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## Commentary

Frank E. Zachos<sup>a,\*</sup>, Les Christidis<sup>a</sup> and Stephen T. Garnett<sup>a</sup>

# Mammalian species and the twofold nature of taxonomy: a comment on Taylor et al. 2019

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**Abstract:** In a recently published paper, Taylor and colleagues discussed different approaches and interpretations of mammalian taxonomy and their bearing on more general issues such as conservation and evolutionary biology. We fully endorse the fundamental importance of taxonomy and its being grounded on scientific principles. However, we also deplore a lack of awareness in the literature of the fact that taxonomy is a twofold enterprise that encompasses not only (i) the scientific description and quantitative analysis of biodiversity but also (ii) an executive decision as to how the results of (i) are translated into names. This has serious ramifications for the conservation of our planet's dwindling biodiversity and when taxonomic names are used as raw data for ecological and evolutionary analyses.

**Keywords:** conservation; species concepts; species delimitation; taxonomy.

## Background of the debate

Taxonomy in general, and mammalian taxonomy in particular, has seen a lively debate over recent years, with a particular focus on the issue of what constitutes a species and how and if species can be delimited objectively. A few papers have triggered criticisms and commentaries, most of all Garnett and Christidis (2017) who, based on their

view that taxonomic decisions pertaining to species status are partly (not completely!) arbitrary, proposed taxonomic governance under the purview of the International Union of Biological Sciences (IUBS). This and other publications dealing with the inherent limitations of taxonomy (e.g. Zachos et al. 2013, Zachos 2018a) stir reactions that appear to follow a common pattern: an outcry from the taxonomic community who consider that we disparage taxonomy as a science, insist that taxonomy is a hypothesis-driven discipline and claim that our views threaten the freedom of scientific research (see the comments on Garnett and Christidis 2017 in the correspondence section of *Nature* as well as Raposo et al. 2017, Thomson et al. 2018, Gippoliti 2019). These arguments generally miss the key points in our various publications (Garnett and Christidis 2018a,b). The most recent case is the paper by Taylor et al. (2019) published in this journal. Our views are variously portrayed as a “condemnation of perceived ‘taxonomic inflation’”, as having received “undue attention” and as defending the Biological Species Concept (BSC). The authors say that “[a]t the heart of the debate is the disagreement about species concepts” and seem to claim that our views are not in line with a consensus among many taxonomists that promotes the Evolutionary Species Concept (ESC) or related concepts. We would like to correct what we believe to be a misrepresentation of our views, and clarify our concerns for taxonomy as a discipline. None of us deny that taxonomy is a scientific discipline that generates and tests hypotheses about the natural world nor wish to constrain that science in any way. Indeed, it is a research field in which we are closely involved: Taylor et al. (2019) cite the research led by one of us (Christidis et al. 2014) as an example of “very high standards of taxonomic description and publication”. Nor do our views depend on any particular species concept, although, like Taylor et al. (2019), Zachos (2016, 2018a,b) embraced and defended the ontological superiority of the ESC. We therefore ask our critics to look at the first part of the reasoning in our respective publications, i.e. the analysis on which our conclusions are based. We believe that there is a misconception of the very nature of taxonomy because the species taxon is conflated with the species category. Here, rather than reprise our previous

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arguments, we think it is worth expanding briefly on these more profound issues involved in describing, delimiting and naming of species (usually called alpha taxonomy). More detailed elaborations and discussions can be found in the references cited.

## Taxonomy's twofold nature and its inherent limitations

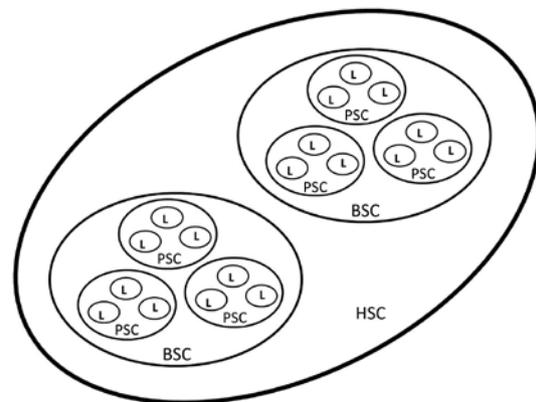
The fundamental issue is that the term “species” is ambiguous because it refers to both a biological entity (e.g. *Homo sapiens*) and a rank in our hierarchical Linnean classification system. The former is the species taxon, the latter is the species category. Species taxa are little twigs in the Tree of Life: portions of biodiversity that exist independently of our efforts to systematise nature. They are real entities that can be discovered as a result of the high-quality taxonomic research reviewed by Taylor et al. (2019). The Tree of Life, however, is an encaptic system displaying a nested hierarchy with a fractal pattern (lineages within lineages). Lineages can legitimately be delimited by grouping individuals together using diverse criteria, but, if criteria for grouping differ, the resulting taxa are necessarily different kinds of entity. However, for the species category (i.e. the class that defines what all species taxa have in common) to be an objective unit, all species taxa must be the same kind of entity. This is the aim of the various species concepts – to create a consistent set of criteria by which species taxa are delimited such that, for example, a rodent species not only has the same kind of name (binomial) but is also the same kind of thing as a species of ungulate, fish or moss, etc.

The ontological framework of the ESC defines species as separately evolving (population-level) lineages; other species concepts provide operational species identification criteria. Thus, the lineage makes the species, but delimiting such lineages requires one of the 30+ operational species concepts (Zachos 2016): if we find two groups of individuals (populations) to be diagnosably different in heritable traits, or if we find a lack of gene flow, or only sterile hybrids, etc., then that is good evidence of two lineages evolving separately. There is no fundamental difference between the various operational species concepts/criteria; they all function within the framework of the ESC. The diagnosability version of the Phylogenetic Species Concept (PSC), which has been advocated particularly strongly in mammalian taxonomy (see, for example, Cotterill et al. 2014, Gippoliti 2019 and references therein), in this respect differs from the others (see Mayden 1997, de

Queiroz 1998, 1999, 2007 who elaborate on the distinction between ontological and operational species concepts) only in that it carves out less inclusive entities along the lineage spectrum than most other concepts. In other words, it is more prone to splitting than to lumping (Figure 1).

The issue facing many users of taxonomy is that different taxonomists favour certain criteria (and thus species concepts) over others with the result that the species category is inconsistent. A single species to one taxonomist is several using the criteria preferred by another. Both are right according to the criteria they adopt but any use of taxonomy that requires grouping or comparison of species suffers from the incommensurability of the basal units (Riddle and Hafner 1999, Faurby et al. 2016, Zachos 2018a). For example, the International Union for Conservation of Nature (IUCN) working groups for East Asian and South American primates have embraced the PSC, whereas the one for African primates prefers the BSC. The underlying diversity in the different regions may be the same, the number of species recognised per unit of variation is not. Yet it is as legitimate to favour diagnosability for delimiting species as it is reproductive isolation at the other end of the definitional spectrum.

The only really different level is the one of the (allopatric) populations themselves: as long as populations are separate, they evolve independently from one another and thus meet the criterion of the ESC. This level also coincides with Willi Hennig's famous tokogeny/



**Figure 1:** Relationship of population lineages and species delimited according to different species concepts.

The only level in the hierarchy of population-level lineages that can be delimited non-arbitrarily is the (allopatric) lineage itself (L). No species concept used in taxonomic practice, however, considers each such lineage to be a separate species. Different concepts lump lineages to varying degrees. The illustration shows three such concepts of increasing inclusiveness: the Phylogenetic Species Concept (PSC), the Biological Species Concept (BSC) and the Hennigian Species Concept (HSC). The latter is based on absolute reproductive isolation and thus may comprise several taxa that, under the BSC, are treated as separate species.

phylogeny divide (Hennig 1966, see Zachos 2016, chapter 6.2). It also is in line with species being the least-inclusive population-level ontological individuals but would equate species with populations. However, as far as we know, no practicing taxonomist classifies every separate population as a distinct species because nobody wants to name ephemeral groups. Nevertheless, strictly following the lineage approach means the only criterion for definition of a species is being a separate lineage; they need not be diagnosable, reproductively incompatible or genetically distinct (de Queiroz 2005, 2007). In theory, this is the only approach that captures natural (“real”) entities at the same objectively and biologically defensible level. Everything more inclusive is to some extent arbitrary, being based not only on the necessary criterion of being a lineage but also on at least one additional criterion that is defined by the taxonomist’s chosen species concept (see Freudenstein et al. 2017 for a similar view). Once we expand from the level of single populations, taxonomists are necessarily selecting the point at which to divide the continuum of stages through which lineages progress after sundering (de Queiroz 1998). They will all, if well done, capture real entities, but of different inclusiveness such that the species category is actually a collection of very different categories. This would make species taxa fundamentally incommensurable, and species counts would face a serious apples-and-oranges problem. The species as the currency for many analyses in comparative biology would be flawed because they would not be based on a single currency, but on an unknown number of them. Alpha taxonomy is thus fundamentally a twofold procedure. First, individual organisms are *grouped* into species *taxa* and secondly, these taxa are *ranked* at the level of the *species* category. Grouping is based on biological realities such as diagnosable differences, ecological adaptations, behaviour, reproductive isolation, etc. As such, grouping is based, like all good science, on scientific hypotheses that are open to refutation. Ranking, on the other hand, necessarily includes some level of arbitrariness. One can test whether a particular grouping really captures a biological entity, but one cannot test whether the resulting taxon is a *species* taxon. This is the reason why there are so many parallel taxonomies where the species in one treatment are subspecies in another. Both are equally right, or wrong. This holds regardless of the existence of ever more sophisticated algorithms of species delimitation. These algorithms detect structure in datasets and thus potential taxa, but not the species rank (cf. Sukumaran and Knowles 2017). Ranking includes an executive decision, not just scientific data and its analysis, a decision that is ultimately a qualitative judgement of significance about

what group is deemed worthy of being assigned a species name. No algorithm can replace this (e.g. Sites and Marshall 2004, see also Mishler and Wilkins 2018).

Taxonomy is thus a twofold process, consisting of the scientific description and quantification of biodiversity and its temporal and spatial distribution, which is often interdisciplinary and highly sophisticated, and an individual preference for the way that the resulting patterns are interpreted and translated into names. More formally, taxonomy consists of (a) grouping of individuals into taxa based on testable hypotheses + (b) an executive decision that the taxon warrants recognition at the *species* level. Rather than saying a new species has been described and named, it would be more accurate to say that a certain portion of hitherto unrecognised biodiversity has been identified (science) and then named *as* a species based on a set of criteria (opinion). While the criteria are usually linked to a theoretical conceptualisation of what constitutes a species (PSC, BSC, etc.), the final choice is an individual preference. We are not alone in sharing our concern about this twofold nature of taxonomy (see, for example, Heywood 1998, Mishler 1999, Hendry et al. 2000, Willis 2017, Mishler and Wilkins 2018) but consider it an inescapable consequence of the fundamental object of taxonomic research: delineating discrete entities out of an evolutionary continuum that inevitably means boundaries are fuzzy. This is an inherent limitation of taxonomy of which users of taxonomy should be more aware.

Given the same raw data, taxonomists often arrive at different species classifications because there is no single correct taxonomic solution above the level of the population itself. If true, this would deal a death blow to the species category as a well-founded currency in comparative biology. Studies highlighting this worrying possibility such as those by Riddle and Hafner (1999), Faurby et al. (2016) or Willis (2017) should be a wake-up call and an alarm signal that we draw the wrong conclusions from alpha taxonomy. Both Garnett and Christidis (2017) and Zachos et al. (2013) (see also Zachos 2018a, 2019) worry that the arbitrary part in the aforementioned alpha taxonomy equation negatively impacts conservation biology because decisions are based too much on the executive-decision part of species and too little on the scientific data that gave rise to that decision. This is why Zachos (2018a) urged conservation biology to put less emphasis on names (i.e. the species or subspecies rank, e.g. in Red Lists) and more on the raw data on which they are based (see also Hendry et al. 2000). This of course would be complicated but would remove the partly arbitrary step of ranking. Taylor et al. (2019) actually present very relevant

data on how insights into biodiversity and its distribution contribute to conservation, but none of what they say necessarily hinges on taxonomic names. It only does so because we have chosen to give different levels of value to the different ranks (interestingly, not a view necessarily shared by the wider public, Garnett et al. 2018). If we continue to do so, then streamlining and standardising our ranking decisions becomes a necessary aspiration. The principles underlying the “Consilient Solution” advocated by Taylor et al. (2019) is a welcome attempt at this kind of standardisation. The problem of incommensurability does not go away, however, and this was exactly what the contentious suggestion by Garnett and Christidis (2017) was about. It is predicated on the same line of reasoning when they conclude that “[i]f species delineations are at least partly arbitrary, deliberations must draw on expertise beyond taxonomy, morphology, systematics and genetics” (p. 27). The commentaries, rejoinders and general indignation were all directed towards the second part, but hardly anybody addressed the first one. For taxonomy to play the role that it should and that we all want it to play, however, it is this first part that needs consideration. Invoking scientific freedom in the name of taxonomy is virtuous, but for the serious problem at hand, it is not enough.

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