Who's related to whom? Recent results from molecular systematic studies

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Similarities among model systems can lead to generalizations about plants, but understanding the differences requires systematic data. Molecular phylogenetic analyses produce results similar to traditional classifications in the grasses (Poaceae), and relationships among the cereal crops are quite clear. Chloroplast-based phylogenies for the Solanaceae show that tomato is best considered as a species of *Solanum*, closely related to potatoes. Traditional classifications in the Brassicaceae are misleading with regard to true phylogenetic relationships and data are only now beginning to clarify the situation. Molecular data are also being used to revise our view of relationships among flowering plant families. Phylogenetic data are critical for interpreting hypotheses of the evolution of development.

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http://biomednet.com/elecref/1369526600100149

Abbreviation
ITS internal transcribed spacer

Introduction

The study of model organisms is generally justified on the grounds that the results will be applicable to all organisms. Testing this assumption requires comparative studies. When laboratory models are compared across kingdoms or phyla, the similarities are taken as fundamental aspects of life. This approach is obviously powerful; it is the source of most of what we know about proteins, cell biology, and genetic structure and function. Such comparison also represents higher-level systematics: the commonalities among kingdoms are the shared derived characters (synapomorphies, in phylogenetic jargon) of life. This broad comparison can easily be performed within kingdoms as well. If a result from *Arabidopsis* is assumed to be common to all plants, then it is simple to compare it to another dicot (e.g. snapdragon or tomato) or to a monocot (e.g. maize) [1,2••]. This too is implicit use of phylogenetic data.

The limitations of the model system approach become obvious when there are differences between plants. Organisms and their characteristics evolve, leading to shared similarities that vary across a near-infinite number of hierarchical levels. This is particularly true as more and more molecular geneticists concern themselves with mechanisms of development, and move closer to the systematist's question — why are there so many different kinds of organisms? Studies of the evolution of development demand that the investigator go beyond the model system and learn the pattern of variation in its relatives [3•]. This requires a reasonable assessment of the relatives' identity.

Knowledge of plant relationships has increased rapidly in the past decade, reflecting partly the development of molecular systematics. It has been known for some time that plant classifications do not reflect phylogeny accurately, even though both phylogeny and classification are hierarchical. The hierarchy of classification was imposed in the late 18th century, well before ideas of descent with modification (evolution) were prevalent [4]. These pre-evolutionary groups were then re-interpreted in an evolutionary context, and were assumed to be products of evolution, rather than man-made artefacts. Thus, every named group represents an historic assumption of relationship that may or may not be accurate but these assumptions can now be tested. Data are accumulating that show, in some cases, historically recognized groups are indeed phylogenetically linked (monophyletic), and other 'groups' are quite miscellaneous and made up of unrelated elements (polyphyletic). In addition, taxa whose placement have been ambiguous can frequently now be placed.

Molecular systematics proceeds by firstly sequencing a gene from multiple organisms, secondly aligning the sequences, and thirdly by constructing a phylogenetic tree from the sequences. There are many methods that can be used to produce the tree; one of the most common is the so-called 'parsimony method,' which assumes that the best inference of evolutionary history is the one that requires postulating the fewest mutations (i.e., the shortest tree). The underlying principle is that scientists prefer explanations that best fit their data. Given the shortest tree, it is often desirable to assess how much evidence there is for particular groups. This too can be done in various ways; one commonly used quasistatistical method is bootstrap analysis. The nucleotide positions in the alignment are sampled randomly with replacement to generate a new 'sequence' and this is analyzed to produce a phylogenetic tree; the randomization procedure is repeated many times and the support for a particular group can be estimated as the percentage of randomised trees in which it occurs. Bootstrap values vary between 0 (no support for a particular group) and 100% (a group well supported by the data).

The phylogeny of sequences from multiple organisms is just that — a phylogeny of sequences, a tree of genes.

Phylogeneticists commonly assume that the phylogeny of sequences is a good approximation of the phylogeny of organisms. There are many cases when this may not be true, however. For example, if introgression occurs, then genes may find themselves in a nucleus different from the one in which they evolved. Similarly, chloroplasts, which are maternally inherited in most plants, may be transferred among species, so that a chloroplast may now share a cell with a nucleus quite different from the nucleus with which it had been associated historically. Such chloroplast transfer can be detected by comparison with the phylogeny of a nuclear gene.

In this review, I focus on the major plant model systems—*Arabidopsis thaliana*, *Antirrhinum majus* (snapdragon), *Lycopersicon esculentum* (=*Solanum lycopersicum*; tomato), *Zea mays* (maize), and *Oryza sativa* (rice)—beginning with recent studies that identify their near relatives. I then comment briefly on progress in determining the 'big picture' of flowering plant evolution. I have highlighted particular studies that use multiple gene and genome comparisons to track the history of organisms. This tests the assumption that all pieces of DNA have similar histories. I have also focused on studies that include large numbers of taxa as these avoid errors associated with biased sampling of species.

Maize, rice and the grass family

Of all plant model organisms, the grasses (Poaceae or Gramineae) are the best understood phylogenetically. There are now seven published molecular phylogenies: five representing markers from the chloroplast [5–12], and two using nuclear markers [13•,14]. These phylogenies are strikingly congruent as can be seen in Figure 1 (see also [15••]). The lack of resolution in relationships among Bambusoideae, Oryzoideae, and Pooideae reflects strongly supported differences among the various gene trees, but this is almost certainly due to sampling problems in some data sets; some gene trees (e.g. the chloroplast-encoded gene for subunit F of NADH dehydrogenase [*ndh*F] and phytochrome B [*phy*B] [11,13•]) indicate that these three subfamilies form a single clade. This phylogeny shows that the panicoid grasses—maize, sugar cane, sorghum, pearl millet—are more closely related to finger millet than they are to rice. Furthermore, if the *phy*B and *ndh*F phylogenies are accurate, the small grains—wheat, barley, rye, and oats, in the Pooideae—are more closely related to rice than they are to maize.

Even at lower taxonomic levels, phylogenies of different genes all indicate the same relationships. Within the subfamily Pooideae, for example, there are four molecular phylogenies, all of which are congruent (Figure 2). This group was identified as monophyletic by cladistic studies of morphology [16], but several genera or small tribes, including the Stipeae, were sometimes placed with the pooids [17] and sometimes in other subfamilies [18]. Two of the molecular studies are based on chloroplast DNA—restriction site polymorphisms [7] and sequences of *ndh*F [19•]—and, as expected, give the same phylogeny because the chloroplast does not recombine and thus has a single history. The other two are based on nuclear genes encoding ITS [20], and phytochrome B ([13•]; SY Mathews, RC Tsai, EA Kellogg, unpublished data). These also support the placement of Stipeae. As all data from both nuclear and chloroplast genomes suggest the same relationships, the gene trees are probably good estimates of the organismal phylogeny.

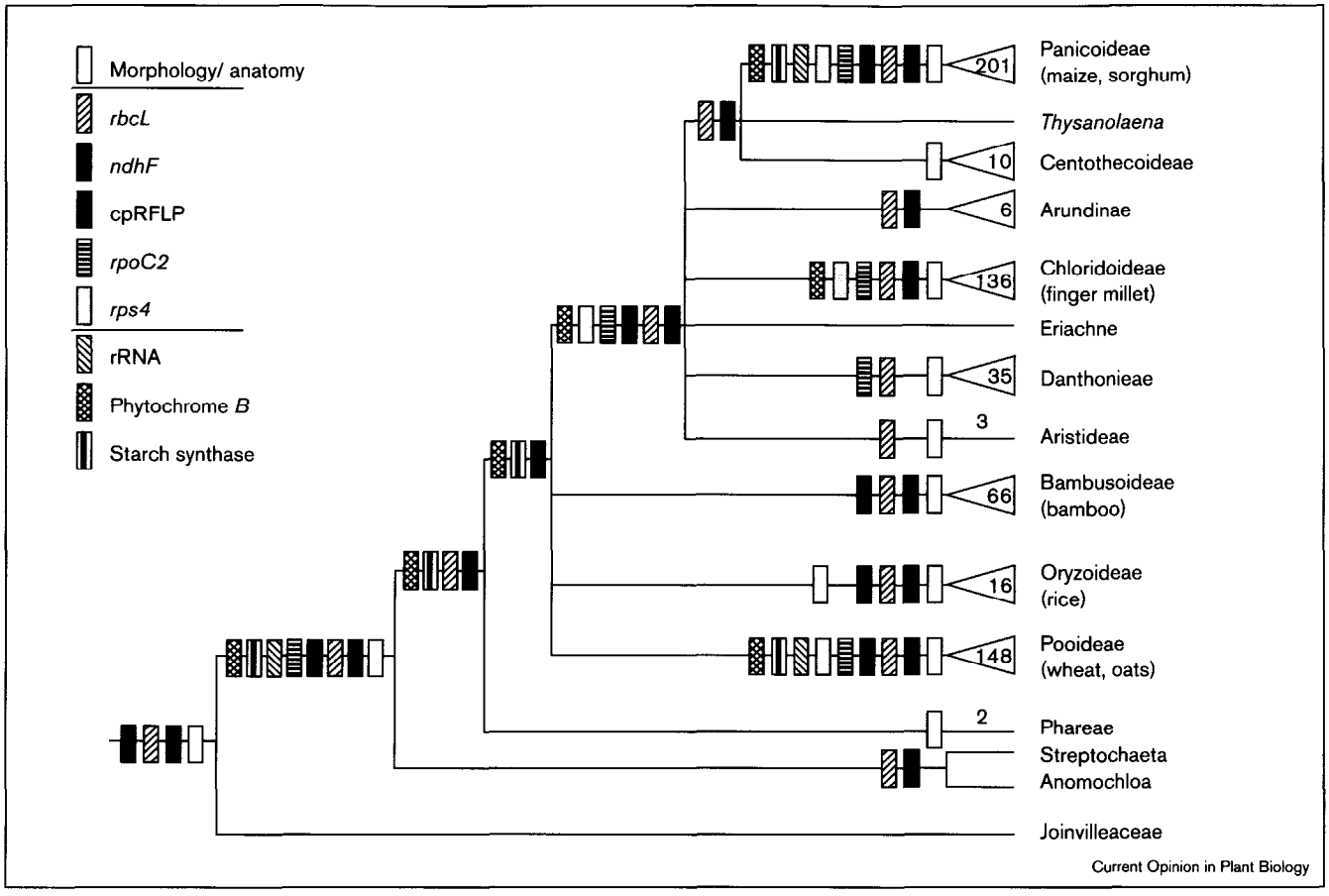
Within the pooid tribe Triticeae, the general congruence among gene trees is lost. This is a cytogenetically complex group, containing 17 intersterile diploid genera from which a number of allopolyploids are derived. For the diploid genera, we have five molecular phylogenies. The two chloroplast phylogenies, based on restriction site polymorphisms [21•] and sequences of the gene encoding RNA polymerase subunit A (*rpoA*) [22•], suggest the same history. The three nuclear gene trees, however, are significantly different, both from each other and from the chloroplast phylogeny ([23••,24••]; Figure 3). The explanation for this is not clear, but may involve a history of rare gene flow among the genera, perhaps across different ploidal levels. The important point is that each gene has a distinct history, indicating that the organismic history is complex and reticulate and is better diagrammed as a network than as a tree. This might have been expected for a group of interfertile species or subspecies, but not for a group of intersterile genera.

Tomato and snapdragon

Tomato, generally classified as *Lycopersicon esculentum*, is a member of the family Solanaceae; next to the grasses, this is the group for which we have the most comprehensive picture of relationships ([25•,26••,27••]; Figure 4). Note, however, that virtually all gene trees to date are based on chloroplast markers. We, therefore, make an assumption that the organismal phylogeny is tracked accurately by this single genome.

The traditional genus *Lycopersicon* clearly represents a single lineage of seven species. It has been known for some time that *Lycopersicon* was closely related to the genus *Solanum* which, in its traditional circumscription, includes potatoes (*S. tuberosum*) and eggplant (*S. melongena*) as well as ~1400 other species. These are apportioned for convenience into seven subgenera each of which is in turn divided into sections [28,29]. *Lycopersicon* is most closely related to section *Petota*, subgenus *Potatoe* [26••,27••,30], which includes the familiar grocery store potato, as well as many other tuber-bearing species. As *Lycopersicon* is derived from within *Solanum* and does not represent a separate evolutionary line, its genetic relationships are more accurately reflected if it is considered a species of *Solanum* (*S. lycopersicum*) rather than an independent genus. If the name *Lycopersicon* were retained, it would imply that it is quite distinct from all other species of

Figure 1



Summary (combinable component analysis) of phylogenetic data on the grass family. Extant taxa are listed on the right of the diagram; points at which lines attach indicate hypothetical ancestors. Triangles indicate large groups and numbers refer to number of genera in the group. Joinvilleaceae is the sister family of the grasses; all other taxa are members of the Poaceae. If more than one line attaches to a particular ancestor it indicates that we do not know the order in which the lineages formed. For example, some evidence [11,13•] suggests that there was a single branch that later divided into Bambusoideae, Oryzoideae and Pooideae, but this is not yet well supported, so the relationship is drawn to indicate that we do not know the order in which the three lineages formed. The diagram synthesizes data from morphology [16,83,84]; *rbcL* [5,8,9]; *ndhF* [11]; chloroplast restriction sites [7]; *rpoC2* [6,10]; *rps4* [12]; rRNA [14]; phytochrome B ([13]; SY Mathews, RC Tsai, EA Kellogg, unpublished data). If a group is found in a particular gene phylogeny, and is not strongly contradicted by any other gene phylogeny, an appropriately patterned rectangle is placed below the common ancestor of the group. For example, both *ndhF* and phytochrome B sequences link *Streptochaeta* and *Anomochloa*, as indicated by the two rectangles just below the pair of genera; no other gene has been sequenced for both genera. Reprinted with permission from [15••].

Solanum, whereas it is in fact more closely related to some members of *Solanum* than to others.

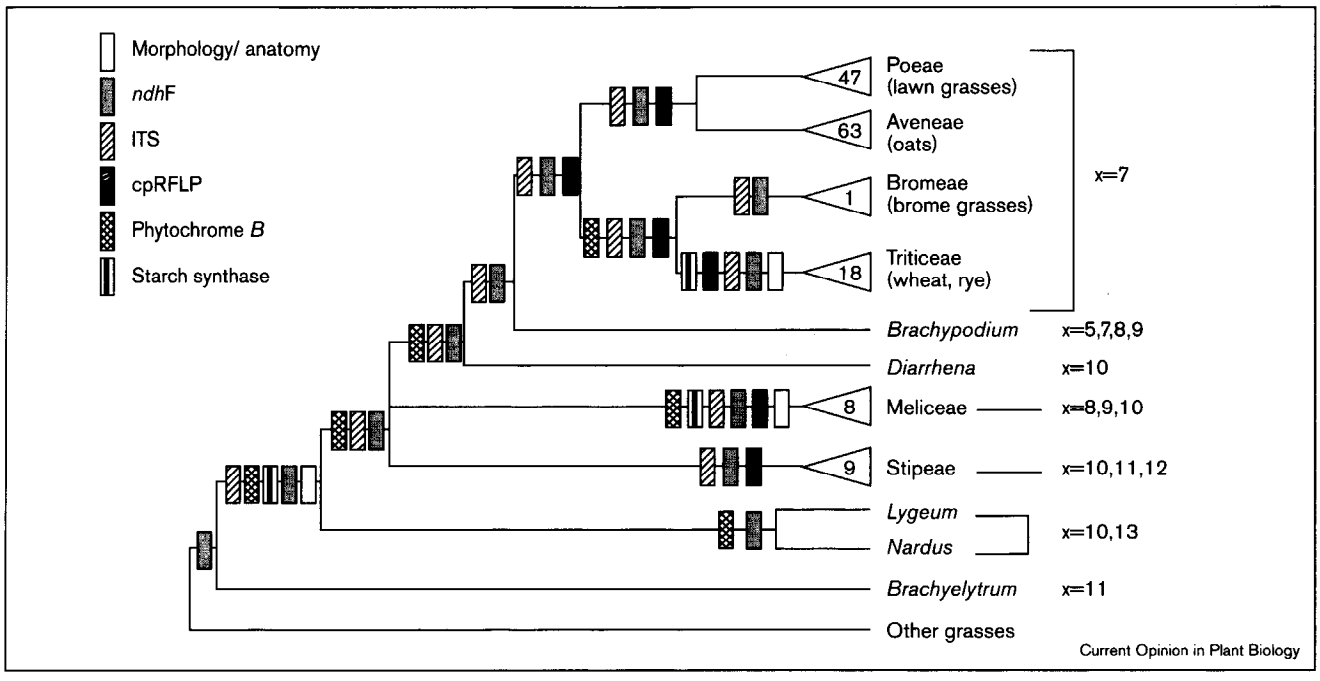
The phylogeny of Solanaceae has obvious implications for the evolution of form. To consider a single example, many species of *Solanum* have compound leaves, as do species of *Schizanthus*, whereas other members of the family have simple leaves. The degree of leaf compounding in sect. *Lycopersicum* is known to be affected by homeobox genes such as *Let6* [31•]. Changes in the regulation of this gene may thus have been involved in the changes leading to the origin of compound leaves in the ancestor of *Solanum*. The phylogeny shows that leaf compounding in *Schizanthus* originated independently; it is, therefore, necessary to test whether it is genetically and developmentally the same.

The Solanaceae is the sister family to the Convolvulaceae (morning glory family) and these, in turn, are closely related to the large group of families including the Lamiaceae (mints) and Scrophulariaceae (snapdragon family) [32,33•]. Both Lamiaceae and Scrophulariaceae are polyphyletic. Scrophulariaceae can be divided into two unrelated groups, one of which contains the genus *Scrophularia* (and thus must be called Scrophulariaceae) and the other of which contains *Antirrhinum*, *Digitalis* (foxglove), and *Veronica* (speedwell) [32].

Arabidopsis

Arabidopsis thaliana is a member of the mustard family (Brassicaceae), a group for which there remains remarkably little phylogenetic information. This is in part because

Figure 2



Summary (combinable component analysis) of phylogenetic data on the grass subfamily Pooideae. An appropriately shaded rectangle marks any clade supported by particular sets of data and not strongly contradicted by any other set of data. Triangles indicate large clades and numbers refer to the number of genera. The overlapping triangles for Poeae and Aveneae indicate that tribal boundaries are unclear. Base chromosome numbers (x) for each clade are shown to the right of the diagram. Sources of data are as follows: morphological data [16,84]; *ndh*F [19•]; ITS [20]; chloroplast restriction sites [7]; phytochrome B ([13•]; SY Mathews, RC Tsai, EA Kellogg unpublished data); granule-bound starch synthase [65].

the existing classification of Brassicaceae, based largely on fruit structure, is proving to be a poor indicator of relationship. In other words, generic and tribal names do not indicate anything about evolutionary history. (An analogous situation in modern society would be if children were not given the family name of either parent but rather a name pulled at random from the 'phone book). Preliminary data from *rbc*L [34]—the gene encoding the large subunit of the photosynthetic enzyme Ribulose-1,5-bisphosphate carboxylase/oxygenase (RuBisCo)—indicate that species in the genus *Arabidopsis* are not closely related to *A. thaliana* and, conversely, that the closest relatives of *A. thaliana* are in the genera *Cardaminopsis* and *Arabis*.

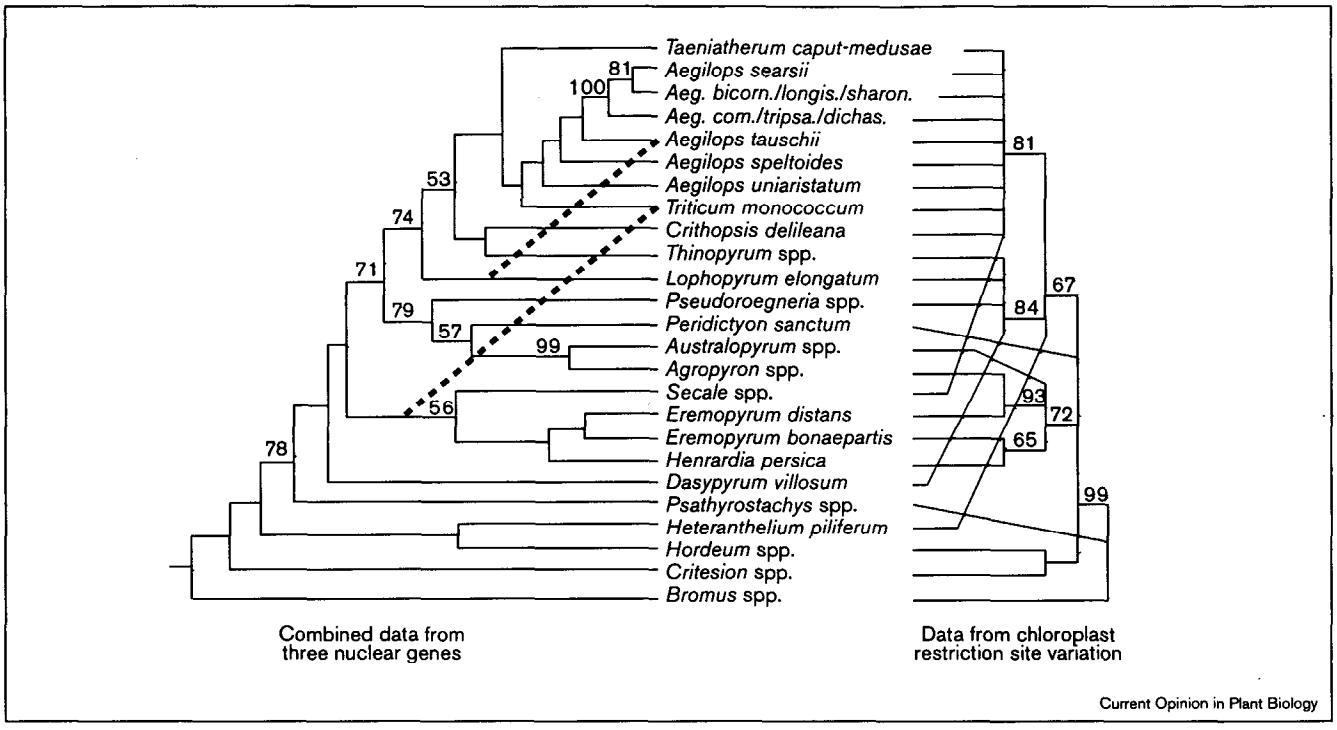
This proposal was recently corroborated by sequences of the nuclear ITS which verified the allopolyploid *Arabidopsis suecica* as being the offspring of *A. thaliana* and most likely *Cardaminopsis arenosa*, or possibly *C. neglecta* [35•]. *C. petraea* is also closely related to *A. thaliana* and *A. suecica* but is not involved in the allopolyploidization event. ITS sequences also verify the substantial evolutionary distance between *A. thaliana* and other species currently classified in *Arabidopsis*.

Molecular data have led to a new classification of *Arabidopsis*, which places *Arabis lyrata* and all species formerly known as *Cardaminopsis* into *Arabidopsis* [36•]. 49 other species, formerly called *Arabidopsis*, are excluded from the genus, with several of them already placed elsewhere (e.g. [37–39]). Molecular phylogenies for a newly circumscribed genus *Arabidopsis* are forthcoming (RA Price, S O'Kane, personal communication).

The one tribe of Brassicaceae that does appear to be monophyletic is Brassiceae [34]. Restriction site data have been used to reconstruct the history of the chloroplast genome in Brassiceae [40••]. If the history of the chloroplast mirrors the history of the organism, then the genus *Brassica* is polyphyletic, with the species *B. oleracea* (cabbage, brussels sprouts, broccoli, etc.) and several other *Brassica* species closely related to the genus *Diplotaxis*, whereas radish (*Raphanus sativus*) is related to *B. barrelieri* and *B. oxyrrhina*.

The Brassicaceae is a member of the glucosinolate clade of angiosperms (see below), members of which produce mustard oils in specialized myrosinase cells. Data from both *rbc*L [41] and from 18S rRNA indicate the same relationships among these families [42], confirming, among other things, that Brassicaceae is sister to or derived from within the Capparaceae (capers), as had long been suspected by morphological systematists.

Figure 3



Evolutionary relationships in the grass tribe Triticeae. Relationships identified on the basis of three nuclear genes are shown on the left, and relationships identified on the basis of the chloroplast genome are on the right. Crossed lines indicate that there are many differences between the chloroplast and nuclear gene phylogenies. The differences among the various sources of phylogenetic data may indicate a history of introgression. Dotted lines indicate well-supported differences among the nuclear genes. Numbers above branches indicate bootstrap support values. Redrawn from [23••].

Relationships among flowering plants

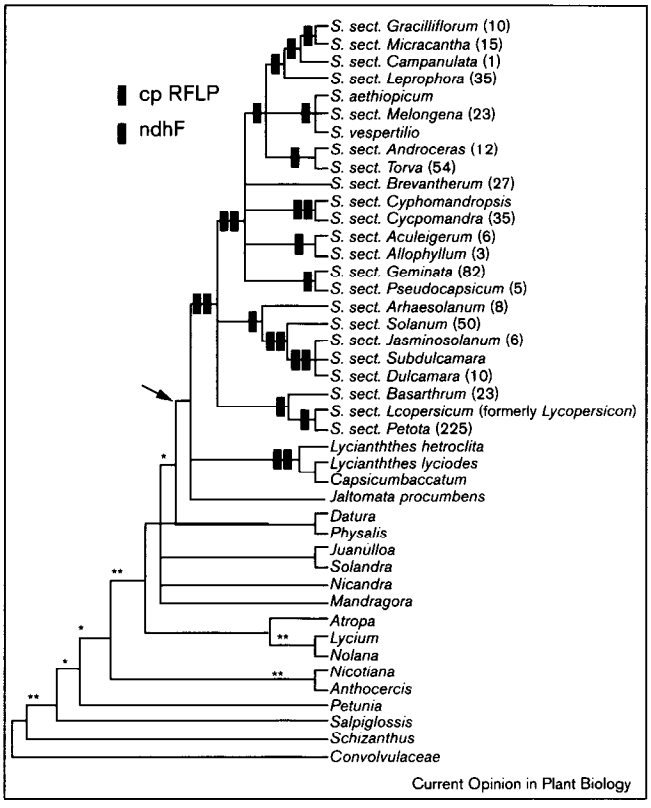
Systematists have grappled for a long time with the relationships among flowering plant families [43–47]. The system of Cronquist [47] is perhaps the most familiar to American botanists, and has the advantage of being comprehensive. It is not at all phylogenetic, however, and many relationships are ambiguous. Molecular systematic data have now overturned many of the proposed higher-level (ordinal and superordinal) groups.

Many plant systematists were involved in a community-wide effort to generate a large database of sequences of *rbc*L, the gene encoding the large subunit of the photosynthetic enzyme ribulose-1,5-bisphosphate carboxylase/oxygenase (RuBisCO). This led to a phylogeny for all seed plants, using 499 *rbc*L sequences [48]. As the authors observed, the results should be interpreted with caution. The published trees turned out not to be the shortest available [49•], and a few of the sequences proved to be pseudogenes [50•]. Nonetheless, the *rbc*L phylogeny is taken as the starting point for many current research projects.

Another large co-operative effort, analogous to that used for *rbc*L, has recently generated a large database of sequences for the small subunit of nuclear ribosomal RNA (18S rRNA; [51••]). This study helps test some of the tentative conclusions of the original *rbc*L study. In broad outline, phylogenies of the two genes find similar groups among angiosperms. Additional data have been generated for the gene *atp*B (a chloroplast gene encoding the subunit B of ATP synthase), and these data have been combined with those from *rbc*L and 18S rRNA [52••,53••]. From the combination of these data sets, a number of robust conclusions emerge.

Many aspects of the *rbc*L, 18S, and *atp*B trees support ideas that had already been formed on the basis of morphology. For example, the Caryophillidae—the group including spinach, beets, cacti, and campion—are monophyletic. The Asteridae, a group that includes many of the plants with fused petals—such as *Antirrhinum*, *Petunia*, *Nicotiana*, and *Solanum*—are also monophyletic. The groups that Cronquist [47] called the Rosidae and the Dilleniidae are largely intermingled, as had been suspected. The well-known family pairs (e.g. Asclepiadaceae/Apocynaceae, Araliaceae/Umbelliferae, Labiatae/Verbenaceae [54]) are supported as being close relatives by molecular data: Asclepiadaceae are derived from within Apocynaceae; Araliaceae and Umbelliferae may be sisters; and Labiatae and Verbenaceae are polyphyletic. Families such as Saxifragaceae (saxifrages, gooseberries,

Figure 4



Phylogenetic relationships in Solanaceae. The diagram was produced by grafting the *ndh*F [26••] and chloroplast restriction site (cpRFLP; [27••]) histories (above the arrow) to a chloroplast history inferred from a combination of three genes ([85]; below the arrow). Above the arrow, an appropriately shaded rectangle marks any clade supported by one set of data and not strongly contradicted by the other. Below the arrow, clades with bootstrap support greater than 90% in the combined phylogeny are indicated by two asterisks; clades with 80–90% support are indicated by a single asterisk.

and hydrangeas) and Caprifoliaceae (honeysuckles) appear polyphyletic, as had also been suspected. The eudicot clade, first identified in morphological studies [55] as including all taxa with tricoplate (three-grooved) pollen, is supported as monophyletic, as are the monocots.

In other cases, the molecular data support relationships that previously appeared ambiguous. For example, the Ericaceae (health family, including rhododendron, blueberries, and cranberries) were placed by 19th century botanists with other fused-petal families (the Sympetalae [56] or Gamopetalae [57]), but systematists of the 20th century thought the groups were unrelated [43–47]. The *rbc*L, 18S, and *atp*B data support the placement of an Ericalean clade in a larger clade with the Asteridae, reuniting much (but not all) of the Englerian Sympetalae. As another example, Juglandaceae (walnuts) are clearly placed with Betulaceae and Fagaceae (birches and oaks, respectively), despite Cronquist's suggestion [47] that the two groups might be unrelated.

Finally, there are a few cases in which the molecular data suggest something that is quite surprising and entirely unexpected. The polyphyly of the Scrophulariaceae was noted above. Another striking example is the fact that the nine families with nitrogen-fixing members fall into a single large clade, along with only ten families that are not nitrogen-fixing [58]. As the nitrogen-fixing families had previously appeared to be completely unrelated, this is unusual and suggests that these families may have more in common than was formerly believed.

The congruence among the 18S, *rbc*L, and *atp*B phylogenies has made it clear that the existing systems of classification [43–47] need to be replaced. In particular, the relationships among families need to be rearranged to reflect the phylogenetic history, some families need to be dismembered, and others reconstituted. Our picture of the evolution of flowering plants is still coming into focus and further changes will undoubtedly be necessary. Fortunately, the technology of the World Wide Web has permitted the construction of Web Sites that provide classifications [59] and descriptions of families and orders (PF Stevens, unpublished data). These place extensive morphological data in the phylogenetic framework provided by molecular studies.

Do gene trees indicate species trees?

With the exception of the grass phylogenies, most molecular systematic studies focus on either chloroplast genes or nuclear ribosomal DNA. In general, they indicate similar relationships among organisms, suggesting that, indeed, the gene chosen does not matter much. For very large data sets (hundreds of taxa), however, more base pairs are needed to identify each branching event [53,60•]. Work on low copy number genes is in its infancy in plant molecular systematics, and no nuclear gene has yet been used across enough groups to provide a clear comparison with chloroplast or ribosomal data. Other nuclear genes that are good candidates for phylogeny reconstruction are the phytochrome genes [13•,61], the small heat-shock proteins [62•], alcohol dehydrogenase (Adh) [63•,64•], granule-bound starch synthase [65], and phosphoglucoisomerase [66•]. In all cases, the history of the gene may or may not be a faithful reflection of the history of the cell in which it resides. Functional constraints, natural selection, and random genetic drift, can under certain circumstances, cause the phylogeny of the gene to differ from that of other genes in the same nucleus or cell. Only by comparison of multiple genes will we be able to discern the history of the organisms that bear them.

Among closely related species or genera, many studies find discrepancies among different gene histories, even if plants are apparently intersterile. The case of the Triticeae [23••,24••] may be the most striking example of this at present, although we have more data on this than on any other similar group so we don't really know how typical it is. If this pattern of discordance is at all general, however, it suggests that any single gene tree may be

quite misleading about the history of organisms. It is not uncommon to find that the history of the chloroplast differs from that of the nucleus in one or more taxa [67–70,71••]. Few studies incorporate sequence data on more than one nuclear marker, however; a notable exception is the study of relationships among species of peony, in which genes for *Adh*1 estimated relationships similar to those from ITS and the chloroplast gene *mat*K [64•]; *Adh2* gene trees, however, had a significantly different history.

Phylogeny and genome evolution

Phylogenies will be critical to the interpretation of the burgeoning data on genome structure and size, because only with a phylogeny is it possible to determine the direction and frequency of change. In a standard genetic study, it is easy to keep track of which plants are mutant and which are wild-type, but over evolutionary time the only way to know which are the 'mutants' (i.e. derived) is to have a phylogeny. For example, with the grass phylogeny shown in Figure 1, it is possible to infer that there exists some mechanism for replacing the centromeric region of one chromosome with an entirely different chromosome and its centromere, such that two ancestral chromosomes are combined by inserting one into the other [15••]. A phylogeny can also be used to show that changes in genome size are frequent, even among groups such as the grasses in which genome structure is largely conserved [15••,72•].

Bharathan used phylogenetic data to study correlates of genome size with reproductive characteristics of monocots [73••]. She found four to nine independent transitions to large genomes (which she defined as those with more than 9.025 pg DNA per 1C nucleus) and up to five reversions to small genomes. She found no strong association between genome size and the presence of nuclear endosperm or the presence of simultaneous microsporogenesis, but did find that genomes were significantly larger in families with bisporic or tetrasporic embryo sacs. Her study relied extensively on available molecular phylogenies, and indeed would not have been possible without them.

Conclusions

As a consequence of space limitation, this review cannot incorporate the many methodological advances that have led to the data cited above. Computational advances have made it possible to analyze data sets that are an order of magnitude larger than was possible a decade ago (e.g. [49•,74••]). It is also increasingly possible to assess support for the data sets [74••,75]. This is critical as assessment of support is necessary for accurate comparison of gene trees [24••,71••]. There has also been much discussion of the relationship between gene trees and species trees [76•,77•] and the methods of incorporating information from different gene trees [24••,71••,78–82].

Relationships among major groups of grasses are now known with some precision, although the history is complex in the Triticeae (which includes wheat, barley and rye). Rapid progress is occurring on relationships within Solanaceae and other sympetalous families, although we must still assume that the chloroplast phylogeny is an accurate reflection of the organismal phylogeny. Understanding of the phylogeny of Brassicaceae lags behind that of other groups. This is partly because the morphological classification is so radically different from the molecular phylogeny that it is impossible to use any one species as a place-holder for a genus or tribe, as can be done in the grasses or Solanaceae; each species must be re-evaluated individually. Finally, our understanding of angiosperm relationships is being revolutionized by molecular data. It is too early to know what new insights will come from these data but they are likely to be profound.

We can now envisage a time in the near future when robust phylogenies will have been constructed for many angiosperm groups. This will permit an entirely new discipline — let us call it "evolutionary genetics" — to test the generality of the model systems, and use comparative data to understand the genetic basis of diversification.

Acknowledgement

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References and recommended reading

Papers of particular interest, published within the annual period of review, have been highlighted as:

- • of special interest
- •• of outstanding interest

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2. •• Meyerowitz EM: **Plants and the logic of development.** *Genetics* 1997, **145**:5-9.
This succinct essay explores current knowledge of plant development and compares it to animal development. In general, the basic cellular machinery is quite similar between the kingdoms. Although the same classes of developmental regulatory proteins are found in both animals and plants, their functions are analogous rather than homologous. Cell–cell and cell–environment communication are substantially different for plants.

3. • Baum DA: **The evolution of plant development.** *Curr Opin Plant Biol* 1998, **1**:79-86.
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13. • Mathews S, Sharrock RA: **The phytochrome gene family in grasses (Poaceae): a phylogeny and evidence that grasses have a subset of the loci found in dicot angiosperms.** *Mol Biol Evol* 1996, **13**:1141-1150.

The grasses have only three phytochrome loci (*A*, *B*, and *C*), in contrast to five in dicots. Sequences of these three loci for a set of phylogenetically disparate grasses indicate that the genes may be useful indicators of phylogenetic relationship, which are similar to those inferred from chloroplast genes.

14. Hamby RK, Zimmer EA: **Ribosomal RNA sequences for inferring phylogeny within the grass family (Poaceae).** *Plant Syst Evol* 1988, **160**:29-37.

15. •• Kellogg EA: **Relationships of cereal crops and other grasses.** *Proc Natl Acad Sci USA* 1998, in press.

Phylogenetic relationships among grasses are becoming increasingly well understood. Changes in genomic arrangement can be mapped onto the phylogeny, which permits inferences about the structure of the ancestral grass genome. The phylogeny also shows that genome size has decreased in several lineages, including rice, whereas it has increased substantially in the tribe Triticeae.

16. Kellogg EA, Campbell CS: **Phylogenetic analysis of the Gramineae.** In *Grass Systematics and Evolution*. Edited by Soderstrom TR, Hilu KW, Campbell CS, Barkworth ME. Washington, DC: Smithsonian Institution Press; 1987:310-322.

17. Clayton WD, Renvoize SA: **Genera graminum.** Kew Bulletin Additional Series XIII. 1986, London: Her Majesty's Stationery Office. 389.

18. Watson L, Dallwitz MJ: **The grass genera of the world.** Wallingford: CAB International; 1992.

19. • Catalan P, Kellogg EA, Olmstead RG: **Phylogeny of Poaceae subfamily Pooideae based on chloroplast *ndh*F gene sequencing.** *Mol Phylog Evol* 1997, **8**:150-166.

Sequences of a portion of the chloroplast gene *ndh*F show that the core Pooideae – tribes Bromeae, Triticeae, Aveneae, and Poeae – form a clade. *Brachypodium* is sister to the core pooids, contradicting existing classifications, but supporting recent molecular phylogenetic data. The earliest diverging branches of the pooid clade, in order of divergence, are *Brachyelytrum*, *Lygeum* and *Phaenosperma*; these three genera had been difficult to place using morphological data.

20. Hsiao C, Chatterton NJ, Asay KH, Jensen KB: **Molecular phylogeny of the Pooideae (Poaceae) based on nuclear rDNA (ITS) sequences.** *Theor Appl Genet* 1995, **90**:389-398.

21. • Mason-Gamer RJ, Kellogg EA: **Chloroplast DNA analysis of the monogenomic Triticeae: phylogenetic implications and genome-specific markers.** In *Methods of Genome Analysis in Plants*. Edited by Jauhar P Boca Raton: CRC Press; 1996:301-325.

Restriction site maps of the chloroplast genome of the diploid Triticeae indicate that *Triticum* and *Aegilops* form a clade. Each genus, which corresponds to a genomic group, is monophyletic. Diagnostic restriction site markers are provided for each chloroplast. These should be useful for tracking cytoplasmic genomes in breeding programs.

22. • Petersen G, Seberg O: **Phylogenetic analysis of the Triticeae (Poaceae) based on *rpo*A sequence data.** *Mol Phylog Evol* 1997, **7**:217-230.

Sequences for *rpo*A from the diploid Triticeae produced a phylogeny generally congruent with that produced by restriction sites [21•]. Genera (genomic groups) are monophyletic. The amount of sequence variation in this region of the chloroplast was quite low (68 total variable nucleotides and seven insertion/deletion mutations among 31 species).

23. •• Kellogg EA, Appels R, Mason-Gamer RJ: **When genes tell different stories: the diploid genera of Triticeae (Gramineae).** *Syst Bot* 1996, **21**:321-347.

Different portions of the genome of diploid Triticeae have distinct histories. The 5S RNA array on chromosome 1 has a history different from that on chromosome 5. Both are different from the chloroplast genome of the same plant. ITS sequences on chromosomes 1 and 5 appear to have undergone concerted evolution. The history of the group is best diagrammed as a net, rather than as a tree. This is unprecedented for a group of intersterile genera.

24. •• Mason-Gamer RJ, Kellogg EA: **Testing for phylogenetic conflict among molecular data sets in the tribe Triticeae.** *Syst Biol* 1996, **45**:524-545.

Gene trees for the diploid Triticeae are compared statistically to determine if they are significantly different. Several tests were applied, all leading to the conclusion that the gene trees available for the Triticeae reflect significantly different histories.

25. • Castillo RO, Spooner DM: **Phylogenetic relationships of wild potatoes, *Solanum* series *Conicibaccata* (Sect. *Petota*).** *Syst Bot* 1997, **22**:45-83.

Accessions from throughout the range of series *Conicibaccata* were studied for morphological and chloroplast restriction site variation. Although the series is currently thought to include 40 named species, the chloroplast data suggest that this may be an overestimate and the actual number may be closer to eight. This affects naming and classification of wild germplasm, as well as studies of evolution in the genus *Solanum*.

26. •• Bohs L, Olmstead RG: **Phylogenetic relationships in *Solanum* (Solanaceae) based on *ndh*F sequences.** *Syst Bot* 1997, **22**:5-17.

Sequences of *ndh*F show that the chloroplasts of *Solanum* species are monophyletic. *Capsicum* (green and red pepper) is derived from within *Lycianthes*. Four of the subgenera of *Solanum* are polyphyletic. *Lycopersicon* (tomato) and *Cyphomandra* (tree tomato) are derived from within *Solanum*. Spines and stellate hairs have evolved more than once in the genus.

27. •• Olmstead RG, Palmer JD: **Implications for the phylogeny, classification, and biogeography of *Solanum* from cpDNA restriction site variation.** *Syst Bot* 1997, **22**:19-29.

Restriction site variation in the chloroplast DNA produces a phylogeny of *Solanum* largely congruent with that produced by *ndh*F sequences [26••]. The genus *Solanum* apparently originated in the New World, and then subsequently spread to the Old World and Australia.

28. D'Arcy WG: **The Solanaceae since 1976, with a review of its biogeography.** In *Solanaceae III: Taxonomy, Chemistry, Evolution*. Edited by Hawkes JG, Lester RN, Nee M, Estrada-R. N. Richmond, Kew: Royal Botanic Gardens; 1991:75-137.

29. D'Arcy WG: **Solanaceae studies II: typification of subdivisions of *Solanum*.** *Ann Missouri Bot Gard* 1972, **59**:262-278.

30. Olmstead RG, Sweere JA: **Combining data in phylogenetic systematics: an empirical approach using three molecular data sets in the Solanaceae.** *Syst Biol* 1994, **43**:467-481.

31. • Chen J-J, Janssen B-J, Williams A, Sinha N: **A gene fusion at a homeobox locus: alterations in leaf shape and implications for morphological evolution.** *Plant Cell* 1997, **9**:1289-1304.

A fusion of a phosphofructokinase gene with a *knotted*-class homeobox gene leads to the dominant mutation, *Mouse ears* in tomato. The homeobox gene, *Let6*, is overexpressed in the gene fusion, leading to increased leaf compounding. This sort of mutation may have led to the origin of novel phenotypes in evolution.

32. Olmstead RG, Reeves PA: **Polyphyletic origin of the Scrophulariaceae: evidence from *rbc*L and *ndh*F sequences.** *Ann Missouri Bot Gard* 1995, **82**:176-193.

33. • Wagstaff SJ, Olmstead RG: **Phylogeny of Labiatae and Verbenaceae inferred from *rbc*L sequences.** *Syst Bot* 1997, **21**:165-179.

The mint family (Labiatae) and verbena family (Verbenaceae) have long been known to be close relatives. This study shows that their evolutionary history is intertwined; neither family is monophyletic. They are part of a large clade that also includes Scrophulariaceae (itself polyphyletic), Bignoniaceae, Acanthaceae, and Gesneriaceae, as well as several other families. If this chloroplast phylogeny is indeed an accurate reflection of the organismic phylogeny, several characteristics of the gynoecium and of the fruit have evolved in parallel.

34. Price RA, Palmer JD, Al-Shehbaz IA: **Systematic relationships of *Arabidopsis*: a molecular and morphological perspective.** In *Arabidopsis*. Edited by Meyerowitz EM, Somerville CR. Plainview NY: Cold Spring Harbor Laboratory Press; 1994:7-19.

35. • O'Kane SL, Schaal BA, Al-Shehbaz IA: **The origins of *Arabidopsis suecica* (Brassicaceae) as indicated by nuclear rDNA sequences.** *Syst Bot* 1996, **21**:559-566.

Arabidopsis suecica has been thought to be an allopolyploid, formed by the cross of *A. thaliana* with *Cardaminopsis arenosa*. This study shows that *A.*

suecica has two ITS sequences, one from *A. thaliana* and the other from either *C. arenosa* or *C. neglecta*. Biogeography points to *C. arenosa* as being the parent, rather than *C. neglecta*. Sequences of other putative relatives of *Arabidopsis* showed that they were more distantly related.

36. • O'Kane SL, Al-Shehbaz IA: **A synopsis of *Arabidopsis* (Brassicaceae).** *Novon* 1997, **7**:323-327.

The genus *Arabidopsis* is redefined to include nine species and five subspecies. Most of these had previously been in the genus *Cardaminopsis*, although two had been in *Arabis*. The remaining names in *Arabidopsis* are excluded from the genus and have been or will be placed elsewhere. The taxonomic realignment is based on unpublished molecular phylogenetic data.

37. Al-Shehbaz IA: ***Erysimum hedgeanum* (Brassicaceae), a new name replacing *Arabidopsis erysimoides*.** *Novon* 1994, **4**:1-2.

38. Al-Shehbaz IA, O'Kane SL: **Placement of *Arabidopsis parvula* in *Thellungiella* (Brassicaceae).** *Novon* 1995, **5**:309-310.

39. Al-Shehbaz IA, O'Kane SL: ***Arabidopsis gamosepala* and *A. tuemurnica* belong to *Neotorularia* (Brassicaceae).** *Novon* 1997, **7**:93-94.

40. •• Warwick SI, Black LD: **Phylogenetic implications of chloroplast DNA restriction site variation in subtribes Raphaninae and Cakilinae (Brassicaceae, tribe Brassiceae).** *Can J Bot* 1997, **75**:960-973.

This study of two subtribes of the monophyletic tribe Brassiceae is the most comprehensive phylogeny for any portion of Brassicaceae. This follows several other papers by the same authors investigating chloroplast restriction site polymorphisms in other subtribes. The analysis shows that subtribe Cakilinae is monophyletic, but Raphaninae is polyphyletic. A lineage that the authors call RAPA-OLERACEA includes *Raphanus*, many economically important species of *Brassica*, and three other genera.

41. Rodman JE, Karol KG, Price RA, Sytsma KJ: **Molecules, morphology, and Dahlgren's expanded order Capparales.** *Syst Bot* 1996, **21**:289-307.

42. Rodman J, Soltis P, Soltis D, Sytsma K, Karol K: **Plastid *rbcL* shouts and nuclear 18S-ribosomal DNA whispers, but the message is the same: Dahlgren cuts the mustard.** *Amer J Bot* 1997, **84(suppl)**:226.

43. Takhtajan AL: **Outline of the classification of flowering plants (Magnoliophyta).** *Bot Rev* 1980, **46**:225-359.

44. Takhtajan A: **Diversity and classification of flowering plants.** 1997, New York: Columbia University Press.

45. Thorne RF: **Classification and geography of the flowering plants.** *Bot Rev* 1981, **58**:225-348.

46. Dahlgren R: **General aspects of angiosperm evolution and macrosystematics.** *Nord J Bot* 1983, **3**:119-149.

47. Cronquist A: **An integrated system of classification of flowering plants.** 1981, New York: Columbia University Press.

48. Chase MW, Soltis DE, Olmstead RG, Morgan D, Les DH, Mishler BD, Duvall MR, Price RA, Hills HG, Qiu Y-L *et al.*: **Phylogenetics of seed plants: an analysis of nucleotide sequences from the plastid gene *rbcL*.** *Ann Missouri Bot Gard* 1993, **80**:528-580.

49. • Rice KA, Donoghue MJ, Olmstead. RG: **Analyzing large data sets: *rbcL* 500 revisited.** *Syst Biol* 1997, **46**:554-563.

Reanalysis of 499 *rbcL* sequences found marginally shorter trees than described by Chase *et al.* [48]. More importantly, this paper describes possible ways to sample large data sets so that the computational problem can be minimized. One solution may be to replace large clades with the sequences of their hypothetical ancestors.

50. • Kellogg EA, Juliano ND: **The structure and function of RuBisCO and their implications for systematic studies.** *Amer J Bot* 1997, **84**:413-428.

Extensive structural data on RuBisCO have been largely ignored by systematists. The protein is under considerable functional constraint, which limits the amount of variation possible in evolutionary time. Protein sequences indicate that some plants may have *rbcL* pseudogenes, and in others the protein may have altered kinetics.

51. •• Soltis DE, Soltis PS, Nickrent DL, Johnson LA, Hahn WJ, Hoot SB, Sweere JA, Kuzoff RK, Kron KA, Chase MW *et al.*: **Angiosperm phylogeny inferred from 18S ribosomal DNA sequences.** *Ann Missouri Bot Gard* 1997, **84**:1-49.

18S rRNA sequences were generated for 223 angiosperms. Phylogenetic analysis of these sequences gave results that were largely similar to those found in a previous study of *rbcL* [48]. The earliest flowering plants had monosulcate pollen. From this group arose the monocot clade and a clade of dicots with tricolpate (three-grooved) pollen (the eudicots).

52. •• Soltis DE, Hibsch-Jetter C, Soltis PS, Chase MW, Farris JS: **Molecular phylogenetic relationships among angiosperms: an overview based on *rbcL* and 18S rDNA sequences.** *J Plant Res* 1998, in press.

Information from a nuclear and a chloroplast gene (18S rRNA and *rbcL*, respectively) are combined to give a phylogeny of flowering plants. The increased amount of data gives stronger support to many groups. General results are similar to those found for each data set alone. In addition, two large clades – Asteridae and Rosidae – are supported as making up the eudicots.

53. •• Soltis DE, Soltis PS, Mort ME, Chase MW, Savolainen V, Hoot SB, Morton CM: **Inferring complex phylogenies using parsimony: an empirical approach using three large data sets for angiosperms.** *Syst Biol* 1998, **46**:in press.

Information from three genes – 18S rRNA, *rbcL* and *atpB* – give the most resolved picture yet for flowering plant relationships. This paper focuses on the effects of combining multiple genes. In general more is better, despite significant incongruence between the data sets. The ability of current computer programs to analyze very large data sets (200 taxa or more) is partly determined by the number of phylogenetically informative characters.

54. Judd WS, Sanders RW, Donoghue MJ: **Angiosperm family pairs: preliminary phylogenetic analyses.** *Harvard Pap Bot* 1994, **5**:1-51.

55. Donoghue MJ, Doyle JA: **Phylogenetic studies of seed plants and angiosperms based on morphological characters.** In *The Hierarchy of Life: Molecules and Morphology in Phylogenetic Analysis*. Edited by Fernholm B, Bremer K, Jörnvall H. Amsterdam: Elsevier Science Publishers; 1989:181-193.

56. Engler A, Prantl K: **Die natürlichen Pflanzen Familien Teil II, Abt. 11889 Teil IV,** 1890-1997, [Title translation: The Natural Plant Families] Leipzig: Wilhelm Engelmann.

57. Bentham G, Hooker JD: **Genera Plantarum, Vol. II.** 1873-1876, London: Reeve & Co.

58. Soltis DE, Soltis PS, Morgan DR, Swensen SM, Mullin BC, Dowd JM, Martin PG: **Chloroplast gene sequence data suggest a single origin of the predisposition for symbiotic nitrogen fixation in angiosperms.** *Proc Natl Acad Sci USA* 1995, **92**:2647-2651.

59. •• A database of phylogenetic knowledge on the World Wide Web URL: http//herbaria.harvard.edu/treebase/index.html

This is a prototype database that incorporates phylogenetic information on green plants. It can be searched by taxon or by author and will ultimately provide current information on relationships of many different plant groups.

60. • Hillis DM: **Inferring complex phylogenies.** *Nature* 1996, **383**:130.

Despite previous suggestions that very large data sets were intractable, simulations suggest that a dense sampling of taxa plus a large number of phylogenetically informative characters (>5000) permit resolution of large phylogenetic problems.

61. Mathews S, Sharrock RA, Lavin M: **Evolution of the phytochrome gene family and its utility for phylogenetic analyses of angiosperms.** *Ann Missouri Bot Gard* 1995, **82**:296-321.

62. • Waters ER, Lee GJ, Vierling E: **Evolution, structure and function of the small heat shock proteins in plants.** *J Exp Bot* 1996, **47**:325-338.

Small heat-shock proteins fall into distinct gene families, corresponding to cytosolic, endoplasmic reticulum, and organellar proteins. The duplications leading to the different families occurred before the origin of angiosperms (>150 million years ago).

63. • Morton BR, Gaut B, Clegg M: **Evolution of alcohol dehydrogenase genes in the palm and grass families.** *Proc Natl Acad Sci USA* 1996, **93**:11735-11739.

Three *Adh* genes were cloned from a palm (*Washingtonia robusta*) and were compared to *Adh* gene sequences from grasses. Independent duplication events occurred in the two families. The history of *Adh* genes is a dynamic process of duplication and loss.

64. • Sang T, Donoghue MJ, Zhang D: **Evolution of alcohol dehydrogenase genes in peonies (*Paeonia*): phylogenetic relationships of putative nonhybrid species.** *Mol Biol Evol* 1997, **14**:994-1007.

*Adh*1 produced a phylogeny similar to that produced by another nuclear marker (ITS) and a chloroplast gene (*mat*K) in species of *Paeonia*, but significantly different from the phylogeny indicated by *Adh*2. This is one of the few phylogenetic applications of low-copy number nuclear gene sequences in plants.

65. Mason-Gamer RJ, Kellogg EA: **Potential utility of the nuclear gene *waxy* for plant phylogenetic analysis.** *Amer J Bot* 1996, **83(suppl)**:178.

66. • Gottlieb LD, Ford VS: **Phylogenetic relationships among the sections of *Clarkia* (Onagraceae) inferred from the nucleotide sequences of PgiC.** *Syst Bot* 1996, **21**:45-62.

A duplication in the gene for cytosolic phosphoglucoisomerase (*PgiC*) precedes the origin of the genus *Clarkia* (Onagraceae). All species investigated appear to retain both gene copies, although one copy is silenced in some and has become a pseudogene. The gene is used to infer relationships among species of *Clarkia*. Gene silencing has occurred at least four different times in *Pgi*C2.

67. Rieseberg LH, Soltis DE: **Phylogenetic consequences of cytoplasmic gene flow in plants.** *Evol Trends Pl* 1991, **5**:65-84.

68. Wendel JF, Stewart JM, Rettig JH: **Molecular evidence for homoploid reticulate evolution in Australian species of *Gossypium*.** *Evolution* 1991, **45**:694-711.

69. Wendel JF, Schnabel A, Seelanan T: **An unusual ribosomal DNA sequence from *Gossypium gossypioides* reveals ancient, cryptic, intergenomic introgression.** *Mol Phylo Evol* 1995, 4:298-313.

70. Soltis DE, Kuzoff RK: **Discordance between nuclear and chloroplast phylogenies in the *Heuchera* group (Saxifragaceae).** *Evolution* 1995, **49**:727-742.

71. •• Seelanen T, Schnabel A, Wendel JF: **Congruence and consensus in the cotton tribe (Malvaceae).** *Syst Bot* 1997, **22**:259-290.
Commercial cotton (*Gossypium hirsutum*) is an allotetraploid with genomes designated A and D. Its diploid progenitors are an A-genome cotton of Africa (*G. herbaceum*) and a D-genome cotton of South and Central America (*G. raimondii*). Among the genera of the tribe Gossypieae, nuclear (ITS) and chloroplast (*ndh*F) markers indicate the same relationships. Within *Gossypium*, however, the chloroplast and ITS sequences have significantly different histories. Some of this can be attributed to known or suspected hybridization, leading to allopolyploids, or hybrid diploids. Other discrepancies are harder to explain. The paper discusses in considerable detail the various explanations for apparent differences in gene trees, including the possibility of spurious differences caused by branching events occurring in rapid succession.

72. •• Bennetzen JL, Kellogg EA: **Do plants have a one-way ticket to genomic obesity?** *Plant cell* 1997, **9**:1509-1514.
The phylogeny of the grasses is used to investigate the possibility that genome size always tends to increase. The answer depends on assumptions about the likelihood of change, which in turn depends on knowledge of underlying mechanisms. If increase and decrease are assumed to be equally likely, then the small genomes of rice and sorghum are inferred to represent reductions from an ancestrally large genome. If, however, increase is assumed to be far more likely than decrease, then rice and sorghum may have retained the ancestral small genome.

73. •• Bharathan G: **Reproductive development and nuclear DNA content in angiosperms.** *Amer J Bot* 1996, **83**:440-451.
Phylogenies of monocotyledons are used to test whether genome size is correlated with several reproductive characters. Bisporic or tetrasporic embryo sacs often occur in families with large genomes; the correlation is not absolute, but is statistically significant. Bisporic and tetrasporic embryo sacs are characterised by a lack of synchrony between nuclear division and cytokinesis; the author suggests that asynchrony may be causally connected to large genome size, perhaps because of changes in the dynamics of tubulin or actin.

74. •• Swofford D: **PAUP 4.0d59, test version.** 1997, Sunderland: Sinauer Associates.
A remarkably flexible computer program with an excellent user-interface. This is the industry standard for phylogenetic studies. Without this program, few of the advances cited would have been possible.

75. Farris JS, Albert VA, Källersjö M, Lipscomb D, Kluge AG: **Parsimony jack-knifing outperforms neighbor-joining.** *Cladistics* 1996, **12**:99-124.

76. • Doyle JJ: **Trees within trees: genes and species, molecules and morphology.** *Syst Biol* 1997, **46**:537-553.
Just as the history of a species may be described by the history of multiple genes, the history of a gene may be described by multiple histories, some as small as a single nucleotide. The central problem in phylogeny reconstruction is reconciling differences among histories at different hierarchical levels. This is also a potential problem for phenotypic characteristics, which may have complex genetic and historical bases.

77. • Maddison WP: **Gene trees in species trees.** *Syst Biol* 1997, **46**:523-536.
Species trees are made up of gene trees, some of which may have the same topology, but some of which may be different. Several reasons are known for discrepancies between gene trees and species trees. Species trees can be viewed as a statistical distribution, or 'cloud', of gene histories.

78. DeQueiroz A, Donoghue MJ, Kim J: **Separate versus combined analysis of phylogenetic evidence.** *Annu Rev Ecol Syst* 1995, **26**:657-681.

79. Kluge AG: **A concern for evidence and a phylogenetic hypothesis of relationships among *Epicrates* (Boidae, Serpentes).** *Syst Zool* 1989, **38**:7-25.

80. Farris JS, Källersjö M, Kluge AG, Bult C: **Testing significance of incongruence.** *Cladistics* 1994, **10**:315-319.

81. Bull JJ, Huelsenbeck JP, Cunningham CW, Swofford DL, Waddell PJ: **Partitioning and combining data in phylogenetic analysis.** *Syst Biol* 1993, **42**:384-397.

82. Miyamoto MM, Fitch WM: **Testing species phylogenies and phylogenetic methods with congruence.** *Syst Biol* 1995, **44**:64-76.

83. Verboom GA, Linder HP, Barker NP:**Haustorial synergids: an important character in the systematics of danthonioid grasses (Arundinoideae: Poaceae)?** *Amer J Bot* 1994, **81**:1601-1610.

84. Kellogg EA, Watson L: **Phylogenetic studies of a large data set. 1. Bambusoideae, Andropogonodae, and Pooideae (Gramineae).** *Bot Rev* 1993, **59**:273-343.

85. Olmstead RG, Sweere JA: **Combining data in phylogenetic systematics: an empirical approach using three molecular data sets in the Solanaceae.** *Syst Biol* 1994, **43**:467-481.