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## Viewpoint: Reconsider Suggested Systematic Arrangements For Some North American Amphibians and Reptiles

Collins (1991) recently proposed that 55 allopatric, morphologically distinct subspecies of amphibians and reptiles be raised to species rank because "a relatively large number of species . . . have been camouflaged by the 'subspecies' taxonomy that I think is an outdated viewpoint." Apparently, field or museum specimens were not examined and changes were based on distribution maps and current subspecific status. Responding to Collins' taxonomic proposals necessarily involves discussion of concepts, methods, and assumptions that cannot be addressed here in full. Here we discuss various aspects including (1) unsubstantiated taxonomic changes based primarily on our knowledge of the animals, and the literature, (2) the significance of geographic isolation as a criterion for recognizing species, (3) the antiquity of species and subspecies, and (4) the validity and importance for taxonomy of several assumptions in cladistic analysis.

Collins' "outdated viewpoint" is the Biological Species Concept (BSC)—species are groups of actually or potentially interbreeding natural populations reproductively isolated from other such groups (Mayr 1942, 1963, and elsewhere). The "actually or potentially" is often left out by BSC critics; the allopatric populations in Collins (1991) are, of course, potentially interbreeding populations. Simpson (1961) defined the species in the Evolutionary Species Concept (ESC) as "an ancestral-descendent sequence of populations evolving separately from others and with its own unitary role and tendencies." His ESC species are BSC species moving through time. For cladistic purposes Wiley (1981) embraced the ESC and would restrict its application to populations defined by "recovered historical relationships"—i.e., cladistic analyses of morphological characters. Collins (1991) stated that "a rigorous application of the evolutionary species concept (as discussed in Frost and Hillis 1990) would also reduce the number of arbitrarily defined subspecies dramatically." Frost and Hillis (1990) state that "intelligent use of trinomials could only follow phylogenetic analyses; otherwise their application in alpha taxonomy would be precluded." A cladistic analysis of

characters is claimed necessary to recognize subspecies, but not to elevate them to species.

Collins' proposed taxonomic changes reflect populations that have been isolated for different lengths of time and have varying degrees of morphological differentiation. He raised the western subspecies, *mormon*, of the widespread polytypic *Coluber constrictor* to a species, apparently following Fitch et al. (1981). However subsequent papers by Greene (1984) and Corn and Bury (1986) provided evidence for intergradation in New Mexico and western Texas south of the Rocky Mountains, and in Colorado, Wyoming, and Utah to the north. They concluded that the elevation of *mormon* to species status was not supported by morphological, reproductive, or zoogeographical evidence. If the predicted global warming of 2°C mean annual temperature by 2000 comes to pass, the intermediate relict populations could well disappear, qualifying the newly isolated *mormon* as a species only under Collins' system. There is no reason to think that widespread subspecies such as *mormon* or *flaviventris* will acquire new characters through natural selection in response to such a climate change or to being separated from each other. In this case, range fragmentation would not be coupled with evolutionary change.

The subspecies of *Tantilla rubra* (*cucullata* and *diabola*) in the United States were elevated to species rank. Degenhardt et al. (1976) have already reported an intermediate population in the Chisos Mountains of Big Bend National Park with the distinctive nuchal collar absent (*cucullata*), complete (*diabola*) or partially present. The intergrade zone actually covers much of the Big Bend from Black Gap to Terlingua (H. K. McCrystal, unpubl. data). With further collecting, the Trans-Pecos populations of these secretive snakes will undoubtedly prove to be continuous, as desertscrub populations tend to be. Using Collins' criteria, would the Big Bend population with characters of both *cucullata* and *diabola* warrant full species status? In contrast, we suspect that if enough specimens were available to assess geographic variation, only a single subspecies would be recognized in Texas.

Collins (1990) and Conant and Collins (1991) followed Gartska (1982) in elevating *Lampropeltis mexicana alterna* to a species using characters (iris color, head shape) that could as well reflect infraspecific adaptive responses (subterranean crevice dwelling, nocturnal activity) to the Chihuahuan Desert. In this case, *alterna* freely interbreeds in captivity with other *L. mexicana* subspecies but not sympatric *L. triangulum*. The presence of alternating reduced markings in Gartska's captive-bred offspring of *L. m. thayeri* from Nuevo Leon could be interpreted as gene flow from *alterna* rather than invalidating the use of color pattern in recognizing subspecies. Gelbach and McCoy (1965) reported *alterna* × *mexicana* (including *greeri*) intergrades from Durango. Collecting bias cannot be neglected when discussing secretive, widely distributed polymorphic taxa; intergrades between *alterna* and *thayeri* were subsequently found in southeastern Coahuila (S. F. Hale, pers. comm. 1989). Would Collins' "species" revert to "subspecies" when intermediate specimens are found in intervening areas?

*Lampropeltis pyromelana infralabialis*, the subspecies isolated north of the Grand Canyon in Arizona, Nevada, and Utah, is a barely distinguishable population raised to species by Collins. Tanner's (1953) description separated *infralabialis* from other subspecies on one less infralabial scale and white annuli complete across the ventrals in 50% or more of the body annuli. A careful study of *L. pyromelana* specimens throughout the species' range (independently by W. H. Woodin and C. H. Lowe, unpubl. data) reveals that color pattern is highly variable throughout the range with *knoblochi* and, *infralabialis* more weakly so, the only populations divergent at the subspecific level. The would-be elevation in rank of little-differentiated subspecies (as by Collins,

and by Frost and Hillis) dilutes and weakens our understanding of species while only appearing to increase biodiversity. Strangely, according to these authors, subspecies are apparently not included in biodiversity. As Cole (1990) correctly pointed out, overestimating the number of species for ulterior motives including conservation will only injure the image and credibility of systematists. We are impressed only that *infralabialis* differs so little from other *L. pyromelana* after 10,000 yrs of isolation and over 2000 generations in the present interglacial; stabilizing selection is very strong.

The subspecies of *Lampropeltis zonata* raised to species (*multifasciata*, *parvirubra*, *pulchra*) in Collins (1991) are examples of slightly differentiated kingsnake populations in isolated mountain ranges with which we are again familiar. An intergrade specimen between *multifasciata* and *zonata* from an intermediate range cited by Zweifel (1952) was overlooked or disregarded, and others are unreported. The extensive fossil record of plants and animals preserved in ancient packrat (*Neotoma* spp.) middens throughout the southwestern United States and northern Mexico have shown that most montane populations have been isolated for about 9000 yrs (Betancourt et al. 1990, Van Devender et al. 1991a). During each of 15 to 20 glacial periods during the Pleistocene, montane woodlands were reconnected in the intervening lowlands. Glacial climates with widespread woodland biotas were the typical situation for perhaps 90% of the last 1.8 million yrs (Imbrie and Imbrie 1979).

Packrat middens have provided records of presently montane reptiles in lowlands in ice age woodlands in Texas: e.g., *Gerrhonotus liocephalus* (Texas alligator lizard) in the Big Bend (Van Devender and Bradley, in press), and *Phrynosoma douglassi* (short-horned lizard) near Van Horn (Montanucci 1987). The middens also record montane animals in Arizona ranges where they no longer occur: e.g., *Gerrhonotus kingii* (Arizona alligator lizard) at 29,000, 14,500, and 9570 yrs B.P. (radiocarbon years before 1950) in the Ajo Mountains, and *Tamias* sp. (chipmunk) at 21,840 and 13,500 yrs B.P. in the Ajos, and 12,430 yrs B.P. in the Tucson Mountains (Van Devender et al. 1991b).

Prediction based on clear patterns in data is an integral part of science; a new glacial could begin any millenium unless man alters the earth's climate system too drastically. Would *multifasciata*, *parvirubra*, and *pulchra* then be reduced to subspecies status again when their ranges reconnect with each other and with *zonata* as they undoubtedly have many times in the past? Reticulate evolution, a common evolutionary mechanism in plants, has occurred in many animal populations currently recognized as subspecies. Cladistics cannot reconstruct the phylogeny of groups with reticulate evolution (Donoghue 1985).

Hundreds, if not thousands, of isolated, slightly and clearly differentiated populations in woodlands and forests on southwestern mountaintops have not been described as subspecies or plant varieties. The divergence may have occurred in the last 10,000 yrs or represent the cumulative natural selection of many Pleistocene interglacials. Under the Phylogenetic Species Concept (PSC) proposed by Donoghue (1985) where species are defined on the basis of monophyletic lineages, isolated populations with any discernible differences whatever are species (see discussion in Echelle 1990). This dubious definition frees the cladist from making troublesome taxonomic decisions—most infraspecific groups including demes, forms, varieties, subspecies, and semispecies become species. The montane populations noted above would become "species" regardless of how slightly differentiated.

*Crotalus lepidus* (rock rattlesnake) is widespread in the southwestern United States and much of northern Mexico. Four subspecies have been described (*klauberi*, *lepidus*, *maculosus*, *morulus*) in broad biogeographic regions. In the United States the ranges

of *klauberi* and *lepidus* span 1030 km from Arizona to Texas. A complex mosaic of modestly differentiated populations in various habitats, rock types, and elevations makes rigorous definition of *klauberi* and *lepidus* difficult, raising the question of whether they should be combined (H. K. McCrystal, unpubl. data). Under Wiley's ESC and the PSC, two variable subspecies of *C. lepidus* would be immediately divided into 20 or 30 species in the United States alone with greater geographic than genetic differences! Again, most of the populations have undoubtedly been isolated only 9000 yrs or less and are likely to be reconnected in the future.

In fact, over 400 species of animals and plants have been identified from packrat midden deposits radiocarbon dated 10,000 to 50,000 yrs B.P. Although species were described on obvious distinctive characters such as color pattern and scalation in snakes, or flower and fruit structure in plants, many other structures are usually distinctive. Teeth, bones, scales, heads, elytra, seeds, fruits, leaves, twigs, spines, etc. in middens are readily matched to modern reference specimens with virtually no differences. Even if a few cryptic species were missed, the last major glacial/interglacial climatic change (the Wisconsin/Holocene) did not produce many new species in the southwestern United States. There is little reason to believe that earlier Pleistocene climatic changes were of greater magnitude with more speciation.

The rich fossil record of beetles in Europe (Coope 1991) and the Rocky Mountains (Elias 1991) has challenged the idea that most living species evolved continuously throughout the Pleistocene with rapid speciation during massive environmental perturbations. All insect fossils dating to the last million years are morphologically identical down to details of the genitalia to existing species. Beetles responded to ice age climatic cycles through great shifts in geographical range rather than evolution of new adaptive types or extinction.

Many reptilian subspecies are mostly restricted to major biogeographical regions, e.g., the Great Plains: *Crotalus viridis viridis*, *Elaphe guttata emoryi*, *Lampropeltis calligaster calligaster*, *L. getulus splendida*, *L. triangulum gentilis*, *Pituophis melanoleucus sayi*; the Chihuahuan Desert: *Lampropeltis mexicana alterna*, *Trimorphodon biscutatus wilkinsoni*; mainland Mexico Sonoran Desert: *Masticophis flagellum cingulum*; Baja California Sonoran Desert: *Arizona elegans pacata*, *M. f. fuliginosus*, *Pituophis m. bimarisi*, *Salvadora hexalepis klauberi*; Sinaloan thornscrub and tropical deciduous forest: *Lampropeltis g. nigritus*, *Rhinocheilus lecontei antoni*; Great Basin Desert: *Crotalus v. lutosus*, *C. v. nuntius*, *Pituophis m. deserticola*; Mediterranean chaparral: *Crotalus v. cerberus*, *C. v. helleri*, *Pituophis m. annectens*. These distributions strongly reflect adaptive responses of species to geologic events and their climatic consequences predating the Pleistocene. The most important geologic events were the uplifts of the Rocky Mountains and the Sierras Madre Occidental and Oriental resulting in regional weather patterns and the modernization of North American biotic provinces—mostly 8 to 20 million years ago in the Miocene (Axelrod 1979).

Pleistocene climates mostly shifted biotic provinces southward with increased species richness under equable climates. Except for tortoises there are very few extinct species of amphibians and reptiles described from the Pleistocene of North America. *Phrynosoma josecitisensis*, a problematic species known from a single squamosal bone from late Pleistocene sediments in San Josecito Cave, Nuevo Leon, México, may be an aberrant specimen of a living species (Montanucci 1987). Even in tortoises, species such as *Gopherus flavomarginatus* (Bolson tortoise) may have evolved in the Pliocene at least two million years ago (Bramble 1982). Thus, subspecies in widespread continental species are more likely to be millions of years old than to have

formed in response to the most recent glacial/interglacial climatic change. Subspecies are undoubtedly much more stable than their geographic ranges—one of Collins' main criteria for species.

We view modern species as fundamental, stable, long-lived evolutionary entities that usually do not evolve or go extinct in response to environmental fluctuations; most species simply shift their ranges. When speciation in isolated populations does occur, the fate of the parent population (extinction, stasis, speciation) is independent of its descendants' fate, and would rarely, if ever, be coupled as they are in the divaricate branching of shared, derived (apomorphic) characters in cladistic analyses (Wiley 1981). In spite of cladistic assumptions, the temporal coexistence of ancestral species or subspecies in older habitats with their descendants in derived habitats is the normal state of affairs. With the first glacial climates about two million years ago, boreal forests moved almost to the Gulf of Mexico, disrupting the Gulf Circumferential Corridor between the southeastern United States and northeastern México (Auffenberg and Milstead 1965), splitting the range of *Drymarchon corais* (indigo snake). There is no reason to believe that the natural selection that formed the southeastern *D. c. couperi*, elevated to species rank by Collins (1991), had any effect on the parental populations in south Texas or northeastern México. Barring other information, *D. c. erebennus* could be the living ancestor of *couperi*.

The subspecies concept has been very useful in describing patterns of geographic variation within species. While concurring, O'Neill (1982) nevertheless incorrectly viewed Mayr's (1963) definition of a subspecies ("an aggregate of local populations of a species inhabiting a geographic subdivision of the range of the species, and differing taxonomically from other populations of the species") to be that of a taxonomic unit rather than an evolutionary one.

Johnson (1982) argues correctly as has Mayr from 1942 onward that a great deal of information on evolutionary variation in species is already cast in a subspecies framework, and that the names call attention to distinctive populations with significant research potential. Difficulty in delineating subspecies in widespread complex species like *L. triangulum* with 25 subspecies (Williams 1988) would in no way justify the elimination of all subspecies with little if any gain in knowledge. *Lampropeltis* would change from a genus with six species with variable numbers of subspecies to over 50 so-called species!

Actually the naming of populations with discontinuous clinal or allopatric variation inherently expresses inferred relationships. We use the concept of "related" in the traditional sense to mean the degree of genetic similarity between two taxa rather than the limited cladistic redefinition of sharing a derived character (Wiley 1981). Because species are as stable and long-lived as the fossil record indicates, the most closely related species are ancestor and descendent(s) that differ only in the new characters evolved by the descendent(s). A single species could be the closest relative of any number of descendants with the same degree of divergence. An ancestor and its descendent will always have a greater genetic similarity and fewer character changes than paired descendants of the same ancestor.

Cladistics or phylogenetic systematics is a methodology guided by rules outlined in an extensive body of literature accumulated in the last two decades. We encourage herpetologists to learn enough about the methodology to be able to evaluate these basic assumptions: (1) all characters are equally important and potentially species characters, (2) the degree of genetic similarity or divergence is irrelevant, (3) most ancestors are assumed to become extinct at the time of speciation, and (4) the most closely related species are paired descendants sharing their ancestors' derived characters. The new "species" proposed by Collins

(1991) reflect a methodology that cannot separate subspecies from species; the species concepts derived from cladistic methodology have an inherent bias toward narrowly defined taxonomic units (Donoghue 1985, Echelle 1990, Wiley 1981).

In practice, populations designated as "species" using Wiley's ESC and Donoghue's PSC are essentially derivatives of the original typological species concept—i.e., groups of organisms that differ from others in constant characters. In the nineteenth century Linnaeus had the advantage of using the degree of divergence to recognize different species. As O'Brien and Mayr (1991) point out "typological species concepts are fraught with interpretive difficulties such as . . . full species assignment to reproductively compatible (BSC) subspecies, arbitrary selection of diagnostic characters, and numerous species designations that err in the direction of excessive taxonomic splitting." Phillips (1982) notes that "subspecies, despite all misleading attacks, remain basic units in ornithology" and "if we cease recognizing subspecies, we must elevate all notable ones, at least, to species rank, thus destroying the biological species and plunging our classification back toward the early 19th century."

We encourage examination of Collins' proposed taxonomic changes on a case by case basis using knowledge of the animals concerned rather than accept such changes wholesale, and to consider the assumptions that they reflect. Regardless of the philosophy embraced by the systematist, a thorough analysis of a taxon with documented evidence should precede any proposed taxonomic change.

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