletic groups in the sense of Hennig (1966). This principle is increasingly finding acceptance among practising taxonomists. Generally, when the paraphyletic nature of higher taxa is brought to light, taxonomists set out to reclassify such taxa into monophyletic ones. Some recent botanical examples are to be found in studies by Fernando & Quinn (1995), Jensen & al. (1995), Linder & Kurzweil (1994), Miao & al. (1995), and Wiegrefe & al. (1994). A phylogenetic classification is not easily achieved, however, under the constraints of current rules of botanical and zoological nomenclature. The problems have been explored in detail by De Queiroz & Gauthier (1990, 1992, 1994) and discussed by a few zoologists, e.g. Bryant (1994, 1996) and Sundberg & Pleijel (1994). De Queiroz & Gauthier (1994) argue that the Linnaean hierarchy of categories (genus, family, order, class, etc.) should be abandoned and a new phylogenetic system of nomenclature developed. Our purpose here is not to discuss De Queiroz & Gauthier's proposal for a phylogenetic system of taxonomy. We agree that current Linnaean classification creates a lot of problems and needs to be changed, but practising taxonomists are at present constrained by the rules of nomenclature. For the ordinary taxonomist working at the family or genus level, it is practically impossible to abandon the Linnaean hierarchy, given that its categories are firmly rooted in everyday taxonomic language and their use is mandatory in the classification of animals and plants. Pending new rules of nomenclature, we need to explore ways of improving classifications under the current nomenclatural constraints without violating the principle of monophyly.

Under the present rules of nomenclature, which stipulate the use of a Linnaean hierarchy, classification is not only a matter of grouping according to the principle of monophyly. There is also the question of ranking, i.e. which clades should be named at the various levels of the hierarchy (e.g. family). In practice, the question is often whether a particular monophyletic group should be recognised as a single unit at a given taxonomic level of the Linnaean hierarchy or subdivided into several monophyletic units at this level. The strategy chosen generally depends on a number of possibly conflicting considerations, subordinate to the principle of monophyly. These include, for example, a desire to maximise the stability and the information content of the system. Below, we list a number of such secondary principles and illustrate their application with reference to two families of flowering plants.

The flowering plants are currently classified in around 400-500 families. Cronquist (1981) lists 383 families, Tahtadžjan (1987) 533. Of these families, 108 to 206

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are monogeneric (Cronquist, 1981; and Tahtadžjan, 1987; respectively), although they may be plurispecific. The differences in classification (see also G. Dahlgren, 1989a-b; Thorne, 1992) are largely due to uncertainties about relationships. For want of knowledge of their precise phylogenetic relationships, there is endless debate about the status of many of the small families. We submit that much of this debate will become obsolete with the rapid strides towards resolving flowering plant phylogeny currently being made by cladistic analysis of morphological and molecular data. For example, dubious families shown to be ingroups of other, well established families may be synonymised with the latter. Other questionable families shown to occupy isolated positions as sister groups of more than one other family will be accepted.

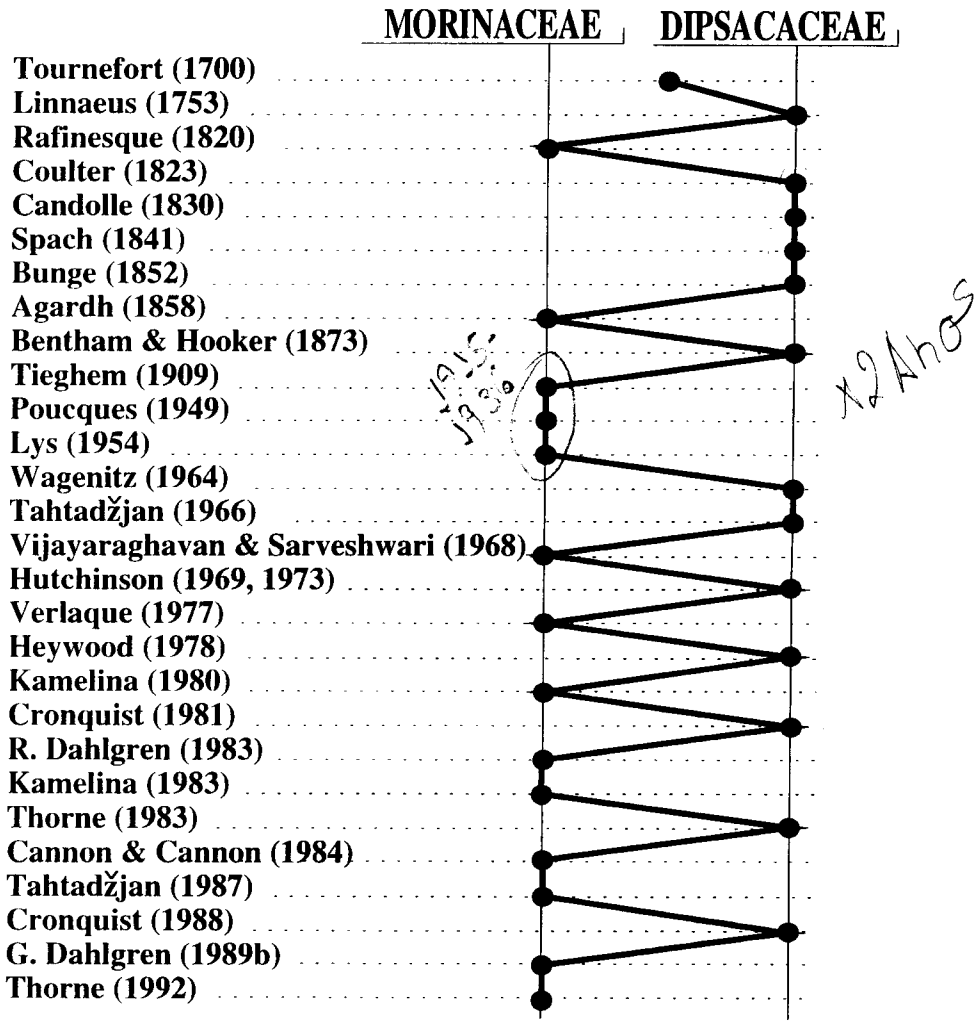

Fig 1. Instability in the familial classification of *Morinaceae*.

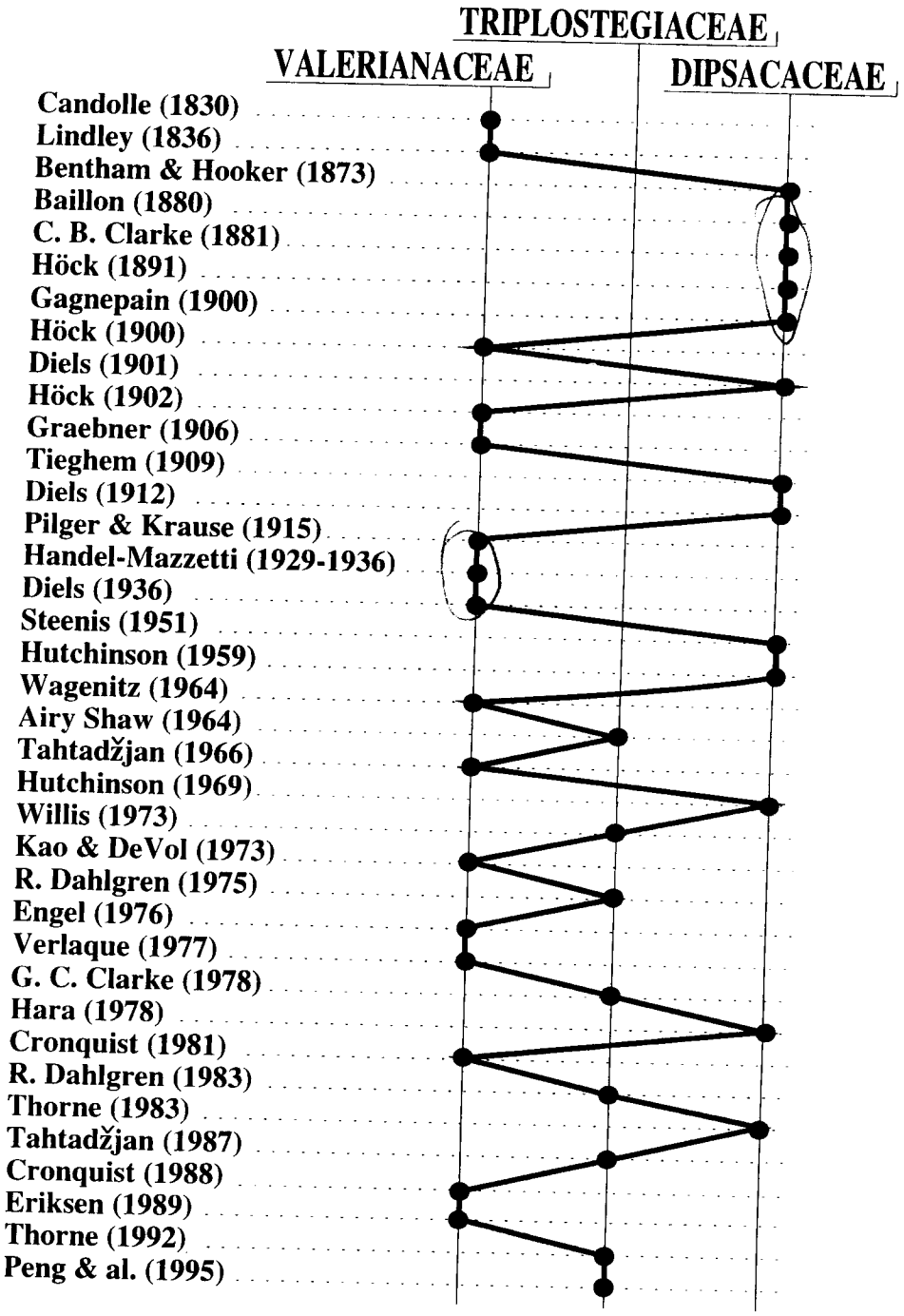

Fig. 2. Instability in the familial classification of *Triplostegia*.

The latter case is exemplified by the family *Morinaceae*. Many controversies in classification may be resolved simply by applying the principle of monophyly, once a corroborated phylogeny is available. In other cases, a ranking problem will remain. This is exemplified by the monogeneric family *Triplostegiaceae*.

Morinaceae *and* Triplostegiaceae

The order *Dipsacales* traditionally comprises three major families, the *Caprifoliaceae* (e.g. honeysuckles, *Lonicera*), the *Dipsacaceae* (e.g. teasel, *Dipsacus*), and the *Valerianaceae* (e.g. valerians, *Valeriana*). In addition to these, there are a number of smaller families which are variably synonymised or recognised, among them *Morinaceae* and *Triplostegiaceae*.

The *Morinaceae* comprise about 15 Eurasian species currently classified in three genera. For a long time this family was treated as monogeneric, with the single genus *Morina*, but Cannon & Cannon (1984) recognised two additional genera, *Acanthocalyx* and *Cryptothladia*, in their revision of the family. The genus *Morina* was established by Tournefort (1700). Vaillant (1724) considered it to be related to his "classe des Dipsacées", including both *Dipsacaceae* and *Valerianaceae* in the modern sense. Linnaeus (1753) classified *Morina* in the *Dipsacaceae*. Rafinesque (1820) treated *Morina* in a separate family *Morinaceae ('Morinidia')*, arguing that it was closer to the *Valerianaceae* than to the *Dipsacaceae*. The family *Morinaceae* was again recognised by Agardh (1858). Ever since Rafinesque (1820), there has been a constant argument about the familial classification of *Morina:* a separate family or a member of the *Dipsacaceae*. This is illustrated in Fig. 1. Even the most recent compilers of major systems of flowering plants disagree (e.g. Cronquist, 1981; Tahtadžjan, 1987; G. Dahlgren, 1989a-b; Thorne, 1992).

The *Triplostegiaceae* comprise two Asian species classified in the single genus *Triplostegia*. The name *Triplostegia* was introduced by Wallich & Bentham (1828), and validly published for a genus of the *Valerianaceae* by Candolle (1830). Bentham & Hooker (1873) transferred that genus to the *Dipsacaceae*. Subsequent authors moved *Triplostegia* back and forth between *Valerianaceae* and *Dipsacaceae*. The situation became even more uncertain with the establishment of the family *Triplostegiaceae* by Airy Shaw (1964). Since then, the classification of *Triplostegia* has been more or less haphazard: in the *Valerianaceae*, in the *Dipsacaceae*, or in a family of its own (Fig. 2). The most recent authors (Peng & al., 1995) accept the *Triplostegiaceae*, and consider the family as related to the *Dipsacaceae*.

Backlund & Donoghue (1996) have undertaken an elaborate cladistic analysis of the *Dipsacales*, including representatives of 58 genera from all families differing in more than 100 mostly morphological characters (including information on gross morphology, anatomy, palynology, embryology, secondary chemistry, and structural rearrangements of the chloroplast genome). In another study, Backlund & Bremer (1998) analysed *rbc*L sequences from 146 genera of the *Asteridae*, mainly in the orders *Araliales, Asterales*, and *Dipsacales*, including 13 genera of the core of the *Dipsacales*, among them *Morina* and *Triplostegia*. These studies support higher familial interrelationships within the *Dipsacales* as shown in Fig. 3. The topology in Fig. 3 is supported by both the morphological and the *rbc*L data sets. Caputo & Cozzolino (1994) made a morphological cladistic analysis of genera of the *Dipsacaceae* using genera of the *Morinaceae, Triplostegiaceae*, and *Valerianaceae* collectively as the outgroup. Their results are largely compatible with the topology in Fig. 3, although

their cladogram is oriented differently owing to their a priori ingroup / outgroup distinction. Apart from the study mentioned above, there is no earlier molecular analysis including *Morina* and *Triplostegia*. The *rbc*L analysis of the *Dipsacales* by Donoghue & al. (1992) focused on the status of the *Caprifoliaceae*, and did not include *Morina* and *Triplostegia*.

There is strong support for the monophyletic group comprising *Morinaceae, Dipsacaceae, Triplostegia,* and *Valerianaceae*. Important synapomorphies for this clade include a largely herbaceous habit, fruits (achenes) crowned by the persistent remains of the calyx, and several anatomical features such as ovular vascularisation and a vascular flankbridge connecting the vascular strands leading into the petioles. All five terminal taxa in Fig. 3 are monophyletic. The *Dipsacaceae* are diagnosed, for example, by flowers in polytelic capitula, a piperad embryogeny (Kamelina, 1980, 1983), and specialised pollen features such as costae surrounding the apertures (G. C. Clarke, 1981). There are also several phytochemical traits characterising the family. The *Valerianaceae* have, for example, a specialised secondary chemistry, with a group of iridoid compounds called valepotriates, a series of reductions in the number of stamens, and a more or less prominent nectar-containing spur.

There is also good support for the monophyly of the group comprising *Dipsacaceae, Triplostegia,* and *Valerianaceae,* and for the pairing of the latter two taxa. All three share a number of morphological, embryological, and palynological features, such as reduction of sepals, chlorophyllous embryo development (Yakovlev & Zhukova, 1980), characters of the anther tapetum (Kamelina, 1980, 1983), and pollen ornamentation. *Triplostegia* and *Valerianaceae* share a partly specialised pollen morphology (Backlund & Nilsson, 1997) and a set of anatomical, ~~morphological,~~ morphological, and embryological characters including simple perforation plates in the primary xylem, sepal vascularisation, and asterad embryology (Johri & al., 1992).

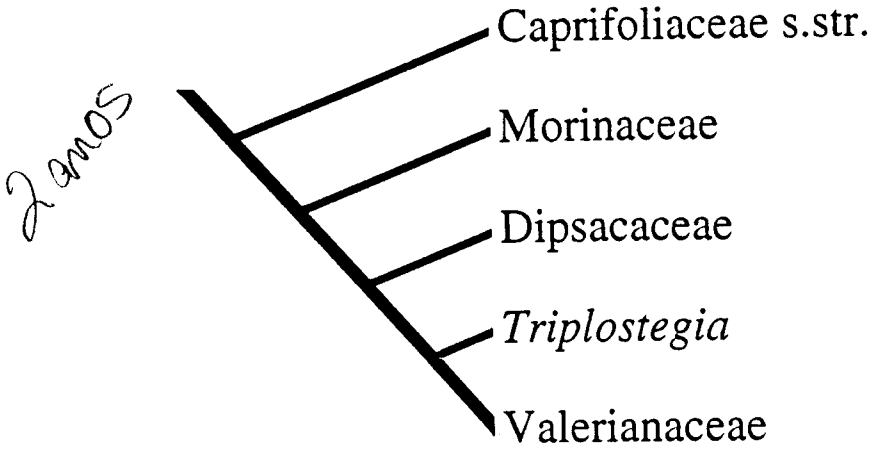

Fig. 3. Phylogenetic interrelationships of the families of the order *Dipsacales,* as indicated by cladistic analysis of morphological (Backlund & Donoghue, 1996) and *rbc*L sequence data (Backlund & Bremer, 1998).

Discussion

As noted above, the four families *Morinaceae, Dipsacaceae, Triplostegiaceae,* and *Valerianaceae* are all monophyletic units and may be retained without violating the primary principle of monophyly. Two of them, *Dipsacaceae* and *Valerianaceae,* are comparatively large and well-known groups. They have long been accepted as independent entities and there has never been any proposal to unite them into a single family (Donoghue & al., 1992 mentioned the possibility of uniting both with the *Caprifoliaceae*). Following the principle of maximising stability in classification, there is a strong case for maintaining *Dipsacaceae* and *Valerianaceae* as separate families. For the purpose of the following discussion, we consider this settled. We realise that this is a decision based on tradition and that arguments may be put forward to change this tradition. To our knowledge, however, there has been no proposal to this effect.

Given the reference phylogeny in Fig. 3, the mandatory use of the Linnaean category of family, and the decision to maintain *Dipsacaceae* and *Valerianaceae* as separate families, it follows that the *Morinaceae* must also be accepted as a separate family. They cannot be included in the *Dipsacaceae* or any other family without violating monophyly. The mandatory application of the Linnaean hierarchy and the independent status of the *Dipsacaceae* and *Valerianaceae* are nothing new in this context. The phylogenetic reconstruction is new, however, and should settle the long-standing debate about the status of the *Morinaceae*. This case illustrates how phylogenetic inference based on cladistic analysis can promote stability in classification.

The status of the *Triplostegiaceae* is not as easily resolved. One of the three alternatives in Fig. 2, viz. inclusion in the *Dipsacaceae,* is excluded, but retention as a separate family and inclusion in the *Valerianaceae* are both possible without violating monophyly. There is no stability in classification to be preserved with either alternative, as Fig. 2 demonstrates. We would argue, however, that monogeneric families like the *Triplostegiaceae* should be reduced in order to increase the phylogenetic information content of the system. "Monotypic" taxa do not provide any information about the relationships of the immediately subordinate taxon, in this case the single genus *Triplostegia*. Consequently, it seems appropriate to avoid "monotypic" taxa. Put another way, this approach minimises redundancy in classification.

It should be noted that it is only possible to eliminate the monogeneric family *Triplostegiaceae* because *Triplostegia* is the sister group of a single family, *Valerianaceae*. If the positions of *Triplostegia* and *Dipsacaceae* were reversed in the phylogeny (Fig. 3), *Triplostegia* would be the sister group of a clade comprising two families and it would not be possible within a Linnaean classification, and following the principle of monophyly, to avoid the use of a monogeneric family for this genus.

The relationship of *Triplostegia* to the *Valerianaceae* is best shown by its inclusion in that family. Alternative ways of expressing this information in a classification, such as the introduction of another taxon, for example a suborder of the *Dipsacales* comprising two families, *Triplostegiaceae* and *Valerianaceae,* are in our opinion less useful. Names at additional levels of the standard Linnaean hierarchy, such as a suborder in between the standard categories of order and family, tend to be ignored. We believe that important phylogenetic information is best conveyed by names at the commonly used ranks of genus, family, order, etc.

Let us suppose that the *Triplostegiaceae* did contain more than one genus. That situation would raise the question of whether the familial classification should inform us about the mutual relationships of those genera by recognising a family *Triplostegiaceae*, or inform us about the mutual relationships of a larger set of genera, including those of the *Valerianaceae*, by including the *Triplostegiaceae* in the *Valerianaceae*. The ranks available within the Linnaean hierarchy can convey only a portion of the phylogenetic information available, and there are no clear criteria for deciding which portion. In this situation, other principles of classification, as outlined below, may be decisive.

Let us also suppose that the monogeneric family *Triplostegiaceae* was widely and consistently known (perhaps commercially) under that name, so that its inclusion in the *Valerianaceae*, in order to increase phylogenetic information, would come into conflict with stability in classification (a consideration that is even more pertinent at the generic level). Such a situation would force us to choose between preserving stability and increasing information, and would raise questions concerning other principles of classification and their relative importance.

One other possible principle of classification is that of maximising support for monophyly. Given a particular phylogeny, and alternatives for taxonomic recognition of particular groups in that phylogeny, for example as families, the groups that are best supported as monophyletic should be preferred for a formal classification. This approach is intimately related both to the primary principle of monophyly and the secondary principle of stability in classification, because naming groups that are well supported as monophyletic reduces the danger that future research will reveal that those groups are not monophyletic, leading to changes and instability.

Yet another principle of classification may be worth expressing: that of maximising ease of identification. A classification comprising easily recognised taxa is naturally to be preferred to one containing taxa identifiable only by characters which are difficult to observe and which require, for example, anatomical dissection or the use of a microscope to be checked. We are not saying that paraphyletic taxa should be accepted simply because they can be easily identified. Maximising ease of identification is of course secondary to the principle of monophyly. However, given a particular phylogeny and alternatives for taxonomic recognition of particular clades in that phylogeny, those clades that are most easily identified should be preferred for a formal classification.

Summarising these various alternatives results in the following principles of classification:

1. Primary principle of monophyly;
2. Secondary principles of
   – maximising stability;
   – maximising phylogenetic information (= minimising redundancy);
   – maximising support for monophyly;
   – maximising ease of identification.

We have listed the secondary principles simply in the order in which they are discussed above. Their relative importance may be vastly different in different groups. With respect to the classification of *Triplostegia*, for example, the principles of maximising stability, support for monophyly, and ease of identification are much less relevant than maximising phylogenetic information. There is no stability to preserve

(Fig. 2), and the *Valerianaceae* are roughly equally well supported as monophyletic and equally identifiable whether or not *Triplostegia* is included.

The cases of the *Morinaceae* and *Triplostegiaceae* demonstrate both the utility and the limitations of the principle of monophyly in resolving controversial questions of classification. The *Morinaceae* are to be maintained, following the principle of monophyly. The *Triplostegiaceae* are better reduced, following the subordinate principle of maximising phylogenetic information. Applying clear principles in this way reduces idiosyncrasy and arbitrariness in classification.

The principles of classification listed above are also applicable within a non-Linnaean nomenclatural system. For example, in choosing between alternative definitions of names (cf. De Queiroz, 1994; Bryant, 1996), we note that widely used names could be defined so that they convey substantial phylogenetic information and are tied to well supported and easily identifiable clades.

Acknowledgements

We thank Birgitta Bremer, Paul Kenrick, Tim McDowell, Bengt Sennblad, Ulf Swenson, and Mats Thulin for constructive criticism and discussion. Michael Donoghue, Kevin De Queiroz, and one anonymous reviewer provided much constructive criticism of an earlier manuscript version. The study was supported by a Swedish Natural Science Research Council grant for *Asteridae* evolution.

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