Species and Subspecies: What Do They Mean and Why Should We Care?

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"Our knowledge of iguanid diversity will likely increase as different philosophical approaches to species are applied and further insights into relationships revealed" (Hollingsworth 2004). Why should we care?

Not too long ago, I wrote an article about animal classification (Powell 2002), in which I suggested that even the experts, systematic biologists who study the evolutionary relationships among animals, differ in their views of species and higher categories. If the experts cannot agree, why should those of us who merely want an accurate name to attach to a particular type of animal seek an inevitably elusive answer or merely put up with what seems like a constant litany of taxonomic changes that accrue when the systematists use new data to change a name that seemed to serve our purposes just fine?

I suggest that we should care and that we also should tolerate — and even welcome — the inevitable confusion that comes with new knowledge, for reasons both philosophical and practical. As an educator, I strongly believe that knowledge for its own sake is valuable, not just because it conceivably could lead to practical applications (pretty far-fetched when discussing lizard phylogenies), but because a knowledge of real relationships reflected in an accurate taxonomy is, in effect, a search for truth. Both in the scientific and human realms, this is a worthy goal, even if no cure for cancer is forthcoming.

The practical aspect reflects our commitment to conserving biodiversity. "Species in peril rightly receive more attention than subspecies [or populations] in peril" (Malone and Davis 2004). Even though any population of an endangered animal is worthy

The three traditionally recognized subspecies of *Cyclura rileyi* , *C. r. rileyi* (above), *C. r. cristata*, and *C. r. nuchalis*, show essentially no genetic differentiation (Malone and Davis 2004) and probably should not be recognized taxonomically. Investing sparse resources to manage them as distinct entities may not be appropriate. *Photograph by John Binns.*

Cyclura carinata bartschi is not genetically distinct from the nominate subspecies (Malone and Davis 2004) and probably should not be recognized taxonomically. *Photograph by John Bendon.*

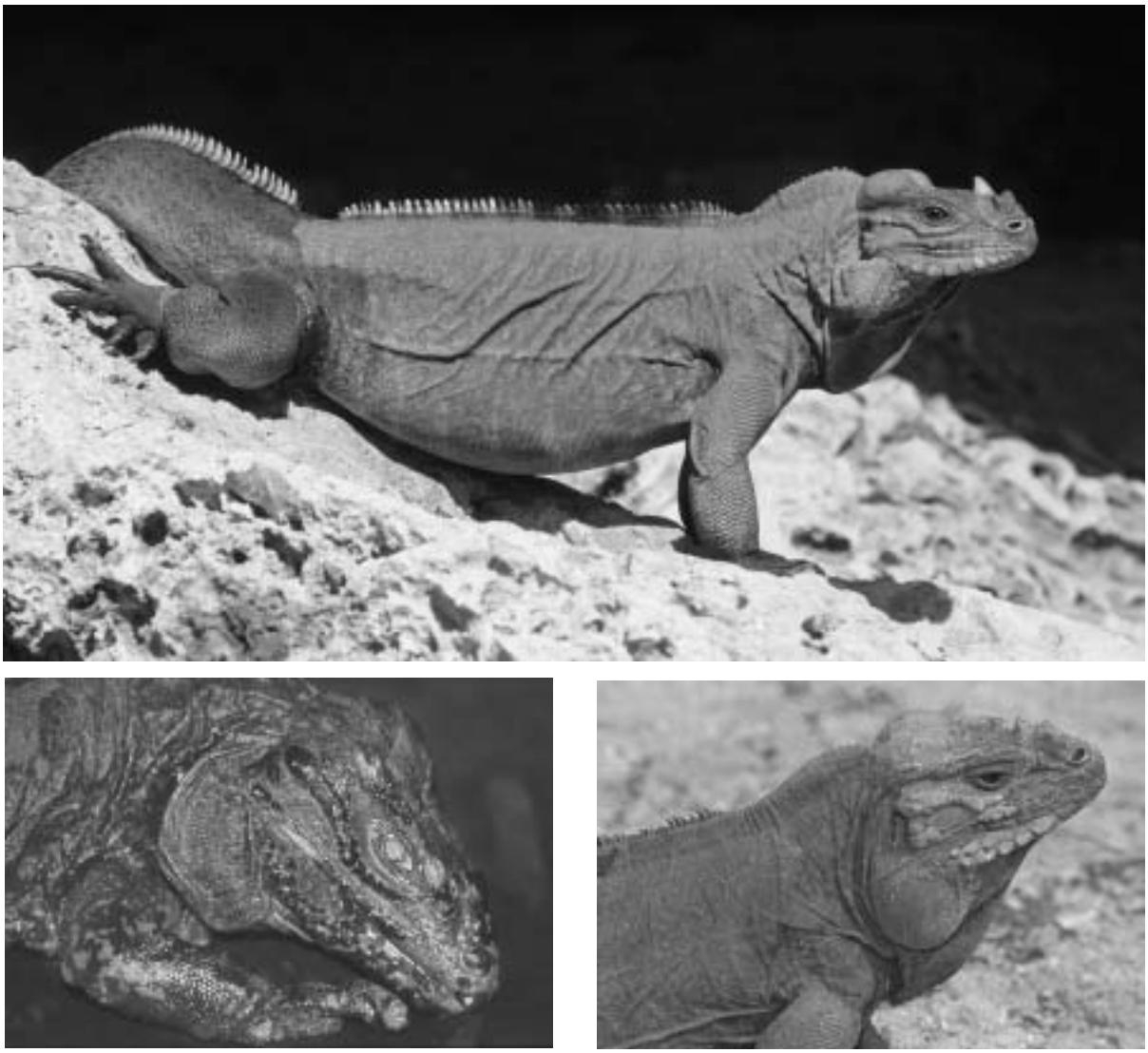
of conservation, especially the very tiny, fragmented populations that characterize the distributions of so many island-dwelling iguanas, that statement reflects the unfortunate reality that resources allocated to conservation are limited and "some form of triage is necessary in any conservation plan" (Malone and Davis 2004). I have heard even professional natural resource managers say that "it's only a subspecies," as if that rendered the entity in question of no value.

So, where should the lines be drawn? Species concepts range from wanting to designate as "full species" every isolated population with its own "evolutionary fate" to a rigid application of the "biological species concept," in which reproductive isolation (an inability to successfully reproduce under natural conditions) is the defining criterion. The former would create an unmanageable morass of new names, many of them applied to populations indistinguishable from one another, whereas the latter leads inevitably to highly subjective conclusions when parthenogenetic groups, asexually reproducing organisms, or geographically isolated populations are considered.

If species are difficult to delineate, what about subspecies? This concept has been variously applied to everything from "incipient species" (itself an undefined entity) to localized pattern variants and geographic isolates of uncertain status (Powell and Henderson 2003a). Because of the ambiguity of subspecies, the entire concept has fallen into disfavor in recent years. For example, only four new subspecies of West Indian amphibians and reptiles have been formally described in the last decade, in stark contrast to the convention that reigned throughout much of the 1950s and 1960s, when hundreds of subspecies were described, many of them placed in the same "species" for reasons no more substantive than an overall similarity in appearance.

If species and subspecies are difficult, if not impossible, to define accurately, how can we distinguish between them? In most instances, the criteria used for this purpose involve "degrees of difference." If two groups of obviously related animals can be distinguished consistently by means of one or several unambiguous characters, most experts would agree that we're dealing with two species. If, however, the diagnostic features are few or don't apply in all cases, especially if we have evidence that hybridization occurs regularly, a dilemma exists. Are we dealing with species

Cyclura cychlura has long been considered to have three subspecies, *C. c. cychlura* (above), *C. c. inornata*, and *C. c. figginsi*, but recent studies suggest that only the latter two genetically and geographically defined units exist (Malone et al. 2003). *Photograph by Chuck Knapp.*



Cyclura stejnegeri (top), from Isla Mona (see article on p. 98), and *C. onchiopsis* (above left), from Navassa Island and extinct since the late 19th century, were considered subspecies of *C. cornuta* (above right) until the application of modern species concepts resulted in a reevaluation of distinctive characters (Powell 1999, 2000). *Cyclura stejnegeri* is less distinctively different from *C. cornuta* morphologically than is *C. onchiopsis*, but biological differences may provide sufficient justification for recognition as a full species (e.g., Wiewandt 1977, Powell and Glor 2000). *Photographs by Robert Powell.*

that have yet to evolve the differences that allow us to accurately distinguish them, are we dealing with something best defined as a subspecies, or are we really only dealing with slight geographic variations unworthy of any taxonomic recognition? What makes this decision even more difficult is the realization that the evolution of new species usually is not a sudden occurrence, but takes time measured in many generations, sometimes extending over millennia or even periods of time best defined by geological means. Consequently, at any time, such as the present, for example, we are likely to encounter populations in various stages of that process, with the almost infinite number of possible variations represented by at least some groups.

Does a solution exist? Not really. In spite of inevitable gaps and errors that will have to be "fixed" down the road, we have to strive to evaluate all of the available and pertinent evidence in an effort to construct a taxonomy that most accurately reflects reality as it currently exists — and we should never recognize a species based on anything other than evolutionary relationships. For example, using the need to protect a population to justify its designation as a full species would be wrong. Similarly inappropriate would be letting a desire to draw hard lines where none are possible or blind allegiance to a traditionally accepted name or concept stand in the way of objectively evaluating new information or interpretations.

So, if we want to conserve imperiled iguanas and we accept the unfortunate reality that populations recognized as species are going to be given more consideration than those that are not, what do we do? We could designate every isolated population a species, but that would not reflect reality nor would it be legitimate or even really helpful. If faced with a large number of

"species" and still-limited resources, the criteria used in the inevitable triage would simply be adjusted. Consequently, the only realistic solution is to evaluate each situation independently, endeavoring to apply the relevant criteria as consistently and accurately as possible, given the uneven states of knowledge and the inevitable disagreements regarding taxonomic ranks.

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Iguana iguana, as traditionally defined, is actually a complex of closely related species (Malone 2000), and all translocations of Green Iguanas between South America, Central America, and the Lesser Antilles should cease in order to prevent the loss of unique genetic variation and disruption of locally adaptive gene complexes (Malone and Davis 2004). *Photograph by Thomas Wiewandt.*

Until about 10 years ago, some authorities thought that the variable morphology and lack of definitive characters used to distinguish *Ctenosaura acanthura* (top), *C. pectinata* (center), and *C. similis* (bottom) would result in these three species being subsumed into a single species that ranged from Sinaloa, México to Panamá (Köhler 2002). Recent, detailed studies have since revealed several consistently diagnostic characters, and these have been confirmed using modern molecular techniques. *Top and center photographs by Gunther Köhler, bottom photograph by John Binns.*

Cyclura lewisi (below) was until recently treated as a subspecies of *C. nubila* (above) (Burton 2004, Malone et al. 2000, Powell and Henderson 2003b). Although considerable effort had been made to conserve what may be the world's most endangered lizard when it was generally considered to be "only" a subspecies, its elevation to full species status is a much more accurate reflection of real relationships within the genus *Cyclura*. *Top photograph by John Binns, bottom photograph by Fred Burton.*

Ctenosaura oedirhina (above) from Isla Roatán, Honduran Bay Islands, was considered a second population of *C. bakeri* (below), known only from Isla Utila, until the distinctiveness of the two populations was recognized (de Queiroz 1987). *Top photograph by Randy McCranie, bottom photograph by Gunther Köhler.*

Ctenosaura conspicuosa, *C. hemilopha*, *C. macrolopha*, and *C. nolascensis* (above), from the circum-Gulf of California region of northwestern México, were considered subspecifically related until reevaluated in light of modern species concepts (Grismer 1999). Of particular interest is the suggestion that *C. conspicuosa* evolved from ancestors whose original populations on islas Cholludo and San Esteban may have had a human facilitated origin (Grismer 2002). *Photograph by John Binns.*

Populations of *Iguana delicatissima* show very little genetic differentiation (Malone 2000). However, because of the ongoing threats that endanger all of the species' fragmented populations and their vulnerability to stochastic events, each should be afforded the highest level of protection possible. *Photograph by Glenn Gerber.*

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