Bot 940 reading for February 7

Taxonomy versus cladonomy, a fundamental controversy in biological systematics

R. K. Brummitt<sup>1</sup>

Brimmit, R.K. 1997. Taxonomy versus cladenomy, a fundamental controversy in biological systematics. Taxon 46: 723-734.

Introduction

In an article in the February issue of this journal, Welzen (1997) has expressed clearly his reservations about my paper 'In defence of paraphyletic taxa' (Brummitt, 1996a) which was originally read at an AETFAT (Association pour l'Etude Taxonomique de la Flore d'Afrique Tropicale) Congress in 1994. In the same issue of this journal, however, Sosef (1997) has come to very much the same conclusions as I had, emphasizing the inevitability of paraphyletic taxa. Essentially the same conflict of views was addressed in a formal debate at the Linnean Society of London on 6 March 1997, when a motion "that this house believes that Linnaean classification without paraphyletic taxa is nonsensical" was proposed by myself and seconded by my colleague Alan Paton. The motion was approved by 69 votes to 43. While this vote itself proves nothing, it does apparently indicate that there is a significant body of opinion in the systematic community (in the U.K. at least) which does not accept the view widely promoted today among followers of 'phylogenetic systematics' that paraphyletic taxa should have no place in biological classification. This is indeed now a matter of major controversy in systematics, and it is timely to review the arguments and further prospects.

### Two contrasting systems

The expression 'Linnaean classification'2, or similar variants using the word 'Linnaean', has become rather widely used in the last half century for the traditional method of biological classification used at least since the time of Linnaeus whereby organisms are referred to species, genera, families, orders and so on. (The fact that the rank of family was not actually adopted by Linnaeus is apparently irrelevant.) An analysis of the logical structure of the Linnaean hierarchy has been given by Buck & Hull (1966, 1969), but an exact definition seems not to have been attempted hitherto.

<sup>&</sup>lt;sup>1</sup> The Herbarium, Royal Botanic Gardens, Kew, Richmond, Surrey, TW9 3AE, U.K.

<sup>&</sup>lt;sup>2</sup> Column Editor's note: It is unfortunate that the expression "Linnaean classification" has come to be adopted for the traditional hierarchical structure of biological classification when contrasting it with alternative systems. The structure of traditional biological classification is in fact based on Aristotelian logic (see Davis & Heywood, Princ. Angiosperm. Taxon.: 12-21. 1963). Apart from his emphasis on and re-evaluation of genera, Linnaeus, himself, contributed little to the conceptual development, per se, of biological classification classes and orders predated him and he did not use the rank of family. While his lasting achievement has been the introduction of our binary system of nomenclature at the level of genus and species, his great contemporary contribution was the introduction of what became known as the "Linnaean Sexual System" of plant classification, which, by primary use of the number of stamens and carpels, permitted the botanical richness that was flowing from 18th century exploration to be readily described and classified. Whereas we reluctantly accept the widespread use of the misnomer "Linnaean classification" for the traditional Aristotelian-based biological classification, it would be extremely confusing to extend this, as some zoologists have done, by speaking of traditional taxonomy as the "Linnaean system" when that expression has a long history referring to the Classes and Orders (e.g. Pentandria Trigynia) that were the cornerstone of Linnaeus's botanical genius, and that ensured such wide use of his work that his binomial shorthand became an established feature of contemporary taxonomy (see Stearn, in Ray Soc. Publ. 140(1): 3. 1957). - [JMN].

Table 1. Comparison of the Linnaean and phylogenetic hierarchies (for further explanation see text).

	Groups recognized (taxa or clada)	Categories (genera, families etc.)
Linnaean hierarchy	mutually exclusive	internesting
Phylogenetic hierarchy	internesting	absent

It will be useful to look at least at the main characteristics of so-called Linnaean classification as it is currently applied to biological organisms (see also Frodin, 1997). They seem to be:

- recognition of classes of organisms, these being arranged in a hierarchy of categories such as genera, families etc. (the word 'class' is here used in a general sense, not in the sense of one category in the hierarchy);
- mandatory adoption of certain principal ranks, notably species, genus, family, order and usually some higher ranks (but not necessarily those below species, those between genus and species and those between family and genus etc., all of which are optional);
- mutual exclusiveness of taxa at each of these ranks, i.e. an organism referred to one species, genus, family etc. cannot at the same time be referred to another species, genus, family etc.;
- a strict sequence in the hierarchy of principal ranks (species are grouped into genera, which are grouped into families, etc.);
- a requirement that, within any particular group, the sum of all taxa at one rank
  must equal the sum of all taxa at the next higher rank recognized (so that if one
  divides a genus into infrageneric ranks such as subgenera or sections, all the
  species of the genus must be accommodated at such ranks);
- binomial nomenclature for species, the specific name including the generic name followed by a specific epithet;
- uninomial nomenclature for principal ranks at and above the genus level, those above genus having a termination which indicates their rank.

Linnaean classification is thus essentially based on class concepts (genera, families etc.). Ranks are fully internested in a hierarchy (species constitute a genus, genera constitute a family etc.), but groups recognized (taxa) at any one rank are mutually exclusive and are not internested. In marked contrast with the Linnaean hierarchy is a so-called hierarchy of descent, also known as a phylogeny, in which there are no classes, only a long series of parent-offspring relationships. The groups which may be recognized (clades) are not mutually exclusive but are internested, and are more or less unlimited in number. Table 1 summarizes how different elements are internesting in the two structures. Whereas in a Linnaean hierarchy each unit at one level is made up of all the units below it, and the apex of the hierarchy represents the totality of the group concerned, in a hierarchy of descent each unit at one level is not made up of all the units below, which may be successively different through anagenetic change, and the apex represents merely a single species (see Fig. 1). To put it more simply, all the species of a genus are equivalent to the genus itself, but all the offspring of a parent are not equivalent to the parent. The two hierarchies are very different. For further reading on hierarchies, see the now much-quoted review paper

by Knc mitted tive pap

Disting

The chies ar a Linna None or phries, were the ized by things speople

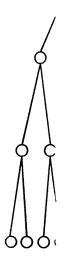


Fig. 1. \text for f

by Knox (1998), written in 1994 but unfortunately still unpublished, but now resubmitted elsewhere. I am grateful to him for letting me have a typescript of his instructive paper, and for discussion of it.

# Distinguishing classification and phylogeny

The main theoretical arguments of my AETFAT paper were that these two hierarchies are incompatible and cannot be equated, and that combining the two to produce a Linnaean classification including only monophyletic taxa is a logical impossibility. None of my opponents has so far disputed these arguments (Welzen, 1997; Humphries, 1997; Forey, 1997; and unpublished correspondence). My main conclusions were that paraphyletic taxa are inevitable in Linnaean classification, as also emphasized by Sosef (1997), and that biological systematics should aim to produce two things side by side, a classification and a phylogeny, and not confuse the two. Many people have now agreed with these arguments and conclusions.

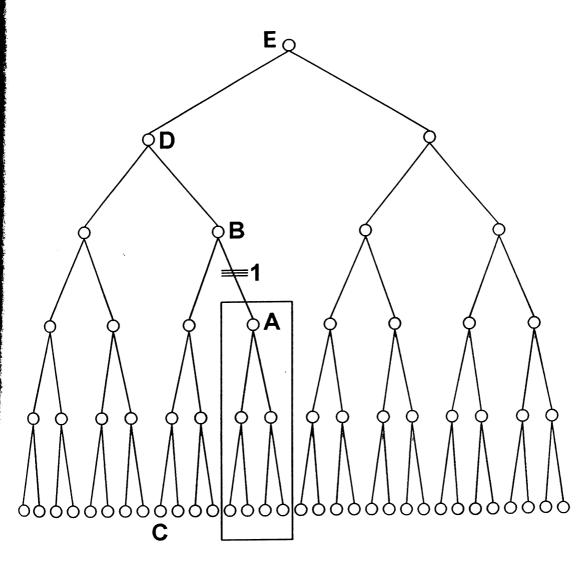


Fig. 1. Very simplified representation of a hierarchy of descent from a stem species E (see text for further explanation).

Those who argue for eliminating paraphyletic taxa from classification, and recogn nizing only monophyletic (in the modern cladistic sense) taxa, are in fact arguing for a classification based on clades, not on taxa, which is a quite different concept Referring organisms to clades is perfectly possible, but it is not Linnaean classification. Clades are not mutually exclusive concepts, and one organism can be simultal. neously referred to many different clades. In an illuminating recent paper Mayr (1995) has stressed the distinction between classifying organisms into a taxon and referring them to a clade, which he has designated a 'cladon'. Even more recently he has referred to a system that recognizes only clades as a 'cladification' rather than a 'classification' (Mayr, 1997: 143-146), noting that it violates almost all the principles of a traditional classification. These are crucial distinctions. In my presentation at the Linnean Society of London debate (Brummitt, 1997) I noted that if 'taxonomy' is the naming of taxa, then the naming of clades should be called 'cladonomy'. This should not be confused with cladistic taxonomy, which would be the naming of taxa (including those found to be paraphyletic) in association with cladistic analysis. I also suggested that we must all decide whether we are taxonomists or cladonomists. But trying to compromise and produce a taxonomy in which all taxa are monophyletic. i.e. are clades, is not a reasonable option.

### The conflict in the situation

I can understand the appeal of monophyletic taxa, and I can sympathize with much of what Welzen (1997) has said. Those who plead for monophyletic taxa can always produce arguments based on information content and character predictability. But to argue that all taxa in a classification must be monophyletic is to ignore one essential factor – the facts of evolution. It is impossible to produce a Linnaean classification of all extant and extinct taxa in which no genus has ever arisen from a species in another genus, and one family from a species in another family, unless one postulates de novo special creation of genera and families. If one believes in evolution, every taxon must have evolved from a precursor which must, by definition, in Linnaean classification, be placed in a different taxon at the same rank. No matter how much we may long for all our taxa to be monophyletic, if we are considering the whole evolutionary process, it is a logical impossibility. Every monophyletic taxon recognized at a principal rank must make another taxon at the same rank paraphyletic. That is inherent in Linnaean classification. In practice, ancestral taxa are often extinct and unknown and then cause us no problems, but this is by no means always so.

The difference between the two contrasting systems may be illustrated by reference to Fig. 1. The diagram is a very simplified representation of a hierarchy of descent from a stem species E. Suppose that a new character, or set of characters, arose at the position marked 1 which would allow recognition of a new taxon for all descendants, as indicated by the box. If we give this box any taxonomic rank – say genus – the genus including A is a monophyletic taxon, which should please everybody. However, we must immediately also create a paraphyletic taxon. In a Linnaean classification the species B must always be referable to a genus, which by definition must be different from that including species A. The genus including B must be paraphyletic. If there has been negligible character change between B and C, the genus of present day species including C will be paraphyletic. In practice there may have been another character change between B and C, allowing recognition of an-

ther genus including C, and all species of the one including B may have become without and be unknown in the fossil record so that we are left with only monophyletic genera. But it is by no means certain that this will happen, and in many cases members of the paraphyletic genus will persist to the present day, or may perhaps be known as fossils.

b But if we look at Fig. 1 from the cladonomist's point of view, we can recognize A and all its descendants as a clade. We can also recognize B-and-all-descendants as a clade, but this includes the clade A-and-all-descendants. We can go higher and recognize a clade taking in D, which will include also B and A, and another to take in E which will include also D, B and A. Clades are not mutually exclusive as genera and other categories of Linnaean classification are. Clades are internesting. As I said in my AETFAT paper (Brummitt, 1996a), a truly phylogenetic classification (a cladification of Mayr) has a completely different structure from a taxon-based system. It has no ranks, no genera, no families, just clades. It divides the phylogenetic tree vertically, whereas Linnaean classification makes horizontal cuts. And as soon as you try to superimpose Linnaean taxa on the phylogenetic tree, paraphyletic taxa are inevitable.

# Hennig's attempted compromise

In his influential book, Hennig (1966) proposed that only monophyletic taxa should be recognized in a classification and paraphyletic taxa should not be allowed. A paraphyletic taxon has been neatly defined as a group which consists of a common ancestor and some, but not all, of its descendants (see, e.g., Queiroz & Gauthier, 1994: 27). Thus if genus Y has evolved from a species within genus X, the latter genus is paraphyletic because it does not include all the descendants of the common ancestor of all its species, since genus Y is also descended from that same ancestor. According to Hennig's view, therefore, the classification must be modified somehow so that the paraphyletic genus is avoided.

Two ways of achieving this have been practised in cladistic literature; either genus Y is sunk into genus X, or genus X is split up into more than one genus. There are two problems with the former option. Firstly, genus X may indeed be made monophyletic by the inclusion of Y, but genus X itself must have originated from a species in another genus, which is thus paraphyletic. If we continue to sink one genus into another to avoid paraphyly, we end up in infinite regression of our classification until the whole tree of life has been sunk into one genus. Secondly, if we still wish to give taxonomic recognition to the group formerly known as genus Y, for example by giving it subgeneric rank within X, we are merely shifting paraphyly to subgeneric rank because then subgenus X would be paraphyletic.

The second strategy, splitting up genus X into two or more genera, has similar problems. It does not matter how many genera are recognized, genus Y must have evolved from within a genus other than itself, which is still paraphyletic. Indeed, the newly recognized genera must also have had their origins outside themselves, and increasing the number of monophyletic genera merely increases the number of potential paraphyletic genera. One can never get rid of paraphyly, though in practice it may not be apparent from a cladogram because the ancestors are not included in the analysis, perhaps because they are extinct (see below for consideration of whether our classification should be only of extant taxa). It may, however, be an unwarranted assumption that there was always a generically distinct group which has become

extinct to which we can relegate the inevitable paraphyly. Cladograms have no ancestors at their nodes, and are far from being phylogenetic trees, as stressed by Donoghue & Cantino (1988: 120) who noted that some species in a cladogram may indeed be ancestral to others. But if a cladogram does not show the ancestor of a taxon, it does not mean that the taxon had no ancestor and was created from nothing. Every taxon must have had an ancestor, and the taxa to which it is referred may or may not be extinct.

The attempts of systematists in the last three decades to produce classifications without paraphyletic taxa have already caused many upsets to previous classifications and consequent nomenclatural changes. But there will be much more to come. With molecular data giving increasing evidence of lines of evolution, paraphyly will be demonstrated at all levels throughout the living world, from subspecies to subkingdoms. The conflict between two incompatible systems of classification will be felt everywhere. What chaos to our taxonomic and nomenclatural system is in store for us if we fail to distinguish classification and phylogeny? Let us consider the logical conclusions.

If, according to the cladistic view, classifications should be based solely on lines of descent, then conversely lines of descent should be directly inferred from classifications. In my AETFAT paper (Brummitt, 1996a) I referred to the situation where one taxon is divided into two subtaxa, such as the flowering plants divided into Monocots and Dicots or any species divided into two subspecies. Except in the rather exceptional circumstance of simultaneous budding off of more than one new species, it is unlikely that both the subtaxa arose simultaneously at the point in evolutionary time when the taxon itself became differentiated from its ancestor, which would require trichotomous branching (the two subtaxa plus the persisting ancestral taxon). It is much more likely that the stem group of the new taxon would be referable to one of the subtaxa and that the other subtaxon evolved from within that at a later stage. when the earliest subtaxon would be paraphyletic. Or it may be that there was another (or more than one) subtaxon which is now extinct, from which the recognized subtaxa evolved, but then that would be paraphyletic. The Monocots are now thought to have been derived from early Dicots, and the present trend in cladistic taxonomy is to abandon the Dicots as a taxon because they are paraphyletic. The Neuracanthus example in my AETFAT paper (Brummitt, 1996a), where the highly specialized N. sect. Leucobarleria makes N. sect. Neuracanthus paraphyletic, is very similar. It is nonsensical to argue that a derived taxon like this cannot be recognized just because it leaves the parental group paraphyletic. Under such a classification there could never have been any evolution of new taxa.

Thus, under the Hennigian principle, any classification in which a family is divided into two subfamilies, or a genus is divided into two subgenera, or a species is divided into two subspecies, is inherently very unlikely. And of course the chances of having more than two subfamilies in a family, or more than two subgenera in a genus, and so on, would be even more remote. Tetrachotomies, pentachotomies and so on do not happen in evolution, and recognition of three or more subdivisions at the same rank under one family, genus or species is certainly theoretically inconsistent with phylogenetic classification. If one wishes to indicate the precise course of evolution in one's system and recognize only monophyletic groups, one must adopt a dichotomous clade-based system which will be very different from our present Linnaean classification. A good actual example of how this may be presented in an

inden given group tion a of its

Are fi

I h that a AETI and d not a paper views raised to me

So accep taxa ? phyly be ra nothir paper ing pl not s€ plant is onl and n which presei which parap! dama conta: Otl

Otl fossilis, ho of W handl (1988 cladis much requires Just a specie specie Simila

indented form has been given by Queiroz & Gauthier (1992: 472), who have also given an excellent review of other literature on the matter. Note that the level of any group in the hierarchy of the classification is indicated only by its degree of indentation and not by any statement of its rank (there are no ranks) nor by the termination of its name.

Are further compromises possible?

I have maintained that Hennig's concept of Linnaean classification is flawed and that attempts to impose it are not only disruptive but will be in vain. Since my AETFAT paper was read in 1994 and published in 1996 I have had correspondence and discussion with many people. A majority have agreed with me, though certainly not all, but none have seriously disputed the logic of the arguments. Meanwhile papers particularly by Mayr (1995) and Sosef (1997) have expressed very similar views, with additional perspectives on the problem. There will be dissenting voices raised for some time no doubt, and several further compromises have been suggested to me. It will be appropriate to consider these here.

Some of my correspondents have agreed with the logic of the arguments and accepted that paraphyletic taxa are inevitable, but have argued that we must make all taxa at the principal ranks of order, family and genus monophyletic and shift paraphyly to the intermediate ranks of suborder, subfamily, subgenus etc. This seems to be rather clutching at straws while admitting that the theory is wrong, and does nothing to avoid the major upheavals which will be necessary at principal ranks. The paper of Judd & al. (1994) gives an idea of some of the changes required in flowering plant families. In this connection I think it worth bearing in mind that there does not seem to be evidence so far from palaeobotany for mass extinction of flowering plant families (Collinson & al., 1993: 810). Indeed, it seems that at the moment there is only one described angiosperm family, Priscaceae, that is known only from fossils and not living plants. While the possibility still exists of major groups in the past which would warrant family recognition if we were fully aware of them, many of our present day families may have been derived directly from others currently recognized which will turn out to be paraphyletic when we have adequate data. Trying to restrict paraphyly to taxa intermediate between the principal ranks is merely an attempt at a damage limitation exercise of very dubious value, admitting that the system does contain paraphyletic taxa and still causing upheavals at principal ranks.

Others have argued that our classification should be only of extant taxa and not fossils or other extinct organisms, and that the problems would then disappear. This is, however, contrary to the view often expressed in cladistic literature, such as that of Wiley (1981: 223) that "a general system of classification must be capable of handling all organisms and not just descendants", and of Donoghue & Cantino (1988: 123-124). Perhaps the view expressed to me that "extinction is the saviour of cladistic classification" may have some credence, for it makes such classification much more plausible if we cannot actually see the ancestral taxa. But this would require that ancestral taxa always die out when a new taxon evolves, which is not so. Just as the residual populations of a species do not necessarily die out if a new species is budded off (despite Hennig's early views on the matter), so all the remaining species of a genus do not necessarily die out if a new genus evolves from one species. Similarly the *Capparaceae* did not become extinct just because the *Cruciferae* evolved

T

I

a

C.

p h

p

g a:

O:

ir

fa

O:

th

aı

tc

 $g_{l}$ 

in

th

W

bı

 $\boldsymbol{P}$ 

pί

cl

lo

W

Q

ha

fa

fo

at of of

pŀ

bi

gi

re

ch

ag

nc

cla

from one of their number. In many cases at all ranks, when a new taxon evolves from one species or population, the residual taxa may persist without significant change. And where would taxonomy of fossils be if our classification were applicable only to modern descendants?

A further compromise, which has frequently been expressed already in the literature on cladistics, is that paraphyly is inevitable at the species level and has to be permitted there, but is inadmissible at higher levels. An extensive review of this position has been provided very recently by Crisp & Chandler (1996), who have supported the view. There is a welcome sense of realism in their discussion. In their section headed 'Are paraphyletic species avoidable?' (l.c.: 832-833) I find some of my own arguments anticipated - mere shifting of paraphyly from one rank to another without eliminating it, inevitable acceptance of recognizable taxa, and conflict between Linnaean classification and the desire for monophyletic taxa only. But while they have concluded that paraphyly is inevitable at specific rank, they have failed to take the obvious next step and see that exactly the same arguments apply at every rank. Their consideration of the problem at higher ranks seems to be confined in their paper to a single sentence (l.c.: 832): "At higher ranks, say genus, the problem can be solved by splitting the residual group further into monophyletic groups, each of which is named as a genus". But, as I have noted above, splitting a paraphyletic genus in a cladogram does not get rid of paraphyly, it merely shifts it somewhere else. The derivative genus causing paraphyly must always have had an ancestor in another genus. The arguments of Donoghue & Cantino (1988: 120-121, 124) on this matter also simply do not answer the point that if a genus has evolved from a species in another genus, not only is that species paraphyletic, the genus it is referred to must be paraphyletic, and the same at family and all other levels. Arguments about gene flow are irrelevant to this. It is a small step to translate the realism of Crisp and Chandler at specific level to higher ranks, and I hope this will happen in due course.

Some correspondents have accepted that the Hennigian theory is questionable but that they prefer to adopt monophyletic taxa "where possible". But this is an admission that there are situations where it is not possible to have only monophyletic taxa. I believe that the theory is so hopelessly wrong, and paraphyly so rife at all levels in the living world, that compromises are not possible. As the saying goes, you cannot fit a square peg into a round hole. And I suspect that if we can just realize this, some of the arguments in the literature about ancestors, stem species, stem lineages, cumbersome taxonomic conventions which never seem to catch on with other people, and proposals to change the codes of nomenclature to accommodate embarrassing situations, will become irrelevant.

#### Obvious absurdities

I can understand the note of exasperation in Welzen's article (1997: 99) in his expression of amazement that those like me who disagree with him prefer to maintain their traditional practices. It is difficult to change long-held attitudes which are deeply felt, and I have the same problem with those who insist on sticking to the traditional but in my view now outdated cladist point of view. Since I find the theory of Hennigian classification to be a logical impossibility, and the practice of it very disruptive to stability, I feel I have a good case for trying to persuade others to see it my way. My instinctive thoughts on paraphyletic taxa are very different from Welzen's.

ntichance bleionly 12 DATE theliter has to b w of this who have n. In their 1 some of to another 1 conflict But while 3 failed to / at everý ed in their em can be , each of aphyletic mewhere ncestor in 4) on this a species d to must out gene Crisp and course. nable but s an adophyletic ife at all goes, you st realize es, stem

MBER, 199

)) in his to main-hich are g to the e theory f it very to see it elzen's.

on with

nmodate

I would prefer to remove any stigma of unacceptability from paraphyletic taxa. Our task is to produce an optimally practical classification, and indicate which genera have evolved from which other genera, which families from which other families, and so on.

Therefore, in my three previous considerations of the problem (Brummitt, 1996a, 1996b, 1997), all delivered verbally at meetings, I have tried to persuade others to change their attitudes by pointing out the absurdity of classification without paraphyletic taxa for anybody who believes in evolution. I have asked how evolution can have proceeded all the way from unicellular algae to highly developed flowering plants if in our classification one genus has never evolved from something in another genus, or one family has never evolved from something in another family. I have asked where families and genera evolved from if they did not evolve from species in other families and genera. I have noted that although evolution is continually producing greater and greater diversity so that new clades (which may represent genera, families, orders etc.) have repeatedly arisen from single species, the cladistic theory of classification holds that descendant taxa can never have a rank higher than any of the taxa to which these ancestral species are referred. This seems to me to be crazy, and a denial of the evolution of new taxa. I have asked what we should do if we were to discover, perhaps alive on a remote hillside like that still harbouring Metasequoia glyptostroboides, or perhaps as a fossil, the species from which the whole of the flowering plants have evolved. Would we have to sink the whole of the flowering plants into the order, family, genus and even species to which that pre-Angiosperm is referred, all of which would be paraphyletic? I have had no answers from opponents, and believe that a broad realisation is emerging that such a theory of classification is nonsensical.

### Proposals to abandon Linnaean classification

I think that the debate must move on from arguments about whether to recognize paraphyletic taxa or not. They are clearly inevitable, as Sosef (1997) has also concluded. The incompatibility between a classification ('taxonomy') and a purely phylogenetic system ('cladonomy') has been stressed by a number of authors including Woodger (1952), Griffiths (1976), Queiroz & Gauthier (1992), Mayr (1995, 1997), Queiroz (1996), Sosef (1997) and myself (Brummitt, 1996a, 1996b, 1997). It may have been Griffiths (1976) who first proposed abandoning Linnaean classification in favour of a phylogenetic system. Queiroz & Gauthier (1992) have argued strongly for this, stressing (l.c.: 453) that "phylogenetic taxonomy may be best served by abandoning the Linnaean categories" and "the development of a phylogenetic system of taxonomy amounts largely to replacing the Linnaean categories with the principle of common descent as the basis for taxonomic conventions", and (l.c.: 454) "a phylogenetic system of taxonomy cannot retain the Linnaean method of forming binomials; specifically the names of genera cannot be parts of the species names", giving references to other authors promoting these views. The ideas of Donoghue reported by Pennisi (1996) seem to reflect the same thoughts, apparently a significant change from his views expressed earlier in Judd & al. (1994). Queiroz (1996) has again favoured abandonment of Linnaean classification, as has Welzen (1997).

Others, however, have been less dismissive of traditional classification. While it is not my purpose here to assess the wide-ranging arguments for and against Linnaean classification and nomenclature, it may be appropriate to point to some of the disad-

vantages of a purely clade-based system which have been mentioned recently and which tend to be overlooked in the extensive more cladistically focused literature. A serious theoretical objection was rightly raised by Sosef (1997) when he noted that reticulate evolution, arising from hybridization followed by speciation in the offspring, cannot be accommodated in a system of clades (see also Hedberg, 1995: 4). This will affect many cases below the Linnaean rank of genus. Paton (1997) has emphasized taxon recognition and communication as strong arguments in a plea for Linnaean classification with paraphyletic taxa from the purely practical point of view. The problem of information retrieval from all the past literature is one of a number of points made by Mayr (1995), and in his latest book (Mayr, 1997: 143-146) his reference to Charlemagne's family emphasizes his point that cladification groups things together which are genetically widely separated while separating things which are genetically very close. Although supporters of a clade-based system will argue that their classification would have objective reality, whereas Linnaean classification is essentially subjective, phylogenetic relationships are not observable and are mere hypotheses, whereas characters used for recognition of Linnaean taxa are directly observable (Brummitt, 1996b).

The lack of class concepts in a phylogeny inevitably results in great proliferation of levels in the classification which at the same time do not have any indication of their position in the hierarchy. Even though Queiroz & Gauthier (1992: 457) have defended this, to me the practicality seems very questionable. In their clade-based classification of the major groups of the *Vertebrata* (Queiroz & Gauthier (1992: 472) it takes 10 steps to reach the birds (Aves), and, as noted above, each step is identified only by a name without a rank. If their suggestion in their 1992 paper that binomial nomenclature be abandoned were adopted, this would be a major blow to stability and practicality. In a more recent paper, however, Queiroz (1996) has presented a revised nomenclatural proposal which uses the names of Linnaean taxonomy but assigns them no rank. It is difficult to see how this would operate in practice, and no comments are made about binomials for species. I have made a plea (Brummitt, 1996b) that any nomenclature devised for a clade-based system should be different, and easily recognizably so, from Linnaean nomenclature. Phytosociology, for example, has developed its own nomenclatural system quite distinct from that for taxa.

In my AETFAT paper (Brummitt, 1996a) I argued that a classification and a phylogeny are both desirable, but that they have different functions and should be allowed to exist side by side, and that abandonment of Linnaean classification in favour of an attempt at a phylogenetic hierarchy must result in loss of anagenetic information and some degree of predictivity. The paper by Mayr (1995) may be recommended for discussion of the different objectives and functions of a classification and a phylogeny. Later, while strongly supporting retention of Linnaean classification, I have pondered the question of how phylogenetic information should be presented alongside it (Brummitt, 1996b). Some method of relating names of Linnaean taxa to a phylogenetic system seems to be required. Great advances have been made from the crude balloon-like representation offered by Bessey (1915: 118) up to the most advanced cladograms of today, but cladograms are still not phylogenetic trees. Until cladistic methodology bridges the gap between presenting a cladogram, with no ancestors at the nodes, and producing a phylogenetic tree (see also Donoghue & Cantino, 1988: 120), the optimal precise way of relating taxa to phylogeny may still elude us. This matter requires further consideration.

### The essential debate

The arguments for or against a classification or a cladification are complex and will no doubt continue for some time. My main purpose here is not to argue that one course must necessarily prevail over another, but to try to focus attention on what the options are. The essential debate seems to resolve itself into three possibilities:

- abandoning Linnaean classification and adopting a purely clade-based dichotomous system;
- retaining Linnaean classification, with paraphyletic taxa, but developing alongside it an independent clade-based dichotomous system with its own separate nomenclature; or
- retaining Linnaean classification, with paraphyletic taxa, and merely assigning the taxa recognized to a position in a phylogenetic system without naming clades.

Those who wish to have a purely phylogenetic classification should read the well argued papers of Queiroz & Gauthier (1992, 1994) and Queiroz (1996) to see exactly what it entails. Both the classification and the nomenclature of a clade-based system will be very different from those of current biological classification. Although the names used will apparently, from the examples given, be based on those currently in use in Linnaean nomenclature, they will have no rank and will be made to define the circumscription of the clade they apply to. Even if that were ideally what we would like, I think that in botany at least we are still so far from having adequate data on phylogeny for most taxa, despite the advances of molecular systematics, that Linnaean classification must persist for a long time yet. Furthermore, the nomenclatural proposals are still only outline ideas and would need a lot more fleshing out before they could be put into practice. To me, the advantages of such a system are far outweighed by the disadvantages, and I do not believe that Linnaean classification and nomenclature will ever be replaced.

But the matter should be properly debated. As Welzen (1997) implies, we should not follow traditional practices just because they are traditional, but neither should we adopt new ideas just because they are new. We need to understand the possibilities and appreciate the different objectives and functions of the different options. In the meantime, it seems to me and to many others that the compromise of maintaining Linnaean classification but trying to eliminate paraphyletic taxa is nonsensical and should be abandoned before any more damage is done to existing classifications and nomenclature.

#### Acknowledgements

I am grateful to a number of people for reviewing the above text, and particularly to A. J. Paton and N. A. Brummitt for detailed comments. Thanks are also due to many correspondents for friendly and constructive comments on this subject over the last three years.

Literature cited (including \*electronic publications)

Bessey, C. E. 1915. The phylogenetic taxonomy of flowering plants. *Ann. Missouri Bot. Gard.* 2: 109-164.

Brummitt, R. K. 1996a. In defence of paraphyletic taxa. Pp. 371-384 in: Maesen, L. J. G. van der, Burgt, X. M. van der & Medenbach de Rooy, J. M. van (ed.), The biodiversity of African plants. Proceedings XIVth AETFAT Congress 22-27 August 1994, Wageningen, the Netherlands. Dordrecht.

- \*- 1996b. Quite happy with the present Code, thank you. In Reveal, J. L. (ed.), Proceedings of a mini-symposium on biological nomenclature in the 21st century. [http://www.life.umd.
- 1997. Proposing the motion 'That this house believes that Linnaean classification without paraphyletic taxa is nonsensical': the theoretical case. Linnean 13 (in press).
- Buck, R. C. & Hull, D. L. 1966. The logical structure of the Linnaean hierarchy. Syst. Zool.
- & 1969. Reply to Gregg. Syst. Zool. 18: 354-357.
- Collinson, M. E., Boulter, M. C. & Holmes, P. L. 1993. Magnoliophyta ('Angiospermae'). Pp. 809-841 in: Benton, M. J., The fossil record 2. London, etc.
- Crisp, M. J. & Chandler, G. T. 1996. Paraphyletic species. Telopea 6: 813-844.
- Donoghue M. J. & Cantino P. D. 1988. Paraphyly, ancestors, and the goals of taxonomy: a botanical defence of cladism. Bot. Rev. (Lancaster) 54: 107-128.
- Forey, P. L. 1997. Opposing the motion 'That this house believes that Linnaean classification without paraphyletic taxa is nonsensical': authority, ancestry and anagenesis as deterrents to progress. Linnean 13 (in press).
- Frodin, D. G. 1997. Preamble to the debate on the motion 'That this house believes that Linnaean classification without paraphyletic taxa is nonsensical': the setting. Linnean 13
- Griffiths, G. C. D. 1976. The future of Linnaean nomenclature. Syst. Zool. 25: 168-173.
- Hedberg, O. 1995. Cladistics in taxonomic botany master or servant? Taxon 44: 3-11.
- Hennig, W. 1966. Phylogenetic systematics. Urbana.
- Humphries, C. J. 1997. Opposing the motion 'That this house believes that Linnaean classification without paraphyletic taxa is nonsensical': what forms of information are to be conveyed? Linnean 13 (in press).
- Judd, W. S., Sanders, R. W. & Donoghue, M. J. 1994. Angiosperm family pairs: preliminary phylogenetic analysis. Harvard Pap. Bot. 5: 1-51.
- Knox, E. B. 1998. The use of hierarchies as organizational models in systematics. Biol. J. Linn. Soc. (in press).
- Mayr, E. 1995. Systems of ordering data. Biol. & Philos. 10: 419-434.
- 1997. This is biology: the science of the living world. Cambridge, MA.
- Paton, A. J. 1997. Seconding the motion 'That this house believes that Linnaean classification without paraphyletic taxa is nonsensical': Paraphyly, taxon recognition and the justification of Linnaean classification. Linnean 13 (in press).
- Pennisi, E. 1996. Evolutionary and systematic botanists converge. Science 273: 181-182.
- \*Queiroz, K. de, 1996. A phylogenetic approach to biological nomenclature as an alternative to the Linnaean systems in current use. In Reveal, J. L. (ed.), Proceedings of a mini-symposium on biological nomenclature in the 21st century. [http://www.life.umd.edu/bees/96sym.html].
- & Gauthier, J. 1992. Phylogenetic taxonomy. Annual Rev. Ecol. Syst. 23: 449-480.
- & 1994. Towards a phylogenetic system of biological nomenclature. *Trends Ecol. Evol.* 9:
- Sosef, M. S. M. 1997. Hierarchical models, reticulate evolution and the inevitability of paraphyletic taxa. Taxon 46: 75-85.
- Welzen, P. C. van, 1997. Paraphyletic groups or what should a classification entail. Taxon 46: 99-103.
- Wiley, E. O. 1981. Phylogenetics. New York, etc.
- Woodger, J. H. 1952. From biology to mathematics. Brit. J. Phil. Sci. 3: 1-21.