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Impacts of taxonomic inertia for the conservation of African ungulate diversity: an overview

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ABSTRACT

We review the state of African ungulate taxonomy over the last 120 years, with an emphasis on the introduction of the polytypic species concept and the discipline's general neglect since the middle of the 20th century. We single out negative consequences of 'orthodox' taxonomy, highlighting numerous cases of neglect of threatened lineages, unsound translocations that led to lineage introgression, and cases of maladaptation to local conditions including parasitic infections. Additionally, several captive breeding programmes have been hampered by chromosome rearrangements caused by involuntary lineage mixing. We advocate that specimen-based taxonomy should regain its keystone role in mammal research and conservation biology, with its scientific values augmented with genomic evidence. While integration with molecular biology, ecology and behaviour is needed for a full understanding of ungulate alpha diversity, we stress that morphological diversity has been neglected despite its tremendous practical importance for some groups of 'utilizers' such as trophy hunters, wildlife tourists and conservationists. We conclude that there is no evidence that purported 'taxonomic inflation' has adverse effects on ungulate conservation: rather, it is taxonomic inertia that has such adverse effects. We stress that sound science, founded on robust taxonomy, should underpin effective sustainable management (hunting, ranching, captive breeding and reintroduction programmes) of this unique African natural resource.

Key words: conservation, morphological diversity, hybridization, phylogenetic species concept, extinct taxa, sustainable utilization.

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I. INTRODUCTION

Conservation biology requires taxonomy for sound scientific guidance. Taxonomic errors have negative impacts on accurate and precise knowledge of species diversity; these errors can mislead conservation evaluations and misinform characterizations of biogeographical history (Adams, 1998; Bernardo, 2011; Cotterill *et al.*, 2014). The taxonomic impediment (Hoagland, 1996) compounds these challenges, so that better surveyed taxa – pertinently vertebrates – are relied on as surrogate indicators to assess biodiversity, notably in gap analyses evaluating protected area coverage. Moreover, conservation assessments increasingly employ estimates of phylogenetic distinctiveness (PD) to characterize historical attributes of taxa to identify biodiversity hotspots. PD estimates expand the traditional focus beyond quantifying extant population diversity to incorporate evolutionary histories of biota across landscapes and continents (King, 2009).

Remarkably, and notwithstanding earlier revisions of a few species complexes (Cotterill, 2003*a*,*b*, 2005), until recently the classification of ungulates (hoofed mammals belonging to the orders Artiodactyla and Perissodactyla) remained almost unchanged from the middle of the 20th century. We here use the term 'taxonomic inertia' to describe this persistence of incomplete knowledge of biodiversity. Fortunately, the taxonomy of ungulates underwent wholesale revision recently (Groves & Grubb, 2011; Groves & Leslie, 2011) leading to a considerable increase in the number of recognized species. Interestingly, this revised classification systematically employs the phylogenetic species concept (PSC) to operationalize the evolutionary species concept (ESC) [the former name for the general lineage concept (GLC) of de Queiroz (1999)]. The application of the ESC has been criticized as 'taxonomic inflation' (a term first used by Isaac, Mallet & Mace, 2004) in recognizing too many false species (Type I errors) (Cotterill *et al.*, 2014). These criticisms invoke two main issues: first, recognizing 'too many species' has negative consequences for conservation biology in that it impedes human-assisted gene flow (e.g. through restocking programs) between threatened 'populations', when the latter are considered to be distinct species (Frankham *et al.*, 2012; Heller *et al.*, 2013; Zachos *et al.*, 2013*a*,*b*). Second, given insufficient funding for biodiversity conservation, an increase in the number of recognized species reduces the resources available per threatened species and thus aggravates the 'agony of choice' for conservation planners and managers (Isaac *et al.*, 2004; Collen *et al.*, 2011). Respondents to both criticisms argue that understanding mammalian diversity must be guided by the best available scientific framework within the available evidence, and condemn artificial lumping of species because it undermines biodiversity assessments, especially where planners rely on recognized species of ungulates as surrogate indicators and/or flagships in conservation planning (Gippoliti, Cotterill & Groves, 2013; Cotterill *et al.*, 2014).

Taxonomic inertia raises critical questions. What are its impacts? In particular, how has taxonomic inertia influenced not just past decisions but prevailing policy? And for the ungulates, why has this debate been so delayed, compared to the other main branches of vertebrate taxonomy, and what are the consequences of this for understanding African ungulate diversity, a unique heritage of this continent?

Here we review the history of ungulate taxonomy to highlight how taxonomic inertia has propagated the remarkable prevalence and persistence of taxonomic errors. Presenting this long-overdue historical context explicates the polarized points of view that shaped the major taxonomic syntheses of African ungulates over the last 120 years. These trends and tensions in taxonomic knowledge further (*i*) distinguish between taxonomic revisions *versus* reviews, and (*ii*) underscore the fundamental roles of available hypodigms on which derived taxonomies ultimately stand or fall. Above all, we show that impacts of taxonomic errors on conservation are hard-hitting, and we highlight problems exacerbated by the mixing of different populations of African ungulates, in the wild and the semi-wild as well as in captivity. These undermine the credibility of repeated translocations of ungulate 'species'.

II. HISTORICAL PERSPECTIVE ON UNGULATE TAXONOMY IN AFRICA

(1) The genesis of ungulate taxonomy

Until the end of the 20th century, an established consensus believed that the living African ungulates comprised 95 recognized species, three of which became extinct recently (summarized in the compilation of Corbet & Hill, 1986), and it followed that the goal to maintain the diversity of ungulate species in Africa was not a 'mission impossible'. This 'orthodox' taxonomy, originating in reviews and checklists (not true taxonomic revisions) of the 1930s, 1940s and 1950s, had come to be perceived as definitive by the scientific community. This tacit belief coincided with a general decline of interest in researching mammal collections, especially in Western European museums. Here, we define 'orthodox' taxonomy as the classification derived from the taxonomic reviews of Allen (1939); Ellerman & Morrison-Scott (1951) and Ellerman, Morrison-Scott & Hayman (1953), which classified previously described mammals using a polytypic species concept [biological species concept (BSC) or morphological species concept (MSC)]. Over the following decades, and despite the addition of little, if any, empirical evidence, the taxonomic arrangements in all three monographs have been unquestioningly accepted and utilized, and often perceived as 'definitive' by users, leading to decades of taxonomic inertia (Gippoliti & Groves, 2012).

The low contemporary appeal of mammalian taxonomy meant that few biologists scrutinized ungulate diversity, unlike the attention paid to the more speciose small mammals such as Rodentia and Chiroptera, even when new potential material and data were available. Thus Cuneo (1965), for example, while describing the breeding at Naples Zoo of

Abyssinian klipspringers *Oreotragus saltatrixoides*, reported that of the four founder individuals, the two received from the Asmara–Keren area had a chestnut-grey pelage, while the two from Senafe had a grey-brown pelage. This remarkable observation – on antelopes originating from within the same country, within a distance of less than 150 km – corroborates evidence of geomorphological controls on diversification of Ethiopian large mammals (*cf*. Gippoliti, 2010). It is unlikely that any of these Naples klipspringer founders was deposited and appropriately labelled in a museum after death – yet another example of taxonomic neglect (Cotterill & Foissner, 2010).

In the 1980s, the first quantitative genetic studies identified an important potential problem for conservation biology. Evaluations of captive populations (such as those of dorcas gazelle *Gazella dorcas*) revealed deficient genetic variation and heterozygosity, highlighting potentially insidious inbreeding depression (Ralls, Brugger & Glick, 1980). This study served to reinforce the prevailing concept of 'biological species', and the conclusion was drawn that the interbreeding of geographically separated populations – purportedly of the same species – would increase genetic variation to minimize the negative effects of inbreeding (Frankham *et al.,* 2012). While Speke's gazelles *Gazella spekei* were used as a model for the elimination of inbreeding depression from a small captive stock (Templeton & Read, 1998), another African mammal, the cheetah *Acinonyx jubatus*, was found to exhibit apparently abnormally low genetic diversity (O'Brien *et al.,* 1985), and in this case interbreeding between southern and eastern African individuals was suggested as a possible countermeasure (irrespective of potential outbreeding depression). Considered in hindsight, preliminary population genetics data together with a simplistic understanding of the small-population paradigm (*cf*. Caughley, 1994) not only exerted a strong influence on thinking among conservation professionals, but also moulded policies toward the perceived sustainability of animal populations – not only in *ex situ* situations but also in protected areas. The case of dwindling species has received high-profile attention.

Significantly, the historical trend towards lumping ungulate species has been compounded by abuse of the subspecies category. Perhaps this was favoured by the impressive flood of mostly spurious 'species' by some late-19th century taxonomists such as Paul Matschie in Berlin, which were often based on single individuals as well as on metaphysical theories about the geographical distribution of species along river basins rather than objective analyses of variation of morphological characters. It was perhaps as a counterbalance that other mammalian taxonomists turned with enthusiasm to the trinomial, following the lead of Lord Rothschild and his colleagues (Rothschild, Hartert & Jordan, 1903; and see Mallet, 2004). Thus Lydekker (1913, p. vi) already adopted 'to a great extent the principle of classing nearly related kinds of animals as races of a single species rather than as distinct species . . . ', and, accordingly, classified the African buffaloes as a single species, *Bos* [now *Syncerus] caffer*, with 21 subspecies. Ernst Schwarz followed the same path of simplification at the species level – as in his paper on duikers and in his otherwise seminal paper on *Alcelaphus* (Schwarz, 1914; Ruxton & Schwarz, 1929). Rothschild himself contributed to the spread of the trinomial in mammalian taxonomy, describing numerous new 'races' (meaning subspecies) of ungulates (e.g. Rothschild, 1921). It is possible that accepting subspecies in a polytypic species served to lower the responsibility for the taxonomist's decision, but it is interesting that already in 1916 this trend to recognize too many ungulate subspecies despite only one (or few) specimens, and without valid morphological characters, was criticized by some (e.g. Camerano, 1916). As a taxonomic category, the subspecies concept became a panacea to deal with problematic situations: especially to characterize differing patterns of morphological variation in (apparently) closely related populations. In reality, conversely to the polytypic species ideal, such variation could represent a population within a metapopulation or a divergent lineage lacking unambiguous evidence (morphological at least) of distinct evolutionary independence.

In important respects, Schwarz was pioneering an evolutionary approach in mammal taxonomy, especially in his *Alcelaphus* paper (Ruxton & Schwarz, 1929), which was part of a series entitled *Stages in the Evolution of Species*. After publication of the influential books of Dobzhansky (1937); Huxley (1940) and Mayr (1942) advocating the BSC, and following the lead of Allen (1939), mammalogists at the then British Museum (Natural History) seemed to take it as their duty to revise the mammal checklists of the Old World mammals in light of the New Systematics and the BSC (Ellerman & Morrison-Scott, 1951; Ellerman *et al.,* 1953). Judging from at least two critical book reviews (Handley, 1954; Ansell, 1958*a*), the immediate response to Ellerman and colleagues was that they had gone too far in lumping 'species' of Old World mammals. One reviewer of their *Mammals of Southern Africa* (Ellerman *et al.,* 1953) observed: "Their 'species' is frequently equal to the 'species group' of American taxonomists. It often appears that to them the criterion of conspecifity is gross resemblance, demonstration of intergradations is unnecessary, and broad overlap of ranges of 'subspecies' is an unimportant detail" (Handley, 1954, p. 460).

For decades, until the molecular biology revolution, a general neglect undermined characterization of challenging and/or cryptic diversity at the species level in vertebrates. It was compounded over the next half century, because taxonomy became 'out of fashion' and museum-based research programs became limited in number and scope, especially in Western Europe. The widespread negative trends across comparative biology over this period hit taxonomy hardest – in what Brooks & McLennan (1999, 2002) term the 'Eclipse of History' (*cf*. Cotterill, 2016).

As a consequence of this dearth of studies of the major museum collections of large mammals, non-specialists tended to assume that the taxonomy of these groups was resolved and definitive. Species boundaries were treated as firmly set. Moreover, it was believed that little if any diversity awaited discovery, especially of large mammals. Illustrative of this viewpoint was the reduction to a care and maintenance policy of the avian and mammalian collections of the Natural History Museum in London after 1989, recounted by Fortey (2008). Viewed today in the context of the prevailing scientific paradigm, there were few tentative advances through the latter half of the 20th century, and only a few descriptions of new taxa, such as the Nigerian pygmy hippopotamus *Choeropsis liberiensis heslopi* by Corbet (1969), occasionally broke through this ominous stagnation.

Since the beginning of the 21st century, a number of more easily recognizable, geographically isolated lineages have been rehabilitated as distinct species. Thus, Grubb (1993, 2005) recognized 100 and 101 species of African ungulates, respectively, in the two editions of *Mammal Species of the World*. In the meantime Cotterill (2000, 2003*a,b*, 2005) questioned the validity of the BSC to describe ungulate diversity in Africa; he advocated the ESC as the only valid solution to discover and describe the true diversity of African antelopes, and also reiterated major problems and challenges in mammalogy identified decades earlier by Ansell (1958*b*). Even if all data from ungulate collections of the major museums were collated – assembled from across the globe – their hypodigms remain inadequate. This general lack of specimens continues to weaken quantitative comparisons of inter-demic variation to inform modern, geographically representative taxonomic revisions.

(2) Molecular contemporary approaches

One might have expected molecular evidence to help solve these taxonomic inadequacies. Instead, it appears the challenges of characterizing ambiguous morphological variation have endured for decades, despite the grand promises of molecular genetics since the 1950s: first karyology, then electrophoresis and more recently estimates of genetic variation from directly sequencing the genome. The latter began with random amplification of polymorphic DNA (RAPD) and related restriction-enzyme comparative mapping, then mitochondrial DNA sequencing, inaugurated by Avise and collaborators in the late 1980s (Avise, 2000), and most recently comparative genomics. The most recent suite of methods enabled by high-throughput sequencing methods – exemplified in restriction site associated DNA sequencing (RADSeq) (Ekblom & Galindo, 2011) – enables hitherto unprecedented characterization of genomic variation. RADSeq has begun to be used in generic revisions, where it vindicates earlier estimates of the widespread incidence of cryptic species. This is underscored by the exemplary taxon sampling in a recent study of African guenons, including many subspecies, synonymized decades earlier; comprehensive genomic evidence evaluated using RADSeq now demonstrates that these subspecies are evolutionarily independent lineages (Guschanski *et al.,* 2013).

Prior to the recent invention of high-throughput sequencing, exemplified in RADSeq, pioneering studies of genetic diversity of the Bovidae (e.g. Arctander, Johansen & Coutellac-Vreto, 1999; Matthee & Robinson, 1999; Alpers *et al.,* 2004; Lorenzen, Heller & Siegismund, 2012) relied on mitochondrial DNA (mtDNA) variation and microsatellites as genetic markers. With the exception of the continental overview of the *Tragelaphus scriptus* and *T. sylvaticus* complexes (Moodley & Bruford, 2007), these preserved the conservative taxonomy of Allen (1939) and Ellerman *et al.* (1953). Actually, uncritically or otherwise, these authors assumed the reality of these 'species', and did not test species boundaries. The common deficiency is the failure of these studies to explicitly genotype topotypical populations of all described subspecies; it is then impossible to anchor phylogeographical findings on the known taxonomic framework. Nearly all phylogeographers continue to evaluate ungulate diversity under a polytypic species concept. This widespread failure to evaluate species boundaries critically in an explicit phylogenetic framework is strange, and raises questions considering expansion of tree-thinking philosophy (*sensu* O'Hara, 1988) into conservation theory (e.g. Erwin, 1991; Vane-Wright, Humphries & Williams, 1991), and increasing investments prioritizing characterization of the evolutionary dimensions of biodiversity in biodiversity assessments and policy (Mouquet *et al.,* 2012).

(3) Why 'taxonomic inflation' is a misnomer

In contrast to the general belief among biologists and conservation practitioners, our actual knowledge of large mammal diversity is poor. Taxonomic inertia has undermined a representative knowledge of ungulate diversity for far too long. There is disquieting evidence that the traditional ungulate taxonomy not only rests on remarkably weak scientific foundations, but also that significant diversity is still unknown and underexplored. Over decades, these repeated failures by professionals flow from the artificial classification of poorly known evolutionarily distinct taxa into single polytypic 'species'. The number of genuine taxonomic revisions that have been conducted on African ungulates – in fact, on any ungulate genera at all – can be counted on the fingers of one hand. Moreover, in these few cases hypodigms were limited, often based on only one museum's collection (almost invariably the Natural History Museum, London). Critically evaluated against this complete lack of revisionary work, it is clear that the term 'taxonomic inflation' is a misnomer, at least as far as ungulates are concerned: quite simply, there has been no taxonomy to be inflated.

Most seriously, many mainstream conservation practitioners appear unaware of these realities. Park managers and zoo directors alike assume that existing knowledge of ungulate diversity is resolved. Thus no species remain unrecognized; for surely, give or take adjustments of the 'subspecies' status of a few populations, is it not true that species lists were completed decades back? Moreover, where their conservation profile is disregarded as just population segments, subspecies

Table 1. Summary of over a century of classification of African ungulates revealing significant shifts in recognized species diversity

Family/subfamily	Sclater & Thomas (1894–1900)	Lydekker & Blaine (1913–1916)	Allen (1939)	Meester & Setzer (1971)	Corbet & Hill (1986)	Grubb (2005)	Groves & Grubb (2011)
Rhinocerotidae	—	2	2	2	2	2	3
Equidae	—	5	5	5	4	4	5
Suidae	—	8	5	4	4	6	8
Hippopotamidae	—	2	2	2	2	2	3
Tragulidae	—	1	1	1	1	1	1
Giraffidae	—	3	3	2	2	2	9
Cervidae	—	1	1	1	1	1	1
Bovinae	14*	10	11	10	10	10	39
Cephalophini	20	33	18	16	17	18	41
Reduncini+	18	12	10	9	9	9	24
Hippotragini	9	7	7	7	7	8	11
Alcelaphini	18	14	10	7	7	10	25
Aepycerotini	2	1	1	1	1	1	2
Antilopini	39	48	34	27	26	24	60
Caprini	—	3	3	2	2	3	3
Total number	120	150	113	96	95	101	235

*Does not include *Syncerus*.

+Includes *Pelea* (following Robinson *et al.*, 2014).

are of negligible evolutionary importance (Corbet, 1997). We argue that all ‘*de facto*’ factors such as these have motivated zoos and wildlife authorities to mix supposedly ‘conspecific’ stocks both *in situ* and *ex situ* (but see Dathe, 1978).

Nothing less than a landmark taxonomic revision was needed to galvanize attention to taxonomic inertia of the ungulates. The incisive synthesis by Groves & Grubb (2011, hereafter G&G) compiled revisions carried out through a collective eight decades of research, within the strictures of available hypodigms in museums. Remarkably, it has met with not just surprise, but hostility, in antagonism against doubling the recognized number of species of ungulates. Unfortunately, too few critics appear to understand not only the motivations but especially the empirical foundations underpinning G&G. One line of criticism seized upon weaknesses perceived in the PSC used to reclassify the ungulates. The PSC was used explicitly as a workable proxy for the ESC. The G&G revision considerably increased the number of recognized species as highlighted by a synthesis of how species diversity of African ungulates has been evaluated over more than a century (Table 1). G&G finally recognized 235 species of African ungulates after studying unprecedented hypodigms of specimens (Cotterill *et al.*, 2014). Although one of the earliest species lists (Lydekker & Blaine, 1913–1916) was already influenced by lumping, it is, nonetheless, interesting to note how its total of 150 species dropped in subsequent years. This finally reached a minimum with Corbet & Hill (1986) of only 95 African ungulate species. Interestingly, the number of global primate species followed a similar trend: decreasing from 532 in 1912 to only 180 in 1967 followed by an increase to 233 in 1993, 370 in 2001, and 480 in 2013 (Rylands & Mittermeier, 2014). With the application of morphometric and genetic methods, in combination with the PSC, we have learned more about primate taxonomy and evolution in the 13 years following Groves (2001) standard work on primate taxonomy than in the 50 years preceding Groves’ book.

It is important to acknowledge that G&G is the precursor and catalyst for much taxonomic work that remains unfinished. This applies especially where hypodigms are small, as the high prevalence of incomplete hypodigms makes the assessments of many populations tentative. These inadequate samples of populational variation of many hypodigms of candidate ungulate taxa are a strident indicator of severe gaps in knowledge of large mammal diversity – poor representation in the available and/or examined museum collections (*cf*. Reddy & Dávolos, 2003). For example, no oribi *Ourebia* sp. from north of the Juba River, Somalia, generally ascribed to the taxon *haggardi*, have been studied and the few existing museum specimens await comparison against the population from southern Somalia and coastal Kenya. Wide-ranging species, such as the bongo *Tragelaphus euryceros*, are mostly known from old museum specimens received from a tiny part of their range −despite this species being nowadays highly prized by trophy hunters in Central Africa. Sample sizes are invariably small and the last original taxonomic work dates from the beginning of the 20th century (Thomas, 1902). In a little-known paper on the African buffalo in southern Somalia, Fagotto (1980) reported the existence of two ‘types’; one lightly built, with horns which never curve downwards below the level of the skull base and resembling the taxon *Syncerus brachyceros*, while the more massive form with horns that curve considerably downwards points to affinities with *S. caffer*. Interestingly, this latter form is present from the borders with Kenya to the lower Sheebeli River (Awai), beyond which the lighter form predominates northwards along the Sheebeli lower course. The small amount of material available in Italian museums is not likely to help us solve this taxonomic question. Similar cases are certainly widespread but, belatedly, G&G have unlocked a new scientific era in large-mammal taxonomy. Important collections in southern African museums, especially the rich collections in the Natural History Museum, Bulawayo (NMZB), have yet to be comprehensively evaluated, with the exception of *Damaliscus lunatus* and *Kobus leche* species complexes studied by Cotterill (2003*a*,*b*, 2005) and unpublished results on *Kobus* cf. *vardoni* and *Hippotragus* (F. P. D. Cotterill, unpublished data). This Bulawayo collection is complemented by significant large mammal collections in Pretoria (TM, Ditsong Museum), East London (Amathole Museum), Cape Town (SAM, Izoko Museum) and Zambia (Livingstone Museum), and smaller but still significant collections in the Kenya National Museum, Nairobi, and the Institut Fondamental d'Afrique Noire (IFAN), Dakar. Regrettably, it seems that the importance of a national repository for natural history collections is not receiving attention in several African countries. There are ample possibilities for European museum collections to contribute to taxonomic studies (e.g. D'Huart & Grubb, 2001; Gippoliti *et al.,* 2014) but this requires a paradigm shift in current perceptions of natural history museums and their collections (Cotterill, 2016).

Finally, apart from the vast amount of morphological data stored in museum collections, molecular studies offer an opportunity to uncover much of the geographical and temporal genetic variation held there. However, genetic studies of historical museum specimens typically rely on extracting highly degraded and chemically modified DNA samples from skins, skulls or other dried samples. Until recently, it was possible only to obtain short fragments of DNA sequences using traditional polymerase chain reaction (PCR) amplification. Recently, however, approaches using high-throughput next-generation sequencing to obtain reliable genome-scale sequence data have been proposed (e.g. Rowe *et al.,* 2011). This allows obtaining data for single-nucleotide polymorphisms (SNPs) or complete mitochondrial genome sequences even from degraded source materials. The biological material required can be as little as 10 mg with high success rates of PCR amplification. This is particularly important when sampling from museum specimens, as it avoids destructive tooth or bone sampling (Wandeler, Hoeck & Keller, 2007; Guschanski *et al.,* 2013; see also Bi *et al.,* 2013). Museum collections allow genotyping of type specimens, as was recently carried out for the lectotype of the Arabian gazelle *Gazella arabica* consisting of a skull and skin, which led to the discovery that it was of composite origin and only the skin should be retained as the name-bearing specimen (Bärmann *et al.,* 2013). Obviously it is now possible to sample museum specimens belonging to extinct taxa/populations to produce more-complete phylogeographic information to resolve taxonomic issues concerning highly threatened species. This has been done with the Nubian wild ass *Equus africanus* (Kimura *et al.,* 2010) and the giant sable antelope *Hippotragus niger variani* (Themudo, Rufino & Campos, 2015).

III. TAXONOMIC INFLATION AND CONSERVATION

Several prominent conservation geneticists who have invested decades of research efforts to the identification and conservation of distinctive and often-threatened evolutionary units (e.g. Frankham *et al.,* 2012; Heller *et al.,* 2013, 2014; Zachos *et al.,* 2013*a*,*b*) are strongly opposed to the shift in mammal taxonomy resulting from adoption of the PSC (Groves, 2001; Groves & Grubb, 2011). The rationale underlying this criticism lies in concerns over dissipation of conservation resources on populations traditionally lumped into single 'species', using the BSC. Such opposition is ironic given the contributions of these and other geneticists to the uncovering of discrete lineages within traditionally recognized species.

Underlying this criticism is the argument of Isaac *et al.* (2004) that excessive taxonomic splitting impacts negatively on macroecological research and conservation. First, we should note that part of their problem lies in the current biased application of ESC in mammalogy. At present we have an ESC synthesis for Primates, Artiodactyla and Perissodactyla while other orders, such as Hyracoidea, remain classified in an overlumped BSC-based taxonomy. This problem is attributed to the present period of transition, not an underlying flaw within the ESC itself.

Regarding the supposed negative effects of a PSC-based taxonomy, we note that a survey by Morrison *et al.* (2009) found no evidence for negative effects of taxonomic splitting on conservation, but rather found the exact opposite: in addition we highlight the dubious record of 'orthodox' taxonomy in creating long-standing *ex situ* problems, e.g. in zoo breeding programs during the 20th century. Here the legacy of 'taxonomic inertia' is manifested by overlooking finer scale diversity and the geographical origins of founder populations, bequeathing chimerical stocks of zoo ungulates of unknown and/or admixed evolutionary lineages. As a potpourri of different populations, the *ex situ* conservation status of these purported 'species' is disputable. For example, two supposed subspecies of East African dikdik *Madoqua kirkii* had different karyotypes and were found to produce infertile offspring when interbred in zoos (Kumamoto, Kingswood & Hugo, 1994; Cernohorska *et al.,* 2011); there are in fact four species, morphometrically distinguishable, within what was lumped as *M. kirkii*, and skulls of dikdik of known karyotype could easily be identified by being fitted in to this scheme (Groves & Grubb, 2011). A study of the karyotypes of the North American zoo population of suni *Nesotragus moschatus* found even greater chromosome variability, with Kenyan animals (*N. m. akeleyi*) exhibiting 2N = 56 and KwaZulu-Natal animals (*N. m. zuluensis*) 2N = 52 (Kingswood *et al.,* 1998). It was sensibly suggested that these two 'subspecies' should be managed separately given evidence of probable breeding problems in hybrids, and they are now classified as different species by G&G. In another study, heterozygosis for three chromosomal changes (centric fusions) was invoked as causing high perinatal mortality in captive Soemmering's gazelles *Gazella soemmeringi* (now *Nanger soemmerringii*) (Benirshke *et al.,* 1984), although, in this case, it is unclear whether chromosomal rearrangements correlate with subspecific status and thus what the possible roles of inbreeding and outbreeding in perinatal mortality might be (see Steiner *et al.,* 2016, who suggested a genetic and chromosomal study of wild populations to clarify the relationship between taxonomic status and chromosomal rearrangements in Soemmering's gazelles). There are at present not many captive breeding programmes for small and medium-sized ruminants representing the Antilopini, Cephalophini and Tragulidae; so opportunities comprehensively to evaluate effects of outbreeding remain severely limited. Nonetheless, available data suggest that the karyotypic diversity of the Bovidae is more similar to that of rodents than to other large mammals such as carnivores (Kumamoto *et al.,* 1999; Pagacova *et al.,* 2011; Robinson & Ropiquet, 2011).

Outbreeding depression (Storfer, 1999) is now recognized to be as great a problem as inbreeding depression in wildlife conservation and captive breeding programmes. Its negative effects persist even after admixture of distant populations of apparently monotypic species such as Arabian oryx *Oryx leucoryx* (Marshall & Spalton, 2000). Pedigree analysis has revealed outbreeding depression in captive populations of Indian rhinoceros *Rhinoceros unicornis* representing separate populations from Nepal and Assam (Zschokke & Baur, 2002); belatedly, these two genetically distinctive populations are now acknowledged to be best managed separately (Zschokke *et al.,* 2011). Although similar cases of breeding incompatibility likely exist in several other rhinoceros populations in Africa and Asia, their classification as 'subspecies' confers a dubious status on these populations. This is most notorious when 'just a subspecies' is declared extinct (Gippoliti *et al.,* 2013). This is the case of the Nile rhinoceros (northern white rhinoceros) *Ceratotherium cottoni*, of which only three individuals are still living in captivity and apparently none in the wild. The species rank accorded by Groves, Fernando & Robovský (2010) has been recently challenged by Harley *et al.* (2016) fearing that the rescue and conservation of *C. cottoni* through hybridization with the southern white rhinoceros *C. simus* may be prevented by taxonomic splitting; yet there is strong evidence that the only female hybrid produced in Dvur Kralove Zoo showed signs of outbreeding depression, never bred and was larger and heavier than any other recorded female (Dvur Kralove Zoo records). As evidenced by a recent proposal to manage Sumatran and Bornean rhinoceros *Dicerorhinus sumatrensis* as a single 'management unit' (Goossens *et al.,* 2013), some conservationists continue the dubious practice of overlooking negative consequences of outbreeding depression. Note, however, that the absence of any perceived negative effect from introgression of two or more closely related taxa does not constitute a criterion for their conspecificity.

The species of African ungulates rated as extinct or near-extinct over the last two centuries makes sobering reading (Table 2). Although the taxonomic status of some of these taxa is still controversial, biogeographical, morphological, and genetic evidence (where known) suggests that these extinctions have extirpated considerable phylogenetic diversity. Orthodox taxonomy stands out as the propagator of several extinctions, especially in the past half a century. Conspicuous losses of phylogenetic diversity among wide-ranging African mammals are exemplified by the black rhinoceros *Diceros* spp. (Moodley *et al.,* 2017). The distinctively long-legged black rhino *Diceros longipes* from the Chad region – presently recognised as *Diceros bicornis longipes* – would certainly have received much greater attention and conservation support had its morphological and taxonomic distinctiveness been thoroughly investigated. Furthermore, given the high value people place on rarity (Angulo *et al.,* 2009), this species should have constituted an exceptional flagship species for conservation in west-central Africa, and an important focus for tourist attraction in a region otherwise neglected.

The case of the Nubian wild ass *Equus africanus* stands unique among all these extinctions. It was treated as one of at least two subspecies (the other being the Somali wild ass *Equus somaliensis*; see Groves & Smeenk, 2007 for a recent synthesis), until the distinction of these lineages was confuted after the mid 20th century. As a result the Nubian wild ass practically disappeared from the scientific and conservation literature (Gippoliti, 2014). Recent genetic studies seeking to resolve the origin of donkeys *Equus asinus* genotyped old museum specimens. These confirm the distinctiveness of the two taxa, highlighting the Nubian wild ass as ancestor of the donkey (Kimura *et al.,* 2010); it is perhaps not too late to save this neglected species from extinction, as there are at least a few individuals, now carefully protected, persisting in south-eastern Egypt (Sultan Mos'ad, personal communication).

IV. TRANSLOCATION 'RESCUE' AND CONSERVATION GENETICS

Several critics of the PSC argue that small and declining populations might be rescued through translocations from other populations, but such conservation 'rescue' efforts are undermined now that these populations are characterized as distinct (Frankham *et al.,* 2012; Zachos *et al.,* 2013*b*; Heller *et al.,* 2014). Besides the failure to find concrete examples to support this fear of a (theoretical) conservation hurdle, this argument overlooks the respective evolutionary histories of populations lumped into single 'species', and runs counter to the increasing role of phylogenetic knowledge in informing conservation decisions. Moreover, the findings of Heller, Okello & Siegismund (2010), on genetic drift in *Syncerus caffer*, confined in isolated protected areas of Uganda and Kenya, clearly show that human-mediated gene flow can be pursued without breaking the deeper phylogenetic barrier that has evolved along the Victoria Nile. On the contrary, we know of a few cases of ecological and behavioural disruptions following mixing of evolutionarily divergent lineages. In a classic case, the translocation of

Table 2. Extinct and near-extinct African ungulates in recent history

Taxon	English name	Original range	Notes
*Diceros bicornis longipes**	Western black rhinoceros	Nigeria, Cameroon, Central African Republic (CAR)	Extinct 2012
*Ceratotherium cottoni**	Nile rhinoceros	W. Uganda, S. Sudan, Garamba NP (Democratic Republic of Congo), CAR, Chad	Three individuals of breeding age in semi-captivity
*Equus quagga quagga**	Quagga	S and E Cape, Free State (S. Africa)	Extinct 1872
*Equus africanus**	Nubian wild ass	N Eritrea, NE Sudan, SE Egypt	Status uncertain, Gebel Elba, Egypt and possibly in Sudan
*Phacocoerus aethiopicus**	Cape warthog	S. Cape (S. Africa)	Extinct
*Choeropsis heslopi**	Nigerian pygmy hippopotamus	Niger Delta, Nigeria	Probably extinct
*Giraffa camelopardalis**	Nubian giraffe	NW Kenya, Ethiopia, Eritrea, Uganda, Sudan (E of Nile)	Survives patchily in Kenya, Uganda, Sudan, far-western Ethiopia
*Kobus robertsi**	Roberts' lechwe	NE Zambia	Extinct by 1950s
Hippotragus leucophaeus	Blaubok	SW Cape, Free State†	Extinct 1800 (1860 if Free State record is valid)
*Alcelaphus buselaphus**	Bubal hartebeest	North Africa	Extinct 1925
*Alcelaphus tora**	Tora hartebeest	Nubia and W Ethiopia	Possibly extinct 2010
*Damaliscus selousi**	Selous' topi	Uasin-Gishu plateau, Karamoja	Extinct sometime after 1930
Eudorcas rufina	Red gazelle	Algeria	Extinct pre-1894

*Denotes taxa not included in Turvey (2009).

†This information comes from a claim of an eyewitness report of what sounds like blaubok in the Free State, in 1858. See Groves & Grubb (2011, p. 198).

three interbreeding members of the genus *Capra* (*Capra ibex*, *C. nubiana* and *C. aegagrus*, the latter two at that time considered subspecies of *C. ibex*) on the Tatra Mountains failed because of a different birth seasonality (Templeton, 1986). Geist, O'Gara & Hoffmann (2000) discussed how wapiti and European red deer (*Cervus canadensis* and *Cervus elaphus* species complexes) differ in their respective habitat requirements and behavioural ecology, suggesting that interbreeding can be advantageous only in semi-captive situations. Such cases imply that the concern expressed by several researchers (Frankham *et al.*, 2012; Heller *et al.*, 2013; Zachos *et al.*, 2013*a,b*) over the conservation consequences of adopting the PSC is misplaced and unwarranted. Paradoxically, wealthier African countries, such as South Africa, face the biggest problems in protecting their original ungulate diversity due to a mix of liberalism in wildlife management and unsound use of scientific knowledge; taxonomic inertia apparently plays a role. It is true that modern conservation biology recognizes the importance of maintaining intraspecific diversity [evolutionarily significant units (ESUs), management units (MUs), subspecies] (Moritz, 1994; Crandall *et al.*, 2000), yet such detailed attention is often accorded only to a few species in particular regions, mostly in North America or Australia (Haig *et al.*, 2006; Gippoliti & Amori, 2007). Most national legislations protect species, and species are the mandatory focus of IUCN *Red List* assessments (see www.iucnredlist.org). Identification of biodiversity hotspots or sub-hotspots is based on endemic species distributions, not on the distribution of subspecies or ESUs (Dubois, 2003). In the few cases where resources are abundant, due attention should be paid to intraspecific variability (e.g. lion *Panthera leo*; tiger *Panthera tigris*; gorilla *Gorilla* spp.; Wilting *et al.*, 2015; Bertola *et al.*, 2016) but this is the exception rather the rule. Even highly charismatic large mammals receive very little attention from this point of view (e.g. African elephant *Loxodonta* spp.; brown bear *Ursus arctos*: see Gippoliti, 2016; Groves *et al.*, 2016). The zoo community has so far allowed the mixing of Sumatran and Bornean elephants within continental Asian family groups, despite the strong phylogeographic structure found in *Elephas maximus* (S. Gippoliti, personal observation).

Although South Africa should urgently adopt new regulations to limit ecological and genetic effects of ungulate translocations in private reserves (Cousins, Sadler & Evans, 2010) with the aim of avoiding further negative consequences for native biodiversity, this still seems far from being achieved. Yet, adoption of an ESC-based taxonomy would be a step in the right direction. For example, the only buffalo native to South Africa remains *Syncerus caffer*, but the G&G taxonomy restricts this species to the southern and eastern African savannahs east of the Western Rift Valley, while Central and Western buffaloes are recognised as belonging to three distinct species (*S. brachyceros*, *S. mathewsi* and *S. nanus*) and, as exotic species, their importation could be easily regulated or even prevented. Unregulated wildlife translocations had severe consequences in North America and Europe (Champagnon *et al.*, 2012), and we may easily imagine negative impacts among ungulates in Africa.

In some cases translocations of rare ungulates become cosmetic initiatives at best; this is the case for 'sitatunga' (*Tragelaphus spekii* complex) reintroduction in The Gambia. In fact, the sitatungas west of the Dahomey Gap seem to represent an undescribed, very-little-known potential species, but apparently no data are available on the origin of the four individuals released at Abuko in 1968 (Starin, 2000). The fact is that one consequence of taxonomic inertia is that of dismissing the role of the whole discipline of morphology-based taxonomy, which some believe is superseded by phylogeographic molecular studies.

Transmission of new diseases or failure to acclimatize to endemic diseases is another widespread problem encountered in the management of translocated ungulate populations (Melter, 1993; Nijhof *et al.*, 2005), and often neglected by population geneticists. Interestingly, Nijhof *et al.* (2005) reported the case of a pair of roan antelope *Hippotragus equinus* originating from Togo and Benin succumbing to a *Theilerosis* infection after release on a game ranch in southern Mpumalanga, South Africa. As Aiello *et al.* (2014) showed with the desert tortoise *Gopherus agassizii*, translocations and augmentation may disrupt existing resident disease dynamics and initiate an outbreak that would effectively offset any advantages accompanying the translocation.

The dramatic recovery of the (southern) white rhinoceros *Ceratotherium simum* in Kwazulu-Natal [but see Rookmaaker (2000) for a critical review of historical data] shows that the paradigm of population genetic theory (see Caughley, 1994) has been overemphasized in conservation biology at the expense of factors such as political stability and effective management and protection. If this is true, the current emphasis on gene flow and human-mediated translocations in ungulate conservation needs to be considered in a wider perspective.

V. THE ROLE OF HYBRIDIZATION IN SPECIES CONCEPTS AND CONSERVATION

In the past, interbreeding or hybridization between animal species was assumed to be of negligible concern, not at least because of a near-universal belief in the infallibility of the BSC as the conceptual tool with which taxonomists classified living diversity; thus fertile interbreeding taxa by definition were regarded as belonging to a single species. Thanks to progress in molecular methods over the last decades, however, it has become obvious that gene flow between species has been widespread in the past, and continues in the present, in various taxonomic groups (e.g. Mallet, 2005; Arnold, 2008; Schwenk, Brede & Streit, 2008; Zinner, Arnold & Roos, 2011). Following in the footsteps of botanists, there is increasing interest among zoologists in the role of hybridization and its evolutionary consequences, ranging from zero gene flow when F1 individuals are sterile to complete admixture or hybrid speciation (Arnold, 1997; Allendorf *et al.*, 2001; Larsen, Marchán-Rivadeneira & Baker, 2010; Abbott *et al.*, 2013). Given that species delimitation is not a simple endeavour, not least because no universal definition of species is yet accepted, despite the arguments of de Queiroz (2007) and others, gene flow among taxa makes it even more complicated. Hybridization can have significant conservation impacts, in particular when conservation is species-based (Simberloff, 1996; Allendorf *et al.*, 2001; Fitzpatrick *et al.*, 2015; van Wyk *et al.*, 2017). Questions arise about the worthiness for conservation of populations with hybrid ancestry, with inherent problems in the legal treatment of hybrid populations (Fitzpatrick *et al.*, 2015; Richards & Hobbs, 2015). Often a distinction is made between 'natural' and 'human-caused' hybridization, although in many cases it remains unclear what proportion of contemporary hybridization can actually be attributed to direct (e.g. purposely introduced species) or indirect (e.g. species range expansion due to human-caused habitat alterations or climate change) human activities (Mallet, 2005).

Molecular techniques can detect past introgressions that shaped the evolutionary histories of lineages (Zinner, Arnold & Roos, 2009; Green *et al.*, 2010), yet such events have not always been suspected on morphological grounds (but see Ackermann & Bishop, 2010; Ackermann *et al.*, 2010). Accumulating evidence of gene flow between both universally recognized species, even of different genera [e.g. in primates (Roos *et al.*, 2011; Zinner *et al.*, 2011); in bovids (Verkaar *et al.*, 2004; Rodríguez *et al.*, 2009)], as well as between 'subspecies', undermines the roots of the BSC with its emphasis on reproductive isolation (Mallet, 2008). This evidence for interspecific gene flow makes it all the more difficult to single out what qualifies as a true species, and why such populations differ from those that comprise a hybrid swarm, as Ruxton & Schwarz (1929) proposed decades earlier for East African *Alcelaphus*.

After studying two specimens of hartebeests from south-west Ethiopia, de Beaux (1943) proposed that, when a hybrid population shows constant characters, it should be recognized as a distinct taxonomic entity. In this specific case, he proposed that *Alcelaphus buselaphus neumanni* (Rothschild) should be accepted with the following synonymy: '*Alcelaphus buselaphus lelwel* (Heuglin) × *Alcelaphus buselaphus tora* (Gray) Ruxton and Schwarz'. More recently, Ouma *et al.* (2011) investigated the genetic status of putative hartebeest hybrids in Kenya. With respect to the declining status of these populations, they affirmed that '... in many African countries, including Kenya, where there has been little mixing of populations by translocation, opportunities to conserve ongoing evolutionary processes persist, and should be pursued' (Ouma *et al.*, 2011, p. 146). A proposed hybrid swarm from divergent caribou lineages (*Rangifer tarandus tarandus* and *R. tarandus caribou*) is considered a conservation target in Canada (McDevitt *et al.*, 2009). These examples, both old and recent, highlight the need to reconsider the taxonomic and conservation implications when we acknowledge that hybridization is an historical process. Moreover, much greater attention should be paid to the possible detrimental effects of wildlife translocations or the further reduction of sympatric populations of closely related taxa that may encounter increased incidence of hybridization due to the absence of conspecific mates. Paradoxically, ungulate managers have often had privileged opportunities to study artificially introgressed populations, yet the intricacies of natural evolutionary trajectories receive little attention.

The complexity of conservation in cases of hybridization becomes clear where human activities induce introgression directly or indirectly, as summarized above (see also Allendorf *et al.*, 2001). The intentional or unintentional introduction of closely related non-indigenous species may lead to hybridization. Similarly, reduced population sizes of related sympatric or parapatric species (through hunting or other human impacts), might increase hybridization risk, eventually leading to the extinction of one or both species (Frankham, Ballou & Briscoe, 2002; Allendorf, Luikart & Aitken, 2012; Fitzpatrick *et al.*, 2015). In South Africa there has been considerable concern about introgression of southern blue wildebeest *Connochaetes taurinus* genes into the local endemic black wildebeest *Connochaetes gnou* following inopportune introductions of the former species into the latter's range (Grobler *et al.*, 2011). But many more taxa seem affected; some cases have been discussed in detail, such as hybridizations between greater kudu and lowland nyala *Strepsiceros strepsiceros* × *Tragelaphus angasi*, or red hartebeest and tsessebe *Alcelaphus buselaphus* × *Damaliscus lunatus* (Robinson *et al.*, 2015). Furthermore, admixtured populations of the Karoo and Kalahari springbok (*Antidorcas* spp.) are purposely farmed for venison and trophy hunting (Van Aswegen, Labuschagne & Grobler, 2012). Zebras are also potentially affected by translocations in South Africa (Castley, Boshoff & Kerley, 2001), with potentially devastating effects for the now-recognized species Cape mountain zebra *Equus zebra* and Hartmann's zebra *Equus hartmannae*. Introduction of scimitar-horned oryx *Oryx dammah* into the historic range of gemsbok *Oryx gazella* puts the genetic integrity of the latter at obvious risk (Castley *et al.*, 2001). Similarly, black-faced impalas *Aepyceros petersi* are also affected by unregulated translocations (Green & Rothstein, 1998).

Introgression over the long term may reduce the abilities of such species to adapt to present and future environmental change (Rhymer & Simberloff, 1996) or may lead directly to cytonuclear extinction (e.g. Gill, 1997; Cordingley *et al.*, 2009). So whether such evolutionarily distinct lineages are termed species, 'subspecies', ESUs (Ryder, 1986), or 'ecotypes' (and so on), it is mandatory that we manage such phylogenetically distinct lineages separately. In summary, the negative impacts of outbreeding depression or introgression underscore how the ESC (=PSC) derived taxonomy of ungulates provides wide-ranging epistemological support to biodiversity conservation. That this is evidently not the current situation is clear from the widespread criticism of G&G when they raised some subspecies to species rank.

VI. HOW CAN A 'NEW ALPHA TAXONOMY' SUPPORT CONSERVATION?

(1) Forgotten taxa, forgotten hotspots

Recent revisions of East African giraffes reveal that the three recognized species are confined to discrete ecoregions, within which synchronization of birth season with rainfall may be one mechanism that reduces gene flow among giraffe species (Thomassen *et al.*, 2013). Belated recognition of the real diversity of *Giraffa* (Brown *et al.*, 2007; Groves & Grubb, 2011; Bock *et al.*, 2014) exemplifies how the taxonomy of these large mammals provides a framework to explore such processes, provided it is founded on a lineage species concept. The new alpha taxonomy of the ungulates provides essential conservation support by highlighting biodiversity hotspots previously overlooked, such as Katanga, the Zambezi and the Nile watersheds (Gippoliti *et al.*, 2013; Cotterill *et al.*, 2014). Equally, it is important to analyse responses of African large mammals to climate change at the level of phylogeographic lineages rather than orthodox 'species', since this level of taxonomic precision is a prerequisite to parse the focal variable in robust models (D'Amen, Zimmermann & Pearman, 2013).

Although the increase in recognized alpha diversity of clades might make 'species conservation' appear more challenging to implement, this is vastly preferable to the converse impacts of imprecise taxonomy fostered by taxonomic inertia. An example of such impacts are species allowed to slip into extinction unnoticed; such as the Tora hartebeest *Alcelaphus tora* (Heckel *et al.*, 2008), because it was lumped as one of several subspecies of *Alcelaphus buselaphus*. Taxonomic inertia has likewise conferred the dubious distinction of complete, or near, extinction on such species as the Nigerian pygmy hippopotamus *Choeropsis heslopi*, the Queen of Sheba's gazelle *Gazella bilkis*, the Nubian giraffe *Giraffa camelopardalis* and the Nile rhinoceros *Ceratotherium cottoni*. Arguably, their conservation status today could have been vastly different had they been accorded species status, or at least had their status openly debated. The same could be said of species in imminent danger of following their slide to extinction. Examples include the West African giraffe *Giraffa peralta*, the Arava gazelle *Gazella acaciae*, the Upemba lechwe *Kobus anselli*, and the Mt. Elgon red duiker *Cephalophus fosteri*.

(2) Taxonomic impacts on the wildlife industry and sustainable conservation

African wild ungulates are worth many hundreds of millions of US dollars as a source of protein for rural communities, as hunting trophies, and as focal subjects of tourist attention (Yasuoka, 2006; Lindsey, Roulet & Romanach, 2007; Nasi, Taber & Van Vliet, 2011). Wild ungulates represent the most notable component of bushmeat consumed in most areas of the humid forest as well as the Zambezian savannahs (Newing, 2001; Fusari & Carpaneto, 2006), and an important source of income for alleviating poverty in rural communities (de Merode, Homewood & Cowlishaw, 2004). Ironically we know very little about the enduring escalating impacts of bushmeat and other depredations on the true diversity of ungulates. Local mismanagement is encouraged by orthodox taxonomy, as exemplified by the report into the decline of blue duiker on Bioko Island (Grande-Vega *et al.*, 2016). According to G&G, the Bioko island blue duiker represents an endemic species *Philantomba melanorheus* (Gray, 1846), but

Grande-Vega *et al.* (2016, p. 49) claimed that 'The blue duiker (*Philantomba monticola*) is an abundant and widely distributed ungulate in continental sub-Saharan Africa'. Later they emphasized that island populations may be more threatened than others, but never used the name *melanorheus* in their paper, even as a subspecific name. This is very different from the attention paid to the endemic primate assemblage of Bioko Island, with the fate of seven species/subspecies a cause of great concern (Butynski, De Jong & Hearn, 2009).

Furthermore, recently, Sarasa (2013) highlighted that previous analyses evaluating trophy prices and the international hunting market are confounded by bias because they overlooked intraspecific diversity of 'traditional species'. For example, among Spanish ibex, trophy prices for *Capra pyrenaica victoriae* are much higher than *Capra pyrenaica hispanica* because the latter has shorter horns. The different IUCN conservation status of these two subspecies underscores why the 'biological species' taxonomy undermines the accuracy of comparative studies and conservation assessments.

We highlight the impact of taxonomic inertia on the classification – and equally on the conservation and management – not only of ungulates but also other charismatic African mega-herbivores, elephants of the genus *Loxodonta*. Recognition of the true diversity of this mega-herbivore obscures the high-profile concern over the plight of the African elephant, traditionally classified during the period of taxonomic inertia as a single species. The reality is that there are two lineages of unequivocal evolutionary distinctiveness, often recognised by those working first-hand on the issue (Frade, 1931; Allen, 1936; Azzaroli, 1966). This is not surprising, given that the genomic evidence dates the divergence between savanna elephant *Loxodonta africana* and forest elephant *L. cyclotis* to the Pliocene (Rohland *et al.,* 2010; Roca *et al.,* 2015); crucially, it is *L. cyclotis* that is most at risk from unsustainable anthropogenic depredations, caused by habitat losses and poaching (Maisels *et al.,* 2013), but taxonomic inertia continues to obscure its conservation plight. Ironically, morphological revisions conclusively demonstrated the distinctiveness of the two species nearly two decades ago (Grubb *et al.,* 2000; Rohland *et al.,* 2010; Shetty & Vidya, 2011).

The role of African ungulates in the maintenance of ecosystems, thus contributing ecosystem services to the value of many millions, even billions of dollars, has only begun to be estimated. The collapse of large mammal populations in Central African forests following overhunting for bushmeat may have long-term consequences for the ecological integrity of the region (Abernethy *et al.,* 2013). Activities such as deforestation and hunting have direct and indirect detrimental effects on ungulate biodiversity in Africa, and a sound knowledge of alpha taxonomy is a *sine qua non* successfully to manage, conserve and study this irreplaceable resource. Pre-G&G taxonomy set a poor foundation that has misinformed and misled sustainable management in too many cases. We have highlighted many conspicuous failures in which the extreme tragedy – species extinction – has occurred repeatedly. In the case of large mammals, an outdated phenetic approach goes a long way to explain this 'domino-impact' of weak science on conservation policy and applied management (Cotterill *et al.,* 2014).

We single out the persistence of a spurious alpha taxonomy as the cause of biotic homogenization across large regions of Africa, in the way that in some countries, such as South Africa, translocations of various exotic or extralimital ungulates is now considered a major risk to native biodiversity (Castley *et al.,* 2001; Spear & Chown, 2009), and hybridization has seriously affected some threatened species such as *Connochaetes gnou* and *Damaliscus pygargus* (van der Walt, Nel & Hoelzel, 2013).

(3) How precise and accurate taxonomy informs a hierarchical conservation strategy

A persistent challenge in conservation is to reconcile the often disparate goals and challenges of single-species *versus* ecosystem management, where the latter aims to maximize biodiversity conservation. Ultimately, any single-species conservation will fail *in situ* where ecosystem integrity is ignored. This is where we highlight the increasing use in conservation biology of decision-making processes relying on phylogenetic diversity (PD) to identify and rank conservation areas. It is no accident that the evolutionary lineage is the core currency of PD calculation to diagnose biodiversity hotspots and evolutionarily vibrant landscapes [as first argued by Erwin (1991) and see Mouquet *et al.* (2012)]. This approach should ideally utilize both ancient and young lineages in combination to map the most complete (i.e. representative) range of unique landscape elements across the continent.

In the case of Africa, there have been major attempts to identify biogeographical patterns using indicators of evolutionary history of representative biota (e.g. Linder *et al.,* 2012), but the lack of primary information still weakens this quest. G&G present a strong data set, where their classified evolutionary species can be mapped out in the most complete detail that locality data permit currently. The strength of this approach is exemplified by Moodley & Bruford (2007) who integrated occurrence maps of the lineages of the *Tragelaphus scriptus* and *T. sylvaticus* species complexes into the matrix of African ecoregions. These lineages of African bushbucks are demonstrated to provide an informative proxy of palaeoecological affinities, and at a finer scale a recent evaluation of endangered okapi (*Okapia johnstoni*) reveals equally instructive evidence linking taxonomy to ecoregions, especially where respective okapi lineages exhibit congruence with other species (Stanton *et al.,* 2014). Ironically today, these ungulates diagnose high conservation values of landscapes in which some indicator lineages appear to have been extirpated.

Much work remains. We single out this evolutionary conservation strategy [the PD strategy] as a significant – if not the primary – practical strength of an ESC-based taxonomy in biodiversity conservation. Following King (2009), application of the PSC at the population level minimizes taxonomic errors, pertinently in applications informing *in situ* planning and policy. At the ecosystem/landscape level, ungulates rank as textbook flagship/umbrella species, and as especially informative indicators, where their evolutionary histories can inform biodiversity maps, and in turn diagnose biodiversity hotspots. Indeed, G&G emphasize this in their Introduction (G&G, p. 17) where they flag some of the main ecosystems revealed by local endemics of ungulates.

VII. CONCLUSIONS

(1) Science informs conservation, not the other way round. In this respect, it is unfortunate that only within the past seven years have conservation decision-makers been able to exploit a sufficiently accurate and precise taxonomy of ungulate diversity.

(2) In its role in revising biodiversity mapping, the new taxonomy complements biogeographical data sets of other indicators (pertinently the herpetofauna and avifauna), but these data are still incomplete, and/or await electronic databasing.

(3) Several salient lessons explain why the revision by G&G has revealed so many new, and significant, findings, issues, and challenges for ungulate conservation.

(*a*) It highlights the application of modern taxonomic methodology whereby high-quality knowledge feeds conservation policy. This is notable where the identification of hitherto-unrecognised evolutionary species at the same time identifies overlooked conservation areas (e.g. Upemba Swamps).

(*b*) Taxonomic assessments remain impossible without tentelic records preserved in museums, especially as the primary data of conservation concern are open to independent checks, and focal studies, particularly using new molecular methods.

(*c*) The largest data set ever assembled for ungulates underscores the primacy of a specimen-based taxonomy over ‘expert’ opinions/assumptions. It is urgent that collecting of specimens such as hunting trophies, bushmeat, cropping exercises and pick-up specimens (e.g. road-killed and predator-killed animals) becomes the norm, where feasible in conservation terms, facilitated by government and conservation authorities. Ultimately, we should aim to collate and utilize all available material in world collections to fill gaps in taxonomic knowledge that can in turn be translated into conservation strategies.

(*d*) Integration of morphology-based taxonomy has the further merit of being potentially ‘palatable’ to exploiters such as wildlife tourists (or indeed trophy hunters), and serves as a vital mechanism to provide DNA to systematists whose revisions are challenged by gaps in representation of populations and/or geographical locations.

(*e*) As argued elsewhere at length (Cotterill *et al.,* 2014) these tentelic data that vouch for the data analysed in G&G were classified employing modern methods of phylogenetic systematics, and not least a species concept that replaces the polytypic BSC with the lineage-based ESC (=GLC) operationalized by the PSC. In short, G&G integrate the complementary strengths of population-thinking and tree-thinking.

(*f*) Contrary to Frankham *et al.* (2012), adoption of the PSC has highly positive rather than negative consequences for conservation science, especially in its characterization of allopatric diversity.

(*g*) With improvements in precision and accuracy (minimizing Type 2 and Type 3 taxonomic errors), G&G sets the precedent to incorporate its classified lineages into conservation-focused databases that integrate measures of phylogenetic diversity to inform policy, especially in implementing the Convention on Biological Diversity at national, regional and global scales.

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