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Commentary on taxonomic inflation, species delimitation and classification in Ruminantia

Frank E. Zachos

Natural History Museum Vienna, Burgring 7, 1010 Vienna, Austria

E-mail: frank.zachos@nhm-wien.ac.at

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The species problem and the debate about species concepts have been shaking up both evolutionary biology and taxonomy for decades or even centuries (Wilkins 2009), but over the last 10 or so years the paradigmatic shift from the biological species concept (BSC) to the phylogenetic species concept(s) (PSC) has added a new dimension to the discussion: taxonomic inflation (Isaac et al. 2004), i. e. the artificial increase of species number of a taxon through splitting, mainly through raising former subspecies to species rank. The debate was initiated in the context of mammalian taxonomy, and a number of studies, commentaries and rejoinders by adherents of the diagnosability version of the PSC and its critics have been published recently (Avice 2000; Meiri and Mace 2007; Frankham et al. 2012; Gippoliti and Groves 2012; Gippoliti et al. 2013; Groves 2013; Heller et al. 2013, 2014; Zachos et al. 2013a, b; Zachos and Lovari 2013; Cotterill et al. 2014; Zachos in press). In this commentary, I raise some of the discussed points that I consider particularly important and then list a number of recent examples of what I consider excessive splitting of some ruminant species.

First of all, it should be made clear that there is nothing wrong with species splitting per se and that taxonomic inflation is not a necessary consequence of splitting. Cryptic diversity and cryptic species are real, and it is also true that many taxa, even among mammals, are understudied and often have not been revised for decades. Thus, the number of species in general and the number of mammal and ruminant species in particular will likely increase for good reasons (some examples of two or more lineages subsumed under a single species at present or until recently include badgers, clouded leopards, probably African elephants and possibly also giraffe,

see Zachos et al. 2013a; but doubtless there are many more). So, my criticism should *not* be misunderstood as opposed to species splitting in general! We certainly possess only superficial knowledge of the biodiversity in many, if not most groups of organisms, and present species lists are consequently often only the tip of the iceberg. The species we have missed so far will not always be those that we have not yet seen, but perhaps equally often (and probably much more often in the case of mammals) those that we have not yet recognised, i. e. those that are subsumed under a single name with one or more other species (cryptic species).

That said, I have serious doubts as to whether the Phylogenetic Species Concept is a scientifically sensible approach to uncovering and taxonomically acknowledging this cryptic diversity. In the case of the Ruminantia, it is mainly the work of Groves and Grubb (2011), whose bovid taxonomy has also been adopted in the ungulate volume of the Handbook of the Mammals of the World (Groves and Leslie jr. 2011), that has triggered a debate. The bovids in particular, of which Groves and Grubb (2011) acknowledge 279 compared to 143 in Grubb (2005), have been contentious. To be sure, the data basis for this work is impressive and the fruit of hard labour over years or decades of measuring museum material throughout the world, but the taxonomic conclusions rest solely on the diagnosability version of the Phylogenetic Species Concept (dPSC). I have argued elsewhere why particularly the dPSC is a poor guide to delimiting species (Zachos and Lovari 2013 and Zachos in press). The main arguments can be quickly summarised as follows:

Practically any and every population will be diagnosably distinct given enough resolution power of the traits analysed (this point has been raised by

others as well, e. g. Heller et al. 2014). That holds for any type of marker, but of course the advent of genomics is what one thinks of first in this context. Thus, it is basically a function of the traits analysed (and the sample size) whether a population is granted species status. The claim of superior objectivity made by adherents of the dPSC is not tenable; they simply ignore that being a lineage is not enough for species status unless indeed every lineage is a species. That, however, is to my knowledge not even claimed by the most ardent PSC proponents. If that were the case, each and every island population, captive breeding group etc. would be a distinct species. The objectivity claim of the PSC simply neglects that there will always be an element of convention or arbitrariness in deciding which hierarchical level of lineages in the Tree of Life (which is nothing but a huge encaptically structured system of lineages!) should be acknowledged taxonomically as the species rank. Apart from the sensible requirement that species be lineages (*ontological* criterion) there must be additional (*operational*!) delimitation criteria. By making diagnosability the yardstick for species recognition (because non-diagnosable lineages are denied species status), diagnosability is no longer an operational proxy for the detection of an evolutionary species sensu Wiley (1978) (as intended) but becomes the ontological definiens of species itself. This is then, ironically, a typological approach – something that the dPSC is believed to overcome by its proponents (see Cotterill et al. 2014) and that they accuse their critics of (Cotterill et al. 2014, particularly pp. 823, 826 and 829). Interestingly, sometimes adherents of the dPSC are very much aware of the inconsistency in their equating species with lineages and vice versa: In this volume, Colin Groves quotes from other publications: „Every lineage is a species“, only to go on by saying that genera and families are also lineages but at a higher hierarchical level. It is very obvious then that *not* every lineage is a species!

This may suffice; a more detailed discussion of this topic and both viewpoints (for and against the dPSC) can be found in the cited publications and references therein. Here I discuss briefly the klipspringer and red deer examples taken from Groves and Grubb (2011) which I consider excessive splitting of ruminant species and which are oddly reminiscent of the famous splitting of North American brown bears (*Ursus arctos*) into 82 separate species by Merriam (1918), which is the archetypical example of taxonomic inflation.

Klipspringer

The klipspringer (*Oreotragus oreotragus*) is perhaps the most obvious ruminant example of what has been regarded as oversplitting leading to taxonomic inflation (Heller et al. 2013; Zachos et al. 2013a). Groves and Grubb (2011) do not just acknowledge a single species, but no less than 11, based on diagnosable morphometric differences. I consider this

a prime example of the shortcomings of the dPSC – practically every population is diagnosably distinct and will have to be assigned species status. This is an unnecessary burden on conservation by reducing population numbers, limiting management measures (genetic rescue, (re)introductions etc. would have to be carried out across species boundaries) and, not least, devaluing the species category in both scientific and public circles. But even if one were to accept the dPSC, this taxonomic revision would be rash because of the very small sample sizes which, for the various populations or species, are mostly < 10, often < 5 and sometimes $n = 1$. No taxonomic conclusion, let alone the erection of 10 new species, is warranted by such a data set.

Red deer

Red deer species have also been extensively multiplied by Groves and Grubb (2011). There has been a long discussion about whether the red deer/wapiti complex should be regarded as a single species (*Cervus elaphus*) or two species: red deer (*Cervus elaphus*) in Europe, western and central Asia and wapiti (*Cervus canadensis*) in eastern Asia and North America. There is actually a cladistically interesting relationship here in that wapiti cluster together with sika deer to the exclusion of the western red deer. This is a borderline case with good arguments for both sides (and perhaps best depicted in the frame of the superspecies concept). In point of fact, this kind of borderline case is exactly one of the predictions of evolutionary theory: if species evolve and give rise to new species, then all gradations of differentiation should be found in nature from a single lineage via a grey area of one or two (or more) lineages to two separate lineages. The grey area will always be something that taxonomy cannot adequately represent – there can be one species or two, but hardly one and a half (it is here that the concepts of subspecies and superspecies have their origin, with all their shortcomings). The picture of well-differentiated taxa on the Tree of Life, separated by gaps, is only true if one zooms out, as it were, so that the often blurred boundaries between species become invisible. Now, instead of two red deer-like species, Groves and Grubb (2011) list 12. This is a nice example of the diagnosability trap and the inconsistency about whether diagnosability is an operational or an ontological criterion (see above). If diagnosability aims at detecting lineages, populations that are known to be distinct lineages must be given species status even in the absence of diagnosability (or absence of a diagnosability analysis). Why, then, are insular red deer from the Tyrrhenian islands (Sardinia and Corsica), that are traditionally classified as *Cervus elaphus corsicanus*, given species status (*C. corsicanus*) while the island population(s) from the British Isles is (are) not? And further, why are Tyrrhenian red deer lumped into the same species *C. corsicanus* with the North-African Barbary deer (usually classified as

C. e. barbarus)? Both are completely isolated, and while they are similar, they are doubtless diagnostically different with high enough resolution markers (and indeed are based on microsatellites, Hajji et al. 2008). The claim of objectivity when it comes to the dPSC therefore turns out to be an illusion in taxonomic practice, even in that of its adherents...

Apart from these two cases, Heller et al. (2014, Table 1 and text) give a list of splittings proposed by Groves and Grubb (2011) (including the klipspringer) where there are statistical problems with the analysis or where genetic data contradict diagnosability, suggesting that even by their own standards their splitting was excessive. Note that certainly not all splittings done by Groves and Grubb (2011) are unwarranted, and an unknown number of those that I consider unfounded based on their data may turn out to be justified in the light of further research. It is not splitting per se that I am criticising, it is the underlying philosophy that, in my view, is responsible for the creation of taxonomic inflation.

Groves' contribution to this volume is a supra-specific classification of Ruminantia, thus not dealing with species delimitation, but he asks the very good question what the criteria are for assigning a certain rank to a taxon, a question that he admits needs a good answer if taxonomy is to be rigorously scientific. Unfortunately, there is no such answer, we must – at very long last – finally rid taxonomy of the burden of this pre-Darwinian legacy. Linnean categories are arbitrary rank designations, and there is simply no feasible way of making them objective (because then only sister taxa could be assigned the same rank, making necessary an almost infinite number of ranks, see Farris 1976 for deterrent examples). Groves offers time-rank associations as a solution (in various versions known as temporal banding and time clipping etc. in the literature: Avise and Johns 1999, Avise and Mitchell 2007), but this does not work either (Avise and Liu 2011; Zachos 2011). The resilience against the abandonment of the Linnean categories is really astonishing, particularly since nothing is gained by using them – other than the illusion of having lots of taxa of, say, family rank that are (falsely!) believed to be directly comparable when in reality one is dealing with apples and oranges. In this regard it is revealing that Groves (and many others) argue that a practical necessity for ranks is that the so-called higher categories are often used as proxies for biodiversity or endemism. There is an argument here, but it is the other way around: precisely because ranks are arbitrary, biogeographers, palaeontologists and macroecologists should *not* rely on them when analysing diversity through time and space; rather, they should in each single case justify exactly which taxa are used and why they are deemed to be all apples or all oranges but not both! Taxonomic surrogacy, as it is called, is very prone to

producing spurious results (Allmon 1992; Bertrand et al. 2006; Zachos 2006).

In conclusion,

- Cryptic diversity is real in many cases and needs to be acknowledged taxonomically! Our species lists at present will often seriously underestimate the true amount of biodiversity.
- Ontologically, species *taxa* are individuals, not classes (while the species *category* is a class, not an individual). These individuals are lineages in the Tree of Life. This is a definition of the species taxon. To delimit species, i.e. to determine the boundaries between two or more species taxa, we need additional operational criteria. These criteria serve to delimit species (not to define them!) and as guidelines as to which hierarchical level of encaptic lineages we want to call species.
- The claims of adherents of the PSC, particularly the dPSC, that their approach enables taxonomists to objectively delimit species is illusory. Because every species is a lineage, but not every lineage is a species, there is always an element of convention as to where to draw the line of the species lineage. The dPSC uses diagnosability to draw that line, but given high-resolution markers, every population lineage becomes diagnosable. Yet, not every population is acknowledged as a species even under the dPSC, which makes it inconsistent. Also, by denying non-diagnosable (if indeed there are any) allopatric populations species status, diagnosability is not anymore an operational criterion to *identify* (i.e. diagnose or discover) lineages/species, but becomes an ontological *definition* of species. This reeks of typology. The dPSC is therefore theoretically and practically inconsistent.
- Linnean categories are a pre-Darwinian relict in taxonomy, and until we finally get rid of them, biological systematics will continue to contain an element of pseudoscience.
- There is a great need for standardised procedures, ideally based on quantitative criteria, to delimit mammalian species. For birds, such a suggestion was recently published (Tobias et al. 2010), but it is still lacking for mammals.

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