



## Commentary

## Mammal taxonomy without taxonomists: a reply to Zachos and Lovari

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### Abstract

Ontological and epistemological properties of the Phylogenetic Species Concept (PSC) as applied in recent mammalian taxonomic works are redefined and defended against criticisms raised by Zachos and Lovari (2013), which we find inapplicable to taxonomy because they relate more to the field of population biology. We summarize the negative impacts of the polytypic species concept for conservation and evolutionary biology, with emphasis on Rhinocerotidae. The priority need to embrace and strengthen museum-based taxonomic research is emphasized.

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The reply of Zachos and Lovari (2013) to our previous opinion paper (Gippoliti and Groves, 2012) provides us with the opportunity to expand our argument.

In 2011 three putative “subspecies” of the family Rhinocerotidae were declared officially Extinct by IUCN: the western black rhinoceros *Diceros bicornis longipes* Zukowsky, 1949; the Nile white rhinoceros *Ceratotherium simus cottoni* (Lydekker, 1908) (with a handful of individuals surviving in captivity); and the Indochinese Javan Rhinoceros *Rhinoceros sondaicus annamiticus* Heude, 1892. We contend that Zachos and Lovari’s reply (2013), and other similar papers (Heller et al., 2013; Zachos et al., 2013a,b), are missing the core point. The taxonomic approach they are defending has some responsibility for the demise of so many unique forms of rhinoceros in Africa and Asia. The raising of *cottoni* to specific level by Groves et al. (2010) is based more on new data (and we should add real interest in a too long forgotten question) than a shift in the species definition adopted. The Nile white rhinoceros deserves species status on any or all species criteria, and we fear that a demonstration of this would be apparent if interbreeding with the southern species will be attempted as a last hope to “save” it. Although even more poorly known due to their historic rarity, and the consequent scarcity of study material, the same predicament may well apply to *Diceros bicornis longipes* and *Rhinoceros sondaicus annamiticus*. Here knowledge of the palaeoclimatological and geomorphological history of both continents (Cotterill, 2003a; Whitmore, 1987; Kingston, 2007; Senut et al., 2009), together with comparative phylogeographic studies of extant biogeographic patterns, strongly suggest that these now extinct rhinoceros taxa actually constituted distinct species. If we look at recent proposals of giraffe taxonomy, for instance (Brown et al., 2007; Groves and Grubb, 2011), all recognize specific status for the West-central African taxa that occurred sympatrically with *Diceros longipes* and remained isolated from eastern populations. This possibly related to an important barrier: Lake Megachad (Hasanin et al., 2007). We are not proposing a formal taxonomic revision, which of course would require detailed research; but we would like to draw attention to how – as exemplified by Roberts’ Lechwe *Kobus robertsi* and Upemba Lechwe *Kobus anselli* (Cotterill, 2003b, 2005)

– a taxon becomes nearly invisible to conservation when it is “only a subspecies”.

That said, we note that the cases cited by Zachos and Lovari (2013) actually contradict, not support, their fear (Zachos et al., 2013a) of the PSC as applied by Groves and Grubb (2011). Their Fig. 1 clearly shows that species in the *Cervus elaphus* complex form monophyletic clades, exactly as maintained by Groves and Grubb (2011) on the basis of common morphological characters. The fact that monophyletic lineages exist within each of these three clades (some of them picked out by rounded squares in Zachos and Lovari’s (2013) Fig. 1) is irrelevant: Zachos and Lovari appear to have forgotten that the species, however defined, is a population concept (“a population or aggregation of populations” – Groves and Grubb 2011:1). And indeed this fundamental ontological nature of the species category was emphasized on the opening page of Groves and Grubb 2011:1: “a lineage ... evolving separately from others and with its own evolutionary role and tendencies” (Simpson, 1961), which is operationalized by the PSC (Cotterill, 2003b, 2005; Groves and Grubb, 2011).

We emphasize that the concept of evolutionary species is a central ontological foundation of phylogenetic systematics; the species-as-lineage concept of the ESC (Evolutionary Species Concept) structures discovery operations – using the PSC and relevant evidence – to characterize those lineages that qualify as individuated species. The realm of organismal more-making, the tokogenic processes that create populations, occupies the hierarchical level below that where species evolve, persist and go extinct (Hennig, 1966; Frost and Kluge, 1994). Zachos and Lovari are broadly correct that events testifying to the circumstances of lineage scission can be challenging to elucidate – but this ontology accommodates such apparent conflicts in evidence (de Queiroz, 2007; Mayden, 2013). At its most fundamental, this is the nature of biodiversity resplendent in the one tree shaped by the genealogical history of life on earth, and it evolved independently of our ability to discover its topology. Alongside the realities of hypothesis-driven biological research, this singularity obviates the credibility of dividing or lumping organisms into artificial groups (Darwin, 1859; O’Hara, 1988; Brooks and McLennan, 2002; Naomi, 2011; Wiley and Lieberman, 2011; Mayden, 2013).

Again, this failure to understand the ontological context of how the PSC is applied in the lineage framework of the ESC (cf. Cotterill 2003b, 2005) is revealed in their Fig. 2 and text (Zachos and Lovari,

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2013), which focus on recent population fragmentation – with the Indian tiger *Panthera tigris tigris* as an example – and its possible genetic consequences. Previously Zachos et al. (2013a) had heavily criticized a three-species arrangement of tigers (Groves and Mazák, 2006) resulting from the complex history of the Sunda Shelf and its sequence of separation from and reconnection with mainland Asia in the Quaternary (Michaux, 2010). Indian tigers may likewise present genetic and morphological substructuring over their formerly vast range, and this is as likely to be maintained by contemporary ecological processes as by drift, as has been shown for boreal grey wolves (Musiani et al., 2007). If today's remnant isolates are discovered to be strongly differentiated genetically, it is likely to be initially a legacy of this previous substructuring, even if drift later modifies populations, and it is important that such processes should be considered in conservation strategy. Unfortunately, too many translocations of wildlife have had detrimental effects on the conservation of biodiversity by introducing alien genetic material (Champagnon et al., 2012) because they are misled as a consequence of prevalent taxonomic views based on the Biological Species Concept (BSC) (Gippoliti, 2004).

We further argue that setting draconian restrictions on the evidence judged sufficient to characterize species underestimates cryptic diversity, especially where such actions seek to reduce “taxonomic inflation” (Bernardo, 2011). The argument that “If an independent evolutionary history, i.e. largely separate gene pools, is what ultimately makes a species, then conclusive nuclear genetic or mitochondrial and nuclear genetic data is what should be required from geneticists before splitting a species” (Zachos et al. 2013a: 5) violates the Precautionary Principle in cases of some real species. Even a surfeit of gene trees can still fail to discover some recently diverged species (Arnold et al., 2013). These include lineages that (1) were founded by hybridization, (2) have experienced introgression, and/or (3) retain ancestral polymorphisms (Norris and Hull, 2011).

In summary, criticism of excessive use of the diagnosability criterion is unwarranted, not least for Groves and Grubb (2011), who maintained subspecific taxa against PSC criteria.

We share the concern against non-peer-reviewed taxonomic decisions (cf. Kaiser et al. 2013) but we maintain the importance of museum based taxonomy to offer solutions even with limited specimens at hand – this Precautionary Principle sets the rule for little-known and threatened taxa. Here, we emphasize that the overwhelming advantage that the PSC has over any other species concept is its testability; the accumulation of further evidence can falsify a taxonomic statement under the PSC. This is a requirement for a credible scientific proposition (Bernardo, 2011). As an historical example from before the advent of the BSC, we highlight the pioneering revisions of Lorenzo Camerano (1856–1917), director of the Zoological Museum at Turin University. Camerano stands out for introducing mathematical methods in taxonomy and ecology (cf. Cohen 1994) and for studying species variability with large museum samples, in particular skulls, in his studies of *Rupicapra* and *Capra ibex* taxonomy. In one of his last papers he lamented the abuse of the subspecies category in several bovid species (Camerano 1916: 4). In a little-known paper, he (Camerano, 1917) challenged the validity of the taxonomic arrangement of the Iberian ibexes proposed by Cabrera (1911: one species and four subspecies); he proposed, on the basis of published data, and the study of two further specimens in the Turin Museum, the existence of two distinct species, *Capra pyrenaica* and *Capra hispanica*, with three subspecies possibly of ancient hybrid origin (Camerano, 1917). This little-appreciated paper (but see García-González 2011) offers an excellent example of a phylogenetic approach to classical taxonomy, and is all the more pertinent today to inform conservation policies of threatened mammal populations.

It is important to reconcile with the circumstances that the BSC (Mayr, 1963) and the Genetic Species Concept (Baker and Bradley, 2006) are constrained by operational strictures as to where a species “appears” in the process of lineage individuation. It is indeed unclear how the BSC can actually discover lineages in the framework of phylogenetic systematics. Only the ESC is free of these operational strictures

(Frost and Kluge, 1994; Mayden, 2013). The poverty of operationalism and its primal failure of systematics was refuted over forty years ago (Hull, 1968; Johnson, 1970; Frost and Kluge, 1994):

... the operational point of view depends for what success it does have on the very element of science which it is designed to eliminate. Operationism was intended as a cathartic to purge physics of all non-empirical wastes, but it proved to be so strong that the viscera were eliminated as well. (Hull 1968: 440).

An extreme version of operationalism has appeared in the Differential Fitness Species Concept (DFSC) of Hausdorf (2011) – unfortunately lauded by Frankham et al. (2012) in a recent publication – which has tried to avoid the species-are-lineages ontology. This stricken attempt to exhume a sterile research program removes the concept of the population from the definition of the species category; the DFSC strips science of the reality of population biology, and ignores the hierarchical organization of biodiversity, represented in the singular species tree that systematics is challenged to discover. We are unconvinced by this strange attempt to overturn a fundamental foundation of evolutionary biology. Ultimately, all these attempts to dismiss the PSC (Frankham et al., 2012; Heller et al., 2013; Zachos et al., 2013a,b; Zachos and Lovari, 2013) are crippled by operationalism. It is unfortunate that this retrogressive perspective is held up as the way forward for conservation policy, considering that the bioGenesis research strategy founded on phylogenetic systematics (Donoghue et al., 2009; Hendry et al., 2010) was developed expressly to guide policy formulated by the Conference of the Parties (COP) to the Biodiversity Convention.

In the light of the consolidation of phylogenetic systematics and its demonstrable progress toward discovering the singular Tree of Life (Bernardo, 2011; Wiley and Lieberman, 2011; Mayden, 2013), all other pretenses at dividing or lumping organisms into artificial taxonomic groups can no longer be defended, at least on scientific grounds. Conservation costs of taxonomic mistakes can be extreme. We cited these historical examples to stress the need to integrate old and new methodologies for the study of mammal diversity – before it is also too late, and more taxa meet the same plight exemplified by *Ceratotherium cottoni*. Especially in Western Europe, demands for knowledge, and improvements in technology (Moodley and Bruford, 2007; Guschanski et al., 2013), highlight the practicalities, and especially the urgency to restore natural history museums and taxonomists into the epicenter of taxonomic research (*sensu* Wheeler 2008; Cotterill and Foissner 2010). We therefore fully support the view that “the headquarters of taxonomic efforts are natural history museums, which need unrelenting support in their fundamental goals to maintain present collections, accumulate new ones, and support alpha-taxonomic and revisionary studies now and into the future” (Reeder et al., 2007). ☺

## References

- Arnold B., Corbett-Detig R.B., Hartl D., Bomblies K., 2013. RADseq underestimates diversity and introduces genealogical biases due to nonrandom haplotype sampling. *Molecular Ecology* (Online First). doi:10.1111/mec.12276
- Baker R.J., Bradley R.D., 2006. Speciation in mammals and the genetic species concept. *J. Mammal.* 87: 643–662.
- Bernardo J., 2011. A critical appraisal of the meaning and diagnosability of cryptic evolutionary diversity, and its implications for conservation in the face of climate change. In: Hodkinson T.R., Jones M.B., Waldren S., Parnell J.A.N. (Eds.) *Climate Change, Ecology and Systematics*. Cambridge University Press: The Systematics Association. 380–438.
- Brooks D.R., McLennan D.A., 2002. *The Nature of Diversity: An evolutionary voyage of discovery*. The University of Chicago Press, Chicago.
- Brown D.M., Brenneman R.A., Koepfli K.-P., Milla B., Georgiadis N.J., Louis E.E.L. jr., Grether G.F., Jacobs D.K., Wayne R.K., 2007. Extensive population genetic structure in the giraffe. *BMC Biol.* 5: 57.
- Cabrera A., 1911. The subspecies of the Spanish ibex. *Proc. Zool. Soc. London* 66: 963–977.
- Camerano L., 1916. I caratteri del cranio, della colorazione e delle corna nella distinzione dei Camosci in specie e sottospecie. *Rivista di Antropologia (Roma)* 20: 3–14. [In Italian]
- Camerano L., 1917. Contributo allo studio degli stambecchi iberici. *Boll. Mus. Zool. Anat. Comp. R. Univ. Torino* 32: 1–30. [In Italian]
- Champagnon J., Elmberg J., Guillemin M., Gauthier-Clerc M., Lebreton J.-D., 2012. Con-specifics can be aliens too: a review of effects of restocking practices in vertebrates. *J. Nature Conserv.* 20: 231–241.
- Cohen J.E., 1994. Lorenzo Camerano's contribution to early food web theory. *Lecture Notes in Biomathematics*, 100: 351–359.

- Cotterill F.P.D., 2003a. Geomorphological influences on vicariant evolution in some African mammals in the Zambesi Basin: some lessons for conservation. In: Plowman A. (Ed.) Proceedings of the ecology and conservation of mini-antelopes: An International Symposium on Duiker and Dwarf Antelope in Africa. Filander Verlag, Ffuirth. 11–58.
- Cotterill F.P.D., 2003b. Species concepts and the real diversity of antelopes. In: Plowman A. (Ed.) Proceedings of the ecology and conservation of mini-antelopes: An International Symposium on Duiker and Dwarf Antelope in Africa. Filander Verlag, Ffuirth. 59–118.
- Cotterill F.P.D., 2005. The Upemba lechwe *Kobus anselli*: an antelope new to science emphasizes the conservation importance of Katanga, Democratic Republic of Congo. *J. Zool., Lond.* 265: 113–132.
- Cotterill F.P.D., Foissner W., 2010. A pervasive denigration of Natural History misconstrues how biodiversity inventories and taxonomy underpin scientific knowledge. *Biodiv. Conserv.* 19: 291–303.
- Darwin C.R., 1859. *The Origin of Species*. First Edition. John Murray, London.
- de Queiroz K., 2007. Species concepts and species delimitation. *Syst. Biol.* 56: 879–886.
- Donoghue M.J., Yahara T., Conti E., Cracraft J., Crandall K.A., Faith D.P., Häuser C., Hendry A.P., Joly C., Kogure K., 2009. bioGENESIS: providing an evolutionary framework for biodiversity science. *DIVERSITAS Report No. 6*.
- Hendry A.P., Lohmann L.G., Conti E., Cracraft J., Crandall K.A., Faith D.P., Häuser C., Häuser C., Joly C.A., Kogure K., Larigauderie A., Magallón S., Moritz C., Tillier S., Zardoya R., Prieur-Richard A.-H., Walther B.A., Yahara T., Donoghue M.J., 2010. Evolutionary biology in biodiversity science, conservation, and policy: a call to action. *Evolution* 64: 1517–1528.
- Frankham R., Ballou J.D., Dudash M.R., Eldridge M.D.B., Fenster C.B., Lacy R.C., Mendelson J.R. III, Porton I.J., Ralls K., Ryder O.A., 2012. Implications of different species concepts for conserving biodiversity. *Biol. Conserv.* 153: 25–31.
- Frost D.R., Kluge A.G., 1994. A consideration of epistemology in systematic biology, with special reference to species. *Cladistics* 10: 259–294.
- García-González R., 2011. Elementos para una filogeografía de la Cabra Montés ibérica (*Capra pyrenaica* Schinz, 1838). *Pinneo, Rev. Ecol. Mont.* 166: 87–122.
- Gippoliti S., 2004. Captive breeding and conservation of the European mammal diversity. *Hystrix* 15(1): 35–53.
- Gippoliti S., Groves C.P., 2012. “Taxonomic inflation” in the historical context of mammalogy and conservation. *Hystrix* 23(2): 6–9.
- Groves C.P., 2013. The nature of species: A rejoinder to Zachos et al. *Mamm. Biol.* 78: 7–9.
- Groves C.P., Fernando P., Robovský J., 2010. The sixth rhino: a taxonomic re-assessment of the Critically Endangered northern white rhinoceros. *PLoS ONE* 5(4): e9703. doi: 10.1371/journal.pone.0009703
- Groves C., Grubb P., 2011. *Ungulate Taxonomy*. The Johns Hopkins University Press, Baltimore.
- Groves C., Mazák J., 2006. A taxonomic revision of the tigers (*Panthera tigris*) of Southeast Asia. *Mamm. Biol.* 71: 268–287.
- Guschanski K., Krause J., Sawyer S., Valente L. M., Bailey S., Finstermeier K., Gilissen E., Sonet G., Nagy Z.T., Lenglet G., Mayer F., Savolainen V., 2013. Next-Generation Museomics disentangles one of the largest primate radiations. *Syst. Biol.* (Advance Access) doi:10.1093/sysbio/syt018
- Gutiérrez E.E., Helgen K.M., 2013. Outdated taxonomy blocks conservation. *Nature* 495: 314.
- Heller R., Frandsen P., Lorenzen E.D., Siegmund H.R., 2013. Are there really twice as many bovid species as we thought? *Syst. Biol.* 62(3): 490–493. doi:10.1093/sysbio/syt004
- Hassanian A., Ropiquet A., Gourmand A.-L., Chardonnet B., Rigoulet J., 2007. Mitochondrial DNA variability in *Giraffa camelopardalis*: consequences for taxonomy, phylogeography and conservation of giraffes in West and central Africa. *C.R. Biologies* 330: 265–274.
- Hausdorf B., 2011. Progress toward a general species concept. *Evolution* 65: 923–931.
- Hennig W., 1966. *Phylogenetic Systematics*. University of Illinois Press, Urbana, Illinois.
- Hull D.L., 1968. The operational imperative: sense and nonsense in operationism. *Syst. Zool.* 17: 438–457.
- Kaiser H., Crother B.I., Kelly C.M.R., Luiselli L., O’Shea M., Ota H., Passos P., Schleip W.D., Wüster W., 2013. Best practices: In the 21<sup>st</sup> Century, taxonomic decisions in herpetology are acceptable only when supported by a body of evidence and published via peer-review. *Herpet. Rev.* 44: 8–23.
- Kingston J.D., 2007. Shifting adaptive landscapes: progress and challenges in reconstructing early hominid environments. *Amer. J. Phys. Anthropol.* 134: 20–58.
- Johnson L., 1970. Rainbow’s end: the quest for an optimal taxonomy. *Syst. Zool.* 19: 203–239.
- Mayden R.L., 2013. Species, trees, characters, and concepts: ongoing issues, diverse ideologies, and a time for reflection and change. In: Pavlinov I. Ya. (Ed.) *The Species Problem – Ongoing Issues*. InTech. 171–191.
- Mayr E., 1963. *Animal Species and Evolution*. Belknap Press, Harvard.
- Michaux B., 2010. Biogeology of Wallacea: geotectonic models, areas of endemism, and natural biogeographical units. *Biol. J. Linnean Soc.* 101: 193–212.
- Moodley Y., Bruford M.W., 2007. Molecular biogeography: towards an integrated framework for conserving Pan-African biodiversity. *PLoS ONE* 2(5): e454. doi:10.1371/journal.pone.0000454
- Musiani M., Leonard J.A., Cluff H.D., Gates C., Mariani S., Paquet P.C., Vilàs C., Wayne R.K., 2007. Differentiation of tundra/taiga and boreal coniferous forest wolves: genetics, coat colour and association with migratory caribou. *Mol. Ecol.* 16: 4149–4170.
- Naomi S.-I., 2011. On the integrated frameworks of species concepts: Mayden’s hierarchy of species concepts and de Queiroz’s unified concept of species. *Journal of Zoological Systematics and Evolutionary Research* 49: 177–184.
- Norris R.D., Hull P.M., 2011. The temporal dimension of marine speciation. *Evol. Ecol.* 26: 393–415.
- O’Hara R.J., 1988. Homage to Clio, or, toward an historical philosophy for evolutionary biology. *Syst. Zool.* 37: 142–155.
- Reeder D.M., Helgen K.M., Wilson D.E., 2007. Global trends and biases in new mammal species discoveries. *Occ. Papers Mus. Texas Tech. Univ.* 269: 1–35.
- Senut B., Pickford M., Ségalen L., 2009. Neogene desertification of Africa. *Comptes Rendus Geoscience*, 341(8–9): 591–602.
- Sharma R., Stuckas H., Bhaskar R., Khan I., Goyal S.P., Tiedemann R., 2011. Genetically distinct population of Bengal tiger (*Panthera tigris tigris*) in Terai Arc Landscape (TAL) of India. *Mamm. Biol.* 76: 484–490.
- Simpson G.G., 1961. *Principles of Animal Taxonomy*. Columbia University Press, New York.
- Wheeler Q.D. (Ed.), 2008. *The New Taxonomy*. Systematics Association Special Volume Series. CRC Press, Boca Raton, FL.
- Whitmore T.C. (Ed.), 1987. *Biogeographical Evolution of the Malay Archipelago*. Clarendon Press, Oxford.
- Wiley E.O., Lieberman B.S., 2011. *Phylogenetics: theory and practice of phylogenetic systematics*. Second Edition. Wiley-Blackwell.
- Zachos F.E., Apollonio M., Bärmann E.V., Festa-Bianchet M., Göhlich U., Habel J.C., Har- ing E., Kruckenhauser L., Lovari S., McDevitt A.D., Pertoldi C., Rössner G.E., Sánchez-Villagra M.R., Scandura M., Suchentrunk F., 2013a. Species inflation and taxonomic artefacts – A critical comment on recent trends in mammalian classification. *Mamm. Biol.* 78: 1–6.
- Zachos F.E., Clutton-Brock T.H., Festa-Bianchet M., Lovari S., Macdonald D.W., Schaller G.B., 2013b. Species splitting puts conservation at risk. *Nature* 494: 35.
- Zachos F.E., Lovari S., 2013. Taxonomic inflation and the poverty of the Phylogenetic Species Concept – a reply to Gippoliti and Groves. *Hystrix (Online First)* 10.4404/hystrix-24.1-8849

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