



Point of view

Species delimitation in mammals: A comment on Zachos (2018)

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ARTICLE INFO

Article history:

Received 11 April 2018

Accepted 18 May 2018

Available online 23 May 2018

Handled by Frank E. Zachos

ABSTRACT

Mammalian taxonomy based on the diagnosability version of the Phylogenetic Species Concept – considered as an operational manifestation of the Evolutionary Species Concept – offers a sound and verifiable base for understanding mammalian classification. There is now strong evidence that a taxonomy dominated by the Biological Synthesis (overlumped) has had deleterious effects on biodiversity conservation, while examples of its benefits remain obscure. It is interesting to note that when dealing with important issues (such as human health) the choice of taxonomy is necessarily analysis-based. In this reply to Zachos (2018), it is emphasized that we should avoid encouraging mistrust in taxonomy that can have negative consequences for taxonomists and taxonomic infrastructures. It is reinstated that while discussion over species concepts is fully legitimate, no doubt taxonomy is crucial to effective monitoring and conservation of mammal biodiversity.

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"I look at the term species as one arbitrarily given for the sake of convenience to a set of individuals closely resembling each other, and that it does not essentially differ from the term variety" (Darwin, 1859[1964, p. 52).

The last decade saw an interesting debate about species concepts in mammalogy, mostly fueled by the publication in 2011 of 'Ungulate Taxonomy' by the late Colin Peter Groves and Peter Grubb (Groves and Grubb, 2011). Their adoption of the diagnosability version of the Phylogenetic Species Concept (dPSC) has been heavily criticized by those that found the Biological Species Concept (BSC), with its emphasis on potential interbreeding, a reasonable delimitation criterion (Zachos et al., 2013; Heller et al., 2010). Conversely, and also surprisingly, concern has been repeatedly voiced for the consequences of a less inclusive species criterion over conservation biology, an issue that led to some strong rebuttals (Groves et al., 2017; Gippoliti et al., 2018).

Zachos (2018) has taken up the subject of these two latter papers (referred to as G & G in his paper). His views may be grouped in main four points:

(i) Zachos (2018) has argued that completely objective species delimitation is impossible due to the grey area after lineage sundering. Species delimitations in these cases necessarily include an element of arbitrariness and are at least partly an

"executive decision". This is true regardless of which species concept is used.

- (ii) If species are separately evolving lineages, then all "defining" characteristics of species named by the different species concepts are contingent with respect to their being a species. They only serve as identification criteria. The dPSC is no different from all the others in this regard; it just uses a particular criterion that tends to delimit species less inclusively ("splitting") than other concepts ("lumping").
- (iii) Claims that the dPSC is ontologically superior are wrong (see point ii), and its application is often not consistent with claims that separately evolving population lineages are all that it takes to be a species. In practice, there are two conditions: being such a lineage *and* being diagnostically distinct. This, however, is ontologically the same as what is done by other concepts (being such a lineage *and* being reproductively isolated: BSC; being such a lineage *and* occupying a distinct ecological niche: EcSC etc.). Hence his example with the Sardinian vs. British red deer (see below).
- (iv) Because species delimitation remains somewhat arbitrary and in lieu of a completely consistent way of delimiting species, Zachos (2018) has suggested to focus more on underlying data and less on taxonomic names when it comes to conservation issues. That recommendation was not to diminish taxonomy but to acknowledge its discreteness as opposed to the continuous process of evolution (Zachos, pers. com).

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<https://doi.org/10.1016/j.mambio.2018.05.007>

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I will comment on the first three of Zachos' points. My main disagreement with his fourth point is separately discussed further below.

The discovery of a 'grey area' in species recognition (Zachos, 2018) makes great heading if we consider that for almost a century most biologists, despite the Hennig revolution (Hennig, 1966) have thought that species boundaries are clearly demarcated by breeding (in)compatibility. With the term 'taxonomic inertia' (Gippoliti et al., 2018), used to characterize a long period of theoretical and practical stasis in mammal taxonomy, it was hoped to move ahead the scientific debate regarding the relationship between species concepts and conservation policies. This debate has been previously dominated by the 'taxonomical inflation' paradigm (Isaac et al., 2004) and more recently by 'taxonomy anarchy' (Garnett and Christidis, 2017) that risked to block refinement of our knowledge of mammal biodiversity. With the 'taxonomic inertia' 'provocation' I feel that a more balanced discussion on the issue is now possible in the best interest of biodiversity conservation.

It is possible to concur with Zachos (2018) that we are far from reaching a consensus on which criteria should be utilized to demarcate species lineages, yet consilience of several lines of evidence may provide critical information on the limits of particular species. However, too often mistrust on species' limits refinements is expressed by researchers from disciplines other than taxonomy, whose main interest is to have a simple, easy to remember and stable list of species as a service for their research or conservation efforts. Stability in species delimitation has nothing to do with science – as opposed to species nomenclature (Dubois, 1998; Padial and De la Riva, 2006; Cotterill et al., 2017) – but these requests probably fueled an overlumped taxonomy that achieved its original aim but cannot be a solid basis for a vibrant conservation policy. Further, taxonomy is a scientific discipline autonomous from other scientific disciplines (Wheeler, 2008; Thomson et al., 2018) although it admits methodological and conceptual progress from other disciplines such as population genetics, population biology, ecology and behaviour. If the issue is consistency, then BSC supporters should be ready to accept only one species in the genera *Capra* and *Ovis*, only one species of bison and so forth.

Although stressing the superiority of dPSC (diagnosability-based Phylogenetic Species Concept) as an operational tool for his own research program, Colin Groves wrote more than once that species are hypotheses that must be tested with all available evidence (Groves, 2013, 2014; Groves et al., 2017). Therefore, the claim was not that Groves and Grubb (2011) represented the last word on ungulate taxonomy for the next half century. Rather, it is highly probable that, as was the case with 'Primate Taxonomy' (Groves, 2001), 'Ungulate Taxonomy' will mark the beginning of a new age of refinement and discovery of the group's actual diversity (Rylands and Mittermeier, 2014). It seems that there is some concern that Groves and Grubb (2011) offered an oversplit species list (Zachos et al., 2013; see also Gutiérrez and Garbino, 2018) but in my opinion any misjudgment has an equal probability of being on both sides. Actually there are probably some cases of 'oversplitting' (e.g. *Rupicapra*) and some cases of 'overlumping' (e.g. *Tragelaphus euryceros*) as a consequence of both inadequate museum samples, limited geographic coverage, and scarce available phylogenetic data (cf. Gutiérrez et al., 2017). As reviewed by Frost and Kluge (1994) diagnosability is important because it is the structure of character variation (hierarchical) that allows us to distinguish between tokogenetic and phylogenetic relations. "We take this to mean that the scalar units of explanation that maximize the power of phylogenetic hypotheses are lineages whose fate is to remain non reticulating. Above this level is the monophyletic group of lineages (past of a historical specification hierarchy) and below are functional scalar levels composed of reticulating sublineages and toko-genetically related organisms" (Frost and Kluge, 1994:

275). The solution to the criticism of dPSC resides in the consilience of lines of evidence showing that multiple character histories match a lineage (cf. Cotterill et al., 2014).

Zachos (2018) cites the specific rank of *Cervus corsicanus* Erxleben, 1777 vs the synonymy of British red deer by Groves and Grubb (2011) but this judgment was complicated due to ancient human-induced translocations (Gippoliti and Amori, 2004). A recent paper (Doan et al., 2017) confirmed that *C. corsicanus* was the original red deer taxon of the Italian Peninsula and both North African, Corsican and Sardinian populations were products of historical anthropogenic activity. Further, there is evidence that *Cervus elaphus* 'subspecies' maintained their distinctiveness from around 50,000 years despite migrations and limited hybridization (Meiri et al., 2018), fully confirming the 'objectivity' of these lineages and thus the defensibility of species rank – a species is a single lineage of ancestral-descendent populations which maintains its identity from other such lineages and which has its own evolutionary tendencies and historical fate (Wiley, 1978: 18). British red deer (and several other allopatric populations) do not deserve to be recognized taxonomically simply because of their short period of separation and because our empirical tools limit what we can discover now (Frost and Kluge, 1994). However, it should be made clear that, for conservation purposes, it is critically important that taxonomic units are first identified and then evaluated for their rank. In agreement with Darwin's sentence at the opening of the article, there is no categorical divide between 'species' and 'variety' (subspecies). Therefore, if the British red deer is perceived as a distinct unit, even if at a much lower degree than *corsicanus*, zoologists may be authorized to label it with the name *scoticus* Lönnberg, 1906 provisionally utilized at the subspecific rank. This is a very important point. Available data shows that *corsicanus* and *scoticus* cannot be considered equipollent, but if both deserve to be recognized, the first should be treated as a species, and the second as a subspecies. Zachos' example is unfortunate because *scoticus* belongs to one of the better known mammal faunas in the world and a detailed taxonomic revision can be easily accomplished. On the contrary, in most regions of the tropics, an inevitable result of overlumping is the disappearance of more-or-less narrow endemic taxa from scientific literature and from the biodiversity research agenda – a fact too often unappreciated by researchers working in Europe, North America and Australia. This may be cause of particular concern from a conservation perspective when an overly lumped taxonomy is proposed at both species and subspecies level, as the one recently presented by the IUCN/SSC Cat Specialist Group (Kitchener et al., 2017). The synonymization of *Colobus guereza poliurus* Thomas, 1900 of the Omo River Valley in Southern Ethiopia with *Colobus guereza guereza* Rüppell, 1835 (cf. Carpaneto and Gippoliti, 1994) is one of the many cases known to the author of how the negative environmental (and social) consequences of dams, irrigation projects and other 'development' megaprojects (cf. Abbink, 2012) are exacerbated by an excessively conflated taxonomy that makes potential endemic taxa invisible and thus proposition of mitigation actions more difficult. The case of the rejected splitting of *Loxodonta* in two species (*africana* and *cyclotis*) when the scientific evidence is now conclusive and overwhelming (Meyer et al., 2017) requires that the conservation community be more cautious when dealing with such a sensitive issue as taxonomy. Zachos (2018) suggested that we cannot speak of 'errors' in taxonomy, but the latter example with *Loxodonta* seems to contradict this, at least if one does not accept *Palaeoloxodon antiquus* as a subspecies of *Loxodonta africana*. Cotterill et al (2014) discussed at length the types of errors that we may have in species delimitation. Yet it is true that while we should be able to identify taxa objectively, every zoologist should be free to establish their rank according to his philosophy. Revising the genus *Rupicapra*, both Camerano (1916) and Lovari (1987) identified the same evolutionary history and major taxa.

Table 1

'Genetic rescue' projects realised (analysed by Frankham (2015)) and proposed for wild mammal taxa. References; 1) Weeks et al. (2017); 2) Frankham (2015); 3) Harley et al. (2016); 4) Goossens et al. (2013); 5) Heller et al. (2010).

Taxon	Taxonomic reference	Taxonomy	Genetic rescue	Ref
<i>Burromys parvus</i>	Jackson and Groves (2015)	Same taxon	accomplished	1
<i>Canis lupus baileyi</i>	Wozencraft (2005)	Same subspecies	accomplished	2
<i>Canis lupus</i>	Wozencraft (2005)	Same taxon	accomplished	2
<i>Puma concolor</i>	Wozencraft (2005)	Different subspecies	accomplished	2
<i>Panthera leo</i>	Wozencraft (2005)	Same taxon?	accomplished	2
<i>Ovis canadensis</i>	Groves and Grubb (2011)	Same subspecies	accomplished	2
<i>Peromyscus maniculatus</i>	Hafner et al. (1998)	Same taxon	accomplished	2
<i>Ceratotherium cottoni</i>	Groves and Grubb (2011)	Different species	proposed	3
<i>Dicerorhinus sumatrensis</i>	Groves and Grubb (2011)	Different subspecies	proposed	4
<i>Syncerus caffer</i>	Groves and Grubb (2011)	Different species?	proposed	5

Camerano decided to accept three species (*R. rupicapra*, *R. pyrenaica* and *R. ornata*) on the argument that *ornata* and *parva* were not of equipollent value. Lovari accepted two species and maintained both *ornata* and *parva* as subspecies of *pyrenaica*. Here I only agree with Zachos that there is no error in either scheme, but only a legitimate difference of scientific views regarding the meaning of 'subspecies'.

However, a strong point of disagreement with Zachos's (2018) view is that species delimitation matters, indeed, and may be objectively assessed in most cases. When zoologist Giovanni Battista Grassi worked on identifying the vector of malaria transmission in Italy, he identified a new species of *Anopheles* mosquito first, then studied its ecology and behavior, and eventually found *species-specific* countermeasures for the target species (Grassi, 1901). This is the same kind of work that is still done today elsewhere in the world (Attenborough, 2015). Extending the example of malaria, researchers studying mammal models for this disease need to know the exact taxonomy of their model host animal (i.e. *Aotus*; Mantilla-Meluk and Jiménez-Ortega, 2011). Malaria is only one of the zoonoses afflicting also our own species - Ebola, Lassa Fever, SARS etc. - having mammal species as potential vectors (DiEuliis et al., 2016). Therefore, an analytic or fine-gravel approach to taxonomy is considered the only one applicable to solve this important issue; G&G (*sensu* Zachos, 2018) are among those mammalogists that consider alpha taxonomy to be an important issue because it informs, according to a precautionary principle, evolutionary studies, comparative biology, experimental biology, and conservation tactics both *in situ* and *ex situ*.

I wish here to respond to point iv of Zachos (2018). Regrettably, lack of taxonomic knowledge is not uncommon, and there are already cases where taxonomy has been abandoned. What exactly are we losing if the South Selkirk mountain caribou herd becomes extinct (Francovich, 2018)? The genus *Rangifer* (caribou) in North America is a classic example of how the lack of a revised taxonomy conducive to the creation of other kinds of designations for conservation units (ESU's, MU's, DU's - Designatable Units - ecotypes, herds etc) in the end only renders more difficult the communication among researchers and conservation bodies without beneficial returns to conservation (Geist, 2007; COSEWIC, 2011). Without a sound understanding of *Rangifer* taxonomy, it is not surprising that the fashionable - and costly - genetic rescue operations have not been able to improve the status of several caribou populations (e.g. Leech et al., 2017). Furthermore, in the framework of international bodies and conventions such as IUCN, CITES and the Convention on Biodiversity, it is of paramount importance that biodiversity is subject to a universal accounting system and consistently applied by different states.

Nobody should be afraid to consider natural history and biogeography data to be integrated with molecular datasets. Zachos's (2018) enthusiasm "for a very good and balanced empirical analysis" of the species problem with reference to a recent molecular

study on the *Muscardinus avellanarius* species complex (Mouton et al., 2017) cannot be shared completely. This paper added crucial elements for a true taxonomic revision of the genus that needs to analyze natural history and biogeographic data among others to reach an integrative resolution of its systematics, a course of action that needs to be revalued especially in Europe (cf. Kryštufek and Vohralík, 2012; Bezerra et al., 2016; Gippoliti and Groves, in press). Mouton et al (2017) do not propose any new taxonomic change although they admitted that there are probably two ESU's for clades estimated to have diverged in the Late Miocene. Incidentally, Gippoliti (2013) already had proposed species status - *Muscardinus speciosus* (Dehne, 1855) - for the Italian peninsula lineage identified by Mouton et al. (2017), because of consilience of available molecular data with morphological evidences (coat color, facial marking, number of molar roots) that had been ignored for too long.

Zachos (2018) repeats the long-standing belief that 'splitting' (I would prefer to say: a more analysis-based taxonomy *sensu* Simpson, 1945: 22) is also dangerous for conservation. It should be wise to offer some examples of species suffering from 'splitting' (sic). Gutiérrez and Garbino (2018) provided a case of a false species, *Mazama bricenii*, but it is unlikely that it (or another taxon) actually suffered from this. Recent papers dealing with the advantages of 'genetic rescue' (Frankham, 2015) also seems reluctant to adopt a dPSC-based taxonomy that they evidently perceive as a threat to moving individuals among populations (Ralls et al., 2018). Yet the mammalian examples of genetic rescue already accomplished (Table 1) have not involved introgression among any dPSC-proposed species. Therefore, it is again stressed (Gippoliti et al., 2018; Gippoliti et al., in prep.) that fighting inbreeding depression remains an achievable goal for mammal conservation also under a dPSC-based taxonomy and that available evidence is inconclusive regarding the prospects for genetic rescue that involves sibling taxa that are much older than the North American puma subspecies often cited in relevant literature.

Finally, it seems that Zachos overlooked the consequences of his operational proposal regarding conservation, instead forging mistrust of species delimitation as a rigorous empirical research program. Taxonomy, preferably based on a fine-grained approach, must be an independent system from conservation that ideally should help to redirect attention towards neglected lineages (and their habitats) aside from human preferences, a well-known bias in conservation (Small, 2011).

Zachos (2018) wrote "... Rather than relying on a one-size-fits-all taxonomy, researchers could decide on a case-by-case basis which biological parameters are most relevant to the conservation of particular populations under study". In an ideal world this should be a possible goal but we live in the age of 'the agony of choice' (Vane-Wright et al., 1991) and so it is imperative to direct resources towards priorities identified through PD (Phylogenetic Diversity) or other objective evidences. Too often researchers working on a sin-

gle species utilize specific biological parameters, including culture (both of humans and animal populations), to attract funding primarily toward attractive species, subspecies or ecotypes. This may be dangerous as an initial bias in geographic location of study sites, for example, is encouraged further and further as more studied populations will certainly lead to interesting discoveries, assessment of conservation threats and so on. This was clearly evident in the first long-term studies of chimpanzees *Pan troglodytes* in the 1990's, most of them situated in East Africa, practically at the eastern limit of their geographic range. Refinement of *Pan troglodytes* taxonomy (Gonder et al., 2006) was instrumental to direct more attention elsewhere, particularly towards the two most threatened West African taxa *Pan troglodytes verus* and *Pan troglodytes ellioti*. For those working in/on species-rich communities, taxonomy is the basal tool to analyze their results and identify conservation priorities (cf. Parnaby, 1991). Establishing conservation priorities among speciose taxa in the framework of the initiatives of the different Specialist Groups of the IUCN Species Survival Commission is often based mainly on a taxonomic revision of the group (Hafner et al., 1998).

'Subspecies' are especially prone to political use and misuse (Gippoliti and Amori, 2007), easily overemphasized in some cases and prone to be dismissed in others. It is perhaps no coincidence that a fine-grained analysis of extinction at the population level shows that Earth's sixth mass extinction is more severe than perceived when looking exclusively at species extinctions (Ceballos et al., 2018). This confirms that a dPSC-based taxonomy with more species and fewer subspecies should allow a more objective monitoring of biodiversity and allocation of resources for conservation.

Acknowledgements

Francesco Angelici, Diego Fontaneto, José Manuel Padiá and Jan Robovský furnished valuable criticism to previous versions of the ms and Bruce Patterson reviewed the last version and greatly helped with English style. I really do appreciate the open mind of the editor-in-chief, Frank Zachos, in considering the present ms for publication. While writing this reply, 'Sudan,' the last known male of Northern white rhinoceros *Ceratotherium cottoni*, died in Kenya. As the fate of this taxon has been influenced also by taxonomy and some of the issues discussed here, I feel appropriate to dedicate this work to 'Sudan'.

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