Chaos out of order in our new Floras?

Clive (C.A.) Stace ('Cringlee', Claybrooke Road, Ullesthorpe, Leicestershire
LE17 5AB, England; e-mail: stace@ullesthorpe.fsworld.co.uk)

Chaos uit orde in onze nieuwe Flora's?

In dit artikel worden de gevolgen van moleculaire gegevens en de daaruit voortkomende interpretaties in de vorm van nieuwe classificaties besproken vanuit het gezichtspunt van de Floraschrijver. Die is voor een bijzonder moeilijk dilemma komen te staan, omdat hij een balans moet zien te vinden tussen het harde bewijs van moleculaire evolutie en het maken van een gebruikersvriendelijke Flora voor een uiteenlopend publiek variërend van amateurs tot professionele botanici. De argumenten voor of tegen het implementeren van moleculaire classificaties in standaard Flora's worden tegen elkaar afgewogen, een afwegingsproces dat Ruud van der Meijden al had afgerond en waarin hij tot een ondubbelzinnige conclusie was gekomen. Daarnaast wordt de vorm van onze toekomstige Flora's bediscussieerd.

Chaos out of order in our new Floras?

The impact of molecular data and their interpretation in the form of new classifications are considered mainly from the point of view of the Flora-writer, who, to use a well-worn phrase, is left between a rock (the concrete evidence of molecular evolution) and a hard place (the provision of a user-friendly plant manual to a wide range of amateur and professional readers). The arguments for and against the adoption of molecular classifications in standard Floras, already considered and answered unequivocally by Ruud van der Meijden, are weighed, and the format of our future Floras is debated.

Introduction

The problem of which plant classification should be adopted in Floras covering any particular region has been addressed many times in the past, with very varied conclusions. Traditionally Floras used the current classification favoured in the region concerned, an obvious approach because until quite recently standard classifications changed rather infrequently, so there was the considerable advantage that comparisons between different Floras (including different editions of the same Flora) were made easily. For example, in Britain and its colonies the system of Bentham & Hooker was favoured, and in many Continental countries that of Engler & Prantl or its later version by Melchior was utilized. *Flora Europaea* (1964–1980)[1] and the first two editions (eds. 20–21) of *Heukels' Flora van Nederland* edited by Ruud van der Meijden (1983, 1990)[2] come into the latter category. A disadvantage of following an established system in a Flora produced over many years can be that by the time that the Flora is completed the classification has become outdated. *Flora Europaea*, and in more recent times *Flora Nordica* (2000–)[3], are notable examples. A more modern system that might have been adopted by these Floras is that of Cronquist (1981)[4], which was the choice of Ruud van der Meijden in ed. 22 of *Heukels' Flora van Nederland* (1996)[2] and of Stace in *New Flora of the British Isles* (1991, 1997)[5]. *Flora of Turkey* (1965–1985)[6] unusually saw fit to follow a system

that was already well antequated before it was commenced. The danger of adopting a new system is that it might prove be short-lived and not only remain unfamiliar but soon appear as outdated as the earlier systems.

Some notable Floras departed from this convention of using established systems where the authors felt strongly that something different was required. *Flora of the British Isles* (1952, 1962)[7], adopted a version of Bentham & Hooker modified in order "to try to bring it more into line with modern ideas", with "the doctrine of evolution in mind", while *Flore de France* (1973–1984)[8] followed Emberger's system, which, then uniquely, placed the monocotyledons within the dicotyledons but which has found little favour outside France. Most authors, however, have not used a novel or little-used classification, and probably most Flora-writers would in fact consider that an identification manual is not the place to introduce new and/or controversial classifications.

A completely different approach has been to order the taxa alphabetically, as in the Floras of Canada[9], North-West U.S.A.[10] and East Texas.[11] In the first two the families are arranged in systematic order, but the genera within them and the species within the genera are ordered alphabetically, whereas in the third even the families are arranged alphabetically, except that the monocots and dicots are treated as separate entities. A similarly artificial method, adopted in some manuals where the primary method of determination is the scanning of coloured illustrations, is to arrange the plants according to their flower colour, habitat or other extraneous information.

The decision now facing future Flora-writers is made difficult by the availability of a radically new and in many respects different classification based on DNA sequences. So far extremely few Floras have adopted this new molecular classification[12], but a notable example is ed. 23 of *Heukels' Flora van Nederland* (2005)[2], which was apparently the first.

Advantages and disadvantages of the APG system

It is generally agreed that an ideal system of classification should be 'natural', i.e. that more closely related taxa should be placed closer together than less closely related ones. The problem, and the scope for argument, lies in deciding how to assess the closeness of relationship. There are two main approaches, the phenetic and the phyletic. In the former case, prosecuted by the methodology of taxometrics, the number or proportion of features that taxa have in common is taken as a measure of their relationship. In the second case the evolutionary history of the taxa is deduced – the more recent is the common ancestor of a group of taxa the closer together they will be classified. Using such principles, the classification should be highly predictive. In my opinion predictivity is by far the best measure of a natural classification, and the best way of assessing the usefulness of a classification, or how 'good' it is.

Whether a natural classification is constructed from phenetic or phyletic methodologies, the same result should be obtained because it is expected and predicted that the more recent is a common ancestor of a taxon the more characters in common the constituents of that taxon should possess. The extreme difficulty in constructing a natural classification from phenetic or more traditional phyletic (deductive) principles

is one of the reasons for the great attractiveness of utilising DNA sequences, which are relatively easy to obtain and to analyse. There are actually many aspects of the methodology of both the gathering of DNA sequence data (especially which regions of the genome to sequence) and their cladistic analysis that are less than ideal[13] and could be discussed at some length, but these avenues are not to be explored here.

The widely accepted classification constructed using DNA sequences has been the result of a consensus within the 'Angiosperm Phylogeny Group' (APG).[12] It should theoretically closely resemble classifications resulting from the phenetic or phyletic analysis of phenotypic characters, and be equally 'natural'. Where they diverge significantly it is generally supposed that the phenotypic characters have misled us for some reason, and that the DNA sequence is a truer measure of relationships. Because of the functional nature of DNA it is difficult to argue with that supposition. It could theoretically be tested by assessing whether the DNA-derived system always grouped more similar taxa together (i.e. is always the more predictive system), but since we have no idea of the proportion of the tens of thousands of genes that differ between any two taxa, no such absolute test can be carried out. Hence we can only rely on the more obvious phenotypic characters, i.e. those that we use to distinguish taxa visually. Since *most* of the families traditionally recognised (e.g. in Cronquist's system) are circumscribed and arranged in the same way in the DNA-based APG system, it seems likely that the different methodologies are leading to the same thing. But there are many examples where the results of the two approaches diverge. In many, probably most, such cases one can, with hindsight, understand how morphological characters might have misled us. Additionally, in some groups, suggestions for a new classification closely resembling the molecular system had been proposed before the DNA data were available (e.g. in the petaloid monocots, in Caprifoliaceae, and in some parts of the Scrophulariaceae). But there are a number of cases where the DNA evidence points to completely new and unsuspected relationships.

Field botanists and Flora-writers will be happy to adopt new classifications where the circumscription of the new taxa can be seen and understood in morphological terms, but a reluctance will become evident where the new taxa are not recognisable. The genus *Orchis* is apparently no longer recognisable as an entity distinct from *Neotinia* or *Anacamptis*[14], and *Senecio* cannot be distinguished from its recent split *Jacobaea*[15], among other examples. Constructing a key to such genera is not possible, except by adopting keys where a genus is arrived at via several routes, effectively a combined genus-and-species key, as utilised by van der Meijden[2], leading to a corruption of the generic concept.

In the above two cases, the traditional concepts of the genera *Orchis* and *Senecio* have been shown to be polyphyletic, so despite the lack of distinguishing exomorphic characters one must assume that splitting them in order to abandon polyphyletic taxa will create more natural, i.e. more predictive, taxa. There are, however, many contentious situations where those taxonomists who wish to follow the strict tenets of cladistics ('strict' or 'extreme cladists') also advocate the abandonment of taxa that are shown to be paraphyletic. This can be done in one of two ways: by amalgamating the paraphyletic taxon with its splits to achieve a monophyletic taxon; or by

retaining the splits and further splitting the paraphyletic taxon into smaller mono-phyletic segregates. In Fig. 1 the first option would involve recognising ABCDE as a single taxon, and the second would involve recognising A, B, and CDE as three separate taxa. The former option is much more commonly adopted. This effectively creates the opposite dilemma to that described above (where a taxon is divided into two unrecognisable taxa), since here two or more well established and widely recognised taxa are amalgamated. In all these cases a communication problem is created, because, wherever the scope of an existing taxon is altered, the user needs to know whether a name is being used to cover the taxon *sensu stricto* or *sensu lato*.

The Flora-writers' dilemma

To what extent should the classification adopted and the sequence followed in an identification manual (Flora) reflect the most modern, i.e. strictly cladistic-molecular, classifications? This question has quite recently been debated by Diggs & Lipscomb[16] and solutions very clearly presented in relation to the *Illustrated Flora of East Texas*.[11] Their answers are not identical to mine, but the similarities by far outweigh the differences. It is argued here (and by Diggs & Lipscomb) that neither extreme (the radical application of every tenet of the strictest form of cladistics, or the conservative use of only phenotypically observable characters) should be followed, but that a pragmatic compromise be adopted. Incidentally, something close to the two extremes is exemplified by the most recent (adjacent) Floras of Belgium[17] and the Netherlands[2]! My compromise solution is as follows:

1. — Since a Flora is a didactic manual concerned with the similarities and differences between taxa, it is surely desirable that the plants should be set out in a natural systematic rather than an artificial sequence, i.e. that more closely related and similar taxa should be placed closer together. This allows convenient comparison of similar taxa. Hence I reject an alphabetical ordering of taxa. Apart from the fact that the alphabet often places unrelated taxa together, and separates closely related ones, name-changes, whether nomenclatural or taxonomic, would often move taxa far from their original position and bring the need for major reorganization. Hence the apparently user-friendly alphabetical sequence can have exactly the opposite effect in practice. The Flora-writer should grasp the nettle and present a biologically meaningful sequence.

2. — I believe that the classification used in Floras should continue to be the same as that in general use in systematic botany, as has traditionally been the case. There is no need for a modified, dumbed-down version especially tailored for use in Floras, but equally the system used should be transparent as well as scientifically accurate. This is effectively a call for a general-purpose classification to remain the goal of taxonomists. Special-purpose classifications still have their important roles in many fields, e.g. dendrology, horticulture, cladistics, but should be seen as just that and no more. I believe that attending to the requirements of the widest audience should be the goal of taxonomists (via general-purpose classifications) and Flora-writers alike. Any system that slavishly pursues one aim and set of principles, and

ignores all other criteria often to their detriment, is by definition a special-purpose rather than a general purpose classification. If the strict-cladistic classification of a particular taxon is not the most predictive available, then it is not fit for general purpose. But in the great majority of cases the expectation is that it will be.

3. — Any taxon unequivocally shown to be polyphyletic should be abandoned and split into its monophyletic constituents. In most cases this presents no problems and will be readily adopted, even in some instances reviving abandoned or minority opinions, e.g. the (re-)splitting of *Nasturtium* and *Rorippa*, of *Ranunculus* and *Ficaria*, or of *Centunculus* and *Anagallis*. In other cases, such as *Orchis* and *Senecio* mentioned previously, real difficulties arise because of the lack of exomorphic diagnostic features. This poses a challenge to the Flora-writer to find visible characters, or failing that to key and present the taxa in a user-friendly manner.

4. — Taxonomic changes indicated by new data or analyses (not only molecular-cladistic) should be adopted in a somewhat conservative manner. In other words, they should only be adopted when the evidence becomes unequivocal. There is little more annoying, or confusing, or liable to generate negative publicity, than for a change to be adopted and then later reversed due to counter-evidence or altered rules or opinions. The example of *Chrysanthemum/Dendranthema/Chrysanthemum* comes to mind, a classic case of taxonomists shooting themselves in the foot. The transient popularity of the genus *Seriphidium* is another glaring example. The amalgamation of *Coeloglossum* with *Dactylorhiza*[14] has been effected on the grounds that the former is nested within the latter, which becomes paraphyletic without *Coeloglossum*, but a more recent analysis[18] has suggested that it is sister to *Dactylorhiza*, which therefore remains monophyletic with or without *Coeloglossum*. In such a case, where addition of the very distinctive *Coeloglossum* changes the circumscription of *Dactylorhiza* considerably, it seems better to retain the traditional classification until the actual relationships are finally clarified.

When the evidence equally supports two or more classifications, one traditional and the other(s) novel, I suggest that the traditional classification should be preferred. The traditional classification of the Apiales separates Apiaceae and Araliaceae, with *Hydrocotyle* included in the former. According to the DNA sequence data this is not sustainable, *Hydrocotyle* falling in the Araliaceae clade but basal within it.[19] Therefore three other possibilities offer themselves: amalgamation of Apiaceae and Araliaceae; maintaining them as separate families, but with *Hydrocotyle* in Araliaceae; maintaining them as separate familes with *Hydrocotyle* forming a third family. Surely the third option, which causes the least upheaval and in any case is not novel, is to be preferred.

5. — The recognition of paraphyletic taxa should not be rejected, despite demand for this by strict cladists. The pros and cons of paraphyletic taxa have been much debated in recent years, often hotly, as a study of issues of *Taxon* (and of other journals) since about 2000 will amply demonstrate, and they will not be reiterated in any detail here. Reference to Brummitt[20][21], Potter & Freudenstein[22], Ebach et al.[23], Hörandl[24], and van Wyk[25] will provide adequate introduction to the arguments. I accept the thesis that paraphyletic taxa are inevitable consequences of evolution (this becomes irrefutable when all the extinct nodes of a cladogram are taken into

consideration), and can justify their recognition as taxa using the criterion of greater predictivity. In Fig. 1 the taxon ACDE is paraphyletic because of the recognition of B as a separate taxon segregated by a number of synapomorphies. This separation of B and ACDE renders each a more predictive taxon than ABCDE would be. Such an example is perhaps the most frequent reason for the recognition of paraphyletic taxa by taxonomists in the past. Often taxa such as B have evolved in special habitats (e.g. water or desert) or where special pollination syndromes (e.g. wind or water) have been exploited. When the taxon that has been segregated from a larger taxon (which then is rendered paraphyletic) is an easily recognised entity widely recognised in the past (and therefore with its own separate literature), I advocate its continued recognition. Examples are the families Lemnaceae/Araceae, Cactaceae/Portulacaeae, Brassicaceae/Capparaceae, and Callitrichaceae/Plantaginaceae/Scrophulariaceae. At the generic level possible parallel cases are *Neottia*/*Listera*, *Tamus*/*Dioscorea*, *Hirschfeldia*/*Erucastrum*, and *Alliaria*/*Thlaspi*.

On the other hand, where the segregated taxon has proved somewhat contentious, due to its addition to the larger paraphyletic taxon not causing any great expansion of the concept of the latter, it is probably better to amalgamate the taxa and attain mono-phyly. Possible examples are Najadaceae/Hydrocharitaceae, Taxodiaceae/Cupressa-ceae, *Eleogiton*/*Isolepis*, *Seriphidium*/*Artemisia*, and *Myosurus*/*Ranunculus*.
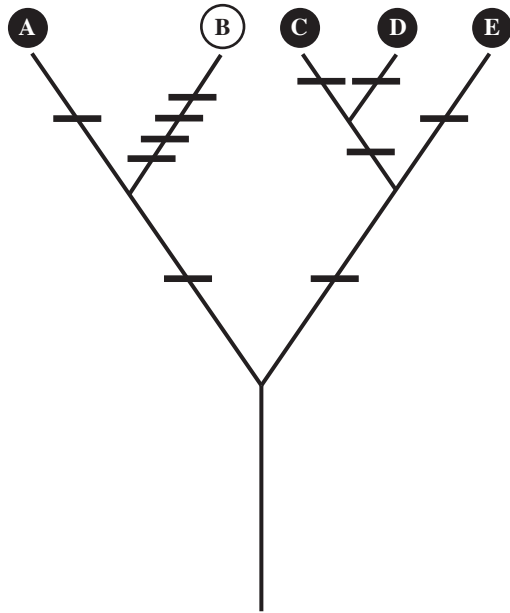

Fig. 1. A cladogram of five taxa, A-E. Taxon ABCDE is monophyletic, as is taxon B, but taxon ACDE is paraphyletic. Synapomorphies are represented by horizontal lines. Taxon B is differentiated by four different synapomorphies, and is therefore likely to be a very distinctive taxon; such taxa have in the past been commonly separated taxonomically from the rest (ACDE) and are the most frequent reason for the existence of paraphyletic taxa.

Admittedly this policy allows for difference in opinions (subjectivity), but taxonomic decisions have always played a big part in taxon delimitation, and the use or even reliance on molecular sequence data does not alter or dilute this fact. Examples where differences of opinion are likely to exist are *Cucubalus*/*Silene*, *Otanthus*/*Achillea*, and *Hebe*/*Veronica*. I am particularly unimpressed by those who use such concepts as 'the *degree* of sequence divergence' to decide on the *level* of taxonomic separation. This is precisely the same concept as deciding that because flower colour is of no taxonomic value in one genus or species, it is never of any value. It is impossible to extrapolate in this way from one taxon to another; *Adonis annua* always has red petals, and *A. vernalis* always yellow ones, but *A. flammea* and *A. aestivalis* can have either. Other examples abound.

Ruud van der Meijden's floristic contributions

Although I knew Ruud for only the last 15 years of his life, our acquaintance and friendship came about because of our common concerns with Flora-writing, and we had many discussions on a range of topics, including the subject of this article. While he would have agreed with most of my suggestions listed above, he was less conservative than I and was determined to follow the latest ideas and tenets of the strict molecular-cladistic school, as evidenced in the 23rd edition of the Dutch Flora[2]. Hence he did not tolerate paraphyletic taxa. How I miss the friendly arguments and discussions that we would have had!

Ruud felt very strongly that a Flora-writer must try to satisfy the requirements of the widest possible audience of users, and that Flora-writers should regularly meet to work out the best ways of achieving this. Indeed, he organised several informal international meetings with such an end in mind. One of his objectives was to produce a consensus check-list of the north-west European flora (north to Scandinavia; east to the whole of Germany; south to the Loire valley). Considerable progress was made on this project, but it was not completed because we could not convince enough colleagues across the region of the need to devote sufficient time to it. Anyone who has written a regional flora is fully aware of the advantages that inter-region collaboration would bring. Recently I compared the accounts of *Salix* in *Flora Nordica*[3] and Kent's *List of Vascular Plants of the British Isles*.[26] I found six cases of nomenclatural disagreements; after investigation I concluded that *Flora Nordica* was correct in three cases, and Kent in the other three! Prior consultation would have corrected three errors in *Salix* in each work.

Ruud's friendly attitude and didactic approach to taxonomy is amply shown by his willing commitment to the production of popular wild flower guides[27], and (in collaboration with ETI, Amsterdam) of electronic interactive Floras.[28] [29] The latter are surely the way forward, and it cannot be long before one can find oneself sitting on top of a mountain with a fully illustrated and interactive Flora of the region contained in a hand-held computer. Taxonomists must continue to strive to provide such ready access to systematic data that are seen by (*inter alia*) molecular systematists, amateur plant-hunters and gardeners alike to be user-friendly. The alternative is the alienation of taxonomy as a fringe or 'ivory tower' science. The adoption of a transparent and

predictive system of classification is a basic requirement of such aims. Classification is supposed to bring order out of chaos. The introduction of a new system that is based on one rigid set of rules that does not render a transparent, multi-purpose predictive classification is in danger of creating chaos out of (relative) order.

1. T.G. Tutin, V.H. Heywood, N.A. Burges, D.M. Moore (vanaf vol. 2), D.H. Valentine, S.M. Walters & D.A. Webb (red.). 1964–1980. Flora Europaea, ed. 1, Vols. 1–5. Cambridge University Press, Cambridge.
2. R. van der Meijden. 1983, 1990, 1996, 2005. Heukels' Flora van Nederland, eds. 20–23. Wolters-Noordhoff, Groningen.
3. B. Jonsell. 2000–. Flora Nordica 1–. The Bergius Foundation, Stockholm.
4. A. Cronquist. 1981. An Integrated System of Classification of Flowering Plants. Columbia University Press, New York.
5. C.A. Stace. 1991, 1997. New Flora of the British Isles, eds. 1 & 2. Cambridge University Press, Cambridge.
6. P.H. Davis. 1965–1985. Flora of Turkey, 1–9. Edinburgh University Press, Edinburgh.
7. A.R. Clapham, T.G. Tutin & E.F. Warburg. 1952, 1962. Flora of the British Isles, eds. 1 & 2. Cambridge University Press, Cambridge.
8. M. Guinochet & R. de Vilmorin. 1973–1984. Flore de France. Centre National de la Recherche Scientifique, Paris.
9. H.J. Scoggan. 1978–1979. The Flora of Canada. National Museum of Natural Sciences, Ottawa.
10. C.L. Hitchcock, A. Cronquist, M. Ownbey & J.W. Thompson. 1955–1969. Vascular Plants of the Pacific Northwest. University of Washington Press, Seattle & London.
11. G.M. Diggs, B.L. Lipscomb, R.J. O'Kennon & M.D. Reed. 2006–. Illustrated Flora of East Texas, 1–. Botanical Research Institute of Texas, Fort Worth.
12. Angiosperm Phylogeny Group. 2003. An update for the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG II. Bot. J. Linn. Soc. 141: 399–436.
13. C.A. Stace. 2005. Plant taxonomy and biosystematics – does DNA provide all the answers? Taxon 54: 999–1007.
14. R.M. Bateman, P.M. Hollingsworth, J. Preston, L. Yi-Bo, A.M. Pridgeon & M.W. Chase. 2003. Molecular phylogenetics and evolution of Orchidinae and selected Habenariinae (Orchidaceae). Bot. J. Linn. Soc. 142: 1–40.
15. P.B. Pelser, B. Nordenstam, J.W. Kadereit & , L.E. Watson. 2007. An ITS phylogeny of tribe Senecioneae (Asteraceae) and a new delimitation of *Senecio* L. Taxon 56: 1077–1104.
16. G.M. Diggs & B.L. Lipscomb. 2002. What is the writer of a Flora to do? Evolutionary taxonomy or phylogenetic systematics? Sida 20: 647–674.
17. J. Lambinon, L. Delvosalle & J. Duvigneaud. 2004. Nouvelle Flore de la Belgique, du Grand-Duché de Luxembourg, du Nord de la France et des Régions Voisines. Jardin Botanique National de Belgique, Meise.
18. N. Devos, O. Raspé, A.-L. Jacquemart & D. Tyteca. 2006. On the monophyly of *Dactylorhiza* Necker ex Nevski (Orchidaceae); is *Coeloglossum* (L.) Hartman a *Dactylorhiza*? Bot. J. Linn. Soc. 152: 261–269.
19. G.M. Plunkett. 2001. Relationships of the order Apiales to subclass Asteridae: a re-evaluation of morphological characters based on insights from molecular data. Edinb. J. Bot. 58: 183–200.
20. R.K. Brummitt. 2002. How to chop up a tree. Taxon 51: 31–41.
21. R.K. Brummitt. R.K. 2006. Am I a bony fish? Taxon 55: 2–3.
22. D. Potter & J.V. Freudenstein. 2005. Character-based phylogenetic Linnaean classification: taxa should be both ranked and monophyletic. Taxon 54: 1033–1035.
23. M.C. Ebach, D.M. Williams & J.J. Morrone. 2006. Paraphyly is bad taxonomy. Taxon 55: 831–832.
24. E. Hörandl. 2006. Paraphyletic versus monophyletic taxa – evolutionary versus cladistic classifications. Taxon 55: 564–570.

25. A.H. van Wyk. 2007. The end justifies the means. Taxon 56: 645–648.
26. D.H. Kent. 1992. List of Vascular Plants of the British Isles. Botanical Society of the British isles, London.
27. M. Blamey, R. van der Meijden & F. Van Rossum. 2009. Wild Flowers of Benelux. A pocket Flora of Netherlands – Belgium – Luxembourg. Domino Books, France.
28. R. van der Meijden. 1999, 2007. Heukels' Interactieve Flora van Nederland, eds. 1 & 2. ETI, Amsterdam.
29. C.A. Stace, R. van der Meijden & I. de Kort. 2004. Interactive Flora of the British Isles. ETI, Amsterdam.