X. A WEBSITE FOR ALL ANGIOSPERM FAMILIES – http://www.mobot.org/mobot/research/apweb/

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Currently both those teaching and those learning about phylogenies face a variety of problems. There are several systems to chose from, yet there is no explicitly phylogenetic system (in the sense of recognizing only strictly monophyletic groups) where all those groups are described. Conventional family descriptions are long, and present a formidable challenge to somebody trying to learn about the family.

This website attempts to deal with such problems. It is a web-based treatment of all flowering plant families and orders that very largely follows the Angiosperm Phylogeny Group (APG) system (APG, 1998, 2002). It contains characterizations of all plant families, some infrafamilial groups, and most of the well-supported nodes above the level of family including those formally recognized as orders. The characterizations consist of hierarchically organized information (see below), and are linked to trees. Associated material consists of a brief discussion of the characters used, indexes of familial and ordinal names, and a bibliography, as well as links to photographs, lists of genera, and other sites.

Systems like those of Cronquist (1981), Takhtajan (1997), and Thorne (1999, 2000) are comprehensive, although the latter is unaccompanied by descriptions, yet all are evolutionary sensu Mayr & Ashlock (1991) in that they recognize paraphyletic groups, and this is particularly true the higher up the hierarchy one goes.

The Angiosperm Phylogeny Group (1998, 2002) is attempting to stabilize the circumscriptions of monophyletic groups at the family level and above, and their names. The APG system is a consensus system based on a conservative, that is, well-supported phylogeny of the Angiosperms; a number of systematists have expressed opinions as to the taxa that should be recognized that are reflected in the make-up of the system. As to the criteria for recognizing taxa, monophyly is essential, but not sufficient, for a group to be named. In addition, individual named taxa should not be too small (monotypic) or too large. In the first case, the name is essentially redundant, in the second, it can be difficult to remember the included groups. After all, the user has to memorize quite a lot, and successful systems in the past have taken the size and number of taxa into account.

Stability should be the result of stable hypotheses of phylogeny; if the phylogeny remains the same, names should not change. This is a principle long recognized by systematists of a variety of philosophies; if relationships do not change, the names should not (Van Steenis, 1978). The phylogenetic tree of angiosperms is (so far!) remarkably stable.

Any tree can support many different classifications. But is there any point in arguing that a family with two monophyletic subfamilies, should be split into two families, or two families we know are related combined? Recent work may have shown that two subfamilies are more different than had been thought, or that there are more features that link a pair of families known to be sister taxa. Well enough, but this does not mean we have to change names.

CHARACTERS AND TREES

No matter how well-supported a molecular tree is, most of us want more. Although it seems that the APG system and the trees on which it is based yield a stable framework, these trees are almost entirely based on analysis of molecular data. There are certainly no combined morphological-molecular analyses of all flowering plant families with the morphological features displayed on the tree. So how do we deal with morphology in the broad sense, including anatomy, chemistry, chromosome numbers, etc.?

If the phylogenetic tree of angiosperms had been produced from morphological data, a tree on which only apomorphies were displayed would be the simplest way of conveying this information. A goal of 'natural' classifications for at least 400 years has been what we can call 'economy of description': a character of a higher-level group is not repeated in the descriptions of lower-level groups, or, in modern parlance, a synapomorphy of an order is not repeated in the descriptions of the families included in that order. How do we attain this goal if the tree is produced by the analysis of DNA sequences?

The starting point for producing the characterizations in /APweb/ consisted of descriptions drawn up for all possibly monophyletic families. These descriptions were then placed on a tree, and characters common to all members of a particular branch were removed from the descriptions and placed on the node subtending the branch. Features such as cotyledon number and presence of double fertilization could be placed straight on the tree, although the position of others, apparently equally unambiguous, such as the presence of triploid endosperm, have since had to be slightly adjusted.

All this is very straightforward in principle, but much more difficult in practice. There are five main problems that I will simply list here.

1. Inappropriate delimitation of character states.
2. Missing data.
3. Variation of a character within the terminals.
4. Lack of resolution of the tree.
5. Optimization of the states or variation on the tree.

The combined effect of such problems made the use of 'characterization' rather than 'apomorphy' seem preferable. However, it is likely that the character states at many of the internal nodes are indeed apomorphies, and when using the trees, we can treat them as such – but always with caution.

NAVIGATION AND INTERPRETATION OF THE SITE

The trees, with their direct links to the characterizations, are the heart of /APweb/. These trees are conservative, and some idea is given on how well supported each branch is. It is possible to move from any node and all the terminals of the main ordinal tree to the relevant point in the characterizations, and back again, and from trees of individual orders to a particular point within the order, or from lists of families at the beginning of each order, from the lists of accepted orders in the sidebar on the main page, or the synonymy lists of orders and families, directly to the appropriate place in the system. Most families and even some orders are accompanied by a brief summary of features that may help you to confirm that a plant you think belongs to a family does in fact belong.

The characterizations of the terminals – family, subfamily, etc. – are often relatively brief and are not written so as to be comparable. Conventional descriptions of such taxa, although much longer and largely comparable, in fact consist mostly of plesiomorphies. In /APweb/, some of these will be within the order and can be established from the ordinal tree. Others will be of nodes below the order, and these are always listed before the characterization of each order. When all the characters are considered in this hierarchical context, it will be found that the information for each family is indeed quite extensive and roughly comparable, it is simply that the information is at several hierarchical levels. Note that I do not expect that all or even most of the features in the characterizations of the terminals to turn out to be apomorphies for the terminals.

When reading characterizations, a side-bar allows the user to move directly to a brief discussion of characters. Few of the references are directly linked to the Reference page, desirable although that might be. For most families, there are links to photographs. There are estimates of the numbers of genera and species in the family, with the larger genera and the number of species they contain mentioned individually. There is also a list of the names of included genera, although these are not up-to-date. Ideally, of course, such lists should be both authoritative and current.

CHANGES AND THE WEB

The basic topology of the angiosperm phylogenetic tree has changed little over the last decade or more, the study by Chase and collaborators (Chase et al., 1993) in particular setting the scene for subsequent work. However, the polychotomies are getting smaller and fewer as more and different genes are sequenced and analyzed. Basically, change has meant that the resolution of the tree is improving, not that everything is moving around. Poorly supported nodes have not been very stable, some are losing what support they had (Saxifragales near Rosids), while others are maintaining or increasing their support (Dilleniales as sister to Caryophyllales). There are still several poorly-known genera which, although assigned to traditional families, may well find a phylogenetic resting place elsewhere.

Conventional books with family descriptions and relationships are out-of-date before they are published. However, it is a fairly easy task to update the site. It takes Hilary Davis, who has been responsible for getting /APweb/ up and running, about an hour to draw a completely resolved tree with 12 terminals, make the links to the family and order lists, etc., and to put the tree online. Papers that have new morphological information can usually be integrated more quickly, since what often has to be done is to adjust the position of a character on a tree and add the reference. Corrections are also readily made. The net result is that anybody with access to the internet can know about the most recent work on the phylogeny of angiosperms – and they can also let Hilary Davis (at hilary.davis@mobot.org) or myself know about additions they would like or mistakes they have found.

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Nepenthaceae, the Asian Pitcher Plant family, consists of a single genus, *Nepenthes*. It is restricted to SE Asia, apart from outliers in Madagascar, the Seychelles, Sri Lanka, India, Indochina, China, New Caledonia and Australia. Of the c. 87 species, 80 (83 including 3 notho-species) are found in SE Asia.

All the species, so far as is known, are carnivorous. Usually insects, but on occasion larger animals such as birds or rats, are attracted, trapped, drowned and digested in the leaf pitchers. The pitchers vary enormously in shape, size and colour and provide the main means for identifying species.

Nepenthes are usually lianas of montane forest, particularly ridge-tops in the cloud zone. The most widespread species however, occur in lowland secondary forest. Several species are shrubs, either terrestrial or epiphytic.

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