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Response to Criticisms of an Updated Subspecies Concept

In an attempt to resolve some contemporary controversies about the taxonomy of incompletely separated lineages, I recently proposed an updated concept of subspecies (de Queiroz 2020). According to that updated concept, subspecies are entities of the same fundamental kind as species (separately evolving metapopulation lineages) that differ from other entities considered species only in that they are incompletely separated from one another and therefore are parts of a more

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inclusive species (lineage). This updated concept of subspecies not only resolves various controversies about the taxonomy of incompletely separated lineages, it also brings the concept of subspecies into congruence with a unified concept of species, gives the concept of subspecies a biologically meaningful definition, and ends the treatment of the subspecies category as an artificial taxonomic rank. Despite these benefits, this new concept of subspecies is at odds with certain taxonomic traditions, and therefore I anticipated that it would meet resistance. In this context, it is not surprising that a criticism of my proposal has recently been published by Hillis (2021). Here I respond to that criticism to clarify both the nature of my proposal and why it is preferable to retaining a more traditional concept of subspecies.

Hillis (2021:49) stated “In de Queiroz’s view, ‘species’ can be used for any historical biological lineage at the population level ... which leads him to accept that there can be species within species (and, by inference, even finer divisions of species within those species).” This characterization suggests that I would support “subdividing these evolutionary lineages into ever-smaller slices that we call species” (Hillis 2020:55), which is not the case. According to the unified species concept (de Queiroz 2007) that serves as the background for my proposed updated concept of subspecies, a species is a separately evolving metapopulation lineage, where a metapopulation is an inclusive population (often) made up of subpopulations; as such, species reside at the higher end of the population-level continuum and are distinguished in this manner from populations at the lower end of the continuum, such as demes and family groups. Admittedly, there is no sharp line of demarcation between the higher and lower ends of the population-level continuum but accepting this fact in no way endorses recognizing every detectable population-level lineage, no matter how small or ephemeral, as a species.

Hillis (2021) raised concerns that my view of species would lead to the conclusion that there are many (incompletely separated) species of living humans within the larger human species. Although I would prefer not to complicate this discussion with the issue of human taxonomy, a politically charged topic that is difficult for people to consider dispassionately, I will mention two things. First, if there happened to be groups of humans that qualified as subspecies under my updated concept (incompletely separated lineages within a more inclusive lineage), they would also qualify as subspecies under Hillis’ concept (incompletely separated lineages within a more inclusive *species* lineage), so adopting Hillis’ view would not avoid the confusion and consternation that he mentioned. Second, my understanding is that the data on human genetic variation do not indicate the existence of distinct but incompletely separated lineages within the human species. Although studies of human genetic variation have inferred the existence of 9–21 population clusters (e.g., Tishkoff et al. 2009; Elhaik et al. 2014; Baker et al. 2017), those clusters do not appear to constitute separately evolving lineages, and they certainly do not possess properties that should be required for taxonomic recognition as subspecies under either my or Hillis’ definition.

Humans are unlike copperheads in this regard. In the copperhead case, which served as an example for my original proposal (de Queiroz 2020), there are large geographic areas occupied by non-admixed members of eastern and western populations with a zone of admixture between them (Burbrink and Guiher 2015, fig. 1A). This pattern suggests a case of incomplete separation between eastern and western lineages. In humans, by contrast, the majority of the individuals exhibiting genetic elements representing any given cluster also possess elements from one or more other clusters (e.g., Tishkoff et al. 2009, fig. 3; Elhaik et al. 2014, fig. 1; Baker et al. 2017, fig. 1). These high levels of admixture indicate that the clusters are not evolving independently and therefore do not constitute separately evolving lineages—not even incompletely separated ones. Put another way, if one were to recognize those clusters as subspecies, almost no individuals would be assignable to those subspecies because almost every individual would be an intergrade. This is a textbook example of a situation in which subspecies should not be recognized.

According to my proposal, the subspecies category is a subcategory of the more general species category (analogous to the distinction between sample and subsample) rather than a mutually exclusive category (analogous to the distinction between adult and subadult), as it has been treated traditionally. More specifically, subspecies are incompletely separated species within a more inclusive species. Hillis (2021:57) argued that this proposal will “lead to confusion.” As an example, he cited my suggestion that *A. contortrix*, *A. c. contortrix*, and *A. c. laticinctus* should all be considered species. On the contrary, if one accepts the updated concept of subspecies in which subspecies are incompletely separated species within a more inclusive species, that suggestion is not confusing at all: *A. c. contortrix* and *A. c. laticinctus* are subspecies (incompletely separated species) within a more inclusive species, *A. contortrix*. The suggestion that *A. c. contortrix* and *A. c. laticinctus* are incompletely separated species is only confusing if one adopts the traditional view that subspecies are *not* a kind of species.

Hillis (2021:57) raised this issue in the context of discussing biodiversity, specifically, in the context of the question “how many species of Copperheads are there in North America?” Of course, if one were counting species for the purposes of assessing biodiversity, it would be misleading to say that there are three species of copperheads, given that one species contains the other two. For that purpose, it would be appropriate to count only non-nested species, of which there are either one or two, with the choice depending on whether maximally inclusive species or incompletely separated species are more relevant to the issue being addressed. For example, the maximally inclusive species would be appropriate to count for a conservative estimate of species richness in North American snakes, whereas the incompletely separated species would be appropriate to count as examples of lineage divergence between snakes inhabiting the eastern temperate forests and the Great Plains.

Under my proposal, the taxonomy of copperheads adopted by Burbrink and Guiher (2015), which recognized two species, *A. contortrix* and *A. laticinctus*, is also acceptable. It is evident from Burbrink and Guiher’s (2015) article that these species are incompletely separated, and according to my proposal, it is neither necessary nor always desirable (see below) to designate all incompletely separated species using trinomina, which are merely representational devices (see O’Hara 1993; de Queiroz 1999). However, if the names proposed by Burbrink and Guiher (2015) are adopted (e.g., in a checklist), I noted that it would be important to indicate that the species designated by those names are incompletely separated. Hillis (2021:57) stated that this approach would require systematic biologists “to introduce a new and potentially confusing system of notation.” On the contrary, such notation is neither new nor confusing. Annotated taxonomies have been in existence for decades (e.g., Wiley 1979, 1981). Moreover, the type of annotation in question has already been used in the Society for the Study of Amphibians and Reptiles (SSAR) list of *Scientific and Standard English Names* (Crother et al. 2008, 2012, 2017), where it is stated in one of the notes that *Aspidoscelis marmorata* and *A. tigris* are incompletely separated species. This information could be conveyed even more simply by using a parenthetical remark after the name, analogous to the notations used in the same list to indicate that some *Aspidoscelis* species are unisexual, for example, “*A. marmorata* (incompletely separated from *A. tigris*).” Far from being confusing, these mechanisms for indicating incomplete separation are clear, simple, and informative.

Hillis (2021) argued that use of the subspecies category under its traditional conceptualization as distinct from the species category is adequate for describing incomplete lineage separation clearly and unambiguously. From my perspective, his argument rests on an oversimplified view of lineage separation. If it were the case that a sharp line existed between lineages that are evolving separately and those that are not, then treating species and subspecies as distinct, mutually exclusive categories, as advocated by Hillis (2021), might make sense. In reality, however, lineage separation is a matter of degree, not of kind—it forms a continuum. That continuum extends from complete lineage separation (absolutely no gene exchange) to extremely limited hybridization to limited hybridization to moderate hybridization in a narrow hybrid zone to more extensive hybridization in a moderately wide hybrid zone to even more extensive hybridization in a broad hybrid zone to more-or-less continuous variation with isolation by distance to absolutely no separation (panmixia with respect to geography). Even this characterization, which is intended to emphasize the continuous nature of lineage separation, greatly oversimplifies both the continuum itself, by using categories to describe it, and its complexity, by focusing on the amount of hybridization and the width of the hybrid zone. Lineage separation can be further complicated by many additional factors, which include (but are not limited to): different types of population structure (another continuum), the strength of selection against hybrids (another continuum), the length (as opposed to the width) of the hybrid zone (another continuum), the number of hybrid (contact) zones, the strength of both extrinsic and intrinsic barriers to gene flow (additional continua), the temporal duration of the hybrid zone (another continuum), and whether the hybrid zone results from secondary contact (thus reflecting potentially greater separation historically) or primary divergence. In addition, some genes or genomic regions move farther and/or faster across hybrid zones than do others (Harrison and Larson 2014, 2016), gene flow between incompletely separated lineages is often asymmetrical (Barton and Hewitt 1985), and a lineage can remain incompletely separated from an older lineage after separating completely (or almost so) from a younger one. The point is that lineage separation is a continuous and complex phenomenon that is grossly oversimplified by division into two mutually exclusive categories—that is, by the traditional view of the relationship between species and subspecies advocated by Hillis (2021).

Returning to the copperhead case, Hillis (2020:54) stated that the two species recognized by Burbrink and Guiher (2015) “clear[ly] ... are not independently evolving lineages” but instead represent a single “geographically variable species” (Hillis 2021:50). I do not consider the situation nearly so clear cut. Burbrink and Guiher (2015) adopted an explicit and objective method of species delimitation that inferred the existence of two species, despite admixture where they come into contact. That inference does not appear to be an artifact of uneven geographic sampling, as the methods used did not further subdivide the two lineages despite their extensive distributions and substantially larger sampling gaps within those distributions than within the inferred hybrid zone. The hybrid zone between these incompletely separated lineages, although not narrow in kilometers, is narrow relative to the distributions of the non-admixed individuals, particularly that of the eastern lineage. The lineages also differ both morphologically and ecologically (Burbrink and Guiher 2015). In addition, further analyses

(Burbrink and Ruane 2021) indicate that the hybrid zone is not neutral—that if it were neutral (e.g., no selection against hybrids, no assortative mating), there has been more than enough time for the hybrid zone to expand to encompass the entire ranges of the two lineages, which it has not done.

In sum, currently available evidence indicates that these incompletely separated lineages of copperheads have been at least partially separated for hundreds of thousands of years and have not hybridized enough to erase that historical signature. Moreover, even if one thinks that copperheads are best considered a single species, there will be other cases in which separation is greater (and greater and greater ...) but still incomplete, and every researcher will accept incompletely separated lineages as separate enough to be considered species at some point along the continuum. Rather than having every researcher draw this artificial line in a different place according to personal preferences, as is currently the situation, biology would be better served by embracing the continuous nature of lineage separation. This can be done by adopting the concept of subspecies as incompletely separated species, which eliminates the artificial line by rejecting the artificial dichotomy upon which it is based.

Hillis (2021) argued that the use of trinomina (as opposed to binomina) to represent incompletely separated lineages would not be confusing, but I consider this conclusion again to overlook the complexities of lineage separation. Because the timing of separation varies from one lineage to another, it is possible for one of two incompletely separated lineages to give rise to a third lineage that is more fully separated from the other two. If the two incompletely separated lineages are designated with trinomina as subspecies of a single species and the third lineage is designated with a binomen as a separate species, the former species would be paraphyletic relative to the latter. This use of trinomina would be confusing in that it would misleadingly imply that the two incompletely separated lineages, as members of the same species, are one another's closest relatives, when in fact one of them is more closely related to a different species. Baltimore Orioles (*Icterus galbula*) and Bullock's Orioles (*I. bullockii*) are an example of this phenomenon. These two species are not each other's closest relatives (Jacobsen et al. 2010), despite hybridizing extensively where they come into contact (e.g., Walsh et al. 2020). Herpetological examples also exist (e.g., Arntzen et al. 2014, 2018; Bell et al. 2015).

Redefining the subspecies category as a subcategory of the species category (reconceptualizing subspecies as a kind of species) more fully acknowledges both the fundamental commonality of species and subspecies as population-level lineages and the continuous nature of lineage separation. By contrast, the traditional treatment of species and subspecies as mutually exclusive categories at worst implies a fundamental difference where none exists and at best represents the artificial partitioning of a continuum. Hillis (2019:8) objected to recognizing Eastern and Broad-banded Copperheads as different species, which he characterized as “the arbitrary slicing of a continuum.” If anything constitutes the arbitrary slicing of a continuum, it is treating the species and the subspecies as mutually exclusive categories.

In closing, I want to point out that Hillis' (2020, 2021) views on subspecies and mine are both fundamentally similar and fundamentally different. We agree that subspecies are incompletely separated lineages, and this point of agreement represents an important departure from several dubious

applications of the subspecies category that have been adopted historically. However, I would argue that Hillis (2021) does not go far enough in adopting a more biologically meaningful concept of subspecies in that he continues to treat the subspecies as a mutually exclusive category relative to the species. That general view about the relationship between the subspecies and species categories has several disadvantages. For one thing, it perpetuates elements of the outdated view that the species and subspecies categories are artificial taxonomic ranks, at least relative to one another. For another, it perpetuates the treatment of the species and subspecies categories as stages in the existence of metapopulation lineages, making them analogous to the categories “adult” and “subadult” rather than to the more general category “organism.” For yet another, it oversimplifies the phenomenon of lineage separation by arbitrarily dividing a continuum into discrete categories, and in so doing, encourages pointless debates about where to draw the line between the two categories. Hillis’ (2020, 2021) definition of subspecies represents an important move toward a biologically meaningful concept of subspecies, but it would be more consistent with a unified concept of species, which is itself more consistent with the importance commonly attributed to the species category (de Queiroz 1998, 1999, 2011), to go a step further and adopt the definition of subspecies as incompletely separated species within a more inclusive species. Taking such a step would more fully embrace the fundamental commonality of species and subspecies as lineages at the population level of biological organization as well as the continuum in degrees of lineage separation.

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