Angiosperm Monophyly

In a recent article in *TREE*[1], V.A. Krassilov reaffirms his view that angiosperms originated several times from different gymnospermous lines. He implies that the conventional view that angiosperms are a monophyletic group is a 'conceptual bias' that has hampered understanding of their origin, and concludes that 'the long-neglected polyphyletic model is in the ascendant'. However, the monophyletic hypothesis is not an unexamined assumption, but rather a conclusion derived from a wide range of morphological, molecular and paleobotanical evidence. Based on the same evidence, the polyphyletic hypothesis is highly unparsimonious.

Morphological cladistic studies[2–4] list numerous derived features shared by angiosperms, including sieve tubes and companion cells, stamens with two pairs of sacs and an endothecial layer, closed carpels, lack of sporopollenin in the megaspore wall, a three-nuclear male gametophyte, an eight-nuclear female gametophyte and double fertilization leading to endosperm formation. Although there are exceptions, they are clearly related to the basic state and/or occur in taxa that are linked with other angiosperms by additional advances.

Krassilov attempts to cast doubt on these data by pointing to precursor conditions in various 'proangiosperms', concluding that 'not a single angiosperm character is unique to the group'. This, we submit, is simply mistaken. For example, he suggests that fusion of both sperm nuclei with female gametophyte nuclei in gnetophytes is homologous with double fertilization in angiosperms. While this may be true[5,6], the resulting formation of triploid endosperm tissue in angiosperms is unknown in other groups. Although Krassilov criticizes previous workers for confused morphological concepts, his own comparisons suffer from similar problems. For example, he states that *Caytonia* has 'cupule[s] ... [bearing] many anatropous ovules', but in fact the ovules of *Caytonia* are orthotropous and it is the cupules that are anatropous.

Recent molecular data also strongly support the monophyly of angiosperms. Studies of ribosomal-RNA sequences from a wide range of taxa[7,8] show that angiosperms are united by at least 25 shared advances (E. Zimmer, pers. commun.). Likewise, in analyses of the chloroplast gene *rbc*L, angiosperms form a well-supported clade (M. Chase and R. Olmstead, pers. commun.). The relevance of these analyses might be questioned because they do not include the fossil 'proangiosperms' discussed by Krassilov. However, they do include one living group that he links with some but not all angiosperms, the gnetophytes. His view would therefore require at least two changes in each of the characters that mark angiosperms as a whole.

Krassilov also claims that the Cretaceous fossil record supports polyphyly by showing that angiosperm lines with uniovulate and multiovulate carpels do not converge going back in time. However, this conflicts with analyses of the much-more-complete pollen and leaf records[9,10], which show progressive morphological divergence of angiosperms from the oldest types through time.

To explain multiple origins of angiosperm features, Krassilov speculates that filling of newly vacated ecological niches by some angiosperms promoted 'similar innovations in other preadapted lineages', while 'viral gene transfer mediated by fungi and bacteria' facilitated '"horizontal" spread of a new trait among coevolving lineages'. However, such exotic mechanisms need to be invoked only if one accepts the polyphyletic hypothesis, which has been tested and found unparsimonious. There are many genuinely unresolved issues in angiosperm evolution (e.g. whether the angiosperm tree is rooted near woody Magnoliales or among herbaceous Nymphaeales, Piperales and monocots[11]), but monophyly is not one of them.

Michael J. Donoghue

Dept of Ecology and Evolutionary Biology, University of Arizona, Tucson, AZ 85721, USA

James A. Doyle

Dept of Botany, University of California, Davis, CA 95616, USA

References

1 Krassilov, V.A. (1991) *Trends Ecol. Evol.* 6, 215–220
2 Crane, P.R. (1985) *Ann. Mo. Bot. Gard.* 72, 716–793
3 Dahlgren, R. and Bremer, K. (1985) *Cladistics* 1, 340–368
4 Doyle, J.A. and Donoghue, M.J. (1986) *Bot. Rev.* 52, 321–431
5 Donoghue, M.J. (1989) *Evolution* 43, 1137–1156
6 Freidman, W.E. (1990) *Am. J. Bot.* 77, 1582–1598
7 Zimmer, E.A., Hamby, R.K., Arnold, M.L., LeBlanc, D.A. and Theriot, E. (1989) in *The Hierarchy of Life* (Fernholm, B., Bremer, K. and Jornvall, H., eds), pp. 205–214, Elsevier
8 Hamby, R.K. and Zimmer, E.A. (1991) in *Molecular Systematics in Plants* (Soltis, P.S., Soltis, D.E. and Doyle, J.J., eds), pp. 50–91, Chapman & Hall
9 Doyle, J.A. (1977) in *Patterns of Evolution* (Hallam, A., ed.), pp. 501–546, Elsevier
10 Hickey, L.J. and Doyle, J.A. (1977) *Bot. Rev.* 43, 1–104
11 Donoghue, M.J. and Doyle, J.A. (1989) in *The Hierarchy of Life* (Fernholm, B., Bremer, K. and Jornvall, H., eds), pp. 181–193, Elsevier

A reply from Krassilov will appear in a subsequent issue. Ed.

Common Interest and Novel Evolutionary Units

In his stimulating article[1], Egbert G. Leigh mentions several cases when a higher-level unit is created by the forceful effect of common interest among the lower-level units. The emerging new units must be able to constrain the evolution of their constituent replicators. In particular, he refers to his model as one of genuine group selection, where he derived the conditions in which selection in one direction on a polygenic quantitative trait at the group level can successfully override selection in the opposite direction at the individual level[2].

While Leigh's model identifies general requirements, a more specific but still general model, showing the feasibility of coexistence of competing units within groups through selection at the group level, exists. The introduction of the stochastic corrector model[3,4] was triggered by Eigen's[5] paradox of prebiotic evolution: in the beginning, genes could not have been linked into long chromosomes, but while they remained unlinked they would compete and so the genome (as an ensemble of genes) would become disrupted. A protocell functions well if (1) the various genes contribute to its function as a whole; and (2) the replicative difference between the genes is diminished. It was shown that both features are favoured by selection for higher protocell growth rate, resulting in an efficient integration of genetic information (cf.