Phylogenetic Approaches to Classification and Nomenclature, and the History of Taxonomy (An Alternative Interpretation)

Herpetological Review has recently featured a series of papers debating the merits of recent developments in the theory and practice of systematic biology, using herpetological examples. In the latest and longest paper in this series, Pritchard (1994) passionately argued against many of these "cladistic" developments. Here I address three issues raised in his paper that bear directly on my own writings concerning systematic theory and practice. These are: 1) the abandonment of paraphyletic higher taxa, 2) the replacement of the current ("Linnean") system of biological nomenclature, and 3) the significance of these proposals in the context of taxonomic history. Contrary to Pritchard's implications, the proposals in question are not based on arbitrary or illogical cladistic dogma but on well-established evolutionary principles. Moreover, these proposals are not passing fads but manifestations of an important trend in the historical development of biological taxonomy.

Paraphyly.—Pritchard opposes the proposal that groups each consisting of a common ancestor and all of its descendants (monophyletic groups, clades) should be recognized as higher taxa, but that groups each consisting of a common ancestor and only some of its descendants (paraphyletic groups) should not. He argues in favor of recognizing paraphyletic higher taxa—for example, a Reptilia that does not include birds—on the grounds that first, they agree with commonsense vernacular concepts, and second, they are congruent with a particular model of speciation, which he illustrates using a human socioeconomic analogy. All of his arguments, however, overlook some important considerations.

Pritchard's first argument for recognizing paraphyletic higher taxa overlooks the fact that much of scientific progress has consisted of replacing commonsense vernacular concepts with concepts derived from corroborated scientific theories. A few examples of commonsense vernacular concepts that were widely accepted in previous times but have largely been replaced in the face of accumulating data are a flat earth, a geocentric universe, solid matter, fixed continents, immutable species, and a single taxon for both amphibians and reptiles. Evolution is often said to be the unifying theory of biology, and most biologists accept the proposition that taxonomy is to be based on evolution. A fundamental component of the principle of evolution is the proliferation of species from common ancestors. Therefore, equating higher taxa with groups of species sharing a unique and exclusive common ancestry constitutes an evolutionary concept of higher taxa (Hennig 1966). The lack of correspondence between these clades or monophyletic groups and commonsense vernacular concepts of taxa is a poor reason for retaining the latter, and it might even be considered resisting scientific progress.

Pritchard also favors the recognition of paraphyletic taxa based on a model of speciation in which an ancestral species remains unchanged while giving rise to a modified descendant species. He argues that the unmodified ancestral species deserves the same taxonomic designation before and after giving rise to the modified descendant, which deserves recognition as a separate taxon (thus rendering the ancestral species paraphyletic). Pritchard's argument suffers from implicitly extending to higher taxa a model that applies properly to species alone. That is to say, although there are accepted evolutionary processes through which species give rise to other species, there is no known evolutionary process through which higher taxa give rise to other higher taxa of the same or greater rank in the Linnean hierarchy (e.g., Wiley 1979). It is this inflated assignment of categorical ranks that results in paraphyly. For example, assigning both Amphisbaenia and Lacertilia to the rank of suborder renders Lacertilia paraphyletic because it implies that Amphisbaenia is entirely separate from Lacertilia rather than being a subgroup of that taxon. Categorical assignments are made by humans. Therefore, paraphyletic higher taxa owe their existence as much to the human mental process of assigning ranks as to any evolutionary process. Systematists who advocate the elimination of paraphyletic higher taxa do so because they wish to recognize as taxa only those entities resulting entirely from evolutionary processes.

Pritchard uses a sociological analogy to illustrate the supposed rationality of recognizing paraphyletic taxa and, at the same time, the supposed irrationality of cladistic practice. He describes a situation in which a lineage of peasants—let us call it the Bauer clan ("Bauer" is German for "peasant")—produces a daughter who becomes educated and gives rise to a lineage of urban professionals. He argues that cladists would insist nonsensically that the urban professionals be called peasants because they are descended from peasants. This characterization of the cladistic position is erroneous and results from Pritchard's failure to distinguish between socioeconomic classes and genealogical lineages (or more generally, between classes and systems, see de Queiroz 1988). Everyone who makes this distinction, including cladists, will classify the descendants of the educated daughter as urban professionals according to socioeconomic criteria, but they will also realize that the descendants' change in socioeconomic status does not remove them from the Bauer clan. An analogous distinction applies to taxonomy. Consider a situation in which a clade composed of insectivores ancestrally—Squamata, for example—produces a descendant lineage that enters a new adaptive zone and gives rise to a clade of herbivores. As long as a distinction is made between classes based on diet and monophyletic entities, there will be no problem classifying the modified descendants as herbivores while at the same time recognizing that they are part of the squamatan clade.

Nomenclatural Systems.—Pritchard also criticizes a recent proposal to replace the current system of biological nomenclature with one based on evolutionary principles (de Queiroz and Gauthier 1990, 1992, 1994). In his view, this as an example of "contortions forced on cladists by...their own arbitrary rules," which represents "iconoclasm that is unlikely to appeal to anyone except highly theoretical cladists" (p. 105). Furthermore, Pritchard implies that the current system promotes nomenclatural stability and that adoption of the proposed alternative would result in "total sacrifice" (p. 105) of that stability. Although adoption of a phylogenetic system of nomenclature would be radical in some important respects, it would not, contrary to the impression given by Pritchard, produce utter nomenclatural chaos. Indeed, adopting a phylogenetic approach to nomenclature would largely solve problems of nomenclatural ambiguity and instability caused by the current system.

Pritchard blames cladistic doctrine for problems stemming from the nonevolutionary nature of the current nomenclatural system, using recent proposals concerning the nomenclature of acrodontan lizards to illustrate his points. Frost and Etheridge (1989) proposed to unite the families Agamidae and Chamaeleonidae into a single family as a result of their conclusions concerning paraphyly of the family Agamidae. Because "Chamaeleonidae" is the older name in the family group, it becomes the name of the new family-level taxon. As a consequence, many species that were formerly members of the family Agamidae will now belong to the family Chamaeleonidae, and the group of species formerly rec-

ognized as the family Chamaeleonidae will either be left nameless or require a new name. Pritchard supposes incorrectly that this nomenclatural ambiguity and instability stems from the cladistic prescription against paraphyletic taxa. In this particular case, the proposal was indeed intended to eliminate a paraphyletic taxon. Nevertheless, the problem is more general in that it applies to all changes involving the taxonomic practices of lumping and splitting, regardless of motivation. Ironically, Pritchard's paper begins as a defense of an earlier paper by Lazell (1992) that included a proposal to unite the families Agamidae and Iguanidae. Although unification of these families was proposed entirely for traditional reasons, it would result in ambiguity and instability very similar to that generated by the cladistic proposal.

In contrast with the current system of nomenclature, a phylogenetic system would promote unambiguous and stable evolutionary meanings of taxon names. The central issue is the manner in which taxon names are defined. Under the current system, names are implicitly defined in terms of a nonevolutionary principle—the Linnean taxonomic categories. For example, the name "Chamaeleonidae" is defined under the current system as the family level taxon containing the type-genus *Chamaeleo*. This genus, however, is contained within each of several taxa in a nested series (i.e.,...Squamata: Iguania: Acrodonta: Chamaeleonidae: Chamaeleoninae: Chamaeleonini...). Consequently, any change regarding assignment of these taxa to the family category will result in a nomenclatural change (e.g., what was once Acrodonta becomes Chamaeleonidae). Under a phylogenetic system, taxon names would be defined in the explicitly evolutionary terms of ancestry and descent. For example, "Chamaeleonidae" might be defined as the most recent common ancestor of *Chamaeleo* and *Brookesia*, and its descendants. Under such a definition, Linnean categorical assignments are irrelevant, and thus the nomenclatural ambiguity and instability caused by changes in categorical assignment would be eliminated. Consequently, the name "Chamaeleonidae" would remain associated with the clade stemming from the most recent common ancestor of the same set of species that has traditionally been included in that taxon (see de Queiroz and Gauthier 1990, 1992, 1994 for further discussion).

Replacing the current system of nomenclature with a phylogenetic one, or as Pritchard puts it "dumping the Linnean system of nomenclature" (p. 105), would not be as disruptive as he makes it sound. Although the Linnean taxonomic categories would be eliminated, the taxa themselves and their existing names would be preserved. For example, I have already indicated that there would still be a taxon Chamaeleonidae made up of all of the same species; the only difference would be that it would be neither a family nor a member of any other Linnean category. The hierarchical component of taxonomy would also remain intact. That is to say, nested series of taxa such as...Reptilia: Squamata: Iguania: Acrodonta: Chamaeleonidae...and...Reptilia: Testudines: Cryptodira: Chelonioidea: Cheloniidae...would continue to be recognized. Although the assignment of taxa to Linnean categories is an old tradition, it is widely acknowledged that this is a highly subjective and artificial practice. In short, reformulating the nomenclatural system with an evolutionary basis would not only promote nomenclatural universality and stability, it would also preserve most of the structure of existing taxonomies, eliminating only their most questionable component.

The History of Taxonomy.—Pritchard views the developments described above as fads "that may well not survive the decade, let alone the centuries" (p. 105). He likens "the hurricane of cladism" to the "storm of pheneticism" with the hope that "this too shall pass" (p. 109). These characterizations and hopes or predictions fail to take into consideration the history of taxonomy, in particular, the changing role played by the principle of evolution. This history suggests both a very different interpretation of the significance of the developments in question as well as a very different prediction concerning their fate.

The idea that living things are related by common descent gained widespread acceptance over a relatively brief span of time during the latter half of the previous century. The influence of this idea on taxonomic theory and practice, however, was not nearly as pervasive or rapid. Historians and biologists have asserted repeatedly that the concept of evolution had little or no impact on taxonomy, but this generalization is oversimplified. The impact of the concept of evolution on taxonomy, though significant, has been difficult to perceive because several of its important manifestations occurred at different times long after initial acceptance of the concept itself.

Immediately after widespread acceptance of the idea that living things are related by common descent, many aspects of taxonomy became evolutionary in only a superficial sense. Specifically, evolution was granted the role of an after-the-fact justification or interpretation for previously existing taxonomic methods and concepts. Throughout the post-Darwinian history of taxonomy, evolution has been granted an increasingly important role in that discipline in that it has come to function, in one area after another, as a central principle or tenet from which fundamental taxonomic concepts and methods are deduced (de Queiroz 1988).

Various occurrences in the historical development of taxonomy are interpretable as manifestations of this trend. For example, during the middle of the present century, concepts of species in which the principle of evolution played a superficial role were replaced by concepts of species in which that principle played a central role. Specifically, concepts of species as groups of similar organisms were replaced by concepts of species as population lineages. This conceptual shift required the rejection of previously recognized species taxa that consisted of reproductively separate populations. For example, morphologically similar leopard frogs that were formerly considered members of a single species are now considered to make up several cryptic or sibling species (Hillis 1988). The same conceptual shift also required the acceptance of previously unrecognized species taxa for phenotypically distinct groups of organisms that nonetheless formed a single interbreeding population. For example, morphologically dissimilar striped and banded kingsnakes in southern California that were formerly considered separate species are now considered morphs of a single polymorphic species (Klauber 1944; Mayr 1944).

The prescription against paraphyletic higher taxa represents an analogous change. Concepts of higher taxa in which the principle of evolution plays a superficial role are being replaced by concepts of higher taxa in which that principle plays a central role. Specifically, concepts of higher taxa as groups of similar species are being replaced by concepts of higher taxa as clades, groups of species sharing an exclusive common ancestry. This conceptual shift necessitates rejection of previously recognized higher taxa that constitute only parts of clades, that is, paraphyletic higher taxa. The same shift also necessitates the recognition of previously unrecognized higher taxa for groups of dissimilar species that nonetheless form a clade. For example, morphologically dissimilar scaled and feathered amniotes that until recently have been recognized as separate higher taxa are now being considered to form a single higher taxon and one of its subtaxa.

The proposed change regarding the system of nomenclature would extend a central role for the principle of evolution into yet another aspect of biological taxonomy. Under this proposal, a nonevolutionary concept of how the names of biological taxa are defined would be replaced with an explicitly evolutionary one.

Specifically, definitions stated in terms of the Linnean taxonomic categories would be replaced by definitions stated in terms of ancestry and descent. This conceptual shift will necessitate abandoning the Linnean taxonomic categories, but it will also increase nomenclatural clarity, universality, and stability.

In conclusion, a consideration of the historical development of taxonomy suggests an interpretation of recent taxonomic events and proposals that differs significantly from the interpretation offered by Pritchard. Both the increasing abandonment of paraphyletic higher taxa and the proposal for a phylogenetic system of nomenclature do not represent passing fads; instead, they represent the most recent stages in a process that has been unfolding for more than 130 years. It is therefore unlikely that these proposals will be abandoned after a brief period of popularity. Moreover, if evolution is truly the unifying theory that many biologists believe it is, then resisting cladistic concepts of higher taxa and the development of a phylogenetic system of nomenclature will be detrimental not only to systematic herpetology but to all of biology.

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