Stems, nodes, crown clades, and rank-free lists: is Linnaeus dead?

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ABSTRACT

Recent radical proposals to overhaul the methods of biological classification are reviewed. The proposals of phylogenetic nomenclature are to translate cladistic phylogenies directly into classifications, and to define taxon names in terms of clades. The method has a number of radical consequences for biologists: taxon names must depend rigidly on the particular cladogram favoured at the moment, familiar names may be reassigned to unfamiliar groupings, Linnaean category terms (e.g. phylum, order, family) are abandoned, and the Linnaean binomen (e.g. *Homo sapiens*) is abandoned. The tenets of phylogenetic nomenclature have gained strong support among some vocal theoreticians, and rigid principles for legislative control of clade names and definitions have been outlined in the PhyloCode. The consequences of this semantic maelstrom have not been worked out. In practice, phylogenetic nomenclature will be disastrous, promoting confusion and instability, and it should be abandoned. It is based on a fundamental misunderstanding of the difference between a phylogeny (which is real) and a classification (which is utilitarian). Under the new view, classifications are identical to phylogenies, and so the proponents of phylogenetic nomenclature will end up abandoning classifications altogether.

Key words: Systematics, classification, phylogeny, clade, cladistics, Linnaeus, PhyloCode, taxonomy, nomenclature.

CONTENTS

I. INTRODUCTION

'In taxonomy, stability is ignorance' (Dominguez & Wheeler, 1997; Gaffney, 1979).
'Linnean binomial nomenclature is logically incompatible with … phylogenetic nomenclature' (Cantino *et al.*, 1999).

The classification of life is an important business.

Systematists argue for the importance of a proper understanding of the relationships of organisms as the basic evidence of evolution, and there are practical applications in properly documenting biodiversity locally or globally and in understanding organism-mediated diseases of humans and crops.

Classification and systematics, once denigrated as mere stamp-collecting or librarianship, have enjoyed a dramatic renaissance in the past 20 years (Hillis, 1997), partly driven by need, and largely driven by the development of new rigorous approaches such as cladistics and the use of molecular characters.

Changes in the methods of systematics have brought in their train a number of revolutionary proposals about the mechanics of classification. The claim has been that the principles of phylogenetic nomenclature (de Queiroz & Gauthier, 1992, 1994) will produce stability in classification, but that claim has been debated. The principles have been developed into a new code of practice (the so-called PhyloCode), and they have been applied vigorously notably by some vertebrate palaeontologists and botanists; now is a good time to review whether they work or not. These proposals would not only affect the community of practising systematists, but everyone who buys a bird book or reads a newspaper report about a new dinosaur discovery. They could really put the cat among the avialian theropods.

The starting points for the modern classification of plants and animals are the comprehensive works of Carolus Linnaeus, or Carl Linné, published in 1753 (Linnaeus, 1753) and 1758 (Linnaeus, 1758), respectively). The importance of these fundamental works, selected by international agreement (International codes, 1992, 1994, 1999), is not so much the listings of animals and plants that Linnaeus gave, but the establishment of a simple scheme for naming organisms and for presenting classification lists. From the works of Linnaeus stem three principles: the binomen, priority, and hierarchical categories. After 1753, every species has been represented by a binomen, a two-part name consisting of the genus and species epithet, such as *Homo sapiens* for the modern human species. The principle of priority has been equally important, that the first-published name for an organism, or group, is the one that is used, except in cases where the first-given name has not been used for 50 years (ICZN Code 1999, article 23.9). Third, the notion of an inclusive hierarchy of group names has also been critical, where each species is contained within a genus, each genus within a family, and so on up through a standard series: order, class, phylum, kingdom.

The purpose of this review is to dissect the principles of phylogenetic nomenclature, and to suggest that they can be discounted as unnecessary and confusing. The tendency of the new idea has already led to the abandonment of the concept of the genus and species. The next logical step is to abandon classification altogether, and to refer simply to cladograms. Before we make this absurd step, it may be worth stopping to consider a little.

II. PHYLOGENY IS REAL, CLASSIFICATIONS ARE NOT

The phylogeny of life is real. There is a single evolutionary tree linking all organisms living and extinct (Darwin, 1859), and relationships are measurable entities that depend on the relative time since any pair of organisms last shared a common ancestor. The key methods for discovering phylogenies are cladistic analysis of morphological characters and phenetic, cladistic, or maximum-likelihood analysis of molecular characters. Like most biologists, I accept that phylogeny reflects the reality of evolution by natural selection, that branching points are the result of real splitting events, and that clades are based on common ancestry. However, no-one can ever see the shape of the tree or put their finger on an ancestor. Cladistics is a method to obtain hypothetical knowledge of relative relationships among organisms, and it is always open to test and change or refinement.

Biological classifications, then, are necessarily entirely human constructs. There is no single, true classification inherent in Nature that is there to be discovered. In this paper, I use the term 'classification' in two ways, as is common practice: first, *a classification* means an ordered list of species or higher taxa, and second, *classification* describes the process of achieving such an ordered list. The usages should be clear from context.

The urge to classify is a deep-seated human attribute. There are different kinds of phenomena in Nature, some discrete and some continuous in character, and classifications must take account of those differences. The chemical elements are discrete and real, and they have discrete and real properties that transcend time, so the separation of one element from another in a classification is inescapable. The ways in which the elements are grouped in the periodic table followed fixed, discrete, and unequivocal properties, like the atomic number. Other higher-order groupings are, however, arbitrary and utilitarian, for example the metals or the rare earth elements. At the other end of the scale is geological time; this is a continuous phenomenon, and there are no essential indicators of how to classify or divide it. The divisions between the geological eras, periods, epochs, stages, zones, and subzones are entirely

arbitrary. Given a different historical development of the science of stratigraphy, the divisions could well have been made in an entirely different way. The divisions of geological time do, however, have agreed international definitions, established by rigid legalistic means, the purpose of which is to maximize their utility.

Biological classifications fall somewhere between the two extremes of the chemical elements and geological time. Most biologists accept that species are real (Darwin, 1859; Huxley, 1940), allowing of course for the complications of incipient species, hybrids, sibling species, and the like. The 'reality' of species is different from that of the chemical elements in many ways, not least in the fact that they are linked by historical lines of descent (Darwin, 1859), and that their existence is finite in time. Equally, larger clades (assemblages of species that all arose from a single common ancestor) are real in that they contain certain species, and not others. These considerations show that it is inappropriate to impose a rigid nomenclatural and definitional system, as if species and clades were static fundamental entities that can be circumscribed once and for all on the basis of inherent law-like properties.

Biological classifications have two functions (Mayr, 1982): practical (to serve as a universal reference system) and general (= evolutionary; the hierarchical structure has immense value in comparative evolutionary biology). The relative importance of these two functions has waxed and waned through time. From the start, classifications were seen to reflect real patterns in Nature, and Darwin (1859) argued eloquently that those real patterns were the result of evolution. Darwin's successors often continued to emphasize utilitarian aspects of classifications. Gilmour (1940), for example, contrasted natural classifications with artificial systems. Artificial groupings of organisms might include succulents, annual plants, flying animals, or poisonous animals. Members of each class share only one or two characteristics, and these groupings therefore have only limited utility. Natural classes are founded on larger numbers of common attributes, and therefore a natural classification has much wider utility. Gilmour (1940) accepted that the natural pattern usually, but not always, arose through evolution. Huxley (1940) took a more Darwinian line, but still argued that classifications of organisms should have 'practical convenience' as well as a close regard for the best current estimate of phylogeny.

The utility-evolutionary tension in definitions of

classifications persisted after these early manifestations of the Modern Synthesis. Mayr (1942, pp. 276–7) was strongly of the view that classifications should be phylogenetic:

Every phylogenetic category should thus, ideally, be monophyletic. Such a phylogenetic system has two advantages: first, it is the only system that has a sound theoretical basis…, and secondly, it has the practical advantage of combining forms…that have the greatest number of characters in common…It is one of the aims of taxonomy to establish and recognize only such categories of classification as are based on phylogenetic relationship. Existing classifications will fall short of this ideal, to a lesser or greater degree, partly for lack of data and partly on account of the impossibility of presenting a phylogenetic tree in a linear sequence.

Simpson (1961, p. 112) similarly argued that classifications should reflect phylogeny, and that they should be updated when new knowledge became available. But he also stressed that: 'A published classification in current use should be changed when it is definitely inconsistent with known facts and accepted principles, but only as far as necessary to bring it into consistency.'

The advent of cladistics might have led to dramatic changes in the rules of biological classification, but it did not. Hennig (1966) proposed a system of numbering instead of ranks, but that scheme was not widely adopted. After much careful work to bring classifications closely into line with cladograms, Eldredge and Cracraft (1980) and Wiley (1981) found that no dramatic changes to classical Linnaean nomenclature were required. Various conventions, such as indented lists, sequencing, and use of plesions for fossil taxa, allowed fully cladistic classifications that retained familiar elements (Patterson & Rosen, 1977). The need for conservatism was stressed, since there was nothing to be gained by making wholesale changes to group names and ranks, if an established classification could be matched to the cladogram by use of some minimal conventions.

The new ideas about classification embodied in the PhyloCode have been presented in a series of papers which have used the terms phylogenetic systematics, phylogenetic taxonomy, and phylogenetic nomenclature. In order to avoid confusion, I shall use the strict term phylogenetic nomenclature to refer to the new system, the practice now followed by the reformist group (Cantino *et al.* 1999). This is correct, and it should help to avoid confusion, since the term 'phylogenetic systematics' is sometimes equated simply with cladistics, and even 'phylo-

genetic taxonomy' could refer to the practice of cladistics by someone who adheres fully to the Linnaean system of nomenclature. The PhyloCode proposals have already been criticized strongly by Brummitt (1997, 1999), who also argues for the retention of paraphyletic taxa in classifications. These are two separate issues: I feel free to reject the PhyloCode, while also preferring to avoid paraphyletic taxa as far as possible.

Much of the debate about phylogenetic nomenclature revolves around the idea of stability, whether stability of content of a named taxon or stability of the taxon name. Linnaean nomenclature achieves the former, phylogenetic nomenclature the latter. Classifications are meant to represent the best current estimate of phylogeny, but they should not drift and evolve infinitely in response to every debate on phylogeny. If classifications slavishly follow such debates, they serve no purpose at all, and they should be dispensed with entirely. In the past 200 years, classifications have tended to change only after some major landmark publication that lays out universally convincing evidence that the previous notion of phylogeny was in error. Changes in accepted classifications, even for much-discussed groups, like roses, birds, or butterflies, have happened only two or three times per century at most. This could be ascribed to human frailty; the fear of the unfamiliar, laziness, or stubbornness. But then classifications have only one purpose: utility. If they lack stability and familiarity, they entirely lack utility.

Phylogenetic nomenclature seeks to remove classification from the realms of utility to the philosophical fastnesses of the rigid pursuit of cladogram shape. In other words, classification equals phylogeny and, in the new view, they really have no independent purpose at all. It is worth looking at the claims of the new method, and to explore whether it works in practice.

III. PHYLOGENETIC NOMENCLATURE

De Queiroz and Gauthier have argued, in a number of papers (de Queiroz & Donoghue, 1988, 1990; de Queiroz & Gauthier, 1990, 1992, 1994; de Queiroz, 1997), that the Linnaean system of nomenclature is non-evolutionary, and that it lacks explicitness, universality, and stability, four features that are claimed of phylogenetic nomenclature.

The argument that Linnaean nomenclature is non-evolutionary is partly word-play, as de Queiroz & Gauthier (1994) admit: Linnaeus of course formulated his principles a hundred years before Darwin (1859), but they have been modified and codified since then, and systematists in the twentieth century have been content with both evolution and with the Linnaean system (Huxley, 1940; Mayr, 1942; Simpson, 1961; Eldredge & Cracraft, 1980; Wiley, 1981). Linnaean nomenclature has been modified both before the advent of cladistics (e.g. exclusion of polphyletic taxa, insertion of additional category terms, inclusion of fossil taxa), and after (e.g. exclusion of paraphyletic taxa, use of indented lists, sequencing, plesions). All these modifications have shared a common principle: that classifications should adhere ever closer to current knowledge of phylogeny, while at the same time remaining conservative.

The PhyloCode has been presented as the next logical step in this succession, from pre-Darwinian, to Darwinian, to cladistic, and now to phylogenetic nomenclature. But the authors of the PhyloCode forget that classification has a phylogenetic *and* a utilitarian function. They assume that classification equals phylogeny. In their agonizing over how to strip out all the inconsistencies in achieving that identity, they have progressively abandoned modifiable taxon definitions, Linnaean ranks, and the species binomen (some even abandon the notion of species as entities), and the next logical step is clearly to abandon classification. They are welcome to it. The wider working world will not be drawn into this downward whirlpool (Brummitt, 1997, 1999). Intelligent people can well cope with pluralism: the search to identify the one true phylogeny, and the acceptance of classifications that reflect that phylogeny, but which retain utilitarian properties (species binomina, ranks, flexible clade definitions).

This consideration should be enough to put an end to the PhyloCode, but it is worth dissecting the principles of phylogenetic nomenclature to see whether it offers the superior qualities that are claimed for it. The focus will shift to the claim that phylogenetic nomenclature is more explicit, universal, and stable than Linnaean nomenclature.

(1) Background to phylogenetic nomenclature

The key proposal in phylogenetic nomenclature is that the names of taxa should be defined with reference to common ancestry, which can be done by referring to characters or to subordinate taxa. The latter method is preferred. So, traditionally, the Class Aves, birds, has been defined in terms of a
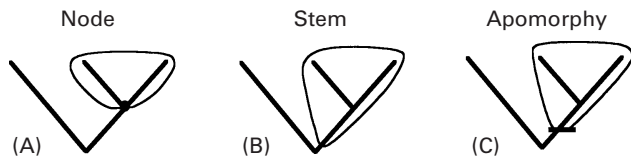
Fig. 1. The three kinds of clade definition, node-based (A), stem-based (B), and apomorphy-based (C). A node-based clade (A) is defined as the most recent common ancestor of two species, or clades, and all other descendants of that ancestor (e.g. Neornithes is the clade stemming from the most recent common ancestor of *Struthio camelus* and *Passer domesticus*). A stem-based clade (B) is defined as all species sharing a more recent common ancestor with one specified organism than with another (e.g. Avialae is the clade consisting of Neornithes and all maniraptorans closer to them than to *Deinonychus*). An apomorphy-based clade (C) is defined as the clade consisting of all organisms to share a particular unique character (e.g. Aves is the clade stemming from the first vertebrate to evolve flight feathers and wings).

number of characters, such as the possession of feathers or wings. This, it is argued, leads to confusion: ornithologists might include only living birds in their taxon Aves, while palaeontologists would include also a string of fossil forms back to *Archaeopteryx* which, fortuitously, has feathers preserved in the fossils. New discoveries, however, show that certain bird-like dinosaurs had feather-like structures (Ji *et al.*, 1998), and even some rather non-bird-like dinosaurs may have had feathers (Xu, Tang & Wang, 1999). Are these to be called birds or not? This is the kind of confusion that leads de Queiroz and Gauthier (1992, 1994) to reject such apomorphy (= character)-based definitions (Fig. 1), and to argue that the classical system is not explicit, universal, or stable.

Character-based definitions of supraspecific taxa were used by Linnaeus (1753, 1758), although the various international codes (1992, 1994, 1999) do not clarify this point. Formally, there is limited advice about how to define taxa above the species level, such as genera, families, or orders, although in practice all systematists have used diagnoses consisting of characters. With the advent of cladistics, such diagnoses have been reformulated to include only apomorphies. It is simple to do this, without rejecting common practice (Lee, 1998): clades can readily be defined unequivocally by reference to an apomorphy, or homologue, of a reference taxon.

The preferred approach in phylogenetic nomenclature is to employ a node-based or stem-based definition (Fig. 1). Instead of defining the taxon Aves in terms of one or more characters, it can be defined with reference to two included taxa. For example, Aves could be defined as 'the clade stemming from the most recent common ancestor of *Struthio camelus* and *Passer domesticus*', in other words, the taxon that stemmed from the common ancestor of the ostrich and the sparrow, and that includes all descendants of that common ancestor. This definition has engineered two changes: first, it is node-based, and second, it is a crown-clade definition, a secondary controversial claim of the new method to which we shall return later. In fact, Class Aves can be given a node-based definition that makes it equivalent to the commonly accepted taxon, namely 'Class Aves is the clade stemming from the most recent common ancestor of *Archaeopteryx* and the sparrow'.

Stem-based taxa are defined in terms of closer relationship to one species than another. Hence, in the bird example (Fig. 2), a stem-based clade Avialae might be invoked to encompass putative fossil birds that had feathers and wings, but were more primitive than *Archaeopteryx* (Padian, Hutchinson & Holtz, 1999). The formal definition of such a stem-based Avialae can then be given as either '*Passer domesticus* and all maniraptorans closer to it than to *Deinonychus*' or 'Neornithes and all maniraptorans closer to them than to *Deinonychus*', the formulation given by Padian *et al.* (1999).

(2) Explicit, universal, and stable?

This simple example must be dissected in detail to examine whether the new definitions are more explicit, universal, and stable than the old. There are numerous current cladograms of birds and their nearest relatives among theropod dinosaurs. Two are shown in Fig. 2, published essentially concurrently (Padian *et al.*, 1999; Sereno, 1998), and representing equally valid, but different, resolutions of current knowledge. Sereno (1999*a*) has already come back with further redefinitions and clarifications of his nomenclatural scheme, and no doubt the discussion will spiral endlessly. In presenting these cladograms, Sereno (1998) and Padian *et al.* (1999) gave explicitly phylogenetic definitions of clade terms. However, two features are clear: the two cladograms demand different nomenclature where the postulated relationships differ, and identical nodes have been given a range of names.

Among birds, both authors agree on the outline of relationships, and yet the node termed Euornithes by Sereno (1998) is termed Ornithurae by Padian *et al.* (1999). Two nodes un-named by one author are
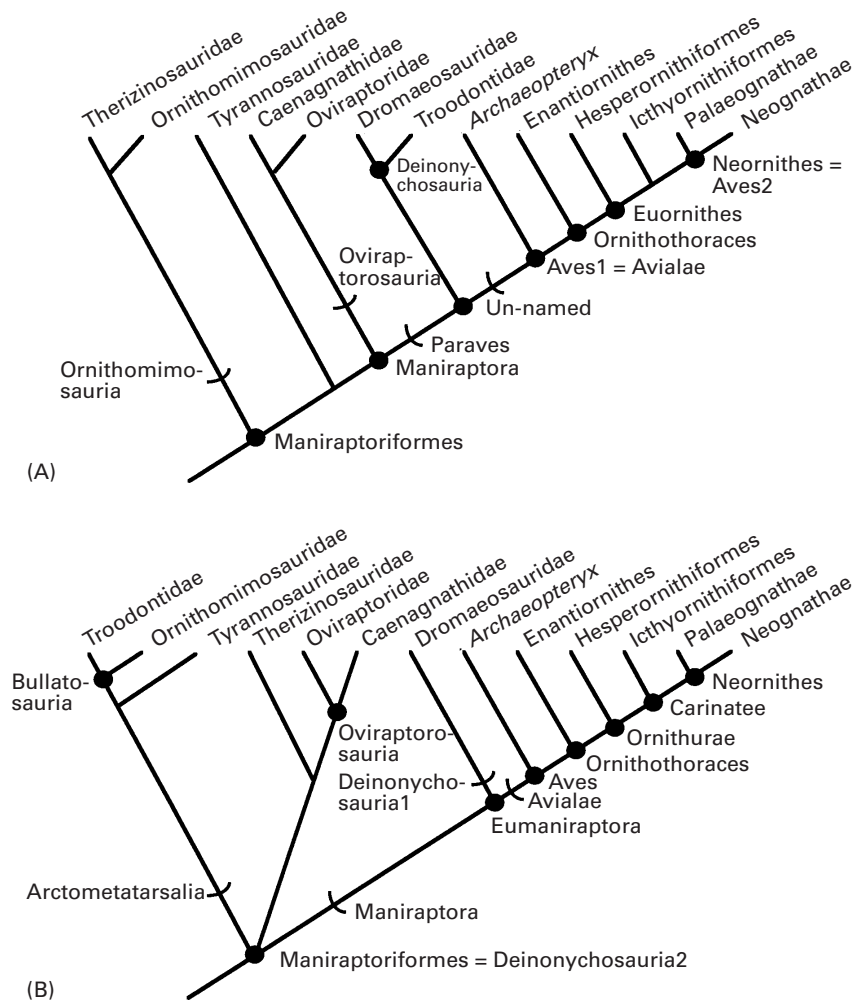
Fig. 2. Comparison of two current cladograms of basal birds and their theropod dinosaur relatives, based on the publications by (A) Sereno (1998) and (B) Padian *et al.* (1999). Node- and stem-based names are shown by solid dots and crescent shapes, respectively, based on definitions given by those two authors. Some disputed terms are also indicated.

named by the other, so there is no confusion there. Both authors agree in using the long-established taxon name Aves to refer to a clade containing birds fossil and Recent, hence *Archaeopteryx*, the sparrow, and everything else in between. However, this is disputed. Gauthier (1986) argued strongly that the term Aves should be restricted to living birds and their subtended ancestors, but that fossil forms lying outside the group defined by ostrich and sparrow, their common ancestor, and all of its descendants, should be excluded. Thus, the term Aves currently has at least two distinct node-based definitions. Crown-clade Aves (Aves2; Fig. 2A) is exactly equivalent in position to Neornithes, and a new taxon term, Avialae, was established to replace the more usual Aves clade name (Aves1; Fig. 2A). Further confusion exists in that Padian *et al.* (1999)

have co-opted the term Avialae, used in a node-based sense by Gauthier (1986) and others, to become a stem-based taxon that includes all bird-like organisms, known and yet to be found, that are more closely related to Aves (or to the sparrow, or to Neornithes) than to deinonychosaurs (or *Deinonychus*).

The definitions of node-based and stem-based taxa can differ, and those differences can have profound effects on their interpretations when applied to conflicting cladograms, as becomes evident when real-life examples are tried (Sereno, 1998; Padian *et al.*, 1999). For example, Sereno (1998) defines a new stem-based taxon Paraves as 'all maniraptorans closer to Neornithes than to *Oviraptor*', and his intention can be seen in Fig. 2A. On the second cladogram (Fig. 2B), stem-based Paraves

is equivalent to stem-based Maniraptora, and hence redundant. Indeed, it is virtually impossible to apply to the second cladogram, since Sereno's (1998) definition makes Paraves a subset of Maniraptora, but Maniraptora of Padian *et al.* (1999) is quite different in content, excluding as it does Oviraptoridae, Caenagnathidae, and Troodontidae.

A second taxon name defined by Sereno (1998), Deinonychosauria, is similarly hard to translate to Padian's cladogram (Fig. 2B). In its first formulation, Deinonychosauria is defined as a node-based taxon consisting of '*Troodon, Velociraptor*, their most recent common ancestor and all descendants'. In the intended version (Fig. 2A), this is a group that includes two families, Troodontidae and Dromaeosauridae. Padian *et al.* (1999) independently redefined Deinonychosauria as a stem-based taxon to include Dromaeosauridae and all other taxa closer to it than to Avialae (Deinonychosauria1; Fig. 2B). Sereno's (1998) definition, when applied to Padian *et al.*'s (1999) cladogram makes Deinonychosauria a much larger concept, essentially equivalent to Maniraptoriformes (Deinonychosauria2; Fig. 2B). Similar confusions arise over clade terms such as Ornithomimosauria (Fig. 2A), Arctometatarsalia (Fig. 2B), and Bullatosauria (Fig. 2B), which are hard to shoehorn onto the other cladogram: if such terms are used, they must always be quoted with reference to the meaning of one or other author.

A further confusion can arise over the exact formulation of terms, where the vicissitudes of author choice can create a monster can of worms. An unnamed node in Sereno's (1998) cladogram (Unnamed; Fig. 2A), identified as Eumaniraptora by Padian *et al.* (1999), could have been given a name defined in nine ways, of which only the first three will be given: (1) 'Deinonychosauria, Neornithes, their most recent common ancestor and all descendants'; (2) '*Deinonychus*, Neornithes, their most recent common ancestor and all descendants'; (3) '*Troodon*, Neornithes, their most recent common ancestor and all descendants'.

If 'Neornithes' is replaced by a genus or species name, such as *Struthio* or *Passer*, a further six formulations could be generated. In this case, potential node-based definitions of Eumaniraptora/ Un-named could enter the millions, depending on which particular pairings of species of troodontids, dromaeosaurids, and birds were selected. However, the implications of each can be utterly different on a different cladogram. The first definition equates to either Eumaniraptora or Maniraptoriformes in cladogram 2 (Fig. 2B), depending on the definition

of Deinonychosauria that is accepted. The second definition is clearly the same as Padian *et al.*'s (1999) Eumaniraptora (Fig. 2B), while the third is the same as their Maniraptoriformes (Fig. 2B). Such variation is inevitable, dependent entirely on the vicissitudes of taxon choice in the definitions: does one use higher-taxon terms as the subordinates (e.g. Deinonychosauria, Neornithes), in which case the new definition is entirely dependent on the stability of those terms, or does one select genera or species as the subordinates (e.g. *Deinonychus, Passer*), and then risk instability if those genera or species are redefined or reassigned at a later time? Instability at any level in a cladogram can feed through a system of phylogenetically defined taxon names and cause chaos.

An analogous case study of the terminology of divisions within Carnivora has been developed to show how confusion in the application of the principles of phylogenetic nomenclature arises (Bryant, 1996). As in the bird-theropod case described here, two essentially concurrent publications (Wolsan, 1993; Wyss & Flynn, 1993) offer alternative proposals on the use of names. Bryant (1996) attempts to fit the taxon names erected by each author to the cladogram of the other, and he has as much difficulty as was found in the bird-theropod case. For example, the clade Carnivora is defined as 'the most recent common ancestor of Feloidea and Arctoidea and all of its descendants' according to one cladogram. On the other cladogram, Canidae, the dogs, are excluded from Arctoidea and form an outgroup to Feloidea + Arctoidea. So dogs are no longer carnivores. Brochu (1999) outlines similar problems with phylogenetic definitions of crocodiles, including the observation that crown clade Crocodylia is included within Eusuchia (eusuchians were hitherto a sub-group of Crocodylia).

These simple practical examples do not confirm that phylogenetic nomenclature offers an 'explicit, universal, and stable' system. Taxon terms *can* be made explicit by the first author who enters the fray, and selects a node-based or stem-based definition that fits the preferred cladogram. An implication of the new system is that, once names have been defined by a taxonomist in explicit terms, that definition must remain. In other words, it is expected by the practitioners of phylogenetic nomenclature that priority will obtain, and that stability is ensured by that means. However, there is no agreement that such priority will exist, and it is likely that debates about the correct usage of existing names, and the correct labelling of nodes in cladograms will continue, as before.

Phylogenetic taxon names, however, suffer from a new problem: if the cladogram changes, the content of every taxon can change radically. This problem is clear to all, and it is accepted (de Queiroz & Gauthier, 1992, 1994; Bryant, 1996, 1997; Brochu, 1999) as a necessary consequence of phylogenetic nomenclature. Bryant (1997) explored this problem, and proposed that phylogenetic clade terms might include a statement of the 'designated phylogenetic context', in other words, the clade-term definition should refer to the included and excluded taxa, but also to the particular cladogram on which it is based. This may appeal to theoreticians, but it is clearly cumbersome and pointless for the users of classifications.

It could be argued that these examples illustrate only the confusion arising from competing concurrent phylogenetic revisions. Surely such debates can happen in any context? However, the requirement of phylogenetic nomenclature imposes a new principle of priority. Without it, Sereno (1998, 1999a) and Padian *et al.* (1999) would not have written those particular papers: they had already presented and debated their alternative phylogenies. In normal times, those debates would continue and they would not seriously impinge on nomenclatural debates until some of the dust had settled. Semantic spats of this kind will become commonplace if the PhyloCode is accepted. It might be suggested that such difficult issues will soon be resolved. However, that is not likely. So long as there are any disagreements over the precise shapes of phylogenetic trees, such pointless exercises will not fade away: the legalistic requirements of phylogenetic nomenclature forces such debates into the open, even when the time is not ripe. So long as particular nodes in a cladogram have low robustness values, or are disputed by other systematists, nomenclature should not be an issue.

The supposedly explicit phylogenetic nomenclature in practice generates confusion and instability. The choice is between a stable and explicit classification that can accommodate changing phylogenetic hypotheses, or an explicit, but unstable, classification that slavishly follows phylogenetic fashion.

IV. EXPLICITNESS, UNIVERSALITY, AND STABILITY

(1) Definitions

It is worth trying to understand the terms 'explicit, 'universal', and 'stable, as principles for an acceptable taxonomic system (de Queiroz & Gauthier,

1992, 1994; Bryant, 1996). Explicitness, or clarity (de Queiroz, 1977), is the requirement that 'the association between a name and a taxon should be clear' (de Queiroz & Gauthier, 1994). This is evidently a feature of phylogenetic nomenclature when applied by a single author, and when everyone accepts that the particular formulation is correct. The theropod-bird example shows that the association between names and taxa is not clear in two senses: (1) in redefining familiar terms in a phylogenetic way, there are as many viewpoints as there are systematists; and (2) while the name and the taxon may be firmly linked, and hence explicit, the content of such taxa is highly variable. As shown in the theropod-bird example, point (1) is illustrated by the fact that Sereno (1998) is explicit in his definition of Deinonychosauria, while Padian *et al.* (1999) are equally explicit in theirs, but the two definitions do not coincide. Point (2) is illustrated by the variable composition of Paraves, Arctometatarsalia, Bullatosauria, Ornithomimosauria, Deinonychosauria, and other node- and stem-based taxa when they are applied to both cladograms. Certainly, the name and the taxon are linked, but the taxon is very different in content according to the cladogram employed: if all species or genera included in the different versions of such taxa were listed, it would be clear that the concepts differed wildly. Explicit in one sense, but not in all senses.

Universality is the requirement that 'all biologists should use the same name for the same taxon' (de Queiroz & Gauthier, 1994), in other words that some priority system has to be imposed to force agreement. Universality is a strong purpose behind the success of the Linnean system. Species names are controlled by accepted rules, so that, for example, no-one can promote a new name for *Canis familiaris* since a valid name already exists. Syonymies (= redundant names) of species may be tested against type specimens, and the boundaries of extant species at least may be defined by testing for viable interbreeding and other criteria; the bounds of species have some reality in nature. The ICZN does not have provisions for resolving disputes over higher taxon names, although such legislative decisions are made under the botanical code.

An aim of phylogenetic nomenclature is to establish firm rules of priority for definitions of supraspecific taxa (Bryant, 1994, 1996; PhyloCode), and in expectation of that, authors are now rushing to be first into print with their definitions. However, a single agreed cladogram of all life, with every last twig worked out and unequivocal, is unlikely to be

achieved. Phylogenetic taxon names are hypothesis-dependent, and so long as alternative hypotheses exist, so too will an equal number of phylogenetically defined taxon names. The only practical way of establishing universality of the meanings of taxon names is to adhere rigidly to a new principle of priority, and for the various international systematics organisations, or some other body, to act as policemen. This is indeed proposed in the Phylo-Code. The committee would have to determine who was first into print, or whether one author's definitions are superior to those of another, whether, for example, we should follow Sereno (1998) or Padian *et al.* (1999), and reject the other.

To add a new principle of priority, priority of phylogenetic nomenclatural redefinition, with the necessary legislation to achieve it (see the Phylo-Code), is bound to be resented. With some three million valid taxonomic terms for species and higher taxa in existence, and few of them formally redefined as node- or stem-based entities, there is scope for decades (if not an eternity) of incredible fighting. And all for what? Better to spend our time discovering new taxa and revising the phylogenies of known taxa. The authors of the PhyloCode (Cantino *et al.*, 1999, p. 806) claim, rather disingenuously, 'Even users of names who have no interest in either phylogeny or nomenclature are likely to appreciate the greater stability that these naming methods offer.' Sorry chaps, but they won't.

In the absence of full explicitness and universality, can phylogenetic nomenclature achieve stability, namely that 'a name should not designate different taxa, nor a taxon be designated by different names' (de Queiroz & Gauthier, 1994)? The theropod-bird example has shown that such a desire is impossible. Node-based and stem-based taxon names are dependent on the favoured cladistic hypothesis. So long as names are hypothesis-dependent, there can be no stability, unless it is predicted that morphological and molecular cladograms are converging on common solutions to the tree of life. Even so, with hordes of phylogenetically defined names in existence, and in preparation, and the content of those named taxa varying with every cladogram that is published, there is currently massive redundancy of names (single names attached to several different taxa, and different names applied to identical taxa).

(2) The Linnean system

A counter-claim is not going to be attempted, that the Linnaean system as widely practised, is itself entirely explicit, universal, and stable. A case will be made, however, that it is as explicit as phylogenetic nomenclature, and that it is currently more universal and stable. Specifically, the claim is made that phylogenetic nomenclature is generating instability and that it cannot ultimately promise an improvement in explicitness or universality that might make such instability bearable in the short term.

The alternative to formalized stable taxon names is stable taxon contents. Hence, Linnaeus (1758) established the taxon name Aves for the animals commonly known in English as birds. He listed characters of birds, such as 'the beautiful voice, the long naked beak, the body covered with feathers, the two feathered wings, and bipedal gait'. This viewpoint, that birds (= Aves) is the group of organisms with wings and primary flight feathers is held by the great majority of ornithologists, biologists in general, and indeed probably by most of the population of the world. Of course Linnaeus did not include fossil birds in his definition since he did not know any such specimens. The discovery of fossil birds, including *Archaeopteryx* in 1861, did not perturb the accepted viewpoint: they were clearly members of the taxon Aves since they had feathers and wings (Sereno, 1999*b*). The advent of evolutionary thinking around that time also did not perturb the classification: it could then be postulated that feathers and wings had arisen in some common ancestor of birds modern and ancient, and that all such creatures that possessed both characters should be included in the taxon Aves. The spread of cladistics and molecular systematics similarly did not perturb this view. Gauthier (1986) listed numerous characters possessed by *Archaeopteryx* and all other birds, including the wing (dissected into 10 more precise anatomical descriptions of the nature of the shoulder joint, the forearm, and the musculature). He expressed uncertainty about the use of feathers as a defining character since some dinosaurs might also have had feathers. Indeed, that has since proved to be the case (Ji *et al.*, 1998; Xu *et al.*, 1999). Clearly, then, the apomorphy-based concept of Aves has remained remarkably stable, in the face of major theoretical (evolution) and methodological (cladistics, molecular systematics) shifts, and in the face of astonishing and unpredicted discoveries of fossils. The critic might ridicule the apomorphy-based concept by arguing that if feathers are retained as an avian character, then a motley assortment of dinosaurs either pops in or out of the clade, depending on whether certain exceptionally preserved integumentary structures in dinosaurs are

accepted as feathers or not. The apomorphy-based concept though can evolve to maintain stability of taxon content: the character 'possession of feathers' can be modified simply to 'possession of primary flight feathers', or Aves can be defined solely on the possession of a wing. Apomorphy-based Aves has survived for 250 years through some remarkable changes in scientific option and method and through an astonishing growth of knowledge: this is stability in practice.

The example of Aves is so familiar that it could be said to be unfair. Surely, for most groups of organisms, there is no such universally used understanding of the meanings of group names? Then it all comes down to authority. A particular apomorphy-based taxon definition is accepted because it was promoted by a particular notable or influential person. However, the PhyloCode provisions are even more draconian and authoritarian, although the decision-making process about which definition to accept, and which to reject, is made explicit and open. I revert to the point that if classifications are utilitarian, then history and human foibles will affect the development of classifications. Better to allow systematists, and users of classifications, to vote with their feet, than to impose a committee decision (which may be unworkable in practice).

In their various discussions, de Queiroz & Donoghue (1988), de Queiroz & Guathier (1990, 1992, 1994), and de Queiroz (1997) do not give a firm reason for rejecting apomorphy-based clade definitions, other than the general remark that defining taxa with characters is non-phylogenetic: 'Definitions of taxon names based on organismal traits are fundamentally non-evolutionary. Such definitions were in use long before the widespread acceptance of an evolutionary world view, and furthermore, they make no reference to common descent or any other evolutionary phenomenon.' (de Queiroz & Gauthier, 1992). That is no criticism, and wholly inadequate as a justification for abandoning a system that works. Indeed, de Queiroz (1997) notes that 'the current systems of nomenclature promote nomenclatural clarity, universality, and stability', but that 'they do so in an inappropriate theoretical context.' This desire for philosophical purity, for classifications that are defined in terms of the geometry of a cladogram-of-the-moment, entirely misses the point that classifications are utilitarian.

Lee (1998) has presented a dissenting view. He makes the important point that node-, stem-, and apomorphy-based definitions all have their place. Apomorphy-based definitions may be impossible in certain cases, for example, in defining a group that contains a clade plus a metataxon (a metataxon is a taxon, often a fossil, that lacks apomorphies), or in expressing a group that is evident only from molecular evidence (as an example, Lee (1998) cites the recent finding of a hippopotamus-cetacean clade). Node-based definitions are ideal when a clade is strongly corroborated, but not when a clade is only weakly indicated and liable to break up on reanalysis: a stem-based definition is then more appropriate. Similarly, apomorphy-based definitions are perfectly explicit when a clade is robust and when a character is clearly an apomorphy, typically a complex present only in members of a clade and not in any members of the outgroup. Subsequent loss, or modification, of such a defining character in some members of a clade is neither here nor there (Lee, 1998).

The proposals of the phylogenetic taxonomists have been valuable in making explicit the new concepts of node-based and stem-based definitions of taxa. Added to cladistic apomorphy-based definitions, systematists now have three ways in which to define clades. There is no reason to reject any of the three, and there is certainly no need to seek to enforce a new concept of priority for the first person who happens to publish an acceptable node- or stem-based definition of a taxon. As systematists revise groups, using cladistic and molecular evidence, they will inevitably provide revised frameworks of nomenclature and definitions, and these will be accepted or rejected on their merits, as is normal. Imposing a legislative procedure will interfere with normal correction procedures in systematics. Once a decision has been made, and a taxon definition logged in the system, corrections will be harder.

The phylogenetic nomenclatural system has led many of its supporters to demand a further series of changes beyond the imposition of priority in taxon definitions. These include the abandonment of Linnaean categories, the end of the binomial, and redefinitions of well-known terms to refer to crown clades. These proposals are essential philosophical consequences of phylogenetic nomenclature. But that is no reason to demand their acceptance; the sole criteria should be (1) do they improve the phylogenetic framework of a classification, and (2) do they enhance the utility of a classification?

Table 1. *Classification lists of major groups of birds, according to a standard Linnaean system applied to a cladogram (A), and listed without category terms (B). Based on the cladograms in Fig. 2.*

(A)	(B)
Class Aves	Aves
Archaeopteryx	*Archaeopteryx*
Infraclass Ornithothoraces	Ornithothoraces
Order Enantiornithes	Enantiornithes
Supercohort Ornithurae	Ornithurae
Order Hesperornithiformes	Hesperornithiformes
Cohort Carinatae	Carinatae
Order Ichthyornithiformes	Ichthyornithiformes
Superdivision Neornithes	Neornithes
Division Palaeognathae	Palaeognathae
Division Neognathae	Neognathae

V. LINNAEAN CATEGORIES, AND THE END OF THE BINOMIAL?

Standard practice among systematists is to produce phylogenetic trees and classifications as representations of their views. A classification, in this sense, is a list of species, genera, families, orders, and so on, organized as an indented, or hierarchical list (e.g. Table 1). In the Linnaean system, taxon names are assigned categorical levels, where the category is a measure of rank, such as species, genus, family, order, class, and so on. The category selected for any particular taxon reflects the significance of the group in some way, and it is determined by the placement of that taxon in a classification list. So the inclusive taxon for all birds is set at 'class' level, equivalent in status to the classes Amphibia, Reptilia, and Mammalia. Included within Class Aves are many orders, such as Order Hesperornithiformes (an extinct group), Order Cuculiformes (cuckoos), and Order Anseriformes (ducks). Other ranks, between class and order, and below order, are set by their positions in the list (Table 1).

The phylogenetic nomenclaturalists argue that ranks above the species have no meaning. Indeed, this is an issue that has long been debated: for example, is a family of mammals equivalent to a family of angiosperms? Among numerous attempts to set criteria, Hennig (1966) suggested geological age. Clades of invertebrates arising from the base of the Cambrian would be termed phyla, clades arising in the Cambrian to Devonian interval would be classes, those arising in the Carboniferous to Permian interval, orders, and so on. This scheme makes little sense, however when applied to tetrapods or land plants. A modification of Hennig's (1966) scheme might take account of the amount of molecular distance between groups (which is dependent on time and rates of change).

But, it is entirely unnecessary to demonstrate that higher category names have any fundamental meaning. Classifications are utilitarian, and inclusive hierarchical categorization is an immensely useful tool in providing a structure that the human brain can comprehend. Nobody has ever pretended that the hierarchical ranks era, period, epoch, stage, and zone have any ontological meaning in the divisions of geological time. But everyone accepts their immense utility, and there are no fatuous calls from semanticists to abandon them. The same is true of the Linnaean categories, and for precisely the same reasons. The critic says, 'if families are not demonstrably equivalent across all organisms, why use them?' I say, 'they work and they offer instant guidance on hierarchical structure, so why abandon them?'

Crane & Kenrick (1997) compare ranked and rank-free classifications of land plants, and they prefer the latter because of problems in determining ranks in the new cladograms and molecular trees, because of a proliferation of different endings on familiar group terms, and because the ICBN is more prescriptive concerning higher taxon names than the ICZN. However, it is not clear that such a radical step is required for botanical classifications. Traditional classifications of vertebrates have been converted into cladistic form (exclusion of paraphyletic groups, use of sequencing, plesions) without abandoning the Linnaean system. The same should be possible for plants.

There is no fundamental reason why a phylogenetic taxonomist should abandon category names, but de Queiroz and Gauthier (1992, 1994) argue that they are simply redundant and contribute

nothing. In response to criticism, de Queiroz (1997) argues that they have not *insisted* on the abandonment of categorical ranks, but abandonment is a strong plank of all presentations of phylogenetic nomenclature. They make a case that the Linnaean system forces taxonomists to create complex hierarchical schemes even for poorly defined taxa, and for basal taxa, such as *Archaeopteryx* (Cantino *et al.*, 1997). Indeed it would be nonsensical to list unique subclass, infraclass, supercohort, superdivision, and division names just for this genus, since they would all be redundant. Following Patterson & Rosen (1977), Wiley (1981), and others, it is accepted practice now not to do such things, and *Archaeopteryx* is simply listed at genus level, and its position in the hierarchy indicates that it is sister group at generic rank to the Infraclass Ornithothoraces (Table 1).

In view of the flimsy reasons for abandonment of category names, are there any advantages in retaining them? There are indeed advantages in terms of information content and in terms of practicality. Linnaean ranks communicate information about inclusiveness of taxa, often by common endings (Dominguez & Wheeler, 1997). For example, animal families usually end in -idae, plant families in -aceae. Among lizards, Family Agamidae is distinct from Family Chamaeleonidae, and neither includes the other. According to some phylogenetic hypotheses, the chamaeleons form a branch within Family Agamidae, and they would typically then be renamed Subfamily Chamaeleoninae. In the phylogenetic system, no such change is necessary, and the names Agamidae and Chamaeleonidae can drift up and down the cladogram according to current hypotheses of inclusiveness. In more dramatic cases, a family or order name could be subsumed in a genus name, if phylogenetic hypotheses changed. As Dominquez and Wheeler (1997) note, the de Queiroz-Gauthier recommendations 'aim for nominal stability at the expense of cladistic information content'. Their proposals 'provide stable names for unstable concepts'.

Practical advantages of the Linnaean hierarchy are manifold. Families and higher taxa prove to be useful proxies for species for large-scale studies of the history of life (Sepkoski, 1998) and of modern biogeography (Gaston, 1991). Biology students have to organise knowledge, and they would have a hard time if they could no longer refer to lists of phyla or classes. In learning about zoology, the list of phyla is manageable, and it is a fundamental way of organising knowledge. Bird watchers rely on lists of orders and families (compare the utility of a list of 20

orders of birds – owls, kingfishers, penguins – with an unranked listing of 9000 species), botanists treat the family as an important division of nature. These may seem rather feeble arguments, allowing the tail to wag the dog. But, of course, a classification is a utilitarian entity, something that has no merit if it does not serve normal requirements: hence it is absolutely right that the tail should wag the dog. The world at large would be mighty puzzled if systematists abandoned their current approach, and insisted that they would only supply category-free lists of taxa that had to be read in conjunction with the favoured cladogram of the moment.

The most scary consequence of phylogenetic nomenclature is the proposal to abandon the Linnaean binomen; abandonment is a logical consequence of the philosophy (Cantino *et al.*, 1999; Mishler, 1999), and it is supported by philosophical scruples about species definitions (Ereshevsky, 1999). Cantino *et al.* (1999), the core PhyloCode team, agree that the Linnaean binomen must go, but they have no clear idea about its replacement. Indeed, they present 13 distinct proposals, each of which has advantages and disadvantages. But they do argue that 'all of the proposed methods for naming species in the context of phylogenetic nomenclature provide names that are more stable than Linnaean binomials.' The 13 methods include a range of proposals, some of which retain the binomial in some form (but with the proviso that the generic term can never be changed as a result of new phylogenetic information), and some of which reduce the binomen to a uninomen.

No longer could one refer to *Homo sapiens*, and compare that species with extinct species such as *Homo erectus* or *Homo habilis*, knowing that the form of these binomina indicates a definite hypothesis, that all three species are close relatives, members of genus *Homo*. *Homo sapiens* becomes, according to various of the 13 proposals, *Homo-sapiens*, *homo.sapiens*, *homosapiens*, *sapiens1*, or *sapiens0127654*. The retention of a quasi-generic term (but which no longer functions as a higher inclusive group term), or the addition of a registration number, resolves the obvious problem of frequently re-used specific epithets (e.g. the snoeshow hare, *Lepus americanus*, the Rocky Mountain goat, *Oreamnos americanus*, the American black bear, *Ursus americanus*, the moose, *Alces americana*, the pronghorn, *Antilocapra americana*, the American marten, *Martes americana*, which all become *americanus*).

Mishler (1999), in an independent proposal, suggests that *Homo sapiens* could be more usefully known as *Sapiens Homo*, or, more formally, as *Sapiens*

Homo Hominidae Primates Mammalia Vertebra Metazoa Eucaryota Life. Mishler's (1999) reasoning for his proposal is that species are hard to define in many cases (problems of reticulation and hybridization) and there is an ontological clash between the biological and phylogenetic species concepts (see also Ereshevsky, 1999). Mishler (1999) then argues that since other Linnaean categories are to be abandoned, then so too must the species category. However, his formal terminology retains the strong hierarchical phylogenetic signal that is opposed in the specific epithet by the PhyloCode group (Cantino *et al.*, 1999).

Which ever of the 13 (or 15) proposed systems is finally incorporated into the PhyloCode, systematists will have to re-define all species so far named, and register them with a central committee. This opens up endless vistas of fruitless timewasting and bickering, and for no benefit whatsoever.

As de Queiroz and Gauthier (1992) conclude, their proposal, elaborated by Cantino *et al.* (1999) to abandon the Linnaean binomen 'would also promote nomenclatural stability'. That is not immediately evident.

VI. CROWN CLADES

The crown-clade concept, where commonly used taxon terms apply to extant species and their ancestors, is treated as a part of phylogenetic nomenclature by many, but not all, of its proponents (de Queiroz & Donoghue, 1988; de Queiroz & Gauthier, 1990, 1992, 1994; Rowe & Gauthier, 1992; Wyss & Meng, 1996). The advantages of crown clades are said to be that (1) they correspond to everyday usage, (2) they allow systematists to have access to the maximum amount of information, particularly soft-part and molecular characters, and (3) they are non-arbitrary and will promote stability.

The proposal to use crown clades is not based on any fundamental philosophical consequence of the phylogenetic system, and the proposal may be accepted or rejected entirely independently of the debate about Linnaean or phylogenetic nomenclature. The first point, that crown clade names correspond to everyday usage, is not established (Sereno, 1999*b*). It is a fact that when people use the word 'bird', they generally use it in a context that includes only living birds. However, the same people, when asked about *Archaeopteryx*, or when shown a picture, would unhesitatingly say that it was also a bird. They would regard it as pure nonsense to deny that it is a bird, since it clearly has primary flight

feathers and wings. This very issue has led to intense confusion among the public and press when new fossil birds have been announced, such as *Mononykus* (Perle *et al.*, 1993). The press releases have tagged these new Cretaceous birds as avialians, and the question is always: 'well, is it a bird or a dinosaur?'. Answer, 'it's a bird in common speech, but properly we now call it an avialian'. Pressmen retire in confusion.

Crown clades, since they are founded on living species, clearly may be characterized by a range of soft-part and molecular characters that are not available in stem taxa. That is a great advantage of such clades, but it is not a reason for migrating names from other clades. The clade Neornithes, including all living birds, does not have to be renamed Aves.

Despite the third claim, the procedure for re-naming crown clades *is* arbitrary, and so too can be the choice of names. In the cases of birds and mammals there is no problem, but what about other groups? Do we call the crown-clade elephants Elephantidae, as at present, or Proboscidea, the ordinal name for all elephants living and fossil? Indeed, would the stone-age phylogenetic systematist who lived 10000 years ago have included mammoths and mastodons in his crown-clade Proboscidea? If the Indian or African elephant were to go extinct in the next century, does the crown clade contract to ignore one of its former members? Analogously, if the duck-billed platypus and the echidnas were to go extinct, as could happen, the definition of crown-clade Mammalia would have to shift (Lucas, 1992). This has been denied (Bryant, 1994; Brochu, 1999), but crown clades are supposed to be delimited by extant taxa, and extinction of Monotremata would make the current crown-clade Mammalia no longer a crown clade.

Proponents of crown clades (Gauthier, 1986; de Queiroz & Gauthier, 1992; Rowe & Gauthier, 1992; Wyss & Meng, 1996; Brochu, 1999) regard them as something special, different from all the other clades that contain basal fossil taxa. However, consider crown-group Mammalia. There are numerous current postulated phylogenies of mammals (Fig. 3), and in each the content of crown-clade Mammalia differs substantially, including and excluding major groups of extinct mammals depending on which current cladogram is selected. This is true, of course, whatever names one applies to the clades; the fact is that basal mammalian phylogeny is far from clear. However, crown clades, if they are to be designated at the risk of considerable upheaval and
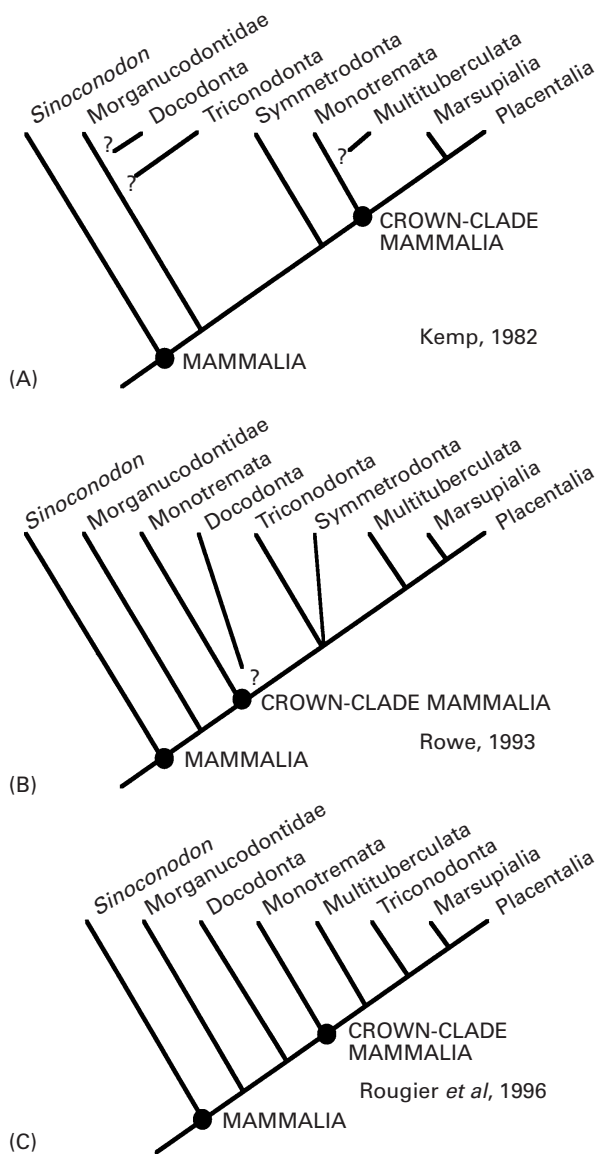
Fig. 3. Three cladograms of basal mammals, by (A) Kemp (1982), (B) Rowe (1993), and (C) Rougier *et al.* (1996). The differing clades designated by 'traditional' Mammalia and crown-clade Mammalia are indicated.

disquiet, ought to be seen to be stable. The supposed stability is often seen as a consequence of their having been based on extant taxa, but crown clades do not consist exclusively of extant organisms. They have a history and include fossils, and those fossils are just as tricky to place in taxa, whether those taxa are crown clades or not (Lee, 1996; Sereno, 1999*b*). So crown clades cannot be more stable than any other clade since they are hypothesis-dependent.

In the end, the advantages of clades founded on living taxa do not necessitate their wholesale renaming. The advantages are certainly not enough

to outweigh the intense confusion that has already been caused by recent redefinitions of terms such as Aves and Mammalia. Indeed, the crown-clade concept has been widely rejected for just this reason (Lucas, 1992; Patterson, 1993; Lee, 1996; Rieppel, 1997; Sereno, 1998, 1999*b*; Benton, 1999; Padian *et al.*, 1999).

VII. CONCLUSIONS

(1) Phylogenetic nomenclature (de Queiroz & Gauthier, 1990, 1992, 1994; Cantino *et al.* 1999) ties phylogenies and classifications firmly together, but it is demonstrably impractical. The language of science is important, and classification schemes have an impact on a much wider group of practitioners than merely on those setting them up. The classification of life is a tool used by many biologists and by non-scientists, and it is understandable that attempts have been made to increase its rigour and informativeness. Cladistics and molecular techniques have greatly improved the transparency of phylogenetic hypotheses.

(2) The introduction of phylogenetic nomenclature wholesale across all disciplines in biology would involve considerable upheaval, confusion, and distress, as has already been evidenced in debates over basal birds and mammals. This short-term pain would be justified if the remedy offered long-term advantages. It does not.

(3) The legislative side of phylogenetic nomenclature, as outlined in the PhyloCode, opens up a nightmare scenario for the future of systematics. New levels of control are proposed, and these will lead to an infinity of meaningless disputes and debates. Not only will priority reside in the first name applied to a taxon, as at present, but also in the first approved cladistic redefinition of all named taxa. Some 1.7 million species have been named to date, and, with all named generic and suprageneric taxa, the global total of available taxonomic entities surely reaches three million. Each and every one of these will have to be re-defined, discussed, disputed, and entered in a global register. The discussions over the terminology of theropod dinosaur clades (Sereno, 1998, 1999*a*; Padian *et al.*, 1999) are an indication of how this will proceed.

(4) The new form of definitional priority encapsulated within the PhyloCode will be a stimulus to certain individuals to engage in a cottage industry of re-definitions. Anyone will be free to rush such definitions into print, and ego might prevail over common-sense in the attempt to clock up as many

redefinitions as possible. At a time when systematists are in demand for useful work, this is hardly a fruitful pursuit.

(5) The PhyloCode proposals will hinder normal systematic work. Once decisions about definitions have been logged in the register, it will be hard to revoke them without a system of appeals, legal debate, and time delays. And yet, the commonest activity of systematists is revision and extension of knowledge about the groups that fall within their expertise. Discovery of new taxa and new characters leads to constant rethinking of clade contents and definitions. At present, systematists are free to make subtle adjustments to clade contents and definitions to accommodate advancing knowledge. Why stop that?

(6) Phylogenetic nomenclature has been advertised as more explicit, universal, and stable than Linnaean nomenclature. However, universality and stability have been achieved for the current Linnaean system in terms of the content of named taxa. Such universality would take a long time to achieve for the new phylogenetic terms and methods, and the end results are no more or less stable than current taxon names. New discoveries might still involve revisions to definitions and to clade contents.

(7) Node-based, stem-based, and apomorphy-based definitions of taxa all have their place, and each has advantages in specific circumstances. Systematists should be free to use each technique as they see fit, and to improve the precision of the definition of clade names as part of normal revision exercises. There is no need to impose an additional legislative framework.

(8) Cognate proposals of phylogenetic nomenclature, such as the abandonment of Linnaean categories, the abandonment of the binomen, and the migration of established names to crown clades, have led to confusion, have reduced the information content of classifications, and yet they offer no advantages.

(9) Phylogenetic nomenclature stems from philosophical, not practical considerations. The PhyloCode team, and other reformers, are most welcome to continue the philosophical debate, and the rest of the world will observe their byzantine disquisitions at a distance. Mediaeval scholars debated endlessly how many angels might fit on the end of a pin, a debate that was incapable of resolution if angels were infinite and infinitesimal in dimensions. Phylogenetic nomenclature similarly offers many opportunities for interesting philosophical debate, but it is patently an absurd proposition as a practical system.

(10) The debate in the end centres on the idea of stability in classification: are we looking for stability of taxon name definitions or stability of taxon contents? Phylogenetic nomenclature pursues lexicographic stability at the expense of utility. As has often been said by many wise philosophers, 'if it ain't broke, don't fix it'.

VIII. ACKNOWLEDGEMENTS

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