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## POINTS OF VIEW

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### Systematics And Subjectivity: The Phylogeny And Classification Of Iguanian Lizards Revisited\*

In 1989, Frost and Etheridge published a cladistic reanalysis of relationships among iguanian lizards along with a new taxonomy of the group. Lazell (1992) attacked this work, questioning its methods and most of all its utility, to which Frost and Etheridge (1993) have recently replied. The latter two papers represent antipodal approaches to systematics generally and iguanian systematics specifically. Because some of my work (Schwenk 1988) has been used to support both points of view and since I, like many herpetologists who work on squamates, have a vested interest in seeing these issues resolved, it seems reasonable for me to explore, and hopefully clarify, the nature of the disagreement.

First, it is worth pointing out that in systematics one is dealing with three overlapping issues: (i) phylogeny reconstruction (identification of evolutionary entities); (ii) classification (what entities are to be named); and (iii) rules of nomenclature (how the entities are to be named). The distinctions among them are at once obvious and complex. Some of the complexity stems from the fact that there are competing schools of thought for each of the three subdisciplines. For example, some traditional systematists ("evolutionary" or "synthetic" taxonomists) have conceded that cladistic methodology is best for character analysis and phylogeny reconstruction, but adopt a non-cladistic approach to classification by promoting paraphyletic taxa in their formal classifications (e.g., a "Reptilia" that excludes birds) in order to highlight subjective degrees of phenotypic difference (Mayr 1981; Mayr and Ashlock 1991). Cladists, on the other hand, insist on classifications based on monophyly (evolutionary entities), but at the same time have heretofore accepted rules of nomenclature based on the non-evolutionary system of Linnean categorical ranks (de Queiroz and Gauthier 1990, 1992, 1994). In his general broadside against the Frost and Etheridge (1989) paper, Lazell (1992) has muddled these three different issues, possibly throwing the baby out with the bath water. A fruitful approach might be to consider iguanian systematics generally, and the Frost and Etheridge (1989) study specifically, in light of these separate issues.

#### Phylogeny Reconstruction

Evolution is the unifying principle of biology and, as Frost and Etheridge (1993) pointed out, each lineage has an evolutionary history (phylogeny) that exists whether or not we attempt to discern it, or whether or not we do so accurately. There is now an overwhelming consensus among biologists that phylogeny reconstruction is central to virtually all aspects of comparative, evolutionary biology (Brooks and McLennan 1991; Harvey and Pagel 1991; Lauder 1981, to name only a few). Therefore, phylogeny reconstruction is not only an end in itself, but is the necessary starting point for many evolutionary questions. Seen in this light, any rigorous attempt to reconstruct phylogeny is laudable. Therefore, Lazell's (1992:109) initial question of "why—what good does it do" indicates a failure to appreciate the fundamental importance of Frost and Etheridge's (1989) attempt to reconstruct the phylogeny of Iguania and that the fragmentation of the traditional family Iguanidae into several, less inclusive taxa follows directly from this attempt. Therefore, we need to separate the attempt to delimit monophyletic groups from the taxonomic decisions based on the results. My sense is that Lazell (1992) (and possibly other herpetologists) is so upset by Frost and Etheridge's

(1989) taxonomy, that he fails to recognize the service they have done by tackling the phylogeny of an historically refractory group. The identification of monophyletic groups, no matter how unresolved the relationships among them, can only be applauded.

In terms of methodology, I have already pointed out that even so steadfast a supporter of "evolutionary taxonomy" as Ernst Mayr has capitulated on the point of phylogeny reconstruction. The recognition that phylogeny must be inferred from synapomorphy (shared derived features; Hennig 1966) is almost universally accepted by practicing systematists, as Frost and Etheridge (1993) have pointed out. Lazell's (1992) use of "gestalt" for "grouping" species is truly anachronistic and can no longer be abided. Certainly gestalt is useful in field identification, but it is anathema to phylogeny reconstruction. There are countless examples to illustrate this. I conclude that Lazell's (1992) criticism of Frost and Etheridge's (1989) cladistic approach is without basis.

What about his criticism of their characters? Character analysis is the soft underbelly of all systematic studies and is always vulnerable to attack. Cladists may be paying the price for years of published polemics that touted the new systematic methodology as an "objective" science. The heavy reliance of cladistics on computer analysis and its associated jargon has done little to diminish this perception. However, relative to previous methods, there is certainly truth to cladists' claims of rigor. Nonetheless, a computer analysis is only as good as its character analysis. And at the heart of any character analysis is investigator subjectivity. Subjectivity is perhaps most apparent at the earliest stages of the analysis: what is a character? Most of Lazell's (1992) criticisms fall into this category. We can rarely identify with certainty a single, heritable unit that could reliably be called a character. Such a unit might be atomized into three putatively independent bits of morphology (characters) by the investigator such that a particular hypothesis of relationship is three times falsely strengthened (we have more confidence in a clade supported by three characters than in one supported by a single character). The opposite is also true (one "character" might actually represent three independent bits). In the face of no opposing evidence, we assume that characters are independent and hope that, in any case, enough "good" characters will outweigh such hidden redundancy. Since we cannot judge the quality of a character (i.e., its "phylogenetic signal") except in light of a phylogeny, we can never test our assumptions directly, only indirectly by their congruence with other character sets.

I digress to this extent because I believe that we have made too much of objectivity in systematic analyses. Character analysis, and therefore systematics, will *always* be subjective to some extent. I think that workers such as Lazell (1992) react to the *impression* of objectivity projected by some cladistic studies. Lazell (1992) is right to nit-pick because it is only through a truly thorough understanding of the morphology and all its manifestations that meaningful character analysis is possible. Frost and Etheridge (1993) concede that some of their characters might be more variable than initially described, although they dispute most of Lazell's (1992) specifics. They also agree with the need for rigorous character analysis. In any case, I believe that this is the most constructive plane on which to base criticism, because controversy in the realm of characters, first, is usually resolvable and second, generates greater breadth and depth of knowledge of the phenotype and therefore can only advance our understanding. The key point then, is not that character analysis is an objective process, but that the *reporting of the character analysis is explicit so that dispute is possible!* Thorough character description, description of multiple character states, the rationale for their attribution as plesiomorphic or apomorphic, and representation of the distribution of the states among all salient taxa are all hallmarks of cladistic studies, including Frost and Etheridge (1989). Gestalt cannot accomplish this level of analytical rigor because it cannot be replicated among investigators. The mere fact that Lazell (1992) is able to dispute

Frost and Etheridge's (1989) character analysis is a testament to the power of their study. While there might be room for disagreement regarding particulars of Frost and Etheridge's (1989) characters, Lazell (1992) is unfair in his wholesale rejection of their study. It would be more useful to see him re-score their characters in a manner consistent with his own interpretation of the morphology, add a few additional characters, justify his decisions with sufficient information (so that others might dispute *him*) and redo the analysis. Then we might have the basis for a real controversy. Until then, we have only an expression of his dissatisfaction.

Finally, Lazell's (1992) accusation of unreasonable emphasis by Frost and Etheridge (1989) on some characters (regarded, without support, by Lazell as trivial) and not others is thought-provoking, but as pointed out by Frost and Etheridge (1993), there is a vast literature, unacknowledged by Lazell (1992), on the pros and cons of character weighting, a controversy that continues to the present moment. Evolutionary taxonomists have long relied on "key characters," (a form of weighting), but one person's key character is another's trivial one. Arguments can be made against any weighting scheme, and it is perfectly reasonable that Frost and Etheridge (1989) did not judge the merit of their characters *a priori*.

The irony is that Frost and Etheridge (1989) and Lazell (1992) have arrived at remarkably similar conclusions about the *phylogeny* of iguanians (so far as we know it): the chameleons form an undoubted monophyletic group; there is a second "group" of non-chameleon taxa that comprises several recognizable (putatively monophyletic) subgroups, some traditionally "iguanaid," others traditionally "agamid," the relationships among which are mostly unresolved. The apparent point of disagreement is that Lazell (1992) argues (but does not support) that the non-chameleon taxa form a monophyletic group, whereas Frost and Etheridge (1989) disallow this possibility, suggesting that some subgroups (traditional agamid taxa) are likely to be more closely related to chameleons than to other subgroups, and further point out that there is no evidence to support the collective monophyly of the remaining subgroups. In fact, even this difference fades upon scrutiny: Lazell (1992) uses the word "monophyly" (with reference to his "Iguanidae") in the traditional sense that includes the cladistic notion of paraphyly (Lazell 1992:109). As such, he allows that his "Iguanidae" may, indeed, be paraphyletic, as Frost and Etheridge (1989; 1993) suggest. Therefore, in terms of phylogenetic conclusions (if not the methods used to arrive at them), the differences between Lazell (1992) and Frost and Etheridge (1989) are trivial. Given this similarity, controversy largely reduces to what to do with the putative, monophyletic taxa once we have them. In other words, we have identified the evolutionary units, now what and how are we to name them?

### Classification

For Lazell (1992), the crucial aspect of a classification is its utility "for highly communicable information about *easily identified groups*" (Lazell 1992:111; italics added). This view, as compared to that of Frost and Etheridge (1989, 1993) represents a fundamental schism regarding the *nature* of the entities to be named—the basis of classification. For Frost and Etheridge (and cladists, generally), the entities to be named must be "recovered evolutionary units," monophyletic in the strict sense. For Lazell, they are phenotypically distinct groups, easy to tell apart. Some of the members of Lazell's group might be more closely related, in an evolutionary sense, to another group (i.e., paraphyletic) so long as the group is not composed of two or more separate lineages (i.e., polyphyletic). Therefore, Lazell (1992) names as a formal taxon his "Iguanidae" in full knowledge that some of its members may be more closely related to his "Chamaeleonidae" than to other members of the "Iguanidae." He bases this classification largely on "gestalt" and argues that it is more useful to him as a field biologist.

I fully accept Lazell's (1992) cry for "utility" in classification, but

like Frost and Etheridge (1993), I cannot agree that utility is better served by a classification that obscures evolutionary history. While I concede that phenotypically uniform groups communicate something, what they communicate is only sensible in light of evolutionary history. As such, concepts such as evolutionary stasis, convergence, parallelism, adaptation, etc., arise from knowing how phenotypic traits are distributed across the phylogeny. Lazell's (1992) classification cannot accomplish this level of communication. While his subjective classification is of use to him in his individual efforts, it is less likely to be of use to another comparative biologist than is a cladistic classification representing accurately the evolutionary history of Iguania. These arguments are now old. Cladists have long suggested that traditional, paraphyletic classifications could lead to erroneous evolutionary generalizations owing to their inaccurate representation of phylogeny. This fear has been realized, for example, very close to home in the literature on squamate sensory modes, in which false evolutionary conclusions followed directly on Camp's (1923) paraphyletic classification of the group (Schwenk 1994).

In sum, Lazell (1992) argues that phenotypically uniform, easily identifiable groups are the most useful for recognition as formal taxa in classification, even though such taxa might not represent evolutionary history accurately, or may, at best, obscure it. Frost and Etheridge (1989, 1993) embrace cladistic doctrine which eschews the naming of paraphyletic taxa and therefore name only cladistically determined, monophyletic (in the strict sense) groups. They argue that a classification reflecting evolutionary history is the most useful. I concur with the latter view and point out that a cladistic classification is arguably of use to the greatest number of comparative biologists, is certainly the least ambiguous, and is demonstrably the least prone to evolutionary misdirection.

#### Nomenclature

It seems likely that many herpetologists will accept cladistic practices as thus far described but are, nonetheless, unhappy with Frost and Etheridge's (1989) taxonomy. This taxonomy is radical not because of the evolutionary entities (monophyletic units) identified, nor because of Frost and Etheridge's (1989) philosophy about which entities are to be named (which, after all, is standard practice; Frost and Etheridge 1993), but mostly because of the particular names chosen to represent the taxa and their elevation to family status. However, the names and family status follow directly from Frost and Etheridge's (1989) interpretation of the rules of nomenclature, as outlined by the International Code of Zoological Nomenclature (ICZN). Nonetheless, taxonomy is dynamic and it is heuristically useful to consider alternatives to the taxonomy proposed by Frost and Etheridge (1989).

(i) *The hybrid approach.*—The recognition of several monophyletic groups within the Iguania is not a recent finding, stemming from the early work of Etheridge and others (Etheridge 1959, 1964, 1966; Etheridge in Paul et al. 1976; Etheridge and Williams 1985; Savage 1958) and given cladistic legitimacy by Etheridge and de Queiroz (1988) and Frost and Etheridge (1989). These works promoted common usage of a series of informal names designating the various groups (e.g., anolines, sceloporines, etc.) which came to be widely regarded as subfamilies within the family "Iguanidae." When Frost and Etheridge (1989) elevated these (or very similar) groups to family status, most of these informal names were eliminated, as directed by rules of priority, and the ICZN. Frost and Etheridge (1989), themselves, acknowledged that this aspect of their work would be most controversial. The new names (Polychrotidae, Phrynosomatidae, etc.) disrupted decades of common usage based on reference to Etheridge's original, informal, "subfamily" epithets and might, therefore, be argued to be "destabilizing." As one of the foremost objectives of the ICZN is to promote stability, it is conceivable that an appeal could be made to recognize as formal family names the previously informal

subfamilial epithets by addition of the Linnean family ending, -idae. As such, Polychrotidae would become Anolidae (preserving the sense of "anoline") and Phrynosomatidae would become Sceloporidae (sceloporine), etc. This is a hybrid approach in the sense that it accepts the cladistic conclusions of Frost and Etheridge (1989) and use of the ICZN, but at the same time seeks to retain the association between existing names and the clade with which they have previously been identified (de Queiroz and Gauthier 1992; see below). There is a formal appeal process for such exceptions to ICZN rules and stability is one of the principal criteria on which exceptions are allowed. In any case, one would still end up with multiple families where previously there were three, a result unlikely to please many, including Lazell.

(ii) *The metataxon approach.*—Relationships among the recognized groups within Iguania remain obscure owing to contradictory or equivocal evidence (Etheridge and de Queiroz 1988; Frost and Etheridge 1989; Williams 1988). In their study of squamate relationships, Estes et al. (1988) accepted the monophyletic taxa identified by Etheridge and de Queiroz (1988) and could not, themselves, find convincing evidence of "iguanid" and "agamid" monophyly. They represented this ambiguity by designating these families *metataxa*, denoted by an asterisk next to the family name (e.g., Iguanidae\* and Agamidae\*). This convention was adopted by Gauthier et al. (1988) and these workers for higher taxa and the concept was then extended to species (*metaspecies*) by Donoghue (1985) (note that Donoghue's paper was published first owing to delay in publication of the Gauthier et al. and Etheridge and de Queiroz manuscripts). Kluge (1989) disputed use of the metataxon convention for taxa in which evidence for monophyly is *contradictory*, as opposed to *absent*. In other words, any evidence of paraphyly would eliminate the possibility of monophyly, even if the characters indicating paraphyly are contradictory (incongruent). Kluge (1989) suggested that, in any case, cladistic conventions already exist for such situations (when polytomies result from character incongruence), namely conventions 4 and 6 of Wiley (1981), which place such taxa within a classification as *sedis mutabilis*, or written with shutter quotes and marked *incertae sedis* (see Wiley [1981] for details). In making the latter suggestion (convention 6), Wiley (1981) was simplifying Patterson's (1973) earlier method of using parenthetical codes next to taxon names in a classification to denote mono-, para-, and polyphyletic taxa, and taxa of unknown status. In so doing, Wiley (1981) lumped together known para- and polyphyletic taxa, on the one hand, with taxa of unknown status. Thus, the metataxon situation (for taxa of unknown status; Patterson's [1973] code, [IK]) is actually obscured by the shutter quote/*incertae sedis* convention. According to de Queiroz (*in litt.*), the *sedis mutabilis* convention reflects unresolved relationships among several taxa (i.e., polytomies) and the *incertae sedis* convention reflects the uncertain position of a taxon within a higher taxon, but neither reflects the uncertain monophyletic status of an individual taxon, i.e. the *metataxon* convention.

Kluge (1989:293) further argued that the metataxon convention (as applied to higher taxa) was overly conservative (contra Frost and Etheridge 1993) and potentially constraining, and that it "merely describes a fact about our ignorance." However, this is exactly the intention of the metataxon concept: to call attention to our ignorance about the status of a taxon.

The metataxon convention and Kluge's (1989) paper are important to consider because the latter is central to Frost and Etheridge's taxonomic decision-making. Following Kluge (1989), they rejected the metataxon status of Iguanidae\* because there is character incongruence (contradictory evidence of paraphyly). They rejected metataxon status of Agamidae\* because it "is not consistent with recovered historical relationships" (Frost and Etheridge 1989:29). It is for these reasons that they chose to recognize as families, *sedis mutabilis*, the largest taxa for which they had reasonable evidence (a strict consensus tree) of monophyly. Once this decision was made, Frost and Etheridge (1989)

used the traditional rules of zoological nomenclature (e.g., the principles of synonymy and priority) and the Linnean system of categorical ranks, resulting in a highly non-traditional classification.

As I indicated above, taxonomic conventions are not writ in stone. For example, one might question Kluge's (1989) restriction of metataxa to groups for which there is merely the absence of synapomorphy. Given contradictory evidence of paraphyly (the situation with "Iguanidae"), monophyly of the taxon might be just as likely as paraphyly, despite the present lack of evidence. Character incongruence is a common phenomenon. Do we dismiss the possibility of monophyly in the face of it? I have shown that Wiley's (1981) conventions do not precisely distinguish this situation. The metataxon convention, using preexisting names (the approach of Gauthier et al. [1988] and Estes et al. [1988]) might more accurately reflect our current understanding of iguanian relationships while simultaneously promoting taxonomic stability. The asterisk tells us, "don't mistake this for a monophyletic group; relationships within this taxon need to be investigated further," and it does this while preserving names that most workers are familiar with. Such stability of names is usually considered desirable, so long as it does not violate known evolutionary history (which is true at least for Iguanidae\*). I am not convinced, as is Kluge (1989), that the metataxon convention will necessarily have a chilling effect, tending to preserve the *status quo*.

(iii) *The phylogenetic taxonomy approach.*—Recent papers by de Queiroz (1992) and de Queiroz and Gauthier (1990, 1992, 1994) propose a radical departure from traditional practices by deriving all taxonomic principles and methods, including those of synonymy and priority, from the central tenet of common evolutionary descent. They show clearly that many aspects of the Linnean system are not compatible with an evolutionary world view and demonstrate that a truly phylogenetic nomenclatural system will have to dispense with many long-held notions. Under their system, taxon names would be very stable because they are defined on the basis of common ancestry and not Linnean categories (de Queiroz and Gauthier 1994). Rules of priority and synonymy would not force abandonment of names traditionally associated with particular lineages, as has occurred with Frost and Etheridge (1989). Both de Queiroz and Gauthier are squamate systematists (Etheridge and de Queiroz 1988; Gauthier et al. 1988; Estes et al. 1988 and other papers) and use the problem of iguanian relationships to illustrate some of their proposals. They note that in a phylogenetic taxonomy, the name Chamaeleonidae would continue to be associated with the undisputed monophyletic taxon with which it has always been associated and that the clade formed by the "agamid" taxa (Agaminae and Leiolepidinae of Frost and Etheridge [1989]) plus chameleons would be named Acrodonta, the name historically associated with that clade. In contrast, in Frost and Etheridge's (1989) taxonomy (based on the traditional use of the Linnean system), Chamaeleonidae is equivalent to "Acrodonta" and therefore includes the traditional agamids, a highly non-traditional usage. Thus, greater taxonomic stability would ensue in the "phylogenetic taxonomic" system, even given Frost and Etheridge's (1989) phylogenetic conclusions. Such stability extends to the fact that lumping and splitting, the latter particularly characteristic of cladistic classifications and deplored by Lazell (1992), would be avoided (de Queiroz and Gauthier 1994).

The proposals of de Queiroz and Gauthier will, undoubtedly, be hugely controversial. One cannot overturn deeply entrenched practices painlessly. However, in my opinion their suggestions need to be considered seriously by all comparative biologists. I urge the readership of *Herpetological Review*, systematists and non-systematists alike, to evaluate "phylogenetic taxonomy" themselves. The pay-off for iguanian systematics specifically and the field of systematics generally is potentially great. Indeed, if ac-

cepted, "phylogenetic taxonomy" would obviate most of the discussion herein; questions of paraphyly and metataxa would be things of the past, as would an Iguania comprising nine families (de Queiroz and Gauthier 1994)!

## Conclusions

What is clear is that we are in a difficult and undoubtedly protracted transitional stage in systematic biology. We have seen cladistics become preeminent among practicing systematists, despite persistent resistance (e.g., Lazell 1992). Lazell (1992) notwithstanding, the battle is won and biologists must adapt or be peripheralized. However, in the arena of classification and nomenclature, there is much to discuss. The newly proposed system of phylogenetic taxonomy (de Queiroz and Gauthier 1992, 1994) may be the next battlefield.

Although I disagree with most of Lazell's (1992) particulars, I share with him a certain dissatisfaction with the iguanian taxonomy proposed by Frost and Etheridge (1989). I am not persuaded by the arguments against the metataxon convention that would have allowed traditional family names to stand until the weight of evidence showed otherwise. I am not convinced that use of formal family names for traditional "iguanid" taxa, rather than informal names, helps us to understand better evolution within Iguania, so long as we are clear about their monophyletic status. However, these feelings are moot; Frost and Etheridge's (1989) taxonomy will stand or fall depending on usage. Its widespread acceptance in the comparative literature indicates that it is here to stay.

It is possible that a rigorous phylogeny of Iguania will elude us. This terrible possibility stems from the fact that fragmentation and speciation of ancestral iguanians may have occurred over a geologically short period of time and in a geographically contiguous area (Williams 1988). Given virtually simultaneous origin of some or most of the major groups within Iguania, we should expect few clear synapomorphies. The situation is analogous to the origin of the mammalian orders which, to this day, defy unambiguous cladistic resolution (e.g., Novacek 1992). The possibility is that contradictory character distributions and unresolved polytomies reflect the reality of the origin of the group (Schwenk and Williams 1989; Williams 1988). Cladistic resolution might be beyond the sensitivity of current morphological and molecular techniques. We must bear this possibility in mind while searching ever deeper for phylogenetic clues.

I have attempted here to clarify some of the issues, as I see them, surrounding current controversy regarding iguanian taxonomy. I conclude that Lazell's (1992) critique of Frost and Etheridge's (1989) methodology is not supportable and suggest that rigorous character analysis is the proper avenue of future investigation. I share with Lazell (1992) some uneasiness about the Frost and Etheridge (1992) taxonomy. I have tried to show, however, that their taxonomy is consistent with current practices, yet is not the only possible outcome. To this end I have explored alternative strategies for dealing with Frost and Etheridge's (1989) phylogenetic results, if only for heuristic purposes, since their classification is a *fait accompli*. Finally, I conclude that a new phylogenetic taxonomy (*sensu* de Queiroz 1992; de Queiroz and Gauthier 1990, 1992, 1994) is sensible and desirable and urge consideration of its proposals.

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\*Note added in proof: I had not seen Lazell's (1994. *Herpetol. Rev.* 25:9-10) reply to Frost and Etheridge (1993) when I wrote this commentary, but its consideration does not cause me to alter the present account.