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Point of view

Species delimitation in mammals: A response to Gippoliti

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ABSTRACT

In a comment published in this issue, Spartaco Gippoliti (2019) presents a critique of a recent perspective paper of mine (Zachos, 2018a). Specifically, he accuses me of diminishing taxonomy and of denying it its proper role in conservation biology. Here I respond to these criticisms and argue that taxonomy is necessary but not sufficient for delineating appropriate units for conservation due to its inherent threshold character that is a direct consequence of imposing a discrete classification system (taxonomy) onto a continuous process (evolution).

In a comment (Gippoliti, 2019), published alongside this response, Spartaco Gippoliti criticizes my views on species concepts and the resulting conclusions I drew pertaining to the relationship between taxonomy and conservation biology (Zachos, 2018a). That latter publication was in turn not only part of the ongoing debate (e.g., Frankham et al., 2012; Zachos et al., 2013; Groves et al., 2013; Heller et al., 2013, 2014; Cotterill et al., 2014), but also a direct reaction to two recent papers about the purported benefits of the diagnosability version of the Phylogenetic Species Concept (dPSC) as applied to the taxonomy of African mammals, including claims about its theoretical and practical superiority over other concepts (Groves et al., 2017; Gippoliti et al., 2018). Although Gippoliti (2019) correctly summarizes my main views, I do not think he addresses them appropriately (particularly my views ii and iii in his list). His arguments do not refute any of my theoretical claims, and I even fail to recognize a concrete response to my concrete criticisms (although he might disagree on this point, of course). I have explicated my views in some detail elsewhere (Zachos, 2015, 2016 – for a discussion of the dPSC, see chapter 5.6.2 –; 2018a; in press) and will therefore not repeat them here but leave the verdict to the readers. Rather, I will clarify what I think is a misreading of my views on taxonomy and its role in conservation. I would also like to emphasize that, although Gippoliti (2019) lists Zachos et al. (2013) among those advocating the Biological Species Concept (BSC), we do no such thing in that paper. While some of the authors might be adherents of the BSC, I can only speak for myself, and I have detailedly discussed the shortcomings of that concept (Zachos, 2016, chapter 5.3; Zachos, in press). It is also worth noting that some explicit advocates of the BSC or related concepts (Frankham et al., 2012) explicitly warn against underestimating outbreeding depression in conservation management (Frankham, 2015) – a point that according to Groves et al. (2017) and Gippoliti et al. (2018) is supposedly particularly detrimental under BSC-based taxonomy. More importantly, however, Gippoliti writes that, according to me, there are "no 'errors' in taxonomy" (as if taxonomy were arbitrary) and that I "forg[e] mistrust of species delimitation as a rigorous empirical research program". This is a serious misunderstanding! My views are based on the inherent limitations of taxonomy (Zachos, 2018b). Evolution, whether gradual or punctuated, is a continuous process. As a consequence, biodiversity, which is both the result of evolution and the target of conservation, comes in degrees. Taxonomy, on the other hand, is discrete – a population or group of populations can be either a species, subspecies etc. or not, but there is nothing in between, and nothing that Gippoliti (2019) or, for that matter, Groves et al. (2017) and Gippoliti et al. (2018) say solves this basic dilemma. This does *not* diminish taxonomy as a scientific discipline, but nature's fuzzy boundaries impose limits on how precise any classification system can be. Biologists in general and taxonomists in particular should not turn a blind eye to this (in the word of Riddle and Hafner, 1999, it is "time to take the blinders off"). Claims that any specific way of "carving nature at its joints" (by means of the dPSC in this case) might solve this problem are flawed and amount to exactly such a "blind-eye" approach. Of course species delimitations are scientific hypotheses, there is no doubt about that, but they are *not only* scientific hypotheses! In

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the grey area of lineage sundering (i.e. the process of speciation), species splitting and lumping are both equally right or wrong, there is no objective scientific solution to the delimitation problem here (for a more detailed discussion, see Zachos, 2016). In these cases of closely related and only recently diverged population lineages, species delimitation is a fuzzy business and ultimately includes not only a scientific hypothesis but also an "executive decision" (Zachos, 2018b; Schlick-Steiner et al., 2010 call it "researcher bias"). It is the realization of this predicament that has triggered both attempts at standardizing species delimitation (e. g. the Tobias criteria, Tobias et al., 2010; see also the discussion triggered by Garnett and Christidis, 2017) and doubts as to whether the species category (not the taxon!) really is an objective level in our classifications. If species taxa are delimited inconsistently (and worse: perhaps necessarily so), then the class of all species taxa (= the species category) might be an artifact (for a discussion and consequences see Mishler, 1999; Riddle and Hafner, 1999; Hendry et al., 2000; Faurby et al., 2016; Zachos, 2016, chapters 6 and 7; Willis, 2017). Species delimitation criteria vary continuously, and hence species delimitation always involves a cut-off criterion. The fact that it can be objectively tested whether that cut-off criterion is met must not be confounded with claims that the criterion itself is objective. There is a threshold analogy with *p*-values in statistics here. Acknowledging a separate species is like rejecting a hypothesis based on a value of lower than, say, 0.05. Apart from the fact that you could have chosen a different threshold (0.001, 0.01, 0.3141592,. . .), a result of 0.051 is treated in the same way as one of 0.99, although it is much closer to 0.049. It is this insight from which I concluded that it should *not only* be taxonomy on which conservation decisions are based. Taxonomy is neither arbitrary nor is it irrelevant to conservation; it is just not precise, due to the rampant vagueness of boundaries in the biological world. This is why I have suggested to include the underlying biodiversity (which can be measured quantitatively) in conservation decisions. I do not want to exclude taxonomy, but rather complement it. Taxonomy is *necessary but not sufficient* for the delineation of appropriate units for conservation. As a scientific hypothesis, a species name is based on an ideally large and diverse dataset – the data "behind the name" that gave rise to it in the first place. These data matter, even if eventually they are not considered sufficient for a separate species name. The fact that Gippoliti (2019) recommends phylogenetic diversity (PD) as a relevant tool in conservation suggests that our viewpoints may in fact be closer than it seems: PD was one of the measures of biodiversity that I explicitly mentioned in my perspective paper (Zachos, 2018a).

Another analogy might drive home the point I am trying to make. Languages are often used in analogies when discussing the species problem, and according to one count, there are 7097 known living languages on the planet (https://www.ethnologue.com/). Now, usually the delimitation criterion for different languages (as opposed to dialects) is the lack of mutual intelligibility (Matthews, 2014, p. 104). However, mutual intelligibility comes in degrees (as does the analogous ability to interbreed and basically every other delimitation criterion) so that the number of 7097 is certainly not the only result one can arrive at. Depending on one's inclinations ("lumping" vs "splitting") one could come up with, say, 6000 or 9000 languages instead. Still, the sum total of the underlying linguistic diversity on which our counts are based remains one and the same. If it is linguistic diversity we want to protect, then we should not simply rely on the number 7097 (the label "language"), but also take that very linguistic diversity into account (by means of one or more appropriate ways of quantification). The analogy with biodiversity, I think, is obvious.

In a nutshell, my views on taxonomy and conservation can be summarized in the plea "focus on data, *not just* on names". This does neither diminish taxonomy nor taxonomists, but it might make a huge difference to science-based conservation.

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