

## POINTS OF VIEW

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# New and Not-so-new Conceptualizations of Species and Subspecies: A Reply to the “It’s Species All the Way Down” View

In a recent Point of View, de Queiroz (2020) claims to present an “updated” concept of subspecies, which he defines (p. 460) as follows: “subspecies are incompletely separated lineages within a more inclusive lineage.” He argues that this is different from the conceptualization of subspecies in Frost and Hillis (1990) or Hillis (2020), which can be paraphrased as: subspecies are incompletely separated lineages within a more inclusive *species* lineage. The difference in the two views is the inclusion of the word “species” in the latter definition. De Queiroz (2020) prefers to equate the word “species” with the more general term of “historical lineage” used by Frost and Hillis (1990), Hillis (2020), and others. In de Queiroz’s view, “species” can be used for any historical biological lineage at the population level (not including organismal or gene lineages), which leads him to accept that there can be species within species (and, by inference, even finer divisions of species within those species).

Although I accept that de Queiroz’s (2020) POV is a novel and philosophically consistent solution to reconciling divergent views on the use and utility of subspecies, I see it as a problematic conceptualization of “species” rather than of “subspecies.” As noted above, the definition of subspecies by de Queiroz’s (2020) only differs from that of Frost and Hillis (1990) or Hillis (2020) in its use of the word “species” to mean any historical biological lineage, regardless of how incompletely or temporarily separated it is from other such lineages. This would result in a radical change in the way that most biologists use the word “species.” Most biologists use the word “species” to refer only to the largest historical biological lineages that are united through tokogenesis (parent–offspring relationships). When a species shows evidence of geographic variation, such that it contains divergent subgroups that intergrade continuously from one form to another (with no evidence of reproductive isolation), those subgroups have traditionally been called subspecies. Species can also be composed of many localized populations that are temporarily isolated from one another in time and/or space. All of these entities (species, subspecies, and populations)

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represent types of historical biological lineages. In de Queiroz’s (2020) view, subspecies, as well as distinct local populations, represent yet more examples of “species.” He might not choose to name all these lineages within larger species with binomials or trinomials, but they would nonetheless be “species” following his logic.

De Queiroz (2020) agreed with my point (Hillis 2020) that trinomials can be used to indicate differentiated but incompletely separated lineages within species (which de Queiroz would consider species within species). He noted (p. 461) that:

THE BINOMINA *AGKISTRODON CONTORTRIX* AND *A. LATINCINCTUS* AND THE TRINOMINA *A. CONTORTRIX CONTORTRIX* AND *A. C. LATINCINCTUS* ARE SIMPLY REPRESENTATIONAL DEVICES... THE PURPOSE OF WHICH IS TO CONVEY OUR CURRENT UNDERSTANDING OF LINEAGE DIVERSITY WITHIN THE *AGKISTRODON* CLADE. IN EITHER CASE, THE NAMED ENTITIES ARE DETECTABLE BUT INCOMPLETELY SEPARATED LINEAGES, AND OUR TAXONOMIES SHOULD REPRESENT THAT SITUATION CLEARLY AND UNAMBIGUOUSLY. THE USE OF TRINOMINA, AS ADVOCATED BY HILLIS (2020), WOULD OBVIOUSLY IMPLY INCOMPLETE SEPARATION UNDER THE UPDATED CONCEPT OF SUBSPECIES PROPOSED IN THIS ARTICLE. IN THE CASE OF BINOMINA, AS ADOPTED BY BURBRINK AND GUIHER (2015), INDICATING INCOMPLETE LINEAGE SEPARATION WOULD REQUIRE SOME ADDITIONAL FORM OF ANNOTATION. (EMPHASIS ADDED)

I note that the trinomials used by Hillis (2020) are not merely consistent with the concept of subspecies presented by de Queiroz (2020), but are also consistent with the concept of subspecies discussed by Frost and Hillis (1990), Hillis (2020), and many other prior authors. The trinomials clearly indicate the broadly intergrading subgroups within the species *A. contortrix*. I agree with de Queiroz (2020) that our taxonomies should represent the situation of subgroups within species (groups that show no evidence of reproductive isolation from one another) clearly and unambiguously. Indeed, I am advocating for the use of subspecies to achieve that purpose. Doing so follows a long tradition in biology, although unfortunately, subspecies have been used in the past for other purposes as well, as discussed and critiqued by Frost and Hillis (1990).

De Queiroz (2020) argues that we could also develop an alternative to trinomials to indicate incompletely separated lineages within species, by adding some form of notation to

binomials to indicate that they are subgroups within larger species lineages. We could do that, but why introduce a new and potentially confusing system of notation, when subspecies already allow us to name and characterize these situations? If we were to do that, binomials would then convey two different meanings, which I think leads to confusion.

I also think de Queiroz's (2020) use of the word "species," which he defines as any historical population-level lineage, even within the traditional bounds of species, will cause considerable confusion and consternation in some areas; indeed, it may well be unintelligible to most biologists and the general public. For example, there are clearly detectable (although in many ways biologically insignificant) historical lineages of populations within the species *Homo sapiens*. In de Queiroz's (2020) conceptualization, these population lineages within *H. sapiens* are also species, leading to the conclusion that there are many species of living humans, within the larger human species. A similar concern was raised by Jackson et al. (2017:802), who referred to the delimitation of such groups with some popular multispecies coalescent methods as a "sanity check" for systematists. I think this is a needlessly misleading and counterproductive way to discuss human diversity. Humans are all one species, and historical population groups within humans are so minor and temporally ephemeral that there is no justification for recognizing even subspecies within modern humans (Templeton 2013). Nonetheless, there are populations of humans that have been historically isolated from other human populations for thousands of years. In de Queiroz's (2020) conceptualization, such populations are also "species." I reject the view that such ephemerally isolated populations of any species should also be considered species, whether or not we assign them formal names.

De Queiroz's (2020) approach also creates unnecessary problems for discussing the biodiversity of geographically variable species, such as Copperheads. Consider the simple question of "how many species of Copperheads are there in North America?" I (Hillis 2019, 2020) argued there is only one species, *A. contortrix*, which contains the geographically distinct subspecies *A. c. contortrix* and *A. c. laticinctus*. Burbrink and Guiher (2015) concluded there are two species, *A. contortrix* and *A. laticinctus*. De Queiroz (2020), however, recognizes three species: *A. contortrix*, *A. c. contortrix*, and *A. c. laticinctus*. I consider the first answer (i.e., one species, with two subspecies) as clear and unambiguous: it tells us that there is no evidence of reproductive isolation among populations of *A. contortrix*, that there are two geographically distinct subspecies within the species, and that we should expect to see a gradual intergradation of intermediate populations where the two subspecies come into contact. This accurately describes Copperhead diversity (Gloyd

and Conant 1990; Burbrink and Guiher 2015). I think the second and third answers (i.e., two or three species) lead to confusion, rather than clarification. The Burbrink and Guiher (2015) answer implies that both species are present across areas of overlap, and that there is evidence for reproductive isolation between *A. contortrix* and *A. laticinctus*, or selection against their hybrids, where they come into contact. Given that the populations in the area of contact actually intergrade from one to the other across hundreds of kilometers (Gloyd and Conant 1990; Burbrink and Guiher 2015), calling these two forms "species" would require (as suggested by de Queiroz 2020) that we add some new means of clarification. The de Queiroz (2020) solution of three species requires that we change the way most biologists (and others) use the word species, and it certainly complicates the enumeration and taxonomy of species.

In conclusion, I understand de Queiroz's (2020) desire to conceptually unify the divergent positions of Hillis (2020) and those who would elevate any detectable and incompletely separated sublineage within a larger species lineage to the level of species. However, his "solution" leads to more practical problems than it solves. We already have a taxonomic system in widespread use (subspecies, designated by trinomials) that can name and characterize these incompletely separated lineages within species.

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