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Species definitions and conservation: a review and case studies from African mammals

Colin P. Groves¹  · F. P. D. Cotterill² · Spartaco Gippoliti³ · Jan Robovský⁴ · Christian Roos⁵ · Peter J. Taylor^{6,7} · Dietmar Zinner⁸

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Abstract The nature of species, especially as applied to large mammals, is of major concern in conservation. Here, we briefly comment on recent thinking in alpha taxonomy, and assert that species are in essence evolutionary lineages, and that the most effective way of recognising them is by their diagnosability, i.e. the so-called Phylogenetic Species Concept. We further assert that the amount of genetic distance is not a relevant datum for distinguishing species, and that the ability to interbreed is not relevant. We consider a few case studies, especially that of the Northern White

Rhinoceros *Ceratotherium cottoni*, and also species in *Loxodonta*, *Giraffa* and *Oreotragus*.

Keywords Evolutionary species · Phylogenetic species concept · *Ceratotherium* · *Loxodonta* · *Giraffa* · *Oreotragus*

The nature of species in mammals

This review examines how reliance on different concepts of the species category (Table 1) holds important, in fact fundamental, impacts on the knowledge informing conservation decisions. We restrict our examples to African Mammalia, whose rich diversity illustrates the primary challenges we identify in how taxonomy either weakens or refines conservation policy. In particular, we single out the impacts of a persistent reliance by many mammalogists on the biological species concept (BSC).

There is no lack of scholarly reviews of the nature of species and the importance of the species category in comparative biology in general (e.g. Claridge et al. 1997; Frost and Kluge 1994; Ghiselin 1997; Howard and Berlocher 1998; Pavlinov 2013; Stamos 2007; Wheeler and Meier 2000; Wilkins 2009; Wilson 1999; Zachos 2016). Rather than reiterating these detailed arguments, our aim here is to focus on major concerns in conservation biology, particularly the challenges presented in the diversity of large mammals, as a flagship example.

The evolutionary synthesis of the 1930s effectively introduced population thinking into many realms of biology, including systematics and taxonomy, and it was in this context that Dobzhansky (1937) and Mayr (1942) argued in detail for a definition of species, which emphasised reproductive isolation, i.e. that species are populations (or series of populations) that do not breed with one another

✉ Colin P. Groves
colin.groves@anu.edu.au

¹ School of Archaeology & Anthropology, Australian National University, Canberra, ACT 2601, Australia

² Geocodynamics Research Hub, c/o Department of Earth Sciences, University of Stellenbosch, Private Bag X1 Matieland, Stellenbosch 7602, South Africa

³ Società Italiana per la Storia della Fauna “G. Altobello”, Viale Liegi 48A, 00198 Rome, Italy

⁴ Department of Zoology, Faculty of Science, University of South Bohemia, Branišovská 31, 37005 České Budějovice, Czech Republic

⁵ Gene Bank of Primates, Primate Genetics Laboratory, German Primate Center, Leibniz Institute for Primate Research, Kellnerweg 4, 37077 Göttingen, Germany

⁶ School of Mathematical and Natural Sciences and Centre for Invasion Biology, University of Venda, P. Bag X5050, Thohoyandou 0950, South Africa

⁷ School of Life Sciences, University of KwaZulu-Natal, Private Bag X54001, Durban 4000, South Africa

⁸ Cognitive Ethology Laboratory, German Primate Center, Leibniz Institute for Primate Research, Kellnerweg 4, 37077 Göttingen, Germany

Table 1 Summary of principal concepts of the species category, including the concepts of ESU and subspecies

Concept	Definition
Biological species concept (BSC)	<p>“A biological species is an inclusive Mendelian population; it is integrated by the bonds of sexual reproduction and parentage.” (Dobzhansky 1970, p. 354)</p> <p>“A species is a group of interbreeding natural groups that is reproductively isolated from other such groups.” (Mayr and Ashlock 1991, p. 26)</p>
Cohesion species concept (CSC)	<p>“...the most inclusive population of individuals having the potential for phenotypic cohesion through intrinsic cohesion mechanisms.” (Templeton 1989, p. 12)</p> <p>“...the most inclusive group of organisms having the potential for genetic and/or demographic exchangeability.” (Templeton 1989, p. 25)</p>
Differential species concept (DFC)	<p>“Groups of individuals that are reciprocally characterized by features that would have negative fitness effects in other groups and that cannot be regularly exchanged between groups upon contact.” (Hausdorf 2011, p. 927)</p>
Evolutionary significant unit (ESU)	<p>“...a population (or group of populations) that (1) is substantially reproductively isolated from other conspecific population units, and (2) represents an important component in the evolutionary legacy of species.” (Waples 1991)</p> <p>“ESUs should be reciprocally monophyletic for mtDNA alleles and show significant divergence of allele frequencies at nuclear loci.” (Moritz 1994, p. 373)</p> <p>“A lineage demonstrating highly restricted gene flow from other such lineages within the higher organizational level (lineage) of a species.” (Fraser and Bernatchez 2001, p. 2742)</p>
Evolutionary species concept (ESC)	<p>“A species is a single lineage of ancestral-descendent populations which maintains its identity from other such lineages and which has its own evolutionary tendencies and historical fate.” (Wiley 1978, p. 18)</p> <p>“...a lineage, comprised of organisms, whose history of individuation has manifested in its unique evolutionary trajectory through space and time.” (Cotterill 2005, p. 115)</p>
Genetic species concept (GSC)	<p>“...population subdivisions concordantly identified by multiple independent genetic traits should constitute the population units worthy of recognition as phylogenetic taxa.” (Avise and Ball 1990, p. 52)</p>
Phylogenetic species concept diagnosable version (PSC1)	<p>“The smallest diagnosable cluster of individual organisms within which there is a parental pattern of ancestry and descent.” (Cracraft 1983, p. 170)</p>
Phylogenetic species concept monophyly version (PSC2)	<p>“...a geographically constrained group of individuals with some unique apomorphous character, is the unit of evolutionary significance” (Rosen 1978, p. 176). Equates with ISC (Internodal Species Concept) of Kornet (1993), which was termed the CSC by Brooks and McLennan (1999)</p>
Phylogenetic species concept diagnosable/monophyly version (PSC3)	<p>“...the smallest diagnosable cluster of individual organisms forming a monophyletic group within which there is a parental pattern of ancestry and descent” (McKittrick and Zink 1988, defined by Mayden 1997, p. 407). This version of the PSC was termed the PSC2 by Brooks and McLennan (1999)</p>
Recognition species concept (RSC)	<p>“...the most inclusive population of individual biparental organisms that share a common fertilization system.” (Paterson 1985, p. 25)</p>
Subspecies	<p>“An aggregate of phenotypically similar populations of a species, inhabiting a geographic subdivision of the range of a species, and differing taxonomically from other populations of the species.” (Mayr 1969, p. 41)</p>

Table 1 (continued)

Concept	Definition
Superspecies	“A superspecies is a monophyletic group of closely related and largely or entirely allopatric species that are too distinct to be included in a single species or that demonstrate their reproductive isolation in a zone of contact.” (Mayr and Ashlock 1991, p. 430)

This classification is a subset of the concepts summarized by Mayden (1997) with concepts listed in alphabetical order. Definitions of the subspecies and superspecies concepts are provided for comparison, and are traditionally applied in combination with the BSC. One might argue that ESUs lie outside of this classification, but ultimately are proposed alternatives to traditional approaches to trinomials in microtaxonomy, which have applied concepts of subspecies, varieties and races

under natural conditions. Mayr (1942) called this the BSC; and this view of ‘what-species-are’ reigned supreme until almost the end of the twentieth century, doubtless because it fits so well with the polytypic species concept (in which there are relatively few species, many of them having subspecies) that held sway during most of the century. Nonetheless, increasing tensions in the application of the BSC built up over the following half-century or so; indeed, Mayr himself devoted two whole chapters of his seminal *Animal Species and Evolution* (Mayr 1963) to listing caveats against applying the reproductive isolation criterion in too wholesale a fashion. Beginning in the 1970s, numerous other “species concepts” (Phenetic, Phylogenetic, Recognition, Ecological, Differential Fitness and others) were proposed out of dissatisfaction with the BSC, and a period of philosophical ferment ensued (Mayden 1997).

It was, however, as early as 1951 that the palaeontologist Simpson (1951, 1961) argued that the nature of species is that they are evolutionary lineages (the evolutionary species concept, ESC). This, in effect, ushered in the concept of tree thinking, to stand alongside population thinking, into systematics. It was not for some 30 years that the logic of Simpson’s vision began to become appreciated; in particular, Mayden (1997), listing the two dozen or so “species concepts” proposed thus far (summarized in Table 1), concluded that the evolutionary species must be regarded as the singular candidate for the primary concept because the ESC recognizes that species are evolutionary lineages, and explains why species have a real existence (Frost and Kluge 1994). Acknowledging that it might be difficult to detect an evolutionary lineage in practice, however, Mayden (1997) followed by Groves (2001) argued that the phylogenetic species concept (PSC1, Table 1) of Cracraft (1983) (under which diagnosability is the criterion) best serves as the means of recognising species. (Note that a different “phylogenetic species concept” requires that the differentiating character states have to be autapomorphic, but this not the usual interpretation; PSC2, Table 1). De Queiroz (2007) concurred: “every [populational] lineage is a species”; and the criteria for the various secondary concepts that have been proposed – distinguishability, reciprocal monophyly, ecological niche differentiation, specific mate recognition

systems, some portion of reproductive isolation fixing species/lineage-specific features – are essentially attributes that evolve in a lineage. Subsequent discussions of “the species problem” have tended to follow this logic that distinguishes between the ontology of the species category versus the discovery tools used to characterize biodiversity: see, for example, Groves and Grubb (2011), Samadi and Barberousse (2006), and papers in Pavlinov (2013) and Fleagle (2014).

The distinction between species concepts and species criteria is much more than a pedantic exercise, because it underpins the consilient solution of species discovery and characterization (Cotterill 2003; Cotterill et al. 2014; see Frost and Kluge 1994 for exhaustive defence of this research strategy). The emphasis in this paper aims to move beyond the persisting confusion that species criteria (as concepts of the species) continue to inject into the taxonomic and applied literature.

Use of the ESC operationalized by the diagnosability criterion, the PSC (strictly, PSC1), is not universally accepted outside of systematics, and some biologists reject the whole idea of the evolutionary species; a common criticism is because more species are thereby recognised than had been “traditionally”, which – it has been maintained – might make conservation efforts more difficult. In response to these concerns, Groves (2012) argued that the PSC offers the only criterion for species recognition that is testable, as a scientific proposition should be.

As for concerns about conservation (see, for example, Frankham et al. 2012), we believe that it is not in fact the PSC but the over-lumped taxonomic schemes that preceded its adoption (Gippoliti and Groves 2012) that were inimical to conservation needs, making numerous species invisible to conservation and risking their extinction unnoticed (Barrowclough et al. 2016; Gippoliti et al. 2013; Gutiérrez and Helgen 2013). As Stevenson et al. (1992) warned, conservation “should try to maximize options and minimize regrets” (Stevenson et al. 1992, p. 11), and, in taxonomy, “splitting rather than lumping maximizes preservation of options” (Stevenson et al. 1992, p. 31). Furthermore, conservation biology rests on the methodology of modern comparative biology, which relies on systematics for

species discovery operations informed with the historical evidence of lineage histories (Frost and Kluge 1994; Brooks and McLennan 1999). In contrast, Frankham et al. (2012) argue that species are best delimited using the criterion of ‘substantial reproductive isolation’ - under aegis of the differential species concept (DFC) (Hausdorf 2011), though this ‘differential fitness criterion’ has yet to counter the weaknesses identified in the DFC (Cotterill et al. 2014).

The notion of subspecies continues to be invoked in conservation policies, often to rank the perceived status of populations. Yet, a strong argument reveals this reliance on subspecies is misplaced. Subspecies are idiosyncratic and, worse, too often misleading – the category is too fallible to evaluate population distinctiveness with a minimum of scientific rigour (Cotterill et al. 2014; Fitzpatrick 2010; Zink 2004). Recently, Wickert et al. (2016, p. 1733) emphasized that as a species is delimited by fixed, diagnostic characters under the PSC1, there is no arbitrary distinction between species or subspecies in a polytypic species. Thus, a subspecies is not “...conceptually equivalent to the “phylogenetic species” (e.g., Remsen 2005)...” And all subspecies concepts are fundamentally different from the PSC1, and they all share the deficiencies of operationalism in practise (Cotterill et al. 2014).

Moreover, there is little credibility in usage of the trinomial, beyond subjective designation of taxa; at most, the subspecies is a kind of “placeholder”, a plea for better information.

In preference to prioritizing the discovery of evolutionarily independent lineages to characterize species, the criterion of reproductive isolation continues to be invoked to lump populations into species (e.g. Frankham et al. 2012). Three issues about the criterion of reproductive isolation are pertinent. First, interbreeding under human control does not give any indication of species status even under the BSC, especially in allopatric populations (see Mayr 1963, especially Chap. 6; Groves and Robovský 2011). Second, Mayr (1963) himself made the point that reproductive isolation has two quite different aspects: prezygotic (do they recognise each other as potential mates?) and postzygotic (having mated, do they produce hybrids, whether fertile, of reduced fertility, or sterile?). Third, and most crucially, we now know that hybridisation—genetic admixture as a consequence of two distinct species having recognised each other as potential mates—is frequent among mammals, yet species maintain their identity in the face of gene flow (Roux et al. 2016). For example, Grévy’s zebra *Equus grevyi* and Plains zebra *Equus quagga* interbreed in the wild (Cordingley et al. 2009). To take another example, especially relevant in the present context (see below, the case study of the Northern White Rhinoceros), Robinson et al. (2005) described a hybrid between a Southern White Rhinoceros, *Ceratotherium simum*, and a Black

Rhinoceros, *Diceros bicornis*, in an 800 ha enclosure at the breeding centre for the South African National Zoo. In both cases, members of different species or even genera recognised each other as potential mates. There are numerous molecular studies convincingly showing that hybridisation has been rife during mammalian evolution and evidence for lateral gene flow has been found in most mammalian orders (for a review see Arnold et al. 2015): e.g. Primates (Tosi et al. 2003; Zinner et al. 2009); Chiroptera (Khan et al. 2014); Carnivora (Cahill et al. 2015; Gaubert et al. 2005; Li et al. 2015), Artiodactyla/“Cetartiodactyla” (Soubrier et al. 2016; Verkaar et al. 2004), Perissodactyla (Jónsson et al. 2014).

Hybridization will lead to incongruence among phylogenies based on different markers or to reticulated phylogenetic relationships (Zinner et al. 2011), making species delimitation based on such markers often ambiguous.

The other assumption is one that is frequently seen, if rarely made explicit, in conservation genetics: that a considerable level of genetic distance (or time of separation) between two populations is necessary before they can be recognised as separate species (Baker and Bradley 2006; Ball and Avise 1992). Reliance on estimates of genetic distance persists despite increasing applications of coalescent models, in which the different markers confer a spectrum of respective genetic distances, and some are often not reciprocally monophyletic across the node(s) of the species tree (Pääbo 2003). However, even if reciprocal monophyly is achieved in a multispecies coalescent model, such a pattern might rather indicate a certain population structure instead of unambiguously delimit species (Sukumaran and Knowles 2017). Furthermore, since reciprocal monophyletic groups might be hierarchically nested in larger monophyletic groups, it is important to consider which of the groups or hierarchical levels one will attribute species status and which population status (Hey and Pinho 2012). Hence, genomic data alone does not solve the problem of species delimitation.

This belief that genetic distance sets an unequivocal criterion on lineages denies the species category its special biological status, and it can only be subjective, given that different levels of genetic distance, for the same or different genetic markers, have been proposed in the past; and indeed different levels of genetic distance characterise “good” (meaning traditionally recognised) species between different mammalian orders and even within orders, a finding that emerges from the compilations in Bradley and Baker (2001) and Lorenzen et al. (2008). When all is said and done, as noted by de Queiroz (2007) and others, “genetic difference is a consequence of speciation, not a primary criterion of it”. Ranges of genetic distance considered to be necessary to recognise species have been specified by Bradley and Baker (2001; Baker and Bradley 2006),

the first biologists to take the “amount of genetic distance” beyond mere assumption and formalise it as the genetic species concept (GSC). Such standardisation would have a chance of being valid only if there would first be consideration of clade-specific life-history parameters (Nabholz et al. 2008) and all variants occurring in nature (cryptic species with limited morphological differences; natural hybrid species; traces of previous, often limited, genetic contacts in mitochondrial DNA [mtDNA]; and so on). For example Bininda-Emonds (2007) and Nabholz et al. (2008) recognized *Perissodactyla* as a group with a significantly slower rate of evolution than that seen in many other mammalian orders.

The question of genetic distance is yet more complicated. It can be that two populations show a large genetic distance between them in certain markers, but, nevertheless, they interbreed freely. Alternatively, two populations can differ in just a few markers or only one marker, but this marker affects, for example, proteins necessary for the sperm to enter the egg. If these proteins do not match, fertilization might be problematic. In such cases, the degree of genetic dissimilarity or similarity in general might not be significant as long as certain important genes are not affected.

In conclusion, it should be clearly understood that one cannot regard “amount of genetic difference” as an absolute criterion for deciding whether two operational taxonomic units are distinct species or not (McDonough et al. 2008). In their reconstructions of histories of gene trees, coalescent methodology moves systematics beyond the conundrums of genetic distance. Coalescent analyses recover each formative demographic event that shaped the encompassing species tree, pertinently those of lineage divergence and introgression (Edwards et al. 2016; Leonardi et al. 2017). Genomic evidence should ideally be integrated with complementary character evidence to test the taxonomic status of candidate populations for specieshood (Cotterill et al. 2014).

Case study: the Northern White Rhinoceros, *Ceratotherium cottoni*

The mania to obtain rhinoceros horn, formerly largely for traditional Chinese medicine, nowadays more as a prestige item in business dealings in Vietnam, has generated a poaching crisis during which at least two taxa of rhinoceros have become extinct, and the Northern White Rhinoceros *Ceratotherium cottoni* (hereinafter NWR) has been reduced to only three known survivors, now (2016) living in a sanctuary at Ol Pejeta in Kenya, outside their natural range.

The NWR was distributed west of the White Nile in Uganda, South Sudan, Democratic Republic of Congo

(DRC), Chad and Central African Republic. It held on longest in Garamba National Park in the DRC, where it was finally exterminated in the early twenty-first century; the tiny group of survivors has been transferred to Kenya from Dvůr Králové Zoo in the Czech Republic. The Southern White Rhinoceros *Ceratotherium simum* (hereinafter SWR), on the verge of extinction a century ago, has been carefully conserved and is now much the most numerous living species of rhinoceros. Its range in historic times was south of the Zambezi, and the present >20,000 population has been used to restock its former range, as well as being introduced outside it, into Kenya, Uganda and Senegal (Rookmaaker and Antoine 2012).

Groves et al. (2010) established the specific distinction of *C. cottoni* (NWR) from *C. simum* (SWR) by characters of the dentition, skull and long bones, body size and conformation, presence or absence of body hair, and genetics. There are consistent differences in vocalizations (Činková and Policht 2014). The two allopatric populations have experienced distinctly different evolutionary histories. The only captive-bred hybrid individual exhibited very poor health, and showed atypical social behaviour (Holečková 2009; Kuneš and Bičík 2002).

Recently, Harley et al. (2016) compared entire mtDNA genomes of both taxa of white rhinos. They sequenced DNA from four NWR and three SWR, and compared them to Rhinocerotidae from GenBank as well as selected out-group taxa - including mtDNA genomes of modern and Late Pleistocene human groups, assuming that the latter are subspecies of *Homo sapiens*, which they are not (Bailey et al. 2014; Foley 2005; Harvati et al. 2004; Hedges 2000; Márquez et al. 2014; Tattersall and Schwartz 2009). The results confirmed that NWR and SWR are reciprocally monophyletic (with 100% statistical support); despite this, they disputed their status as separate species, the main argument being that accepting them as different species would be “a problem for conservation”. If some of the genes of NWR were to be saved, they argued, the only hope seems to be that the last survivors should be interbred with SWR – unless advanced techniques of reproductive technology could be tried, namely in vitro fertilisation or stem cell technology (in fact, such is already planned: see Saragusty et al. (2016), who also pointed out that the three remaining NWR are unable to breed naturally).

Distinguishing subspecies using genetic distance as in the case of *Ceratotherium* perpetuates phenetic approaches in molecular genetics (Cotterill et al. 2014). The new mtDNA evidence presented by Harley et al. (2016) for *C. cottoni* and *C. simum* is very welcome, indeed overdue. Analogously to *Loxodonta africana* and *Loxodonta cyclotis* (see next section), the combined genetic and morphological data confirm that the two rhinoceros lineages are evolutionary distinct species. The

extirpation of *C. cottoni* holds austere lessons for conservation, where policy and decision invokes misleading taxonomic concepts, and ignores or misconstrues pertinent evidence (Gippoliti et al. 2017).

Case study: the African Forest Elephant, *Loxodonta cyclotis*

The history of the taxonomy of African elephants was recounted in Groves and Grubb (2000) and Grubb et al. (2000). In summary, a detailed analysis by Frade (1955) showed striking and consistent differences between African Savanna and Forest Elephants and established them as two distinct species (*L. africana* and *L. cyclotis*, respectively). Although largely endorsed by Morrison-Scott (1947), Frade's analysis was overturned by Ellerman et al. (1953), followed up by observations of apparent intermediates in north-eastern Congo by Backhaus (1958). Grubb et al. (2000) compiled a long list of diagnostic characters distinguishing the two species of African elephants, and Groves and Grubb (2000) performed a multivariate analysis of skull measurements, showing that the two species, sex for sex, do not overlap. They found evidence of limited hybridisation in populations along the forest-savanna boundary.

The re-establishment of the Forest Elephant as a separate species from the Savanna Elephant was corroborated by Roca et al. (2001) on the basis of a DNA study. The same authors (Roca et al. 2007) found a degree of cytonuclear disassociation in places: implying that, when forests receded, local Forest Elephant populations had undergone nuclear swamping from Savanna Elephants. Most recently, Rohland et al. (2010) and Roca et al. (2015) calculated that the divergence time between the two species of *Loxodonta*, at 2.6–5.6 million years ago is not much less than that between *Elephas* (Asian Elephant) and *Mammuthus* (the recently extinct Woolly Mammoth).

Given all this overwhelming data, we disagree with the assertion that “The African Elephant Specialist Group believes that more extensive research is required to support the proposed re-classification” (IUCN Red List 2016a, b), given how the deep evolutionary distinctiveness of the two species has consolidated the solid empirical evidence and further developed a complementary microsatellite library to enable genotyping of *L. cyclotis* (Gugala et al. 2016). We feel it is fitting here to draw attention to a parallel case in ornithology, where the noted bird systematist Peterson remarked that a critic “considers it necessary to defend the taxonomy that the conservation establishment creates and approves of against any change from outside, particularly if it would require conceptual rethinking and reconsideration” (Peterson 2007, p. 117).

Case study: giraffes, *Giraffa* spp.

It was assumed for well over half a century that the genus *Giraffa* has only one species, until a multi-species model was put forward by Brown et al. (2007). This was followed up and formalised by Groves and Grubb (2011), who proposed that there are eight species. A further multispecies model, drawing extensively, but without acknowledgement, from these two predecessors, was proposed by Fennessy et al. (2016). The IUCN Red List dubs “*Giraffa camelopardalis*” as Least Concern, although it does in this case, unlike that of African elephants, acknowledge that “recent genetic work suggests that several subspecies may even represent distinct species (Brown et al. 2007)”, and lists two of the “subspecies” separately as Endangered. Although research is still necessary to elucidate how many species of giraffe really exist and which factors have been responsible for their diversification (cf. Thomassen et al. 2013; Berco-vitch et al. 2017), Fennessy et al. (2017) concluded that the consilience between pelage patterns and genetic evidence demonstrate four distinct giraffe species, which have experienced limited gene flow.

Case study: klipspringers, *Oreotragus* spp.

Groves and Grubb (2011) recognized at least 13 species of *Oreotragus*. No critique has tested this revision comprehensively in a scientific context, using empirical evidence; although it can be noted that photographs of the nine best-known species (collated by Castelló 2016) go some way towards substantiating the claims by Groves and Grubb (2011), because they reveal the ear patterns of klipspringers to be an additional diagnostic character (these are of signalling significance in static-optic advertising).

Klipspringers are diminutive stenotopic antelopes, with exactly the ecological specializations of allopatric lineages to rupicolous habitat islands which could encourage speciation—as in the cases of *Procapra* (Prinsloo and Robinson 1992), *Pronolagus* (Matthee and Robinson 1996), the rodent genus *Otomys* (Taylor et al. 2014) and the lizard genus *Agama* (Matthee and Flemming 2002). One klipspringer species, *Oreotragus schillingsi*, is unique among the genus in both sexes presenting horns. Zachos et al. (2012) point out the small samples studied; we may add that probably some populations have not been sampled at all (for instance in Central African Republic) and new taxa may await discovery, once the hypodigm of *Oreotragus* in museums represents these under-collected populations. Maintaining the outdated ungulate taxonomy by rejecting this hypothesis, that there are multiple species of Africa's klipspringers, illustrates three factors: (1) resistance to the Consilient Solution that is grounded in the ESC, and

despite an alternative and notwithstanding widespread application of its arguments to classify biodiversity, notably many other vertebrate clades (Cotterill et al. 2014); (2) the notion that species complexes, exemplified by *Oreotragus*, are polytypic “species”, a belief maintained even in the absence of empirical tests; and (3) the inadequate support for urgent taxonomic revisions of such poorly understood species complexes. Instead of rejecting the reclassification of *Oreotragus*, we remark that the appropriate scientific response is to test this hypothesis. Collection-based research, marginalized over the last 30 years or so, needs to be paralleled by DNA studies; preliminary genetic work by Le Roex (2008) suggests that there are indeed divisions between klipspringers in different southern African regions.

Conclusions

We have given an all too brief survey of taxonomic problems in a few groups of African large mammals. We show that their taxonomy has been beset by assumptions about reproductive isolation, or a certain arbitrary degree of genetic distance, being necessary for recognition of species. Instead, we assert that a species is an evolutionary lineage, this status being objectively operationalised by diagnosability. Not only does this meet the scientific requirements, but it also highlights units for conservation, which are liable to be missed under reproductive isolation or genetic distance criteria.

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