Mammal taxonomy without taxonomists: a reply to Zachos and Lovari

Spartaco Gippoliti\textsuperscript{a,}\textsuperscript{b}, Fenton P.D. Cotterill\textsuperscript{b}, Colin P. Groves\textsuperscript{c}

\textsuperscript{a}Viale Liegi 48A, 00198 Roma, Italy
\textsuperscript{b}AEON – Africa Earth Observatory Network, Geocodynamics Research Hub, c/o Department of Botany and Zoology, University of Stellenbosch, Stellenbosch 7602, South Africa
\textsuperscript{c}School of Archaeology & Anthropology, Australian National University, Canberra, Australia

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.

The reply of Zachos and Lovari (2013) to our previous opinion piece (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 \textit{Diceros bicornis longipes} Zukowsky, 1949; the Nile white rhinoceros \textit{Ceratotherium simus cottoni} (Lydekker, 1908) (with a handful of individuals surviving in captivity); and the Indochinese Javan Rhinoceros \textit{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 \textit{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 \textit{Diceros bicornis longipes} and \textit{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 phyleogeographic 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 \textit{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 \textit{Kobus robertsi} and Upemba Lechwe \textit{Kobus anelsi} (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 \textit{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, as shown by 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, 2013).
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) re-
sulting from the complex history of the Sunda Shelf and its sequence
of separation from and reconnection with mainland Asia in the Qua-
ternary (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 differ-
etiated genetically, it is likely to be initially a legacy of this previous
substructuring, even if drift later modifies populations, and it is impor-
tant 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 conse-
cuence of prevalent taxonomic views based on the Biological Species
Concept (BSC) (Gippoliti, 2004).

We further argue that setting draconian restrictions on the evid-
ence judged sufficient to characterize species underestimates cryptic
diversity, especially where such actions seek to reduce “taxonomic in-
flation” (Bernardo, 2011). The argument that “If an independent evolu-
tionary 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 be-
fore splitting a species” (Zachos et al. 2013a: 5) violates the Precau-
tory 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 hybrid-
ization, (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 de-
cisions (cf. Kaiser et al. 2013) but we maintain the importance of mu-
seum 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 advant-
age 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 proposi-
tion (Bernardo, 2011). As an historical example from before the advent
of the BSC, we highlight the pioneering revisions of Lorenzo Camer-
ano (1856-1917), director of the Zoological Museum at Turin Univer-
sity, who launched an effort for introducing mathematical methods in
taxonomy and ecology (cf. Cohen 1994) and for studying species vari-
ability 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
(Camaron 1916: 4). In a little-known paper, he (Cameron, 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 (Cameron, 1917). This little-appreciated pa-
per (but see García-González 2011) offers an excellent example of a
phylogenetic approach to classical taxonomy, and is all the more per-
tinent today to inform conservation policies of threatened mammal pop-
ulations.

It is important to reconcile with the circumstances that the BSC
(Mayr, 1963) and the Generic 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 phylo-
genetic systematics. Only the ESC is free of these operational strictures
(Frost and Kluge, 1994; Mayden, 2013). The poverty of operational-
ism and its primal failure of systematics was refuted over forty years

…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 catharctic to
purge physics of all non-empirical wastes, but it proved to
be so strong that the viscera were eliminated as well. (Hull

An extreme version of operationism has appeared in the Differential
Fitness Species Concept (DFSC) of Hausdorf (2011) – unfortunately
lauded by Frankham et al. (2002) 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 hierarchi-
cal 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., 2002; Heller et al., 2013; Zachos et al., 2013a,b; Zachos and Lowari,
2013) are crippled by operationalism. It is unfathomable how a pro-
gressive 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. Con-
servation costs of taxonomic mistakes can be extreme. We cited these
historical examples to stress the need to integrate old and new method-
ologies 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 improve-
ments 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 taxon-
omic research (sensu Wheeler 2008; Cotterill and Foisnier 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).