

Distinguishing Intraspecific Geographic Variation from Distinct Species Boundaries

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As the accompanying articles in this issue indicate, Charles M. Bogert and Charles H. Lowe did not always see eye-to-eye about taxonomic issues. One apparent flashpoint in their relationship revolved around the recognition of taxa of Patch-nosed Snakes (*Salvadora*), which Bogert (1939) had studied for his Master's thesis. In truth, one could say that Bogert was self-conflicted about *Salvadora* taxonomy, as he treated certain populations of Arizona Patch-nosed Snakes in at least three distinct ways at various points in his career: as intergrades between *S. hexalepis* and *S. grahamiae* (Bogert 1939); as a subspecies of *S. hexalepis*, which he called *S. h. deserticola* (Bogert 1945); and finally, as a distinct species, *S. deserticola* (Bogert and Degenhardt 1961, Bogert 1985). Unfortunately, however, although Bogert used the name *S. deserticola* in print across nearly a quarter of a century (from 1961-1985), he never published his evidence that the taxon was specifically distinct. At least in part, this may be because of his limited access to specimens in the University of Arizona herpetology collection, which was controlled by Lowe (see Bradley, this issue). As a result, this taxonomic case is controversial and undecided to this day. Various authors either consider the taxon *deserticola* a distinct species (e.g., Hernández-Jiménez et al. 2019, Hernández-Jiménez et al. 2021) or as a subspecies within *S. hexalepis* (e.g., Jones et al. 2020, Holycross et al. 2022). Why do different herpetologists continue to disagree on this issue, and what are the criteria that we use to recognize taxa as species versus subspecies?

How is a species defined and delimited?

Most widely distributed species exhibit geographic variation (in both morphological and genetic character sets) throughout their range. This is entirely expected; selective conditions differ in different regions or habitats, and so it is unsurprising that features like color patterns will vary geographically within a species (Hillis 2020). If we take samples from the opposite ends of the range of almost any species, it is likely that we can distinguish these two samples by their morphological features, and almost certainly we can distinguish the samples if we sequence the DNA in their respective genomes. Additionally, within the range of almost any single species, we can also likely sample intermediate populations, and find the observed differences are part of a continuum from one part of the species range to another. Gene flow

among adjacent populations of the species mean that these two different samples are not evolving within evolutionary separated lineages, but instead are part of a single, genetically and geographically structured, evolutionary species (Hillis et al. 2021).

Although biologists often argue about what methods or data are best to distinguish species, there is a surprising amount of agreement about what we are trying to distinguish. In recent decades at least, most taxonomists would say (probably each using different words) that species are the lineage segments on the tree of life: the distinct, independently evolving lineages of organisms that are connected through time by parent-offspring relationships (also called tokogenetic relationships). Within such a lineage (at least in sexual species), the relationships among individuals form a complicated network of genealogical reticulations (a tokogeny), rather than a bifurcating hierarchy of diverging relationships (a phylogeny).

A species is generally considered to be the largest lineage of individuals and populations that are connected by tokogenetic relationships (Frost and Hillis 1990, Mayden 1997, de Queiroz 1998). As an analogy of species on a phylogenetic tree, consider the individual rivers within a river basin. Although water in a river basin runs in the opposite direction from time on an evolutionary tree, otherwise there are many similarities in the two examples. We call each lineage segment in the basin a river (even though we might not give all of them different names). Similarly, we consider each lineage segment in the evolutionary tree a species. Rather than a river valley, individual organisms within a species are united in an evolutionary lineage by reticulating, tokogenetic (parent/offspring) relationships. This is what we mean when we say that species are the lineage segments on the tree of life.

Over time, ancestral species sometimes divide into two (or more) descendant species. This happens when genetic and reproductive barriers (anything that inhibits reproduction among individuals) arise within a lineage. This leads to two or more distinct lineages that evolve independently of one another. When this happens, the two lineages are no longer connected by tokogeny, but instead are historically related through phylogeny (the relationships of splitting events among lineages). We call all the lineages that descend from an ancestral lineage a clade, or monophyletic group. We name major clades as genera or other higher taxonomic ranks. *The important point is that the boundary between species and clades is the boundary between tokogenetic*

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and phylogenetic relationships, or in other words, between population genetics and phylogenetics (Baum and Shaw 1995, Hillis 2022).

What is a subspecies?

What about the variation *within* species? Often the morphological or genetic differences in different parts of a species range are different enough that we wish to have different names to describe different geographic phenotypes or genotypes (i.e., a polytypic species). Without evidence of any genetic or reproductive barriers, however, then clearly the taxa in question cannot be considered distinct species, but rather as parts of the same evolving lineage. If we wish to designate geographically and morphologically distinct taxa within species using formal scientific names under the rules of the International Commission of Zoological Nomenclature (ICZN), our only option is to call those taxa subspecies. However, it is important to remember that recognition of subspecies within species is always optional under ICZN rules; some biologists prefer not to recognize any taxa below the level of species. Often, subspecies are recognized (in field guides, for example) if they exhibit geographically distinct color patterns that might otherwise be confusing in identification of specimens. Such variation is often the result of different selective conditions within different parts of a species range.

If we use enough information (whole genome sequences, for example), we could divide geographically distinct units within species at many different levels, from relatively large groups to very localized populations. For this reason, subspecies names can be taken to excess, for example in designating extremely minor differences among populations within a species. Unlike the boundary between species and clades, there is no clear lower limit

for how much we might want to divide geographically variable populations within a species. For this reason, subspecies are traditionally restricted to major consistently distinct geographical forms within a species. It is up to individual taxonomic experts in a group to decide how much of the geographic variation within species is worthy of formal names.

Deciding between species and subspecies

What data or tests can we use to decide if two taxa are subspecies (part of the same tokogenetic lineage) or if they are sufficiently isolated to recognize them as independently evolving lineages (i.e., different species)? If the taxa in question come into geographic contact, the definitive test is to examine the contact zone between them. If they are species, then we should be able to detect evidence for reproductive isolation (barriers to free gene flow) where they come into contact (i.e., they do not form a genetic continuum). Note that the reproductive isolation need not be complete; hybrids may still form from occasional interspecific (between species) crosses. If there is no evidence for any barriers to interbreeding, however, then we say that the forms intergrade across the contact zone (form a genetic continuum), and therefore are part of a single evolutionary species. If we choose to name these as formal intraspecific taxa, then our only option (under ICZN rules) would be to call them subspecies of the parental species.

Some people prefer to name distinctive populations as species, rather than subspecies, even if the taxa in question clearly are part of a reproductive continuum. One common reason for this is that conservation-minded individuals feel that the taxa in question are more likely to receive formal legal protection if they are named as species, than if they are named as subspecies. However, this practice is deliberately misleading and

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Button created by Charles Lowe, and given to David Hillis at the University of Arizona, to express Lowe's displeasure with the changing taxonomic practices of the early 1990s.

deceptive about the biology of the respective taxa. In addition, many conservation laws (including the U.S. Endangered Species Act) can be applied to distinct population segments within species (whether they are formally described as subspecies or not). Our taxonomy should reflect our best information about the biology of the respective taxa, rather than be used to advance a particular political agenda (even one as important as conservation).

Salvadora solutions?

How does all this relate to the argument about the Big Bend Patch-nosed Snake (variously known as *S. hexalepis deserticola*, or *S. deserticola*)? In Bogert's 1945 paper, he identified both pattern differences and scalation differences between the subspecies he designated *hexalepis* and *deserticola*. For example, Bogert (1945) noted differences in the modal width of the median stripe, as well as the location of the lateral strips, between these taxa. Moreover, when he grouped snakes using these pattern differences, he also found differences in the modal number of loreal scales (one versus two) as well as in the modal number of supralabials in contact with the ocular (the scale over the eye). However, he found considerable overlap in all of these characters between the two taxa, and he noted that the variation appeared to be clinal from north to south within the range of the species. Bogert's (1945) data appeared to be consistent with a continuous transition from *S. h. hexalepis* to *S. h. deserticola*. Bogert (1945) described the transition as a "step-cline," to indicate that the region of intergradation between the two forms occurred over a relatively short distance compared the remaining range of the two subspecies. This is why he treated these taxa as subspecies of *S. hexalepis*. He also noted, however, that his sampling was highly biased and largely limited to particular areas where collecting was common (i.e. around Tucson). He clearly needed more consistent sampling of taxa at the contact zone of the two taxa, and as he noted, that was lacking in his 1945 paper.

In a completely unrelated paper (the first report of *Crotalus willardi* from New Mexico¹), Bogert and Degenhardt (1961) made a passing reference to a specimen that they called *S. deserticola*, without further comment or explanation. After that reference, some herpetologists began recognizing *S. deserticola* as a species distinct from *S. hexalepis*. Decades later, Bogert (1985) wrote in an informal snake systematics newsletter that he had evidence to support this taxonomic change. Without showing any data, he argued that the ranges of *hexalepis* and *deserticola*

closely abut one another, and that he had found no intermediate specimens.

Bogert's (1985) statement that he had found no intermediate specimens seems to conflict with the data he had presented in Bogert (1945), which showed considerable overlap in morphological characters between the two taxa, although he did not report the specific localities for those intermediate individuals. Clarifying all this might have been the purpose of Bogert's 1985 visit to the University of Arizona collections described by Bradley (this issue). Unfortunately, any supporting data that Bogert had were never published. Other authors who have recognized *S. deserticola* as distinct have likewise presented no evidence from the critical contact zone between *hexalepis* and *deserticola*, which is what we need to definitively decide if these taxa are species or subspecies.

Hernández-Jiménez et al. (2021), who also recognized *S. deserticola* as a distinct species, noted in their acknowledgements that Bogert gave his "copious unpublished notes" to Jonathan Campbell (a co-author of Hernández-Jiménez et al. 2021) prior to Bogert's death. Although Hernández-Jiménez et al. (2019, 2021) treated *S. deserticola* as a distinct species from *S. hexalepis*, they did not analyze the contact zone of the two taxa, and their maps do not indicate any sampled specimens of the two taxa in close proximity. The phylogenetic analysis of Hernández-Jiménez et al. (2019), based on molecular data, placed *S. deserticola* as a closely related sister-taxon of *S. hexalepis*, although it is unclear which subspecies of *S. hexalepis* they sequenced. Based on morphological characters, Hernández-Jiménez et al. (2021) placed *S. deserticola* embedded within a group that included the other recognized subspecies of *S. hexalepis*, with *S. deserticola* more closely related to some subspecies of *S. hexalepis* than to others. So, their tree was consistent with recognizing *deserticola* as a subspecies of *S. hexalepis* as well (although they recognized it as a distinct species). Hernández-Jiménez et al. (2019, 2021) may well be correct that *S. deserticola* is a distinct species, but what data do we have to suggest that Bogert (1945) was wrong, and Bogert (1985) was right?

The diagnosis of *S. deserticola* by Hernández-Jiménez et al. (2021) states that it "[d]iffers from the other species in the genus by having a single loreal, usually not divided; tail shorter (less than 24% of the total length) and fewer subcaudal scales." In the diagnosis of *S. hexalepis*, they note that this species "differs from *S. deserticola* by having a divided loreal and 75–103 subcaudals." In their key they note that the loreal of *deserticola* is "normally single" and that of

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¹This paper referred to the New Mexico population of Ridge-nosed Rattlesnakes as *C. willardi silus*, despite some differences with known populations of that subspecies. It was later described as a distinct subspecies, *C. willardi obscurus* (Harris and Simmons 1976). Workers subsequently supported it with genetic and phenotypic data, treating various populations of Ridge-nosed Rattlesnakes as subspecies (e.g., Barker 1992, Holycross and Goode 2020) or as distinct species (Barker 2016).

hexalepis is “normally divided.” This appears to be the most consistent character that differentiates the two taxa, but clearly it varies to some degree in both. The tail length of *deserticola* is listed as <24% total length, whereas that of *S. hexalepis* is listed as 20–26% total length, so that character does not seem to differentiate the two taxa. The subcaudals in *deserticola* are reported as 66–87, compared to 75–103 in *hexalepis*, so again there is considerable overlap. The pattern differences noted by Bogert (1945) are discussed as well in Hernández-Jiménez et al. (2021), although it is unclear how much variation exists in these patterns, especially near the critical contact zone.

Why would anyone argue over whether the Big Bend Patch-nosed Snake is a species or a subspecies? Why does it even matter? This question may have been a point of great disagreement between Lowe and Bogert, and it remains a point of some (although hopefully less acrimonious) disagreement among herpetologists today. The issue is not so much about the taxonomy *per se*, though. Taxonomy is a tool to tell others about the biology of the snakes. If we call *deserticola* a subspecies of *S. hexalepis*, then we are expressing the view that these snakes are all part of reproductive continuum. In that case, the geographically distributed phenotypic differences we observe are likely the result of different selective conditions, or different population histories, in different environments across the species’ range (Sonoran versus Chihuahuan deserts, for example). If we call *S. deserticola* and *S. hexalepis* distinct species, we are expressing the view that there are reproductive/genetic barriers between the two species, which we take as evidence that they are evolving on independent evolutionary paths. The names, then, reflect our best information and current understanding on the biology of the snakes.

Which position is best supported?

After considering the published data, which opinion is best supported: should we consider *S. deserticola* a distinct species? Or a subspecies of *S. hexalepis*? I’d say that the issue is not clearly resolved. The critical point is that the patterns of character expression discussed above, different or not between the two taxa, could exist within OR between species. What is still needed is a careful analysis of the contact zone between the two taxa. We are left with the varied taxonomic opinions that Bogert (1945, 1961, 1985) expressed throughout his career, but still with no definitive analysis that would tell us which of those opinions is best supported by data.

Jones et al. (2020) and Holycross et al. (2022) took the position that since no one has ever presented and published clear evidence to support *hexalepis* and *deserticola* as distinct species rather than subspecies (i.e., morphological or genetic data from the contact

zone of the taxa that supports two distinct species), we should continue to treat these taxa as subspecies of *S. hexalepis* (as argued by Bogert 1945). Indeed, Bogert’s (1945) data look fairly compelling on this issue; none of the characters that are used to separate the taxa are diagnostic (consistently different between the taxa), and that seems to be confirmed by Hernández-Jiménez et al. (2021). In counting loreals, or supralabials in contact with the ocular, it is hard to have an intermediate number between one and two, so intermediate states cannot occur. Although Bogert’s (1945) first key couplet distinguished these taxa on the basis of one (*hexalepis*) versus two (*deserticola*) supralabials in contact with the ocular, Bogert nonetheless recorded 23.4% of *hexalepis* specimens, and 2.7% of *deserticola* specimens, with the opposite conditions. He hinted (Bogert 1945:12) about “other data that need not be discussed here,” but all the data he presented showed two taxa with overlap in their distinguishing characters. That seems to be the case as well with the analysis by Hernández-Jiménez et al. (2021), which appears to include any subsequent data obtained by Bogert.

I think that Jones et al. (2020) and Holycross et al. (2022) take a reasonable stance. But I acknowledge that an analysis of the contact zone could certainly show that there are genetic barriers between these taxa, which would support their recognition as distinct species. Hernández-Jiménez et al. (2019, 2022) followed the opinion that, as Bogert (1985) expressed late in his life, the two taxa are different species – although Bogert never published data to support that position.

I’m friends with people on both sides of the issue, and disagreeing about taxonomy is not a barrier to friendship for most reasonable people (even though it appears to have caused tensions in the relationship between Lowe and Bogert). I’m more interested in the answer, and in an analysis, of the contact zone, than I am in anyone’s opinion of what an analysis *might* show. I think such an analysis should be a priority for anyone interested in systematics of the snakes of Arizona. We should make this decision on the basis of data and analysis, however. This is a golden opportunity for a field biologist who willing to sample carefully across the contact zone.

Until someone carefully examines the contact zone of these taxa, different herpetologists will likely make different taxonomic choices about the status of the Big-Bend Patch-nosed Snake. It is important to understand that neither side is obviously wrong; different people just disagree about which solution is best supported by the current evidence. Hopefully as new and better evidence is published, taxonomic opinions will converge on a single solution. Until then, ICZN rules allow individuals the freedom to pick the solution that they think best reflects the current evidence. No one (including reviewers, editors, or

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famous biologists with strong opinions) should be allowed to force a subjective taxonomic decision on others. Whether you choose to call a taxon a species or subspecies should depend only on what you think the current data best supports.

Lowe and the irony of taxonomic cycles

Lowe was a big supporter of the concept of polytypic species: the idea that a species can often exhibit different forms or phenotypes across different environments. So, I suspect that he was unhappy with Bogert and Degenhardt's (1961) unsupported elevation of *S. deserticola* to a full species. When I first met Lowe in the early 1990s, it is ironic that he considered me to be an opponent of the taxonomic use of subspecies. I had co-authored a paper (Frost and Hillis 1990) that argued that the subspecies category had been over-used and applied to subjective splits of continuous clines within species (including some examples that he had named). But Frost and I also discussed appropriate uses of subspecies in that paper. Nonetheless, Lowe had buttons printed up that read "Save a Subspecies; Kill a Cladist." When we met, he gave a button to me, and made it clear that my 1990 paper with Frost had been the inspiration for the button. I still have the button today and display it in my office. The experience was ironic, as three decades later, I am now seen by some as one of the current supporters of the use of subspecies. In truth, my position hasn't changed much since 1990. I still think many biologists of the 1940s to 1980s over-used the subspecies category to name some trivial geographic variation, including the subjective splitting of continuous, gradual clines. Nonetheless, as we argued in Frost and Hillis (1990), subspecies are an appropriate way to name distinct geographic races of polytypic species that nonetheless maintain reproductive cohesion. I don't care if people recognize geographic races with a formal name or not, but I am opposed to designating such geographic races as "species" when there is clear evidence that they constitute a reproductive continuum, without any reproductive barriers between the taxa.

Looking ahead

I'd argue that there are other cases, similar to the *Salvadora* story, of proposed species splits among Arizona herps that are poorly supported, or unsupported, by available data. This suggests that there is still a lot of work to do in understanding the species boundaries of Arizona reptiles and amphibians. For example, Holycross et al. (2020a, b) and Holycross et al. (2022) followed the proposed recognition of two species of Mountain Kingsnakes in Arizona: *Lampropeltis pyromelana* in the north (Colorado Plateau and Mogollon Rim), and *L. knoblochi* in the southeastern Madrean Sky Islands. However, they also noted that

these two taxa cannot be reliably distinguished on the basis of any morphological characters. Instead, they were proposed as distinct taxa based on DNA sequence differences and coalescent analyses in northern versus southern samples (Burbrink et al. 2011). However, geographically intermediate populations in the Pinaleno, Rincon, and Santa Catalina mountains have not been examined genetically, so it is impossible to tell if the reported differences are part of genetic continuum (i.e., there is a single species), or if two species actually overlap and coexist in the intermediate mountain ranges (Holycross et al. 2022). Furthermore, the multispecies coalescent approaches used to distinguish these taxa as species have subsequently been shown to over-split species (Sukumaran and Knowles 2017, Campillo et al. 2020, Chambers and Hillis 2020, Mason et al. 2020). As the purported species can't be distinguished based on morphology, and intermediate populations have not been examined genetically, existing data are inadequate to determine the status of these taxa. This is another example where careful field work and analysis could answer this open question. Of course, populations of Mountain Kingsnakes are isolated in discrete patches of habitat, so contact zones may be much harder to assess than in more continuously distributed species (such as *Salvadora*, or *Pantherophis obsoletus* in the eastern United States; Hillis 2022). But there are plenty of geographically intermediate populations that have not yet been examined, so there are certainly data that could be collected that are relevant to the question of the taxonomic status of Mountain Kingsnakes in Arizona. Data are so much more useful, and often definitive, than opinions.

Bogert and Lowe were both forceful individuals with strong opinions, and we continue to have such individuals in herpetology today. Hopefully, however, times are changing for the better, and biologists will begin to base their taxonomic decisions on published data and analyses, rather than on a particular person's forceful opinions. If people disagree about taxonomy, the force of an individual's personality should have nothing to do with which arrangement we follow. Rather, we should look at the relevant data and analyses, and decide for ourselves which arrangement is best supported by the evidence. The good news is that the ICZN rules clearly leave subjective taxonomic decisions in the hands of individuals. We should examine published data and analyses, and decide for ourselves if we think evidence is sufficient to consider taxa as species or subspecies, or if we should recognize them at all. No one is required to accept a taxonomic decision, or follow someone's list of taxon names, if they believe that the taxonomic decisions are insufficiently supported by published evidence.

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