VIEW FROM THE FIELD

PHYLOGENETIC NOMENCLATURE AND PALEONTOLOGY

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THAT *TAXONOMY* should be phylogenetic—i.e., that named taxa should be restricted to monophyletic groups—is widely accepted throughout systematic biology. A recently proposed phylogenetic *nomenclatural* system (de Queiroz and Gauthier, 1990, 1992, 1994; Cantino and de Queiroz, 2000) goes further by specifying that all supraspecific taxon names be explicitly defined on the basis of common ancestry. This phylogenetic nomenclatural system would eventually replace the Linnean system currently in use. In this note, we discuss why this is a good thing for paleontology and suggest ways in which we, as a community, can make the transition from typological to evolutionary systems while minimizing confusion.

PRINCIPLES OF PHYLOGENETIC NOMENCLATURE

The Linnean system appears to have served us well for more than two centuries, and its abandonment makes many uneasy. But phylogenetic nomenclature follows from a view all of us share—that taxa are the dynamic products of descent with modification rather than static classes of objects sharing some arbitrary set of physical membership criteria (Griffiths, 1974; Ghiselin, 1984; de Queiroz, 1988; de Queiroz and Gauthier, 1990). Because the hierarchical pattern generated by evolution creates natural groups that we discover (or whose presence we hypothesize), taxa should be viewed as historically-bound entities. An evolutionary group exists because of common ancestry. The only natural boundaries for these groups are speciation and extinction. This is why monophyletic groups are individuals, but paraphyletic assemblages above the species level are not; to create a paraphyletic assemblage, we are forced to create an artificial upper bound on the basis of characters we deem significant for group exclusion.

Modern applications of Linnean taxonomy acknowledge the individuality of species and recognize the fact that higher taxa are the products of evolution, but as long as taxa are based on their physical characters and not common ancestry, they continue to be viewed as classes of objects. Individuals are products of history; we can recognize an individual on the basis of particular features, but these features are not the reason an individual exists. In the phylogenetic nomenclatural system, there is a clear distinction between a taxon's *diagnosis* and its name's *definition* (Ghiselin, 1984; Rowe, 1986). The name definition explains what the taxon is historically (a product of evolution), and the diagnosis lists the characters that tell us how to recognize one of its members.

This seems to represent a massive departure from other current nomenclatural systems. But a good analogy for this kind of conceptual shift can be found in sequence stratigraphy. For most of the 19th and 20th centuries sedimentary rock units were based on overall sedimentological or faunal similarity rather than on the underlying system that formed them. Modern sequence stratigraphy recognizes sedimentary units based on a genetic model of their formation (packages of system tracts bounded by unconformities and their correlative conformities), not unlike the way phylogenetic nomenclature recognizes taxa on the basis of their hypothesized relationships. Sequence stratigraphy predicts the spatiotemporal order of packages of system tracts within a depositional system, just as a phylogenetic hypothesis allows the generation of predictions, for example about the characters expected in undiscovered members of a clade or in the unpreserved parts of a fossil. The original pre-sequence rock units are directly analogous to character-based typological taxa, and sedimentary sequences are akin to phylogenetic definitions. That rock unit names are redefined to reflect the newer sedimentological paradigm (and that unit names may mean very different things in different references, based on the paradigm under which they are used) is widely accepted in the geological community.

Three different kinds of group name are recognized in the phylogenetic system (de Queiroz and Gauthier, 1990, 1992, 1994; Fig. 1). The draft PhyloCode (Cantino and de Queiroz, 2000), which will govern the application of phylogenetic nomenclature, covers names based on all three.

BENEFITS TO PALEONTOLOGY AND SYSTEMATICS

Explicit taxon meanings.—The most important benefit of phylogenetic nomenclature is explicitness. Universal meanings can only be imparted by explicit taxon name definitions. Universality is an important concept in the Linnean system as well, but Linnean names have not always been universally applied (Rowe and Gauthier, 1992). As long as the meaning of taxon names is based on similarity, there will be a level of ambiguity caused by the arbitrary and subjective nature of the characters chosen to delineate group boundaries—individual species may belong to a taxon under one person's concept, but not another's, depending on how the boundaries are drawn by different researchers.

This is especially true when names are used by both paleontologists and neontologists. The ranges of characters and taxa considered by both groups differ—neontologists can apply soft-tissue morphology, behavior, and molecular evidence to taxon diagnoses, but often disregard the fossils that sometimes represent a large proportion of their study group's diversity. Explicit, universal meanings are critical if paleontology is to play a central role in systematics and evolutionary biology.

Many recent debates between paleontologists and neontologists have been based more on miscommunication than on real conflict between data sets. The "conflict" between molecular and fossil estimates on the age of the taxon *Crocodylus,* for example, was based entirely on conflicting meanings of the name; molecular divergence estimates of 5 to 10 m.y. were addressing the divergence of living species only and hence regarded *Crocodylus* as a node-based crown group, while paleontologists used *Crocodylus* as a form-taxon including a wide array of crocodylians as old as the Late Cretaceous. Recent phylogenetic analyses indicate that the only fossils belonging to crown-genus *Crocodylus* are within the five- to ten-million-year window indicated by molecular data
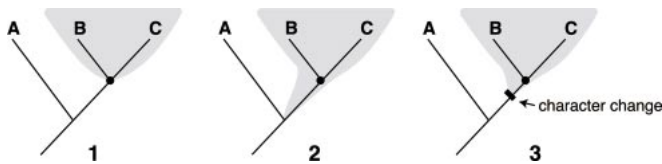
FIGURE 1—Diagram showing the three kinds of group recognized in phylogenetic nomenclature. *1,* a node-based group name is based on an ancestor and all of its descendants; *2,* a stem-based group name is based on a terminal taxon and everything more closely related to it than to another terminal taxon; *3,* an apomorphy-based group name is based on the first organism to possess a certain derived trait and all of its descendants.

FIGURE 2—Conflicting meanings of Glyptocystitida in the literature.

(Brochu, 2000). The data sets actually agreed with each other, but because the name being discussed lacked a precise meaning, a debate ensued that had nothing to do with the evidence itself. Similar miscommunication may be confusing discussions over the origin and diversification of modern mammalian clades (Bromham et al., 1999; Alroy, 1999) and flowering plants (Doyle and Donoghue, 1993; Crane et al., 1995; Sytsma and Baum, 1996).

Stability.—The properties of a taxon (diagnosis, membership, estimated time of origin) will always change as we learn more, regardless of the nomenclatural system used. As long as taxon names are based on membership or diagnosis, we risk having the meaning of the name itself change as new information surfaces. In phylogenetic nomenclature, the underlying meaning of a taxon name remains stable—the name still refers to a specific evolutionary entity, even if our understanding of this entity's properties change (as it always will).

Glyptocystitida, an extinct group of stemmed echinoderms, provides an example of instability in Linnean nomenclature. The diagnosis found in standard references (e.g., Kesling, 1968) included the presence of unique respiratory structures, but problems arose because the putative glyptocystitid *Macrocystella* lacks them. Ubaghs (1968) and Sprinkle (1973) interpreted the diagnosis of Glyptocystitida literally and considered *Macrocystella* to be an eocrinoid with strong affinities to glyptocystitids. Conversely, Paul (1968) considered *Macrocystella* to be a glytpocystitid lacking that diagnostic feature. Paul (1968) rediagnosed Glyptocystitida to include taxa either possessing or lacking these structures. This renders the diagnosis uninformative—all living and extinct organisms either possess or lack these structures. These authors agreed on the important point—*Macrocystella* has a close phylogenetic relationship to derived glyptocystitids—but disagreed on how to adjust the diagnoses to express this. Sumrall (1996) defined Glyptocystitida as the stem-based group including all echinoderms closer to *Cuniculocystis* than to *Ridersia.* Using a stem-based definition, the set of characters becomes irrelevant to the meaning of the group and *Macrocystella* lies within Glyptocystitida (Fig. 2).

The most common criticism of phylogenetic nomenclature is the potential instability some fear might arise because of the labile nature of our phylogenetic hypotheses (Dominguez and Wheeler, 1997; Moore, 1998; Nixon and Carpenter, 2000; Benton, 2000). Some changes in phylogenetic hypothesis result in radically different group memberships and diagnoses (Schander and Thollesson, 1995; Wyss and Meng, 1996; Bryant, 1996, 1997; Brochu, 1999). But we do not believe this to be the serious problem some fear it to be. Systematists are usually aware of regions of the tree that are unstable, either because nodal support is very low or because other data sets support different hypotheses of relationship. Phylogenetic nomenclature does not require a name for every node.

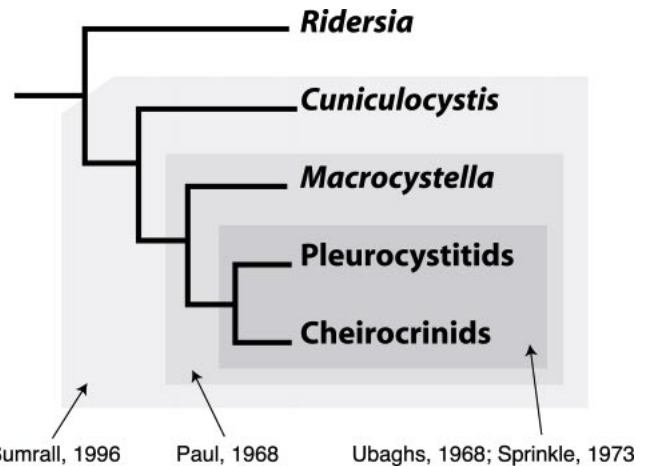Another potential problem is the establishment of different names for what look like the same groups of organisms. The reasons for this problem are various, including application of new names on what appear to be different phylogenies and disagreement over the appropriateness of some names. This has been a particularly acute issue among dinosaur taxonomists (Gauthier, 1986; Holtz, 1994, 1996; Sereno, 1998, 1999a, 1999b; Padian et al., 1999). But abandonment of the Linnean nomenclatural system does not mean abandonment of the principle of priority, although in the phylogenetic nomenclatural system priority is based on definitions rather than memberships or diagnoses (de Queiroz and Gauthier, 1992; Cantino and de Queiroz, 2000). Cases where multiple names have been applied to the same clade can be resolved simply by publication date.

Consider, for example, controversies over the names applied to derived theropod dinosaurs. Most systematists regard troodontids and dromaeosaurids, small-bodied theropods closely related to birds, to be close relatives within a group named Deinonychosauria, but a few analyses suggest a more distant relationship (e.g., Holtz, 1994). Benton (2000, p. 639) argued that Sereno's (1998) node-based definition of Deinonychosauria (last common ancestor of dromaeosaurids and troodontids and all of its descendents) was "hard to translate" onto the theropod phylogeny preferred by Padian et al. (1999), in which dromaeosaurids and troodontids are distantly related. In fact, the solution is rather simple—Deinonychosauria becomes synonymous with another phylogenetic name (Maniraptoriformes), and the definition having publication priority (in this case, Maniraptoriformes Holtz, 1996) takes priority.

Incompletely known fossil taxa can often be very labile in an analysis; hence, contents of clades including large numbers of fossils may fluctuate over time. Rather than arguing over whether a group should include a particular species, we should argue whether a particular species belongs to a group. These sound the same, but they are fundamentally different. Consider, for example, the various arguments over the content of Mammalia (Rowe, 1988; Rowe and Gauthier, 1992; Bryant, 1994; de Queiroz, 1994). Arguments from a rank-based perspective, in which content and diagnosis "make the group," involve different parties holding very different meanings of the same name. Tritylodontids (an extinct group of small Triassic mammal-like animals) may move in and out of Mammalia only because groups of experts may diagnose Mammalia differently (and thus may mean very different things by the name "Mammalia"). When tied to a specific monophyletic group, the name Mammalia has a stable, universal meaning, and the argument is streamlined to the question of where tritylodontids fit on the tree. If tritylodontids belong to the clade

we have named Mammalia, they are mammals. If their position is unresolved relative to that clade, then our ignorance is given an explicit description.

The recent practice of restricting some prominent names to crown clades bound by living representatives (e.g., Maisey, 1986; Gauthier, 1986; Gauthier et al., 1988; Rowe, 1988; Benton and Clark, 1988; Brochu, 1997, 1999) has been controversial (Miao, 1991; Lucas, 1992; Bryant, 1994; Lee, 1996; Sereno, 1998, 1999a; Benton, 1999, 2000). Names such as Mammalia supposedly have widespread meanings that, ostensibly, include several extinct taxa that would be excluded under a strict crown-group definition. In this sense, phylogenetic nomenclature seems outwardly to detract from the cause of universality. Mammalia sensu Rowe (1988) would exclude tritylodontids, even though some previous authors regarded them as mammals, because they are not descendents of the last common ancestor of monotremes, marsupials, and placentals. But this is not an integral aspect of phylogenetic nomenclature. Arguments against crown-group nomenclature are not arguments against phylogenetic nomenclature.

Abolition of mandatory ranks.—Mandatory ranks are fundamentally incompatible with phylogenetic taxonomy (Griffiths, 1976; de Queiroz and Gauthier, 1992; Sundberg and Pleijel, 1994; de Queiroz, 1996; Cantino et al., 1999). Divergence events in phylogeny create natural hierarchical groupings of ancestors and descendents, but the ranks are purely human constructs that have nothing to do with the groups themselves. Ranks express the subjective opinion of an expert of the perceived importance of a group relative to another, often based on group diversity, biogeographic or stratigraphic range, or some major morphological innovation. This implies an unrealistic expectation of rank equivalency across taxa.

Mandatory Linnean ranks are a cause of taxonomic redundancy (de Queiroz and Gauthier, 1992, 1994). A genus must belong to a family; a new monospecific genus, not belonging to any pre-existing family group, forces the taxonomist to erect a monotypic family that is completely redundant with the genus and species. Benton (2000) argues that one could simply neglect such ranks, but we fail to see how this differs from not using ranks at all. Ranks are a source of instability—if one family-level group is subsumed within another, the subsumed family must be changed to a subfamily, causing its name to change (de Queiroz and Gauthier, 1994). Furthermore, Linnean ranks add another dimension of nonuniversality. Features thought to be significant at the ''family'' level by one specialist may only be significant at the ''subfamily'' level of another.

The common counterargument is that ranks are useful for communication. But even though the present system allows for an infinite number of ranks by adding prefixes, there are simply too many levels to the real hierarchy created by evolution to be efficiently accounted for by Linnean ranks, even if we choose to leave most nodes unnamed (Crane and Kenrick, 1996; de Queiroz, 1996). The potential confusion from the assumed equivalence, in our view, outweighs any benefit for data retrieval. In any case, the information contained in a phylogenetic taxonomy without ranks can be made just as explicit as that in a Linnean hierarchy (Sundberg and Pleijel, 1994; Crane and Kenrick, 1996; Kron, 1996; Ereshefsky, 1999).

We are deliberately restricting our comments to supraspecific taxa. There is still much discussion over the issue of species and binomials in the phylogenetic system (Schander and Thollesson, 1995; Graybeal, 1985; Pleijel, 1999; Cantino et al., 1999; Mishler, 1999), and at present, the draft PhyloCode (Cantino and de Queiroz, 2000) only addresses supraspecific taxa. *Linnean* binomials are incompatible with phylogenetic taxonomy for the same reasons that any Linnean rank is incompatible with phylogenetic taxonomy, but most proposals for translating Linnean binomials into the phylogenetic system preserve the binomial format (contra Benton, 2000). The form species names will take in the PhyloCode is undecided, and we encourage all paleontologists to participate in the decision-making process.

RECOMMENDATIONS

We believe phylogenetic nomenclature represents an extremely beneficial change for the paleontological community, but we also recognize some of the confusion that might arise as we move from the Linnean to a phylogenetic system. As with any nomenclatural system, various human weaknesses, ranging from carelessness to selfishness, can make phylogenetic nomenclature cumbersome.

First, we do not advocate the naming of all nodes in a cladogram, and strongly urge workers to apply phylogenetic nomenclature only after a thorough phylogenetic analysis has been conducted. In our experience, clades are named if two criteria are met—the clade is stable and unlikely to collapse, and there is a need to discuss the group. Bryant (1996), Cantino et al. (1997), and Schulte et al. (1998) provide some guidelines for the establishment of names, including the application of methods for measuring nodal support, careful consideration of those taxa that are likely to move around in different analyses, and use of multiple basal taxa as specifiers for node-based groups.

Second, we strongly urge paleontologists to join with other systematic biologists and discuss how the names of various groups of organisms are to be translated into the phylogenetic system. Taxonomy is important enough to be handled at the level of the community. We call for specialists on particular groups to meet and work on standard nomenclatural protocols jointly. We further suggest that these protocols be published. These need not be formal symposia; all it takes is a roomful of systematists, a blackboard, and a few pitchers of beer.

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