

How to chop up a tree

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Over the past 50 years it has been pointed out with increasing frequency that our traditional Linnaean system of classification and nomenclature is incompatible with a phylogenetic system which recognises only monophyletic groups. Dividing up an evolutionary tree into mutually exclusive families, genera, and species which are all monophyletic is a logical impossibility. Darwin had emphasised that evolution is descent with modification. The rise of cladistic thinking in the last 40 years has promoted an obsession with monophyletic taxa, with classification based solely on descent at the expense of modification. Despite strong psychological pressures on a generation of biologists who have been brought up on the dogma of monophyly, the Hennigian view of classification is now increasingly seen as illogical and out-of-date. Some are therefore supporting the *PhyloCode*, which is based on a logical position but is impractical for general purpose classification and communication since it recognises no ranks and abandons binomials. Others still cling to the nonsensical concept of recognising families, genera, species, etc., and all being monophyletic. Linnaean classification is the optimal tool for cataloguing biodiversity and will inevitably be maintained, but this requires recognition of paraphyletic taxa and some rethinking of the practice and purposes of biological classification. Those who want a classification to recognise only monophyletic taxa should adopt an appropriate nomenclatural system such as is offered by the *PhyloCode*. To do otherwise will tend to lead to bad taxonomy.

KEYWORDS: cladistics, classification, monophyly, paraphyly, *PhyloCode*, phylogeny, taxonomy.

INTRODUCTION

I must thank the organisers sincerely for inviting me to speak in this symposium¹, which is very timely since it confronts fundamental practices in biological taxonomy which are currently under serious debate. When I thought of what I wanted to say and looked for an appropriate title, I remembered a little riddle which was once popular in my house. When my children were young, we often had visitors whose first language wasn't English. They often had a better knowledge of English than the family did, so to test their abilities in vernacular expression the children would ask a little question: What is the next thing you do after you chop a tree down? The answer of course is that once you've chopped a tree down the next thing to do is to chop it up, which had some of our visitors amused and others bemused. The only reason I recall this is to emphasise that there is more than one way to chop a tree. This is my message, of course talking about the evolutionary tree, the Tree of Life. One should not actually push these analogies too far, and, as others have said often enough, the tree of life

is really more of a bush than a tree. I could have called the talk "How to Chop up a Bush", but I thought that if I flew into Washington with a document with this title, the CIA might begin to take too close an interest in me. So let us not take the analogies too literally.

I assume that I am expected to present my now stand-up routine on paraphyletic taxa, with some consideration of the *PhyloCode*. I have actually been dining out on paraphyletic taxa ever since I was first persuaded to put forward my then heretical views on the subject at an AETFAT Congress in 1994 (Brummitt, 1996). This is in fact the twelfth time I have addressed an audience on the matter, and I would like to think that my views are no longer so heretical. I have had a great deal of support wherever I have spoken on the subject, and many have told me to just go on saying it until the matter is properly and generally understood.

In fact, if this audience is anything like most previous audiences I have faced, one third will think that what I say is so obvious that it hardly needs saying, one third will think my views are so way off the establishment line that they needn't bother to listen to such stuff at all, and

¹The following text was prepared as a verbal presentation at a symposium, and is reproduced here more or less as spoken. It is here dedicated to the late Arthur Cronquist, who understood these things better than most people do.

one third might be undecided which way to jump. So I am mainly talking to those who want to hear the arguments and need to be persuaded. I am not attempting to give a formal scientific paper. I am here to persuade people, to persuade them to look at some very simple facts and ask themselves how best to interpret them taxonomically, because I believe that there has been a lot of muddled thinking in the past and our taxonomy is in danger of going rather seriously off the rails as a result. And I can honestly say that when I have spoken on this subject before, I have always gone away afterwards sure that more people agreed with my point of view than when I arrived.

The *PhyloCode* is also under discussion in this symposium. From my point of view, the *PhyloCode* is just part of the argument about paraphyletic taxa. It is all part of the same question of how we want to chop up the tree of life. Some commentators have criticised the *PhyloCode* without ever considering the broader question. A nice paper on phylogenetic nomenclature by Moore (1998) did raise the matter of paraphyly, but he declined to come to any conclusion on the matter. I don't think we can argue about Linnaean taxonomy and the

PhyloCode without talking about paraphyletic taxa. The issues are too closely intertwined. We need a broad perspective of what we are doing.

INCOMPATIBILITY

Nearly 50 years ago a paper was published in the *British Journal of the Philosophy of Science* by Woodger (1952) entitled "From biology to mathematics". The concluding sentence was clearly stated: "The taxonomic system and the evolutionary phylogenetic scheme are quite different things doing quite different jobs, and only confusion will arise from identifying or mixing them". Since then, at regular intervals, some biologists have come to the same conclusion and made statements to the effect that our Linnaean system of classification is incompatible with a system which recognises only monophyletic taxa, otherwise known as clades. Notable among these have been the zoologists Griffiths (1976) and de Queiroz & Gauthier (1992) and (1994), and in botanical circles Cronquist (1987), Sosef (1997), and recently Cantino (1998, 1999; Cantino & al., 1999) in

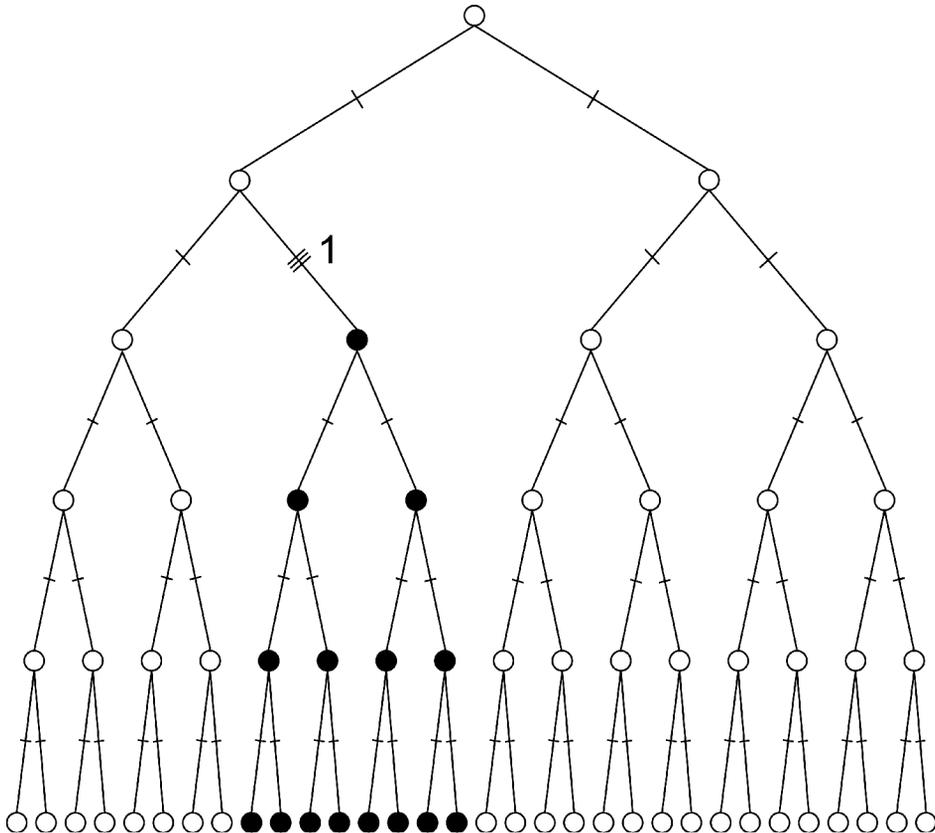


Fig. 1. Stylised diagram of a phylogenetic tree in which a major character change has occurred at point 1, giving rise to descendants indicated by darkened circles.

various papers promoting the *PhyloCode*. I agree completely with this (Brummitt 1996, 1997). But as far as I know, attempts to explain this incompatibility to practising taxonomists have been few and far between. May I make an attempt?

Let us look at the diagram (Fig. 1). This, I emphasise, is a diagrammatic representation of a phylogenetic tree, not a cladogram (I will comment later on the differences). One position of major character change is marked at point 1. It is just a model of a situation that has arisen millions of times in evolution, where a major character change has given rise to a group which differs significantly from its ancestors, while other descendants have remained comparatively little changed or unchanged. The whole diagram is one clade, and the dark circles together form a readily recognisable lesser clade within the larger clade. It doesn't matter what rank we are talking about, so, just for the sake of convenience, let us think in terms of genera. If I call all the dark circles one genus defined by the characters at 1, then the open circles must be a different genus. In Linnaean classification one species cannot be referred simultaneously to more than one genus, all taxa at the same rank being mutually exclusive. But then the genus of open circles is paraphyletic, because it is not a complete clade. The cladistic principle that one cannot have paraphyletic taxa requires that the taxon of dark circles cannot be recognised as a genus if the open circles are also recognised as a genus; the dark circles have to be sunk into the open circles. And you can imagine that if I had drawn the diagram bigger and included the higher part of the tree, then the genus of open circles must be similarly derived from another genus which differs from it by whatever characters we use to define the genus of open circles. And so on, right back to the year dot. So without paraphyletic taxa, the whole classification telescopes into the original genus and species.

If we are classifying all the products of evolution, i.e., the whole evolutionary tree of life, every taxon we recognise must make another taxon paraphyletic. That is a simple logical fact. It is obvious to most people that if you cannot have paraphyletic taxa, you cannot have a classification showing anything beyond one original species, genus, family, etc. This is why my fellow-thinker Marc Sosef and I entitled a short note in *Taxon* in 1998 "Paraphyletic taxa are inherent in Linnaean classification", which we finished by saying "Until somebody can draw for us a phylogenetic tree (as distinct from a cladogram) divided fully into Linnaean taxa without any of them being paraphyletic, we will continue to believe that our arguments on the inevitability of paraphyletic taxa are correct" (Brummitt & Sosef, 1998). That was three years ago. We have had no takers. The offer is still open. If anybody here thinks they can draw a phyloge-

netic tree and divide it into families and genera without creating paraphyletic families and genera, they are welcome to come up here and do so. Surely the theory of cladistic classification, which has dominated parts of biological taxonomy for the past forty years, must at least be open to serious question.

So what do we have to do to avoid paraphyletic taxa? We have seen that if the dark circles are one genus in our classification of the evolutionary tree, there must be a paraphyletic genus somewhere from within which it evolved. And of course exactly the same argument applies if we call them a family or a species. As soon as we assign a rank to a group, we create paraphyly. But if we just call the dark circles a clade without giving it a rank, and say that the group from which it evolved is part of a higher clade, we can get away without paraphyly—because we have no taxa, or at least we have no ranked taxa. As you go back through the tree of life you just build up bigger and bigger clades, but you cannot impose Linnaean classification on the tree without creating paraphyletic taxa. It is a logical impossibility. This is the fundamental incompatibility between Linnaean classification and a system of monophyletic taxa, or clades.

This is why the *PhyloCode* recognises that if a system of only monophyletic taxa is required, you have to abandon ranks. Some supporters of the *PhyloCode* want to abandon all ranks above species but retain the species—see for example Cantino & al. (1999) where 13 different methods for naming species were discussed and neatly keyed out in a dichotomous key—with none of them being considered ideal. But the view of Brent Mishler's recent paper (Mishler, 1999) that species also have to be abandoned seems to me to be a necessary logical extension to abandoning all other ranks. The principle is the same at every rank. There can be no orders, no families, no genera, and no species, just clades, in a clade-based classification. It is perfectly logical. If you are prepared to make the sacrifice of abandoning ranks, then you can have a phylogenetic system without paraphyletic taxa, but this will be very different from a traditional Linnaean classification.

CHOPPING TREES

To try to get this idea across to people, I have resorted to the analogy of chopping up the tree, or bush. What Linnaean taxonomy does is to cut horizontally across the grain to make a series of building blocks, with smaller ones aggregated into bigger units in a hierarchical series. A system of clades chops the tree in a quite different way. If one does not push the analogy too far, I would suggest that the system of clades creates not a set of building blocks like the Linnaean system but a series

of Russian dolls, each one nesting within a bigger one. Or if you want to put it in terms which many of us may have learned in first-year undergraduate classes thirty or forty years ago, Linnaean taxonomy divides the tree into grades, whereas a phylogenetic system divides it into clades. Whatever happened to grades? We hear a lot about clades these days, but to present-day students grades are only the assessments you get in your exams at the end of the course. Anybody uncertain of the differences between clades and grades may check the numerous references to the matter in Davis & Heywood (1963).

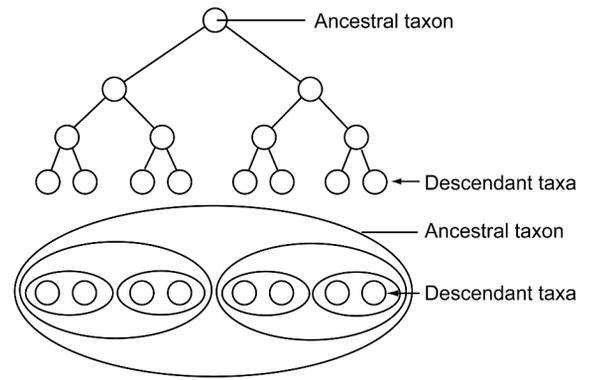
HIERARCHIES

If you want further convincing about this incompatibility, let us consider hierarchies. It has been said in the past that the Linnaean ranks form a hierarchy, and the tree of life is a hierarchy, and all we taxonomists need to do is to combine the two into one. This is what Hennig thought. But, as Knox (1998) has said, there are different sorts of hierarchies. Consider Fig. 2. The upper diagram shows a phylogeny, which can be represented as a hierarchy with the original ancestor at the top and the descendants on the lower line. If we convert this into a Venn diagram, the outer ring is the ancestral taxon and the descendant taxa are the small circles in the middle. The lower diagram shows the hierarchy of ranks of Linnaean classification, with “all taxa” at the top of the tree and the ancestral taxon just one of the units on the bottom line. In the upper hierarchy the top of the pyramid is a single taxon, the original species, and diversity increases as you move downwards, whereas in the other hierarchy the top of the pyramid represents the whole of the plant kingdom and diversity is the same at every level. There is no way that these hierarchies can be equated. They are incompatible.

ABSURDITIES

I have been having some correspondence recently with a zoologist who shares my views on paraphyletic taxa. He wrote a short time ago that it seemed very strange that such counter-intuitive ideas as those of our opponents had become so widely accepted. I liked the word “counter-intuitive”, which is a nice non-confrontational expression for something which is completely contrary to plain common sense. Unless there are some special-creationists in the audience, I think we all understand that evolution has continually been throwing up greater and greater diversification of plants and animals, and yet the cladistic idea of classification requires that all successive descendant groups have to have lower and

(a) Phylogeny



(b) Linnaean classification

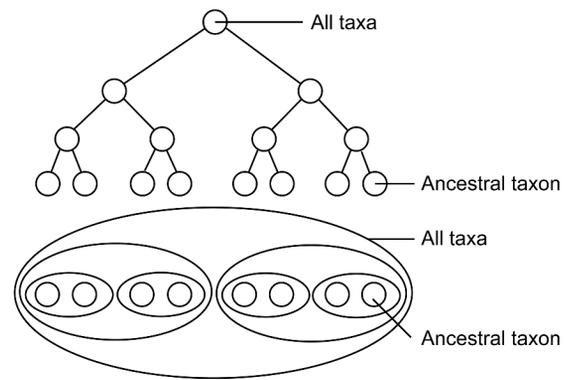


Fig. 2. Hierarchies and corresponding Venn diagrams for (a) phylogeny and (b) Linnaean classification.

lower taxonomic rank. Something which has evolved from within one genus must have a rank lower than genus. Is this view of taxonomy really a sensible idea? How can we apply lower and lower ranks when evolution is producing wider and wider variation? In a clade-based classification you can go on extending your clades as evolution progresses *ad infinitum*, but if you are using a traditional taxon-based classification you can't keep on giving them lower ranks. This is related to the incompatibility of the two hierarchies working in opposite directions in Fig. 2.

Every monophyletic genus we recognise in the tree of life must have arisen from a single species in a different genus, which must be paraphyletic; every monophyletic family we recognise has been descended from one species which is referable to one genus which is in a different family, and all must be paraphyletic; and so on. That is the nature of evolution, always producing bigger and more diverse groups from narrowly defined origins

(a species or population). So how can the taxonomic rank we give the products of evolution become successively lower? Is this not a silly idea? I wish those who argue for Linnaean ranks without paraphyletic taxa would answer these questions, but they never do so.

If we stand back and think of the whole line of evolution all the way from unicellular green algae to highly developed angiosperms, is it credible to suggest that we can classify this line into taxa in such a way that no genus ever evolved from within another genus, or one family ever evolved from within another family? That line of evolution would be just one long succession of paraphyletic taxa. Cladistic classification, without paraphyly, would mean that all the flowering plants would have to be included in one family in which we also place a lot of unicellular algae. Or supposing somebody were to discover at last a primitive angiosperm referable to the family and genus from which all the rest of the angiosperms evolved, perhaps as a fossil or perhaps even on some far hillside previously not explored, wouldn't we have to sink all the angiosperm families into that one family and genus? If we can't have paraphyletic taxa, these are the only logical conclusions. Do I convince you that this cladistic theory of classification is indeed open to serious question? If some still need some gentle convincing, I ought to remember to use the nice word "counter-intuitive" to describe the cladistic position. But I have to admit that in a recent publication (Brummitt, 1997) I actually used the word "crazy" instead, and on other occasions I have used the words "absurd", "daff", and "nonsensical". And I am afraid I have referred to the arguments of those who vainly try to equate two completely incompatible systems, as "futile mental gymnastics".

PRESSURES

I hope at least that you see why there is an inherent incompatibility between Linnaean classification and a system recognising only monophyletic groups. But in certain circles the pursuit of monophyly has become an obsession to the point of being almost a religion, as others have said often enough (e.g., Buck, 1986). If I am right and there is a fundamental fallacy in the idea of a Linnaean classification which recognises only monophyletic taxa, how is it that this idea has become so deeply ingrained into the thinking of one sector of the taxonomic community over the last 40 years? Is it just a case of he or she who shouts loudest wins? This might be a nice area of research for those who are interested in academic attitudes or the history of science. Hennig's book, translated into English in 1966, was very influential. He takes credit for introducing a rigorous methodol-

ogy into phylogenetic analysis, but his views on taxonomy were, in retrospect, naïve. Ernst Mayr has pointed out (Mayr, 1995) that Hennig fatally ignored Darwin's observation of 100 years earlier that evolutionary classification depends on two factors, descent and modification. Hennig ignored modification and thought classification could be based only on phylogeny irrespective of characters. He tried to equate the hierarchy of descent directly with the hierarchy of Linnaean classification, but, as I hope I have demonstrated, these are incompatible. But his book appeared after a decade or more when numerical taxonomy was the fashionable answer that would solve all our problems in systematics, and now the attractive ingredient of evolutionary reality was added to the scene.

As computer methods became widely adopted, Hennig's ideas seemed to offer objectivity to the study of systematics, and his ideas on taxonomy were followed blindly by many. Cutting-edge science embraced the idea of recognising only monophyletic taxa for 30 years or more. The advent of molecular data, which of course have enormously clarified relationships of taxa in the last decade, has unfortunately also fuelled this obsession with phylogeny as the predominant or only consideration for systematic work at the expense of characters. Very few authors have raised the obvious "counter-intuitive" aspects of the cladistic theory of classification for serious consideration, though the writings of Ernst Mayr, the critique of cladism by Cronquist (1987), and the paper by Sosef (1997) are notable among those that did.

However, the nagging incompatibility which had been noted by a few commentators over a longish period has now come to the fore. Hennig's views on classification (as distinct from phylogeny) are now increasingly seen as old-fashioned, and the *PhyloCode* is now catching the attention of the modern cutting-edge. I can understand that there are intense psychological pressures involved. We all find it difficult to change the habits of a lifetime. Those who like to think of themselves as being at the cutting-edge, who have practised and preached monophyly of Linnaean taxa all their life, naturally are not all going to accept easily that the whole theory behind their views is a logical impossibility. A whole generation of taxonomists has been reared on the dogma that all taxa have to be monophyletic, despite what I see as the obvious absurdity of this.

But they are now split. Those who can see the fundamental incompatibility and are prepared to go the whole hog in arguing for monophyly are now arguing for a clade-based classification governed by the *PhyloCode*. Those who want a taxon-based classification and do not like the idea of giving up formal ranks and binomial nomenclature are now seen to fall between two stools, and they try to justify their position with increasing diffi-

culty. They continue to think that monophyletic taxa, or clades, are more real and more predictive than paraphyletic taxa and therefore must be adopted throughout a classification at all cost, but they fail to see the absurdity of this in the light of evolution. I believe there is no middle way which will combine universal monophyly with formal Linnaean ranks, and this is now increasingly being realised. Why do you think the *PhyloCode* supporters would be advocating such revolutionary and disruptive—and some would say impractical—ideas as abandoning ranks and binomials if there were any logical way of retaining these and still having only monophyletic taxa?

PRACTICALITIES

I hope I have shown that the theoretical arguments for a completely monophyletic Linnaean system are illogical. But what happens at present in practice? One of the jobs I still do in the institution where I work is to convene what we fondly like to call the Family Planning Committee. This decides which plant families the institution should recognise (but not, I am glad to say, in which sequence they should be arranged). The group includes those who hope for only monophyletic families and those like me who see it differently. We had a preliminary meeting two years ago, and what struck me very forcibly at the time was the very high level of agreement there was in the whole group. Only a relatively small number of cases involving paraphyly were put aside for further consideration. I asked myself why it was that botanists with such widely divergent theoretical positions could come up with such a high level of *agreement*. The answer, I think, is that in dealing only with extant taxa we are looking only at the tips of the phylogenetic tree. Most of the twigs we want to cut off as families at the branch tips are both grades and clades, so there is no problem about everybody recognising them. Extinction has meant that we don't have to deal with the rest of the tree—unless of course we are classifying fossils. Then we would really have problems.

This probably applies at all taxonomic levels. It seems to me probable that perhaps 80% of extant taxa currently recognised at the major ranks of family, genus, and species will turn out to be both grades and clades and so will be acceptable to both sides of the argument. At the intermediate ranks of subfamily, subgenus, etc., I think the figure may be lower. So I am guessing that around 20–30% of traditionally recognised taxa may turn out to be paraphyletic. In a previous publication (Brummitt, 1996) I quoted from the zoological literature (Carroll, 1988: 14) an estimate that 50% of taxa are paraphyletic. Rieseberg & Brouillet (1994) speculated that

nearly 50% of plant species are not monophyletic. Similar estimates of up to 50% were given by Crisp & Chandler (1996) who accepted the inevitability of paraphyletic species, though not higher taxa. If my guess is about right, of the 20–30% paraphyletic taxa, perhaps half will cause only relatively mild arguments between the two different camps, but for the remaining 10–15% one group is going to say “This is ridiculous. No way am I going to accept this”. It is because the majority of traditionally recognised taxa will usually be monophyletic anyway that there has been a tendency for those wanting monophyly throughout to push for the final 20–30% as well. It is when this happens that, in my opinion, taxonomy starts to go off the rails. Excessive insistence on monophyletic taxa in this minority of cases promotes, I believe, poor or bad taxonomy.

EXAMPLES

Examples will occur at all levels in the hierarchy. At family level I cannot help referring to the case of Cactaceae and Portulacaceae reported on by Hershkovitz & Zimmer (1997) from work done at the Smithsonian. It seems that Cactaceae nest within Portulacaceae, so of course I asked my cladistically inclined colleagues what we should do about it. I was told that we cannot sink Cactaceae so we will have to split the Portulacaceae. But Portulacaceae are a very natural and easily recognised family, and there are no characters by which anyone has ever thought to divide it into two families. Furthermore, and to my delight, Cactaceae were found to nest within one previously recognised genus of Portulacaceae, *Talinum*. Here is the classic example, with a fairly large family nesting within what was at the time considered to be one genus. It matters not that the paraphyletic genus was actually split as a result of the study and that other authorities in the family are happy to accept this. The point is made, and when the classification of Portulacaceae settles down it seems certain that the whole of Cactaceae will nest at least within one tribe or subtribe of the family. If anyone wants to maintain the previous broad concept of *Talinum*, they will have to sink the whole of Cactaceae into the one genus. It is cases like this which emphasise the need to resist the obsession for universal monophyly in our existing classification. [Note added in proof: Applequist & Wallace (2001) have presented a further analysis of the Portulacaceae clade showing a somewhat different topology, but still commenting that the traditional concept of Portulacaceae is paraphyletic in respect to Cactaceae, and also to Didiereaceae.]

Even more striking family examples are provided by some aquatic families. The diminutive rapid-water-

loving Podostemaceae are now found to nest within my institution's concept of Clusiaceae, a family of largely broad-leaved trees and shrubs (Savolainen & al., 2000: 267). So are we to sink Podostemaceae into Clusiaceae? Another river-loving family, Hydrostachyaceae, with reduced flowers and finely divided leaves, are found to nest within Hydrangeaceae (Hempel & al., 1995; Xiang, 1999; Albach & al., 2001). These would also be very strange in one family. It is apparent that the aquatic habitat has wrought dramatic morphological changes on some of its inhabitants. Surely we have a right (or obligation) to recognise these as families.

At subfamily level there are many examples, but the one which caught my attention is in Compositae (Asteraceae) where I am told that Eupatorieae make the Heliantheae paraphyletic. So what? I very much hope we are not going to have the tribal classification totally upset by the cladistic dogma on monophyly. In legumes Caesalpinioideae are paraphyletic with respect to the other subfamilies. So what? Evolution had to start somewhere. Something always had to be the primitive group.

As an example at generic level, I can now quote my favourite genus, *Calystegia* in Convolvulaceae, which I am told makes *Convolvulus* paraphyletic according to the molecular data. There is nothing at all surprising in that, but I have no doubt that *Calystegia* is monophyletic and it differs from *Convolvulus* in having very strikingly different pollen, different ovary structure, and different corolla characters, while all but a few plesiomorphic species are even more readily recognised by their bracteoles, so there is no way I feel persuaded to sink them as one genus. That would be poor taxonomy. Other examples at generic rank abound. Probably many of the endemic genera of evolutionary hot spots such as Hawai'i would have to be sunk because their parental groups are still extant elsewhere.

Similarly at infrageneric levels. In the genus *Neuracanthus*, which I revised with my colleague Sally Bidgood a few years ago (Bidgood & Brummitt, 1998), we intuitively recognised three sections. Two were characterised by what we presumed to be apomorphies (reduction from four seeds to two in one, and development of conspicuous spiny inflorescences in the other). Our cladogram confirmed our natural thoughts, and the third section, which we intuitively thought of as being primitive, was thus doubly paraphyletic. I have said in the past (Brummitt, 1997) that this is a situation which may be expected to be found commonly wherever infrageneric ranks are recognised. When we asked our cladist colleagues how we should treat this taxonomically, we were told we could not recognise a paraphyletic section, so we should give formal names to the two monophyletic sections and refer to the third only by an informal name. We did not take the advice.

TINKERING

This last case illustrates one way how the old school now tries to by-pass the issue. Giving paraphyletic taxa only informal names has often been adopted in recent times at higher levels, and terms like "Dicotyledones" or "lower Asparagoids" have remained or become widely accepted where it has been thought desirable to refer to a paraphyletic group. But while at the higher levels nobody really cares too much what you call groups, adopting this approach below family level would, I think, be regarded as unacceptable and unnecessary by many people on practical grounds.

Another approach adopted particularly at higher ranks has been to avoid placing some taxa at all at some ranks. A recent paper discussing phylogenetic nomenclature within the Linnaean framework by Bremer (2000) has advocated extending use of this practice to generic rank. Some species would not be included in any genus, so "avoiding the danger of creating non-monophyletic genera and avoiding nomenclaturally redundant monotypic genera", though it is not clear whether this should be used expressly to avoid paraphyly. I wonder if we all think this would be good taxonomic practice.

Attempts to cling to the traditional ranks in the face of inherent difficulties only emphasise to me that it is a big mistake to think that the Linnaean ranks ever can be used for a monophyletic system. Can we not simply recognise the fundamental incompatibility of the two approaches, rather than try to force a square peg into a round hole? If people insist on monophyly, the clade-based *PhyloCode* will provide a logical solution. If they want to use the traditional ranks, the answer is very simple: recognise paraphyletic taxa. The absurdities of the Hennigian idea of classification would then be avoided. Tinkering around the edges of the established system will never resolve the problem, and I think will only debase the Linnaean method and perplex users.

CLADOGRAMS

You may have noticed that I base all my arguments on phylogenetic trees, not on cladograms. They are quite different things. A phylogenetic tree has a time axis, ancestors, and a stylised branching pattern showing descent, and is a diagram of what actually happened in evolution. A cladogram does not have a time axis or ancestors, and is merely a diagram of the inter-relationships of characters from which a range of possible ancestors and evolutionary relationships may be hypothesised. I assure you I have nothing against making cladograms. They are a very valuable way of analysing your data, which I have used in my own work. But it has been said

often enough that a cladogram may represent many different phylogenetic trees. Can true relationships not actually be hidden by cladograms? I think the situation in my Fig. 1 could easily appear in a cladogram as two sister taxa, with neither paraphyletic, if only extant taxa are analysed. To think only in terms of cladograms rather than phylogenetic trees may ignore many other evolutionary patterns and obscure reality.

I think it is because so many people think only in terms of cladograms, and not phylogenetic trees, that they cannot see the absurdity of what they are saying in arguing for universal monophyly in Linnaean classification. I don't want to push this point, but I do feel that it is often too superficial to simply chop up a cladogram into supposed clades (can one really call them clades if there are only extant taxa and no ancestors included in the analysis?) and assume that this makes either good taxonomy or an accurate representation of what actually happened in the evolution of the group. All I want to say is that there should be more to taxonomy than this, and I think a more critical assessment of what cladograms mean, both in terms of proving phylogeny and of creating a taxonomy, would often be welcome. Cladograms are not phylogenetic trees. They need interpretation. This must particularly be the case if my views on paraphyletic taxa are correct.

Furthermore, if our taxonomy at specific level in the 21st century is going to be dominated by cladograms, we should note the warning of Sosef (1997) that in many cases the concept of clades does not apply because of reticulate evolution through past interspecific hybridisation. Cladograms then become meaningless in terms of monophyly. But we often see cladograms published in papers on species-level taxonomy together with claims that clades can be recognised within them. It seems to me that assumptions that such cladograms accurately reflect phylogeny of the group must often be very naïve, but the journals continue to publish new taxonomies based on them. Sosef's final thoughts are also worth repeating: "The quest for monophyletic taxa and the splitting of former paraphyletic ones should halt immediately, as they unnecessarily deteriorate classifications which will often prove to be valid". Amen to that.

ADVANTAGES

Although the preference for monophyletic taxa has been loudly trumpeted for several decades, I am not sure that the advantages have necessarily been proven. The matter has been too often emotive rather than rational. Linnaean classification chops the tree so that the parts (taxa) have the greatest possible attributes in common. The monophyletic system divides the tree according to

lines of descent. The difference was emphasised recently by Mayr (1997: 143–146) when he noted that sister groups to a taxon, even though genetically more closely related to that taxon than are its far distant descendants, may be excluded from a clade which embraces that taxon and the distant progeny. Or as Mayr put it "According to cladistic principles, the modern descendants of Charlemagne are more closely related to him than he was to his brothers and sisters". I call this the principle of Charlemagne's family. I have no idea why Ernst Mayr used Charlemagne as the eponymous hero.

To put it in a more extreme botanical context, there is (or was) a unicellular green alga that a cladistic classification would group with its distant descendants the Compositae (Asteraceae) before it would place it with its own sister unicellular alga. Is this sort of thing necessarily desirable in a classification? Again, I think serious questions have to be raised. A Linnaean classification would certainly place the two unicellular algae nearer to each other than either would be to the Compositae. Does that not have something to commend it? Are we sure that the cladistic classification will always be more predictive than the Linnaean one? Recognisability has often also been stressed as a factor for delimiting taxa. Are families based on long phylogenetic lineages as recognisable to users of taxonomy as families defined by possession of characters? I doubt it. The *PhyloCode* is not just a new nomenclatural system; it also requires a classification which is different from that traditionally used.

The practicalities of recognising paraphyletic taxa have been discussed recently by Ghiselin (1997: 185–189), who added an aphorism (p. 307) that "Systems with paraphyletic taxa may be simpler, better in accord with vernacular language, and more conveniently expressive of features deemed important (such as major changes in organisation)", as already quoted by Moore (1998). The practical advantages he found included bringing scientific terminology into line with the vernacular, but also extended as far as his filing system for reprints.

PHYLOCODE

If we are talking about cataloguing biodiversity or providing a general purpose reference system for the plant (or animal) kingdom, with convenient names as handles, I have no doubt that the traditional Linnaean system is vastly superior to that offered by the *PhyloCode*. Phylogeny is of interest, of course, and is an essential part of systematic research, but it is a different thing from a classification. And it is not necessary to abandon Linnaean classification and paraphyletic taxa in order to make a phylogeny available to users. One can

have a phylogenetic tree and mark on it the various taxa, so getting the best of both worlds—a classification which places like with like and a phylogeny showing lines of descent.

The *PhyloCode* is an interesting intellectual exercise, but is it a realistic practical alternative to what we have always done? If people feel the need to name clades, then it is difficult to argue that they should not do so, but they should not think this is going to displace traditional classification, particularly at the lower taxonomic ranks. It is not going to do so. I personally am not convinced of the need for the *PhyloCode* at all, although I might consider whether some of its principles could be useful above family rank (where already the principle of priority of publication does not apply under the present International Code). But at least there is a logic behind the *PhyloCode* which is lacking for attempts at Linnaean classification into monophyletic taxa. I think that what is currently being proposed would at best be a parallel development alongside the Linnaean system, as acknowledged as inevitable at least in the short term by its supporters (Cantino, 2000). But do we really have to have two systems simultaneously? Are we trying to confuse all of the people all of the time?

The lack of ranks and binomials is, I think, an insuperable barrier to the present *PhyloCode* ever being a day-to-day system for general use. It lacks the clear structure and convenient names of our traditional classification. In the long term, the disruption that displacing the present nomenclature would bring to information retrieval and to scientific and non-scientific communications about plants would be a horrific prospect. Any hopes that it would introduce greater stability to names of plants are, I think, just wishful thinking, for few of the nomenclatural problems that I have to deal with on a daily basis have any solution in the *PhyloCode*. We would surely just add a new set of problems to that already existing. And recognising clades rather than grades runs contrary to man's natural instincts. Linnaean classification and nomenclature offer a well established, well ordered, relatively easily comprehended and communicated series of reference points for plants for a multitude of practical purposes. The *PhyloCode* emphasises phylogeny at the expense of practicality.

I would like to mention briefly one other disadvantage to recognising only clades. Paraphyletic groups exist, defined by characters, and it is often desirable to refer to them. How does one do this in a clade-based system? Capparaceae are paraphyletic with respect to Cruciferae. If we name the clades Cruciferae sensu lato and Cruciferae sensu stricto (with whatever names the *PhyloCode* comes up with for them), how do we tell somebody that a plant belongs among the 42 or so genera we now call Capparaceae? It seems that the only way to

refer to this group is to say that it is referable to the big clade but not to the little clade. This problem will occur at all levels. So the accurate placement of any plant will have to be in terms not of a single name but in the form of “clade X excluding clade Y”. This is very cumbersome and impracticable. The same difficulty applies, of course, when attempts are made to use Linnaean ranks in a wholly monophyletic system, but those who advocate sinking families seldom bother to tell us what the resulting infrafamilial classification is going to be. The adoption of paraphyletic taxa in a Linnaean system overcomes all such problems and gives a maximally practical way of classifying and naming plants.

Of course taxonomy must always keep modern methods and ideas in mind. Cladistic analysis and use of micromorphological and molecular data are now standard procedures alongside traditional methods. But new ideas are not necessarily good ideas, and we should beware of being pushed into things just because they seem to represent cutting-edge science. As I see it, at the moment we have half of the supposed cutting-edge in taxonomy still pursuing a theory which is a logical impossibility, and the other half leading us towards taxonomic and nomenclatural chaos. Perhaps our Health and Safety regulations should include a warning that cutting-edges can be dangerous.

Those who dislike the way things are going have an obligation to express their views loudly and not merely accept the latest fashions. The dogma of monophyly and the *PhyloCode* both need our very critical assessment if taxonomy is to get back on the rails.

PARAPHYLY

Now I would just like to return quickly to the question of paraphyletic taxa and refer back to Fig. 1. This is a picture of paraphyly. It is a situation which must have arisen very many times in evolution. Within the bigger clade we have a smaller one easily recognised by a suite of characters which arose at the point marked 1, the other descendants being changed little or not at all. How may we treat this situation taxonomically? If I have some opponents, I hope they will answer this question for me. I mentioned earlier Arthur Cronquist's well known critique of cladistics (Cronquist, 1987), in which he said that paraphyletic taxa have to be recognised. In one of the replies he got to his paper, two commentators implied that even if the derived group (dark circles) differs by 50 or 100 characters from the parental group, it cannot be recognised in a classification at the same rank as the parental group because the latter would be paraphyletic. What they meant, of course, was that possession of 100 characters does not put a derived group into a different

clade, which is obvious, but they hopelessly confused phylogeny with classification, which is what Cronquist was talking about.

Now, I have been a taxonomist and Flora-writer for over 40 years, and if I have to key out two genera I often consider myself mighty lucky to find a couple of good characters to use in the key. Is somebody now telling me that even if there are 100 characters to separate these groups, I still can't make them two genera because one is going to be paraphyletic? What is going on here? How does a normally reserved Englishman express his reactions to this to an American audience? Do I just say, "Oh deary me, this does seem to be a little bit disturbing!"? Do I look for slightly stronger words to attract your concern? Or do I borrow some phrases from your own sporting heroes who come over to Britain and take away all our silverware? What was it Mr. MacEnroe taught us? "You can *not* be serious. Man, you can *not* be *serious*. This is the pits! The ball was on the line. The chalk flew up. Everyone here could see it. Just open your eyes". So if this clade has got 100 characters to distinguish it, to hell with calling it a genus, I'm gonna make a new family at least.

This situation arises all over the place. A classification has to be based on characters. If you say you cannot give a group like this the same rank as the ancestral group no matter how many characters you have, it means you are effectively eliminating characters and relying solely on phylogeny to create your classification, when, as Knox (1998) has pointed out, a phylogeny has no classes. So everything collapses into one original taxon. If you can't use characters to recognise newly evolved groups as taxa, you are denying that any new taxa have ever arisen in evolution. You are denying evolution! If anyone thinks that families and genera in a classification did not arise from within other families and genera in the classification, we really have got some special creationists!

Think of these two groups in Fig. 1 as Cactaceae (dark circles) and Portulacaceae that we were talking about. If you decide on sinking, you can't make them two subfamilies, because then Portulacoideae are just as paraphyletic as the family Portulacaceae was, or even two tribes for the same reason. If you decide on splitting the Portulacaceae into two in the curious hope that the Cactaceae will fall through the gap between them and not nest in anything, there are no characters that any sensible taxonomist would ever use to recognise families. Why should there be any reason to expect that there will be characters to split the Portulacaceae into two families at this point just because the Cactaceae took off from here? It makes no sense to me. The bottom line in interpreting Fig. 1 must surely be: *If you have good characters you should recognise good taxa; if you have no characters*

you shouldn't recognise taxa at all. To me the whole idea of cladistic classification into Linnaean taxa without any being paraphyletic is a logical absurdity. Or do I have to remember to be nice and say "counter-intuitive"?

CONCLUSIONS

In conclusion, I refer again to the final sentence of the paper by Woodger (1952) that I quoted earlier: "The taxonomic system and the evolutionary phylogenetic scheme are quite different things doing quite different jobs, and only confusion will arise from identifying or mixing them". As I see it, taxonomy has got itself in a mess over the last 30 or 40 years through not understanding this. But now that so many people are talking about the incompatibility of the two ways of chopping up the tree, the message is coming home. Certainly we need both a classification and a phylogeny, but we need to keep them separate and decide which we need for different purposes. I hope those tempted by the *PhyloCode* will give this serious thought.

For some decades, paraphyletic taxa have received a very bad press in certain quarters of the taxonomic community. There have even been T-shirts printed about it. But, as I suggested in my introduction, I think there has always been a substantial part of the community that is perfectly happy to accept paraphyletic taxa. When I recently asked the committee of the Species Plantarum Project whether we should be considering an account of Cruciferae (Brassicaceae) to include Capparaceae, which are paraphyletic in respect to Cruciferae, there was not one among 23 members present who supported combining the two families. We need to reverse the bad press and make paraphyletic taxa perfectly socially acceptable to all. They should even be acceptable in doctoral theses. They are after all just a product of the evolutionary process, what is left behind as evolution moves on to a new level of organisation. Perhaps we now need a counter T-shirt campaign saying "Evolution is parapyly all the way". Or have you other suggestions?

Four years ago I felt confident enough of my arguments to challenge one of my opponents to a debate at the Linnean Society of London. The motion was thought up by a colleague, not me, and was "That this House considers that Linnaean classification without paraphyletic taxa is nonsensical". To the surprise of many people, this motion was passed by a vote of 69 in favour to 43 against. When the vote was announced, three people present separately said to me that the only surprising thing was that 43 people could vote against the motion. But old habits die hard, and one still sees statements in taxonomic papers that genus A nests within genus B and therefore has to be sunk irrespective of the

characters by which it is distinguished. This is why I said I thought that our taxonomy was going off the rails. However, I think the pendulum is swinging away from what I call the old-fashioned Hennigian view of taxonomy into a more modern and realistic view appropriate for the 21st century. If I have done anything here to give the pendulum a little further push, and if I have commented sensibly on the *PhyloCode*, I shall be happy.

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