Systematic Biology Advance Access published January 11, 2014

Running head - WHY ONE CENTURY OF PHENETICS IS ENOUGH

WHY ONE CENTURY OF PHENETICS IS ENOUGH: RESPONSE TO 'ARE THERE REALLY TWICE AS MANY BOVID SPECIES AS WE THOUGHT?'

Fenton P. D. Cotterill[1], Peter J. Taylor[2], Spartaco Gippoliti[3], Jacqueline M. Bishop[4], Colin P. Groves[5]

[1]*AEON - Africa Earth Observatory Network, Geoecodynamics Research Hub, c/o Department of Botany and Zoology, University of Stellenbosch, Stellenbosch 7602, South Africa. email: fcotterill@gmail.com*

[2] *SARChI Chair on Biodiversity Value & Change in the Vhembe Biosphere Reserve & Core Member of Centre for Invasion Biology, School of Mathematical & Natural Sciences,University of Venda, P. Bag X5050, Thohoyandou, 0950, South Africa*

[3]*Viale Liegi 48, 00198 Roma, Italy*

[4]*Department of Biological Sciences, University of Cape Town, Private Bag, Rondebosch 7700, South Africa*

[5]*School of Archaeology & Anthropology, Australian National University, Canberra 0200, Australia*

ABSTRACT

The real diversity of the Bovidae is not only underestimated, but holds many surprises in its richness of diversity, especially overlooked and misclassified cryptic species. Our argument refutes the recent paper (Heller et al. 2013) condemning Groves & Grubb's (2011) revised taxonomy of the Bovidae as "taxonomic inflation" that is bad for conservation. The recent collective condemnation of this bovid revision misunderstands taxonomic theory and concept, and disregards how the unprecedented revision of material evidence informs the new bovid taxonomy. Unfortunately, the criticisms are likely to mislead conservation efforts. Contrary to taxonomic conservatives' denigrations of the Phylogenetic Species Concept (PSC), we explain how evolutionary species - ontological realities - can be discovered and characterized using the PSC, with a minimum of taxonomic error. Taxonomic conservatism weakens conservation policy because it throws a great deal out of biology. It is best understood as a political reaction to taxonomic revisions replacing non-historical characterizations of biodiversity (reliant on the polytypic Biological Species Concept and/or the morphological species concept) with historical ones based on the PSC. Further, accelerating discoveries of cryptic species unnerve conservative traditions in taxonomy and conservation biology. Taxonomic conservatism has no place in modern biology, let alone phylogenetic systematics, because its deficiencies undermine the consilience of comparative biology. Most seriously, taxonomic conservatism ignores the fundamental role of the Individuality Thesis in fostering robust understanding of biodiversity. We argue that rejections of G&G defend an obsolete taxonomy of large mammals, which testifies to the remarkable persistence of a folk taxonomy weakening 21st century science. Our consolidated argument underscores the challenges of improving scientific knowledge of cryptic biodiversity, exemplified in the extant (and historically extinct) Bovidae.

Keywords: evolutionary species concept; cryptic diversity; conservation; Individuality Thesis

INTRODUCTION

Heller et al. (2013), hereafter H&A, argue that the recent revision of the Bovidae (Groves and Grubb 2011), hereafter G&G (and see also Groves and Leslie 2011) is rife with Type 1 taxonomic errors (assigning the rank of species to a population that it is actually part of a metapopulation). Purportedly, G&G raise ecotypes or subspecies to the level of full species in the absence of credible evidence. Distinctly unwelcome, this increase in recognized species is labelled "taxonomic inflation" and apparently also causes taxonomic instability: altogether bad for conservation. We label this position “taxonomic conservatism” (Padial et al. 2009) and our criticism of the pejorative usage of "taxonomic inflation" echoes what Bernardo (2011) calls “inertial bias”. H&A is one contribution among recent rebuttals (Zachos & Lovari 2013; Zachos et al. 2013a,b) condemning G&G: described as “a mess” of taxonomic artefacts created by a “splitting frenzy” (Zachos 2012). All these rebuttals reject the Phylogenetic Species Concept (PSC), of which G&G used the diagnostic version (cf. Wheeler & Platnick 2000) to discover species[1].

Nevertheless, H&A pose an important question. Our overarching objective is to explain why the real diversity of the Bovidae is not only underestimated, but holds many surprises; not least because its richness of cryptic species has been overlooked and misclassified. We argue G&G has undertaken the first comprehensive test of what we define as the Phenetic Hypothesis. We emphasize why the benefits of a precise, accurate classification of bovid diversity are far-reaching. Our response is motivated by the quest to characterize cryptic biodiversity – to obtain an objective knowledge of extant (and historically extinct) bovids. Whilst the magnitude and significance of cryptic diversity is well known, and accepted without question for small mammals, its prevalence in large mammals

---

[1] We struggle to reconcile several contradictory statements by H&A that invoke central concepts in comparative biology and systematics. An explicit ontology of the species category is not defined, indeed they “acknowledge that no consensus exists”, but they endorse “an integrative taxonomy” in citing Padial et al. (2010) who argue strongly for the Evolutionary Species Concept (ESC). Conversely, H&A dismiss the PSC, even though it is the primary species criterion that operationalizes tests of evidence to characterize species under the aegis of the ESC. They condemn the PSC “as unstable and unsuitable for biodiversity assessment”, yet claim “…we do not advocate static species lists”. It is further unclear how the tree-thinking framework of integrative taxonomy accommodates the notions of subspecies and ecotypes; obsolete, these are not real evolutionary entities but artifacts of polytypic species concepts.

awaits due recognition. The magnitude of the knowledge gap stands out when we compare the neglect of large mammal taxonomy against the continuing explosion in discoveries of cryptic species of African small mammals (e.g. Stoffberg et al. 2012; Taylor et al. 2011, 2012; Koubínová et al. 2013; Van Daele et al. 2013). Besides G&G, recent exceptions include revisions of *Loxodonta* (see below) and *Giraffa* (Brown et al. 2007) and the *Kobus leche* complex (Cotterill 2005, 2006); not all cryptic species of mammals are "small" and some are "medium" sized such as *Philantomba walteri* (Colyn et al. 2010). These burgeoning reports of overlooked mammal diversity exemplify how a New Age of Discovery challenges 21st century biology (Donoghue and Alverson 2000; Baker and Bradley 2006; Helgen 2011), and G&G represents long overdue progress to close many knowledge gaps, not least overlooked cryptic species of Bovidae.

Expanding on Groves (2013), Gippoliti & Groves (2012), and Gippoliti et al. (2013), we reject criticisms of G&G, which dismiss the PSC as error-prone and condemn a significant proportion of bovid species as artefacts of "taxonomic inflation". This view weakens accurate and precise knowledge of biodiversity, and in turn misleads conservation policy. We first (1) summarize the nature of real species (their ontology); (2) explain how errors mislead species discovery and characterization; and (3) respond to specific errors in H&A. We then (4) argue that extreme operationalism is the common cause of Type 2 and 3 errors in bovid taxonomy, which (5) collectively undermine the purported scientific credibility of the idea of "taxonomic inflation". These insights lead us to propose an explanation (6) for why an obsolete taxonomy of the Bovidae has persisted for decades.

EVOLUTIONARY SPECIES AND THE PHYLOGENETIC SPECIES CONCEPT

In consolidating phylogenetic systematics, a widely recognized outcome of the "Systematics Wars" through the late 20th century was its discarding of phenetics (Hull 1989; Felsenstein 2004). The maturation of phylogenetic systematics both motivated and was founded on a significant revolutionary breakthrough; this entailed the elucidation of the Individuality Thesis that continues to change comparative biology irrevocably. Contemporary comparative biologists, systematists especially, cannot ignore its central importance. It began with the argument that species are, ontologically speaking, individuals. Species are not classes (Ghiselin 1974). Formalized decades after 1859, the elucidation of the Individuality Thesis was distinctly belated, and its reshaping of science is by no means complete (Ghiselin 1997, 2005a,b,c). Its fundamental strengths in restructuring science can be gauged by the plight of converse attempts to refine an ontology (equally, an epistemology) for biology that ignores the Individuality Thesis. These all end up in the wilderness, appealing to essentialism and operationalism (Barbieri 2002; Ghiselin 1997, 2005a,b,c; Jenner & Wills 2008). The Individuality Thesis frames the revised bovid taxonomy. Explicit characterization of lineages replaces the classification of polytypic species, each comprising allopatric populations lumped together because they look morphologically similar. For example, the principal allopatric populations of Wildebeest (gnu) *Connachaetes*, Topi *Damaliscus*, and Hartebeest *Alcelaphus*, distributed across Africa's savannah grasslands were classified into respective polytypic species (Grubb 2005); they each comprise a species complex of divergent lineages: exemplified by *Connachaetes mearnsi* and *Damaliscus jimela* both endemic to the Serengeti-Mara ecosystem (G&G). The taxonomic revision compiled by G&G exemplifies how biology's New Age of Discovery demands universal standards for biodiversity characterization, not least for a universal species category, especially when we acknowledge the dimensions of cryptic biodiversity (Trontelj & Fišer 2009).

The fundamental impact of the Individuality Thesis on systematics is evident in how the tree-thinking paradigm replaced group-thinking (O'Hara 1988, 1997); tree-thinking frames the discovery and characterization of individuated populational lineages, with minimum error. The Individuality Thesis provides us with the conceptual scaffolding to discover these time-extended lineages, which qualify as evolutionary species. Contrary to Hausdorf (2011) and H&A, we acknowledge the consensus that has solved the species problem: the species category[2] comprises individuated populational lineages. A species is that segment of a populational lineage that has persisted between critical events of individuation; a unique evolutionary history has shaped its topology. Obviously, the

---

[2] The distinction between species - as individuals - and the species category - as a kind - is fundamental to systematics, especially given the considerable heterogeneity in the immense diversity of individuated lineages qualifying as members of the species category (De Queiroz 1999, 2007; Haveman 2013; Mayden 2013).

multitude of species we encounter differ in lineage age and relative divergence. These challenges of characterizing species are accommodated in the ontological scope of the Evolutionary Species Concept (ESC) – accounting for geographical variation, clines and sexual dimorphism; wherever this variation can be quantified using phenotypic and phylogeographical evidence to evaluate the contiguity, and history, of populations (Frost et al. 1992; Frost & Kluge 1994; Adams 1998, 2001; De Queiroz 1999, 2005, 2007; Brooks & McLennan 2002; Padial & de la Riva 2010; Naomi 2011; Norris & Hull 2011; Yeates et al. 2011; Wiley & Lieberman 2011; Haveman 2013; Mayden 2013; Pavlinov 2013).

The epistemological strengths of consilience (cf. Gould 2003) proved fundamental to solving the species problem; consilience classifies mutually reinforcing facets of evidence into a singular relationship that resolves the ontology of the species, the real products of evolutionary processes comprising the Tree of Life (sensu Cracraft 1989; Kluge 1990; Adams 2001; Brooks & McLennan 2002; Wiley & Lieberman 2011). Likewise, it invites those interested in biological conservation (which, we hope, means all practising biologists) to consider seriously what we aim to conserve; are these the spurious wide-ranging all-purpose “species” falling into the IUCN “least concern” category, or the evolutionary species, the units themselves, many of which are likely to be vulnerable or endangered?

The ability to discover and classify evolutionary species follows from consilient classification of actual evidence - morphological and molecular (Cotterill 2003a; Wiley & Lieberman 2011; Haveman 2013; Mayden 2013). As the battery of species discovery methods expands (Wiens 2007; Yeates et al. 2011; Camargo and Sites 2013), this understanding is enhanced and becomes all the more important. We call this the Consilient Solution, and apply it to characterize allopatric lineages of African mammals. The ESC frames operations employing the PSC to compare diagnostic characters to test whether or not candidate populations represent distinct lineages (Cotterill 2002, 2003a,b, 2005). In taxonomy, such comparisons are contingent on available museum material, and the available sample of populational variation comprises the hypodigms (Simpson 1940) for respective taxa underpinning respective taxonomic decisions, as is detailed in G&G. The hypodigms for

Damaliscus (Cotterill 2003a,b) and the *Kobus leche* complex (Cotterill 2005, 2006) exemplify how diagnosable characters test null hypotheses framed by the ESC. In contrast, proposals that promote delineation of species using thresholds of divergence in delimiting taxa (e.g. Baum 2007; Carstens et al. 2013) misrepresent a fundamental tenet of the Individuality Thesis. Seeking a nontrivial level of biologically relevant differentiation – prescribing divergence thresholds to try and define exclusive groups of organisms – can hide the more cryptic species from discovery; this distinction between delineation versus discovery is not semantic, because the misinterpretation perpetuates group-thinking. As expanded on below, group-thinking prescribes restrictive thresholds (only those populations that meet a threshold in lineage divergence qualify as species), and it also perpetuates the notions that subspecies are real entities.

Accurate, precise taxonomy organizes our knowledge about the real things causally involved in evolutionary processes (Ghiselin 2005c), and further promotes discoveries that consolidate and expand the web of knowledge. In contrast, without such outward flows of consensible[3] information, scattered facts and events remain insignificant until classified into consilient context (Ziman 1978; Cotterill & Foissner 2010). The veracity of classified taxa recovered in modern systematics reflects on the actual individuals causally involved in evolutionary processes; their classification is fundamental toward exploring Earth history, and our understanding expands as we incorporate more evidence of causal mechanisms (e.g. geological determinants of biogeographical patterns). So this broadening of knowledge interlinks sciences. This strength of systematics is too rarely acknowledged, especially in how it enables unforeseen discoveries (unanticipated patterns and mechanisms), where consensible knowledge is consolidated and refined across sciences. Invariably, ramifications of consensible knowledge aid and abet surprising, if not radical, discoveries; so it is difficult to overestimate where and how precise, accurate taxonomies of biodiversity will improve knowledge (Cotterill & Foissner

---

[3] In its broad usage, an item of consensible information minimizes obscurity and ambiguity in its meaning, which is critical if recipients are "either to give it whole-hearted assent or to offer well-founded objections." (Ziman 1978:6). In the context of biodiversity characterization, consensible knowledge meets this criterion of falsibility where real individuals (species and clades) are classified into an accurate, precise taxonomy; and enable new discoveries through consilient explorations of Earth history. Antithetical examples include fictitious polytypic species, superspecies, ecotypes and subspecies.

2010). Moreover, these unprecedented, far reaching demands underwrite critical standards to minimize taxonomic errors, which, unchecked, exact pernicious costs.

ERRORS IN THE DISCOVERY AND CHARACTERIZATION OF SPECIES

Science strives to minimize ambiguity in its communication – underscoring the important contribution by Adams (1998), who identified the three categories of error that undermine the precision and accuracy of taxonomy; Bernardo (2011) has endorsed their importance. Type 1 errors assign the rank of species to a population that is in reality part of a metapopulation. Type 2 errors erroneously lump together evolutionarily discrete lineages. Type 3 errors misclassify the relationships among real species by lumping them into phenetic clusters labelled superspecies or polytypic species (Adams 1998; Cotterill 2003a; Bernardo 2011; Mayden 2013, Fig. 1); this is especially where high levels of homoplasy and convergent evolution in bovid morphology have proved spectacularly misleading, when employed to classify populations on criteria of overall similarity (a phenetic methodology). These three categories of error are more specific than the alpha and beta distinction drawn by Padial et al. (2010). Under the framework of the Consilient Solution, comparisons of candidate populations aim to minimize classification errors. Type 2 (underestimates) and Type 3 (misclassifications) errors misrepresent biodiversity to generate taxonomies with undesirable impacts on scientific knowledge; these deficiencies in taxonomic accuracy and precision mislead conservation strategy (Cotterill 2003a,b, Fig 1). We agree with the undesirability of Type 1 errors in taxonomy (Kaiser et. al. 2013), including their potentially negative impacts on conservation policy and actions; and we describe below how the Consilient Solution minimizes Type 1 errors.

A most remarkable example of Type 3 errors in mammal taxonomy was revealed in the time-honoured original generic classification of the Tragelaphini (spiral-horned antelopes); G&G (pp 125-144) employed genetic evidence (Willows-Munro et al. 2005) to rectify these errors, and reclassify *Tragelaphus* into four distinct genera (see below). Moreover, just one polytypic species of "bushbuck" was previously recognized until mtDNA evidence unravelled Type 2 errors, revealing 23 cryptic allopatric lineages, tellingly individuated into respective ecoregions (Moodley & Bruford

2007; Moodley et al. 2009). Subject to exhaustive revision, G&G provisionally reclassified these lineages into a minimum of eight evolutionary species, representing two divergent, potentially paraphyletic *Tragelaphus scriptus* and *T. sylvaticus* clades. The challenges entailed in reclassifying these two clades (the collective "bushbucks") are by no means an isolated problem.

In summary, we concur with Adams (1998) that too many taxonomies still use species concepts that produce serious errors. The solution lies in progression "to using the discovery operations of the PSC to recover the 'largest integrating lineages' of the ESC (Frost and Kluge, 1994)." (Adams 1998:14). Type 2 and 3 errors have weakened bovid taxonomy for far too long, but are now yielding to the Consilient Solution, resolving over a century of misrepresentation (see below). Correcting this plethora of taxonomic errors is by no means complete, and G&G have taken the first steps; their evaluation of extant bovid diversity examined unprecedented hypodigms of museum material. Most importantly, this entailed the long overdue application of the methods of phylogenetic systematics.

SPECIFIC RESPONSES TO HELLER ET AL.

We now respond to specific criticisms directed at G&G by H&A:

1. "*…the excessive splitting of species is unconvincing in many cases*…[pg 490]

This statement does not justify why it is unconvincing, because it lacks not only analytical foundations, but alternative empirical evidence to reject classifications that G&G founded on analyses of hypodigms. Standard scientific practice revises a taxonomic classification with new and/or reanalysed evidence (museum collections and/or genomic sequence data). G&G employed such a hypothesis-testing methodology, evaluating sampled populations in the framework of the ESC. The Introduction to G&G and Groves (2013) describes how these designations were tested, within the limits of empirical evidence, including published revisions.

2. "*To systematically describe biodiversity, we need criteria to assess what level of character variability merits species designation. ….where primarily morphological data are available*

> *and a quantitative model linking character variability to speciation processes is lacking, it is vital that characters used for species delimitation are otherwise evaluated to ensure that the term species is reserved to describe a certain level of biologically meaningful diversity*" [pg 491]

This statement by H&A is correct, but only if based on a credible ontology of the species category. To test their reliability in species diagnosis, G&G evaluated specific characters against available hypodigms. This methodology tests the status of two or more populations against the null hypothesis that they are conspecific. The validity of taxonomic characters is the outcome of appraising intra-populational variation, categorised by age-specific variation and sexual dimorphism. Taxonomic resolution is nevertheless contingent on available samples – ideally the hypodigm includes all known museum specimens. Ultimately, these analyses should encompass representative phylogeographic sampling of geographical variation. In its collation of hypodigms, the sampling of G&G is unprecedented.

3. "*Although we support data driven species delimitation, we do not see the biological justification of using diagnosability as a proxy in itself without a conceptual or quantitative framework linking it to speciation processes*" [pg 491]

An unfortunate habit of hostile critics is a failure to actually read what the subjects of their denigration have written. In this case, H&A clearly failed to read the following:

> "In essence, a species is 'a lineage . . . evolving separately from others and with its own evolutionary role and tendencies' (Simpson 1961). This is true, in the sense that it says why species are important in the grand scheme of things (as the units of biodiversity), but it is not useful when it comes to actually identifying them and discriminating them from each other. *We are in need of an operational definition*. One of us has argued extensively (Groves 2001a,b, 2004) that what is known as the Phylogenetic Species Concept (PSC) fills this need." [Groves and Grubb 2011: 1 *italics added*].

Here we read the quintessence of the Consilient Solution; it defines the conceptual framework of the ESC that accommodates relevant processes of speciation. Most importantly, G&G justify their usage of diagnosability – employing the PSC to evaluate null hypotheses, and test whether or not populations qualify as evolutionary species. This epistemology is diametrically opposed to invoking the BSC or its surrogates, which include the Genealogical Species Concept (GSC) – a lineage defined by exclusive coalescence of its alleles (Baum 2007), and the Genetic Species Concept (GeSC) – a lineage with an independent evolutionary fate, in which accumulated genetic changes produce genetic isolation, so the species exists when the integrity of its gene pool is protected as a consequence of genetic differences in its genome (Bradley and Baker 2006). All these species criteria delimit populations as reproductively isolated sets or groups (Hausdorf 2011; Frankham et al. 2012; Zachos et al 2013a).

4. "*This serves as an illustration that PSC* [sic] *is unsuitable and causes taxonomic inflation.* [pg 490]….*It has been shown that such approaches lead to taxonomic inflation, as there is no lower limit to the resolution of the variability used to partition populations (Avise 2000; Isaac et al. 2004; Zachos et al. 2013)*" [pg 490]

Their criticism, like that in Zachos et al. (2013a,b) and Zachos & Lovari (2013), fails to acknowledge how population thinking underpins the Consilient Solution, especially where the PSC operationalizes the ESC (see Groves & Grubb 1911:1: "A species is the smallest population or aggregation of populations…"). Its application is underscored by Hennig's distinction (1966) between tokogeny and cladogenesis (Wiley & Lieberman 2011). Groves (2013) has already questioned how Avise (2000), Isaac et al. (2004) and Zachos et al. (2013a) justify the impression that there is no lower limit to the partitioning of populations! These three cited papers lack any direct clues. Beyond arm-waving, all fail to appreciate how characters are evaluated in samples of populations in a population-thinking framework (cf Wiley and Lieberman 2011). We reiterate that quantification of geographical variation – and testing for clines - is a tenet of taxonomic practice. This discovery process identifies species informed by analyses of the hypodigm of museum specimens available for compared taxa.

Where the hypodigm is too limited, we argue, as advocated by Brooks and McLennan (2002), that insufficient evidence cannot overwrite the Precautionary Principle in conservation decisions.

Characterization of the eleven allopatric species of klipspringers, *Oreotragus* spp., exemplifies how this research strategy classified a species complex of small antelopes whose distribution is discontinuous, with each species confined to an island of rocky habitat. Diagnostic characters compared in available museum material of the vicariant populations reveal geographically isolated lineages with divergent evolutionary histories, and behavioural studies may well be relevant to an understanding of these (G&G pp. 275-279). Moreover, a preliminary study revealed highly significant phylogeographical structure among ten of the sampled lineages, but did not include the West African *O. porteousi* (Le Roex 2008). It would be hard to explain why *Oreotragus* speciation is not similar to that of rupicolous Caprini (see G&G) as characteristic of habitat specialists. Future research is challenged to test G&G with more thorough geographical sampling of klipspringers and associated endemics of rocky landscapes.

5. "*By basing the bovid section on only one primary source, HMW have disregarded a vast number of experts in the field (including the current assessment of the bovid species list by the IUCN)…. We urge the IUCN to consider other opinions on bovid taxonomy before making any changes to their species list.*" [pg 491]

Here we extend our response to Criticism 2. It is unclear who these "vast number of experts in the field" might be, or indeed what they are experts in. Certainly, we know of few who have studied the available material (in museum collections); on the other hand we do know of vast numbers who have contributed their own data sets while simply accepting the most recent available taxonomic statements (usually dating from the middle of the 20th century), a reasonable position considering the absence of original material on which to base revisions of their own. G&G, on the other hand, studied original material, and so are well qualified to offer new taxonomic revisions.

Revealing phylogeographical studies have also contributed materially to our understanding of interrelationships among African bovids (e.g. Lorenzen et al. 2006, 2007, 2008); and where available G&G used their contributions and findings in conjunction with their own museum-based datasets to elucidate evolutionary species. It is precisely these new analyses that inform revision of previous bovid classifications.

As for the IUCN's qualification as a body of "experts in the field", it is pertinent to note that IUCN's African Elephant and Rhino Specialist Group has yet to come to terms with the fact that recognized "experts in the field", who have indeed studied the available material, recognize two species of *Loxodonta* (Grubb et al. 2000; Rohland et al. 2010; Shetty and Vidya 2011), while its enduring subspecific classification of *Diceros bicornis* is totally spurious, lacking any material evidence (Rookmaaker 2011).

6. "*traits are not evaluated but are used as long as they are diagnosable…ecotypes or subspecies have been raised to the level of full species based not on new data, but solely on a change in the species concept used.*" [pg 490]

This claim is simply wrong. To qualify our preceding responses, H&A reveal a failure to appreciate how G&G analysed unprecedented hypodigms with the explicit aim of evaluating characters: an intensive investment in data collection from the world's collections of extant Bovidae (let alone other Mammalia, see below). In short, the taxonomy of G&G has set a new threshold, by analysing the breadth and scope of series of specimens in the world's museums. The reclassification is underscored by *new data*, analysed in the theoretical framework of phylogenetic systematics. Groves (2001a) described this methodology in detail, and it underscores strengths of the Consilient Solution. Dismissal of this investment reveals poor appreciation of taxonomic methodology, despite it being well established and described (e.g. Winston 1999; Wiley & Leiberman 2011). To reiterate the Preface of G&G:

> "We do not intend to present this book as a finished proposition. Time and again, we remark that "more research is necessary"; we want, above all, to stimulate more taxonomic research on ungulates. In some cases we have been able to break new ground, and we hope that these examples will be examined by colleagues and, if found acceptable, used as templates for other studies." [Groves and Grubb 2011: vii].

Attempts to retain an error-ridden bovid taxonomy raise poignant questions, not least in how the paradox of overlooked cryptic diversity contrasts against the reticence of taxonomic conservatives. It calls for scrutiny of the failures of the popular species concepts that cause Type 2 and 3 taxonomic errors.

OPERATIONALISM: THE CRITERIA OF REPRODUCTIVE ISOLATION AND RECIPROCAL MONOPHYLY FAIL SPECIES DISCOVERY

Contrary to the Consilient Solution, the BSC and equally the GSC and GeSC prescribe a certain degree of distinctiveness – a delimitation – if a population is to qualify for species status (see Pastorini et al. 2001; Bradley & Baker 2001; Baker & Bradley 2006; Baum 2007). In so doing they fail to detect cryptic species (Type 2 errors), and/or misclassify populations (Type 3 errors). Yet, as diagnosed by de Queiroz (1999, 2007), their popularity (and ironically, their epistemological weaknesses) lies in three interleaved misconceptions in taxonomic thought and practice that reappear repeatedly throughout the voluminous species debate: (1) the mistake that one among many secondary species criteria qualifies as the universal concept of the species category; (2) an inflated faith in one's favourite criterion or criteria results in overestimates of its epistemic capabilities and scope; such that (3) it is under appreciated that some degree of epistemic parochialism afflicts every secondary species criterion, including the PSC. The complex attributes of "specieshood" explain why no species criterion alone qualifies as a universal discovery method.

Reproductive isolation has been (and indeed still is by some) ranked supreme as the *sine qua non* among criteria distinguishing a population as a species. It is really a proxy, if not a caricature, for suspected genetic discontinuity between closely related lineages (see Bernardo 2011). Beyond practicable challenges to obtain scientific evidence to test the criterion, detailed arguments explain why reproductive isolation fails as the singular determinant of specieshood (Cotterill 2003a; Padial & de la Riva 2010; Norris & Hull 2011; Pavlinov 2013). Nevertheless, the notion is resurrected in the species literature: pertinently in the GSC, GeSC and DFSC (see below). Like the BSC itself, these all impose a subjective cut off; a population only qualifies as a "species" above an arbitrary yardarm of genetic divergence. An equally common misconception occurs in applying genomic evidence to define the ontology of the species category (e.g. Baum 2009) because the topology of the singular species tree sets inescapable constraints: gene trees can only approximate the topology of the species tree (Wiley & Lieberman 2011).

The Differential Fitness Species Concept (DFSC), cited as a principal authority in critiques of G&G (Zachos & Lovari 2013; see also Frankham et al. 2012, further cited by H&A), strongly advocates the population fitness criterion to evaluate whether an allopatric populations qualifies as a conservation target. The DFSC defines a species as a group of individuals reciprocally characterized by features that would have negative fitness effects in other groups and cannot be regularly exchanged between groups upon contact (Hausdorf 2011); but it suffers from the same weaknesses as the BSC, GSC and GeSC (not least operationalism), and the DFSC is crippled by its attempt to avoid using the population to define the ontology of the species category.

Errors in bovid classification reveal how all these species criteria overlook important categories of species, not least morphologically similar lineages (i.e. cryptic species) that have experienced episodes of introgression and/or retain ancestral polymorphisms. Adherence to reproductive isolation, reciprocal monophyly or population fitness as preeminent criteria for specieshood *invariably* overlooks lineages represented by allopatric populations (cf Nadler 2002; Cotterill 2003a, 2006; Norris and Hull 2011).

Populations that fail to meet strictures of a criterion (only accepting purported species above its threshold) are relegated to conspecific status, and frequently classified as subspecies or Evolutionary Significant Units (ESU). Whether or not explicitly defined as subgroups within a polytypic species, the belief that subspecies and ecotypes have an ontological reality continues to persist (not least under the GeSC) without asking the question: ‘what justifies membership of a distinct ontological category, distinct from that occupied by species?’ An allied mistake by Bennett (2013) similarly misunderstands the Individuality Thesis - arguing that species only exist in the present but that their antecedent lineages are entirely different entities.

The Consilient Solution resolves this subjectivity. It overcomes challenges encountered in classifying speciated lineages of different ages; each lineage has a heterogeneous history shaped through its unique context of tokogenic descent. In contrast, if ecotypes or subspecies do indeed exist as autonomous lineages – thus comprising a recognizable category in the economy of nature – then how do they differ from those lineages individuated into species? Their usage in any convenience category does not preclude their failure to fit them into classifications of individuated phyla. This question reveals why notions of subspecific entities do not correspond to real entities (Cotterill 2003a,b). Some biologists might well wish the nature of biodiversity shaped by Earth history does not present such mordant challenges.

We agree with Padial & de la Riva (2010) that insistence on operationalism motivates the futile search for the "golden species concept". Despite the reality that each species discovery method has finite constraints (Adams 1998, 2001; De Queiroz 1999, 2005, 2007; Haveman 2013; Mayden 2013), ignorance or abuse of these constraints continues to inject problems of extreme operationalism into taxonomy (Hull 1968; Johnson 1970; Frost & Kluge 1994; Wiley & Lieberman 2011). Unjustifiable claims for the BSC, DFSC, GeSC and GSC share the same subjective weakness that: "*...the operational point of view depends for what success it does have on the very element of science which it is designed to eliminate*. Operation[al]ism was intended as a cathartic to purge physics of all non-empirical wastes, but it proved to be so strong that the viscera were eliminated as well." (D.L. Hull 1968:440 *italics his*). Unfortunately, it still undermines comparative biology, because too few seem cognisant of how modern systematics was shaped by classic rebuttals of operationalism (Hull 1968; Johnson 1970).

In summary, notwithstanding the inability of the criterion of reproductive isolation to define the quintessence of the species category, its popularity propagates mistaken beliefs: only reproductively isolated populations qualify as species, and/or sister populations must qualify against criteria of genetic divergence to be species. Equally, the lack of practicable evidence for reproductive isolation leads to unsubstantiated taxonomic decisions. Leaps of faith replace direct tests. Thus, a high incidence of Type 2 and 3 errors still undermines ungulate taxonomy, especially where the test for species membership invokes subjective inferences of overall similarity. Such interpretations of biological patterns perpetuate the philosophy and methods of phenetics, discredited decades back (Brooks & McLennan 2002; Wiley & Lieberman 2011).

THE SCIENTIFIC POVERTY OF TAXONOMIC CONSERVATISM

We now scrutinize the credentials of the argument that “taxonomic inflation” has pejorative impacts (promoted by Isaac et al. 2004), especially given its high literature profile (with attendant bibiliometric inflation). Criticisms of G&G argued that inflated species counts result from elevating subspecies to species status in the absence of revision (!) but they instead endorse “expert decisions” to inform conservation policy. Will political decisions by expert committees replace real taxonomy? Carried to the extreme, taxonomic conservatism suppresses the quest for new evidence. What superior knowledge of biodiversity shapes this brave new world, freed of phylogenetic systematics? Does the idea of minimizing “taxonomic inflation” possess any credibility to justify suppressing precise, accurate knowledge of biodiversity?

Condemning perceived “taxonomic inflation” in the long overdue reclassification of the Bovidae typifies the response of quasi-taxonomic conservatives (e.g. Collar 2007; Rosenberger 2012) to progressive taxonomic revisions (e.g. Groves 2001a; Navarro-Sigüenza & Peterson 2004; Peterson 2006). Remarkably, taxonomic conservatism is touted as an important principle of conservation policy, despite disquieting evidence that its taxonomic errors exact negative impacts on conservation. Accelerating discoveries of cryptic diversity unnerve conservative traditions in taxonomy and conservation biology, as testified in critiques of the very concept of cryptic species (Bernardo 2011). Cryptic species still awaiting discovery are either overlooked, or dismissed as “subspecies”. How many more will join the ranks of the extinct – not only bovids such as Roberts’ lechwe *Kobus robertsi*, but also Niger Delta pygmy hippopotamus *Choeropsis heslopi*, Western black rhinoceros *Diceros longipes* and Northern white rhinoceros *Ceratotherium cottoni* (Gippoliti et al. 2013)?

Sangster (2009) evaluated the role of empirical evidence in taxonomic revisions, based on conclusions from a meticulous analysis of the characterization of new avian species recognized since

1950; of 747 proposals, new taxonomic data supported 84.6% of newly recognized species. Moreover, 63.4% of these newly recognized species were not based exclusively on PSC-based criteria (Sangster 2009). Alongside benefits of new technologies and intensive researcher effort, Padial and de la Riva (2006) concluded that increases in newly recognized species reflect the long-delayed adoption of an evolutionary classification shaped by phylogenetic systematics.

Critical reading of Isaac et al. (2004) reveals that two axioms of taxonomy – both obsolete - underwrite the belief that a taxonomy can be “inflated” by deleterious Type 1 errors. One sets reproductive isolation as the criterion that qualifies a population as a species; the second believes that a trinomial taxonomy yields a precise and accurate classification of biodiversity (in reality Type 2 and 3 errors hamstring trinomial classifications). Both highlight the ontological distinction between classifying non-historical groups versus individuated lineages. In preserving deficiencies of the obsolete BSC and its proxies, the belief that taxonomic stability is a paramount requirement for conservation policy countermands strengths of the research programme of phylogenetic systematics, and discards the Consilient Solution as the optimal scientific procedure to discover and characterize organismal biodiversity. Is purported morpho-similarity of populations the superior method over one that diagnoses individuated lineages?

It is further unclear how taxonomic conservatism can coexist with increasing usage of phylogenetic distinctiveness to inform conservation planning. Maximizing precision in species characterization confers a fundamental strength on the spatial resolution of biodiversity mapping, and quantifies the geospatial attributes of complementarity, representation and uniqueness (King 2009; Collen et al. 2011; Rosauer & Mooers 2013), and this is where evolutionary lineages reveal hotspots of endemism and vibrant speciation. In this respect, G&G recovered indicator species that flag the significance of several biodiversity hotspots across Africa (e.g. Serengeti-Mara, Luangwa Valley, western Chad). Molecular dating of speciation events in all these bovids will further refine our knowledge of these conservation targets.

In contrast, a “stable taxonomy” obscures attempts to reconstruct Earth history. Error-ridden taxonomies confer far reaching costs where real individual species (populational lineages) are misclassified into artificial groups. This weakens the ability to map biodiversity in explicit spatio-temporal detail, and exemplifies how taxonomic errors curtail consensibility to mislead and even prevent communication of knowledge, and its derived applications in science. Ironically, these deficiencies undermine the self-proclaimed goal of taxonomic conservatism – to facilitate “universal communication” in biology! The profound distinction between the old versus modern systematics is the ability to foster discoveries of biodiversity that expand, and simultaneously refine, knowledge across science.

Equally, scientific propositions must be testable. We remind Frankham et al. (2012), Heller et al. (2013), Zachos et al. (2013a,b) and Zachos & Lovari (2013) that the singular advantage of the PSC in operationalizing the ESC is the testability of its propositions; assess the available evidence and amass further evidence to refute the multi-species hypothesis of klipspringers, as for any other organisms. This arm-waving about “taxonomic inflation” is founded on naive operationalism and worse (Gippoliti et al. 2013).

The idea of “taxonomic inflation” undermines biology. We concur with Bernardo (2011) who concluded that when one acknowledges the realities of characterizing biodiversity with minimal error, the mandate to minimize “taxonomic inflation” lacks scientific credibility. It repeats the eclipse of evolutionary history from comparative biology (Brooks & McLennan 2002), and ignoring tree-thinking will set science back by decades; at worst, classifications shaped by political demands subjugate discoveries of real species. Yet these arguments raise important questions; why subjugate robust science (i.e. the Consilient Solution), and maintain an obsolete classification of large mammals? What causes the reality of cryptic diversity to be widely misconstrued, and worse, suppressed?

REMARKABLE PERSISTANCE OF A FOLK TAXONOMY

Prior to the revision by G&G, the taxonomy of the Bovidae stabilized after Ellerman et al. (1953) with little change by Ansell (1972), nor even by Grubb (2005), who saw his responsibility as being to reflect the most recent taxonomic revisions. In short, bovid taxonomy lapsed into a state of torpor: highlighting the desperate need for updating (P. Grubb pers. comm.). We suggest the reasons lie in ambiguous relationships between the species concepts and empirical evidence applied to classify these large mammals. Persistence of trinomials is symptomatic of this torpor, because there was scarcely any critical reappraisal of the status of the diversity they attempt to classify.

Few, if any, of the inaugural classifications of the Bovidae stated their underlying taxonomic philosophy; nevertheless it is clear that they used a morphological species concept (MSC). This is exemplified in treatments of allopatric populations of antelopes, which applied observations of perceived overall similarity as the criterion to recognize polytypic species; this lumping into morphospecies is evident in Ellerman et al. (1953) even though they endorsed the polytypic BSC. It is the unambiguous morphotypes that qualified as species, almost invariably inclusive of two or more subspecies. The BSC was cited in the belief that a lack of reproductive isolation (suspected not tested) explained geographically widespread morphotypes. In reality, phenetics substituted for the BSC. Evaluation of these populations had to await analyses by G&G, comparing hypodigms that had taken several decades to collate from the respective specimens scattered amongst the world's museums. Thus, prior to application of the Consilient Solution, taxonomy of the Bovidae relied on a subjective overall similarity to delimit a "species" and its apparent conspecific populations.

To date, this explanation does not appear to have received formal recognition to explain the taxonomic errors that have misclassified many species complexes of bovids for far too long. It can be formally stated as the Phenetic Hypothesis. A complex of cryptic species of large mammals are classified subjectively into a single morphospecies, where the high degree of apparent morphological similarity between its allopatric populations was invoked as evidence for how rampant trans-continental gene flow could shape a widespread morphotype. Tacit belief in this apparently ubiquitous pattern explains how geographical isolates have *actually* been classified as subspecies or ecotypes. Invoking the currency of the polytypic BSC, geographical representatives of the morphospecies are simply labelled as variants of the familiar typological model. Widespread subscription to the Phenetic hypothesis – rarely if ever articulated – maintains a persistent dogma. This has persistently shaped large mammal classification and its usage; moreover, criticisms of G&G implicitly invoke the Phenetic hypothesis (e.g. that there is only one species of "klipspringer"). In practice, the identification of species boundaries has continued to rely on phenetic evidence (subjective similarity) as the proxy to invoke the existence of reproductive isolation (Corbet 1997; Gippoliti & Groves 2012; Gippoliti et al. 2013). For example, the combined evidence of allopatric distributions and overall similarity of topis, korrigum and tsessebes had justified classifying them all as subspecies of *Damaliscus lunatus* (Cotterill 2003a,b). On phenetic criteria, all populations of klipspringers (*Oreotragus oreotragus*), wildebeests (*Connochaetes taurinus*) (albeit distinct from *C. gnou*, which is, however, quite capable of introgression with *C. taurinus*) and hartebeests (*Alcelaphus buselaphus*) comprise in each case a single polytypic "species", simply because they look somewhat similar (Zachos et al. 2013a). A proxy of the many pervasive errors in bovid classification is obtained by comparing the taxonomy of G&G against the distribution maps in Kingdon & Hoffman (2013), mostly prepared before the publication of G&G. To revisit our earlier example of Type 3 errors in the Tragelaphini, the notion that "Lesser" and "Greater" kudu are sister "species" illustrates how the Phenetic Hypothesis fosters remarkable errors. G&G reclassify these lineages into distinct genera as the *Ammelaphus imberbis* and *Strepsiceros strepsiceros* species complexes, respectively.

This situation raises the equally important question - why was the reappraisal of ungulate diversity by G&G so delayed? Moreover, why does it incite such antagonism? A paradoxical naivety, if not ignorance, of the persistent dogma underlies neglect of large mammal taxonomy:

> "In most biota, ungulates are among the most visible fauna on the landscape. In national parks they are readily spotted and much admired by visitors, and it is easy to assume that because these animals are so familiar, everything is known about them, especially how many species there are. Such an assumption would be wrong. Mammalogists expect diversity among small mammals, and seek it out, but they have grown used to accepting that larger ones, because they are thought to be highly mobile (and indeed they may be), are bound to be much less

> diverse and thus will yield up less information about ecosystems, biogeography, and so on." [Groves and Grubb 2011: vii].

Furthermore, a first-order observation reveals that recognized species of Bovidae (Ansell 1972; Grubb 2005) are matched with few exceptions by the local names for extant antelopes in a maximum total of 46 indigenous African languages sampled. This comprises one language for Botswana (Smithers 1971) and two for Zimbabwe (Kenmuir & Williams 1975), and local names for respective species vary between 10-28 languages across Kenya, Tanzania and Uganda (Kingdon 1982) and 4-15 in Zambia (Ansell 1978); so the totals of local names differ between species, contingent on distributions of antelope populations relative to ethnic boundaries.

Such typological congruence raises interesting questions about the origins of scientific classification, especially where Taxonomic Conservatives do not acknowledge that large mammals classifications, which they seek to preserve, have scarcely advanced in over a century since first monographed. This state of torpor seems to be bound up in the Phenetic Hypothesis. We attribute this typological congruence between vernacular names and the obsolete scientific taxonomy of the Bovidae to the persistence of a folk taxonomy (cf Atran 1990; Yoon 2011). This folk taxonomy was likely invaluable to local hunter-gatherers, and may indeed supply contemporary society with sufficient, albeit superficial knowledge (such as field guides). Prior to G&G, we conclude the BSC was used primarily as a convenient moniker to lump allopatric populations of large mammals into respective morphospecies (comprising a high proportion of imaginary taxa).

Remarkably, a vociferous lobby continues to invoke subjective morphological resemblance to delimit, and especially to lump, individuated lineages of bovids into fictitious taxa, at the cost of ignoring real species. The Phenetic Hypothesis provides a plausible explanation for this predicament in mammalogy that undermines the consilience of comparative biology. Defended by no shortage of prominent biologists, the time-honoured bovid classification is founded on what amounts to little more than untested myths; some have persisted for decades. They could indeed be ancient. This quaint typological classification of large mammal diversity continues to dominate both mammalogy and conservation biology. Unfortunately, it maintains a plethora of Type 2 and 3 errors. Will subscription to a phenetic taxonomy (which has remained largely untested for decades) continue to underestimate and misclassify knowledge of the real diversity of the Bovidae into the 21st century?

IMPROVED THEORY OR EVIDENCE?

In science, the way forward to improve biodiversity knowledge, and resolve uncertainty, is to replace obsolete concepts, theory and methods, and/or improve empirical evidence. These are the axioms that guide and shape taxonomic revision. Critiques of G&G have failed to present any credible alternative to replace its theoretical foundations. This situation recalls the thoughtful review of Ellerman et al. (1953) that: "Time, additional specimens, and more comparisons, will test their classification" (Handley 1954:461). The urgent priority is to resolve glaring knowledge gaps, and especially sample populations of bovids poorly represented in collections. Persisting neglect of museum focused research on large mammals further compounds these collecting gaps. An expanding century of neglect of large mammal taxonomy also stands as harsh testimony to impacts of the Taxonomic Impediment (as defined by Hoagland 1996) on science and conservation.

The logical solution lies in reviving taxonomy, in which there has been too little investment for far too long. No shortcut suffices. This argument for increased investment in primary taxonomy is strengthened, when we recognize how order-of-magnitude increases in sample sizes in recent revisions discovered several previously unrecognized species; this is a positive outcome of comprehensive revisions sampling collections that were previously overlooked, neglected and/or studied in isolation (Gippoliti & Groves 2012). Not least, unprecedented sampling of existing specimens underpins the timely revision published in G&G: over a collective eight decades of researching museum collections, their research entailed repeated visits by both authors to work out material that by its very nature is nearly impossible to loan. This testifies to the remarkable dedication of Peter Grubb (1942-2006), who sadly did not live to see publication of the greater portion of a lifetime of work; and we highlight the rediscovery of the long-forgotten Somali warthog in his revision of *Phacocoerus* (d'Huart & Grubb 2001; Grubb & d'Huart 2010); reinstatement of *P.*

delamerei (whose close ally, *P. aethiopicus,* was shown to be historically extinct in South Africa) ranks as a major advance in African mammalogy.

G&G is not and was explicitly never intended to be the final word, especially given the gaps in museum representation. The state of knowledge of ungulate taxonomy underscores the urgency to catalyse taxonomic revision, yet the plethora of taxonomic problems reveals that there are far too few taxonomists to carry out intensive revisions. We reiterate the call by G&G for committed support to reinvigorate this research. Unfortunately, too few biologists responded to pleas (Harrison Matthews 1954; Ansell 1958a,b) to where possible exploit opportunities to preserve museum specimens from bovid populations before their extirpation across Africa, and so improve museum collections; indeed, reactivating and fulfilling this quest will likely identify, and mitigate extirpation of restricted-range taxa - especially cryptic species. Deficient knowledge calls for long overdue investment in museum collections, and allied genomic research; nothing less than unprecedented investment in primary, idiographic research in natural history will do (Brooks & McLennan 2002; Cotterill & Foissner 2010). Elucidating the real diversity of the Bovidae requires much more work, in the field, museum and laboratory. Integrative taxonomy is challenged to collate and analyse key morphological and genetic evidence at biogeographical scales sufficiently fine to reappraise geographical variation, and seek out undiscovered cryptic species. It already appears too late for many victims of taxonomic errors; some cryptic species of African mammals classified as "subspecies" are destined to remain unknown, but pertinent voucher specimens, if preserved, will continue to reveal where taxonomic conservatism failed. The new age of discovery is realizing remarkable opportunities in genomics to genotype museum specimens (Helgen 2011; Guschanski et al. 2013), and it underscores the fundamental roles and values of tentelic[4] evidence in science (Cotterill 1999, 2003a).

CONCLUSIONS

---

[4] 'Tentelic' means ''holding together a web'', describing how a preserved specimen anchors consensible information. Specimens have a core epistemological role in science as tentelic tokens of verifiable information; the veracity of a particular item of knowledge causally relates to the existence and provenance of voucher specimens, and their other affinities with the real world. Specimen preservation enables independent checks of these attributes. Specimens preserve knowledge. These curated materials of reputable fidelity and integrity will be available to future technologies yet to be developed (Cotterill & Foissner 2010).

> “The notion that classification is based on similarity is an epistemological myth, and one that could only be corrected by ontological considerations. It was evolutionary theory, with its historical ontology, that led Darwin to reject that notion altogether and insist that classification be strictly genealogical.” (M.T. Ghiselin 2005c:168)

The Phenetic Hypothesis is mythology. Belief in polytypic species of bovids faces a dilemma; systematics discarded phenetics long ago. If subspecies and polytypic species are real, then how does one characterize them objectively? A pervasive belief in their ontological reality has weakened comparative biology for far too long. The Individuality Thesis structures the complementary threads of evidence explaining why there are *at least* twice as many species of Bovidae, over and above those traditionally recognized. G&G has undertaken the first comprehensive evaluation of Bovidae diversity; the empirical evidence is unprecedented in hypodigms compared. A significant contribution to mammalogy, it implements modern theory and methods of systematics to minimize taxonomic errors; the ontological and epistemological linkages that empower this approach shape the Consilient Solution, and provide straightforward guidelines to discover evolutionary species.

One might expect 21st-century scientists, especially conservation biologists, to put this long overdue revision of the ungulates to work. Instead, rejecting G&G, defenders of a folk taxonomy preserve taxonomic errors, and so weaken conservation biology, especially its capacity for scientific decisions. This is doubly counterproductive, given how the realities of bovid taxonomy present austere challenges, poorly appreciated in conservation policy. We agree that the notion of “taxonomic inflation” is a political reaction to science moving beyond non-historical characterizations of biodiversity. Subjugating progress toward robust knowledge, taxonomic conservatism treats the taxonomy as an artefact, subservient to priorities of information management. The pursuit of taxonomic stability employs weak science, in the obsession to purge “inflated” taxonomies. Arguments invoking “taxonomic inflation” perpetuate the eclipse of evolutionary history from biology, to overlook cryptic diversity, and detract from taxonomic accuracy and precision. Although reproductive isolation of bovid “species” has been inferred, in practice the phenetic criterion of overall similarity delimits polytypic species, in decisions invariably entailing pure guesswork. The species discovery operations that inform objective biodiversity characterization cannot use the BSC, MSC, GeSC, GSC nor DFSC; dismissals of the PSC cannot provide an alternative epistemology that minimizes errors in species discovery.

Scientific tenets of the Individuality Thesis appear conspicuously underrepresented, if not ignored, in parts of mammalogy and conservation biology. This is strange. Catalysed by cladistics, tree thinking was adopted rapidly through the 1980s, and continues to empower increasingly powerful advances, abetting no end of surprising discoveries of biodiversity. Underpinned by the Individuality Thesis, systematic biology has occupied the fulcrum of this revolution, propagating progress toward the interdisciplinary synthesis of knowledge of biodiversity and Earth history. Growth of tree-thinking continues to overturn a plethora of misclassifications of Life's diversity; these correct many taxonomic errors grounded in mythology (cf. Nee 2005), not least the Great Chain of Being.

Nevertheless, future generations will rightly be bemused at why it took so long before phylogenetic systematics began to classify biodiversity in a whole new light, and revolutionized comparative biology. Future pedagogy will illustrate this history with a bizarre example from the biodiversity crisis; its explanation of the protracted delay in realizing the Darwinian Revolution will recount how badly phenetics misled biology. Notwithstanding reconstructions of the Tree of Life, group-thinking persisted in the shape of pheneticism into the 21st century - in cul-de-sacs of self-deception that had pernicious impacts. Future textbooks will reveal that although a folk taxonomy of the large mammals, in all respects prehistoric, served our hominin ancestors perfectly well, it deceived zoologists for centuries after the Scientific Enlightenment. Obsolete ideas about species, subspecies and operationalism weakened theory, so suppression of "taxonomic inflation" suppressed knowledge of cryptic diversity. Bad taxonomy misinformed conservation biology. Overlooked and unrecognized species of ungulates were hardest hit. As tropical wilderness dwindled through the Anthropocene, a deficient taxonomy aided and abetted megafaunal extinctions.

Today, many years after 1859, the real evolutionary diversity of large mammals is finally being revealed. In the age of genomics, with tree-thinking as its keystone, phylogenetic systematics impels the revitalized Natural History. It is opening up and opening out to reshape the entirety of biology; this unfurling revolution ratchets across each life science - irrevocably - as we reconcile with the realities of the Individuality Thesis.

ACKNOWLEDGEMENTS

Cotterill has been supported by the NRF, !Khure, InkabayeAfrika, the ERANDA Foundation, the Claude Leon Foundation, the Bay Foundation, and the Josephine Bay Paul and C Michael Paul Foundations, New York City. Taylor has been funded by the NRF and the University of Venda. This is AEON Publication No. 0120.

REFERENCES

Adams B.J. 1998. Species concepts and the evolutionary paradigm in modern nematology. J. Nematol. 30:1-21.

Adams B.J. 2001. The species delimitation uncertainty principle. J. Nematol. 33:153-160.

Ansell W.F.H. 1958a. The need for better study collections of African ungulates. Mammalia 22:338-347.

Ansell W.F.H. 1958b. On the study of African Mammalia. J. Mammal. 39:577-581.

Ansell W.F.H. 1972. Order Artiodactyla. In: (eds) J. A. J. Meester and H. W. Setzer. The Mammals of Africa: an Identification Manual. Washington DC: Smithsonian Institution Press,. p. 1-84.

Ansell W.F.H. 1978. The Mammals of Zambia. Chilanga: Parks and Wildlife Service.

Atran S. 1990. Towards an Anthropology of Science: Cognitive Foundations of Natural History. Cambridge: Cambridge University Press.

Avise J.C. 2000. Cladists in wonderland. Review of: “Species Concepts and Phylogenetic Theory” by Quentin D. Wheeler; Rudolf Meier. Evolution 54:1828–1832.

Barbieri M. 2002. The Organic Codes: An Introduction to Semantic Biology. Cambridge: Cambridge University Press.

Baker R.J., Bradley R.D. 2006. Speciation in mammals and the Genetic Species Concept. J. Mammal. 87:643–662.

Baum D.A. 2009. Species as ranked taxa. Syst. Biol. 58:74–86.

Bennett K.D. 2013. Is the number of species on Earth increasing or decreasing? Time, chaos and the origin of species. Palaeontology doi: 10.1111/pala.12057

Bernardo J. 2011. A critical appraisal of the meaning and diagnosability of cryptic evolutionary diversity, and its implications for conservation in the face of climate change. In: Hodkinson TR, Jones MB, Waldren S, Parnell JAN (eds.) Climate Change, Ecology and Systematics. Cambridge University Press: The Systematics Association. p. 380-438.

Bradley R.D., Baker R.J. 2001. A test of the genetic species concept: cytochrome-b sequences and mammals. J. Mammal. 82: 960-973.

Brooks D.R., McLennan D.A. 2002. The Nature of Diversity: An evolutionary voyage of discovery. Chicago: The University of Chicago Press.

Brown D.M., Brenneman R.A., Koepfli K.-P., Míla B., Georgiadis N.J., Louis E.L., Grether G.F., Jacobs D.K., Wayne R.K. 2007. Extensive population genetic structure in the giraffe. BMC Biol. 5: 57

Camargo A., Sites J.J. 2013. Species delimitation : a decade after the renaissance. In: The Species Problem - Ongoing Issues. I. Ya. Pavlinov (Ed.), InTech. p. 225-247.

Carstens B.C., Pelletier T.A., Reid N.M. Satler J.D. 2013. How to fail at species delimitation. Mol. Ecol. doi: 10.1111/mec.12413

Collar N. 2007. Phillipine bird taxonomy and conservation, a commentary on Peterson (2006). Bird Cons. Intern. 17:103-113.

Collen B., Turvey S.T., Waterman C., Meredith H.M.R., Kuhn T.S., Baillie J.E.M., Isaac N.J.B., 2011. Investing in evolutionary history: implementing a phylogenetic approach for mammal conservation. Phil. Trans. R. Soc. B 366:2611–2622.

Colyn M., Hulselmans J., Sonet G., Oudé P., De Winter J., Natta A., Tamás Nagy Z., Verheyen E.K. 2010. Discovery of a new duiker species (Bovidae: Cephalophinae) from the Dahomey Gap, West Africa. Zootaxa 2637:1-30.

Corbet G.B. 1997. The species in mammals. In: M.F. Claridge, H.A Dawah & M.R. Wilson (eds). Species: the Units of Biodiversity. London: Chapman & Hall. p. 341-356.

Cotterill F.P.D. 1999. Toward exorcism of the ghost of W. T. Thistleton-Dyer: a comment on "overduplication" and the scientific properties, uses and values of natural science specimens. Taxon 48:35-39.

Cotterill F.P.D. 2002. A new species of horseshoe bat (Microchiroptera: Rhinolophidae) from south-central Africa: with comments on its affinities and evolution, and the characterization of rhinolophid species. J. Zool., Lond. 256:165-179.

Cotterill F.P.D. 2003a. Species concepts and the real diversity of antelopes. In: A. Plowman. Proceedings of the Ecology and Conservation of Mini-antelope: An International Symposium on Duiker and Dwarf Antelope in Africa. Füürth: Filander Verlag. p. 59-118.

Cotterill F.P.D. 2003b. Insights into the taxonomy of tsessebe antelopes, *Damaliscus lunatus* (Bovidae: Alcelaphini) in south-central Africa: with the description of a new evolutionary species. Durb. Mus. Novit. 28:11-30.

Cotterill F.P.D. 2005. The Upemba lechwe *Kobus anselli*: an antelope new to science emphasizes the conservation importance of Katanga, Democratic Republic of Congo. J. Zool., Lond. 265: 113-132.

Cotterill F.P.D. 2006. The Evolutionary History and Taxonomy of the *Kobus leche* species complex of south-central Africa in the context of Palaeo-Drainage Dynamics. Unpublished PhD thesis, University of Stellenbosch.

Cotterill F.P.D., Foissner W. 2010. A pervasive denigration of Natural History misconstrues how biodiversity inventories and taxonomy underpin scientific knowledge. Biodiv. Conserv. 19:291-303.

Cracraft J. 1989. Species as entities of biological theory. In: M. Ruse (Ed.). What the Philosophy of Biology is - Essays for David Hull. Netherlands: Kluwer. p. 33-54.

De Queiroz K. 1999. The general lineage concept of species and the defining properties of the species category. In: R. A. Wilson (Ed.). Species: New Interdisciplinary Essays. Cambridge MA: MIT Press, p. 49-89.

De Queiroz, K. 2005. A unified concept of species and its consequences for the future of taxonomy. Proc. Calif Acad. Sci. Suppl. 56 I (15):192-215.

De Queiroz K. (2007) Species concepts and species delimitation. Systematic Biology 56:879-886.

Donoghue M.J., Alverson W. S. 2000. A new age of discovery. Ann. Miss. Bot. Gard. 87:110-126.

Ellerman J.R., Morrison- Scott T.C.S., Hayman F.W. 1953. Southern African Mammals, 1758 to 1951: A Reclassification. London: British Museum (Natural History).

Felsenstein J. 2004. Inferring Phylogenies. Sunderland: Sinaeur.

Frankham, Richard, Jonathan D. Ballou, Michele R. Dudash, Mark DB Eldridge, Charles B. Fenster, Robert C. Lacy, Joseph R. Mendelson, Ingrid J. Porton, Katherine Ralls, and Oliver A. Ryder. 2012. Implications of different species concepts for conserving biodiversity. Biological Conservation 153:25-31.

Frost D.R., Kluge A.G. 1994. A consideration of epistemology in systematic biology, with special reference to species. Cladistics 10:259-294.

Frost D.R., Kluge A.G., Hillis D.M. 1992. Species in contemporary herpetology: comments on phylogenetic inference and taxonomy. Herp. Rev. 23:46-54.

Ghiselin M.T. 1974. A radical solution to the species problem. Syst. Zool. 23:536-544.

Ghiselin M.T. 1997. Metaphysics and the Origin of Species. New York: State University of New York.

Ghiselin M.T. 2005a. The Darwinian revolution as viewed by a philosophical biologist. J. Hist. Biol. 38:123–136.

Ghiselin M.T. 2005b. Homology as a relation of correspondence between parts of individuals. Theor. Biosci. 124:91-103.

Ghiselin M.T. 2005c. Taxonomy as the organization of knowledge. Proc. Calif. Acad. Sci. Suppl. 56 I (15):161-169.

Gippoliti S., Groves C.P. 2012. "Taxonomic inflation" in the historical context of mammalogy and conservation. Hystrix, It. J. Mamm. 23:6-9.

Gippoliti S., Cotterill F.P.D., Groves C. 2013. Mammal taxonomy without taxonomists: a reply to Zachos and Lovari. Hystrix, It. J. Mamm. 24:3-5. doi:10.4404/hystrix-23.2-8685

Gould S.J. 2003. The Hedgehog, the Fox, and the Magister's Pox: mending and minding the misconceived gap between science and the humanities. London: Jonathan Cape.

Groves C.P. 2001a. Primate Taxonomy. Washington DC: Smithsonian Institution Press.

Groves C.P. 2001b. Why taxonomic stability is a bad idea, or why are there so few species of primates (or are there?). Evol. Anthrop. 10:192–198.

Groves C.P. 2004. The what, why, and how of primate taxonomy. Intern. J. Primatol. 25:1105–1126.

Groves C.P. 2013. The nature of species: A rejoinder to Zachos et al. Mamm. Biol. 78:7-9.

Groves C., Grubb P. 2011. Ungulate Taxonomy. Baltimore: The Johns Hopkins University Press.

Groves C., Leslie Jr. D.M. 2011. Family Bovidae (hollow-horned ruminants). In: Wilson D.E., Mittermeier R.A. (Eds.), Handbook of the Mammals of the World. Hoofed Mammals, vol. 2. Bellaterra (Spain): Lynx Edicions. p. 444–779.

Grubb P. 2005. Order Artiodactyla. In: Wilson, D.E., Reeder, D.M. (Eds.), Mammal Species of the World. A Taxonomic and Geographic Reference. 3rd edition. Baltimore: The Johns Hopkins University Press. p. 637–722.

Grubb P., d'Huart, J.P. 2010. Rediscovery of the Cape Warthog *Phacochoerus aethiopicus*: A review. J. East Afr. Nat. Hist. 99:77–102.

Grubb P., Groves, C.P. Dudley J.P., Shoshani J. 2000. Living African elephants belong to two species: *Loxodonta africana* (Blumenbach, 1797) and *Loxodonta cyclotis* (Matschie, 1900). Elephant 2:1-4.

Guschanski K., Krause J., Sawyer S., Valente L.M., Bailey S., Finstermeier K., Sabin R. et al. 2013. "Next-Generation museomics disentangles one of the largest primate radiations." *Systematic Biology* 62:539-554.

Handley C.O. 1954. Review of Southern African Mammals 1758 to 1951: A Reclassification by J. R. Ellerman; T. C. S., Morrison-Scott; R. W. Hayman. J. Mammal. 35:460-461.

Harrison Matthews L. 1954. Research on the mammals of Africa. Nature 174:670-671.

Haveman R. 2013. Freakish patterns – species and species concepts in apomicts. Nord. J. Bot. 31:257–269.

Hausdorf B. 2011. Progress toward a general species concept. Evolution 65:923–931.

Helgen K.M. 2011. The mammal family tree. Science 334:458-459. doi:10.1126/science.1214544

Heller R., Frandsen P., Lorenzen E.D., Siegismund H.R. 2013. Are there really twice as many bovid species as we thought? Syst. Biol. 62:490-493.

Hennig W. 1966. Phylogenetic Systematics. Urbana, IL: University of Illinois Press.

d'Huart J.-P., Grubb P. 2001. Distribution of the common warthog (*Phacochoerus africanus*) and the desert warthog (*Phacochoerus aethiopicus*) in the Horn of Africa. Afr. J. Ecol. 39:156–169.

Hoagland, K.E. 1996. The Taxonomic Impediment and the Convention on Biodiversity. Assoc. Syst. Coll. News 24:61-62,66-67.

Hull D.L. 1968. The operational imperative: sense and nonsense in operationism. Syst. Zool. 17:438-457.

Hull D.L. 1989. Science as a Process: An evolutionary account of the social and conceptual development of science. Chicago: University of Chicago Press.

Isaac N.J.B., Mallet J., Mace G.M. 2004. Taxonomic inflation: its influence on macroecology and conservation. Trends Ecol. Evol. 19:464–469. doi:10.1016/j.tree.2004.06.004

Jansen Van Vuuren B., Robinson T.J. 2001. Retrieval of four adaptive lineages in duiker antelope: evidence from mitochondrial DNA sequences and fluorescence in Situ hybridization. Mol. Phyl. Evol. 20:409-425.

Jenner R.A., Wills M.A. 2007. The choice of model organisms in evo-devo. Nat. Rev. Genet. 8:311–319.

Johnson L.A.S. 1970. Rainbow's End: the quest for an optimal taxonomy. Syst. Zool. 19:203-239.

Kaiser H., Crother B.I., Kelly C.M.R., Luiselli L., O'Shea M., Ota H., Passos P., Schleip W.D., Wüster W. 2013. Best practices: In the 21st Century, taxonomic decisions in herpetology are acceptable only when supported by a body of evidence and published via peer-review. Herpet. Rev. 44:8-23.

Kenmuir D., Williams R. 1975. Wild mammals: a field guide and introduction to the mammals of Rhodesia. Longman Rhodesia.

King I. 2009. The need for the incorporation of phylogeny in the measurement of biological diversity, with special reference to ecosystem functioning research. BioEssays 31:107-116.

Kingdon J. 1982. East African Mammals. Volume IIIC and IIID. Chicago: University of Chicago Press.

Kingdon J. 1997. The Kingdon Field Guide to African Mammals. London: Academic Press.

Kingdon J., Hoffman M. (eds) 2013. Mammals of Africa. Volume 6. London: Bloomsbury.

Kluge A.G. 1990. Species as historical individuals. Biol. Philos. 5:417-431.

Koubínová D., Irwin N., Hulva P., Koubek P., Zima J. 2013. Hidden diversity in Senegalese bats and associated findings in the systematics of the family Vespertilionidae. Frontiers in Zoology 10:48 doi:10.1186/1742-9994-10-48

Le Roex N. 2008. Phylogeographic Analysis reveals Strong Structuring in the Klipspringer, *Oreotragus oreotragus*. MSc Thesis, Cape Town: University of Cape Town.

Lorenzen E.D., Simonsen B.T., Kat P.W., Arctander P., Siegismund H.R. 2006. Hybridisation between subspecies of waterbuck (*Kobus ellipsiprymnus*) in zones of overlap with limited introgression. Mol. Ecol. 15:3787-3799.

Lorenzen E.D., de Neergaard R., Arctander P., Siegismund H.R. 2007. Phylogeography, hybridisation and Pleistocene refugia of the kob antelope (*Kobus kob*). Mol. Ecol. 16:3241-3252.

Lorenzen E.D., Arctander P., Siegismund H.R. 2008. Three reciprocally monophyletic mtDNA lineages elucidate the taxonomic status of Grant's gazelles. Conserv. Genet. 9:593-601.

Mayden R.L. 2013. Species, trees, characters, and concepts: ongoing issues, diverse ideologies, and a time for reflection and change. In: The Species Problem - Ongoing Issues. I. Ya. Pavlinov (Ed.), InTech. p. 171-191.

Moodley Y., Bruford M.W. 2007. Molecular biogeography: towards an integrated framework for conserving Pan-African biodiversity. Plos One 2.5 (2007): e454.

Moodley Y., Bruford M.W., Bleidorn C., Wronski T., Apio A., Plath M. 2009. Analysis of mitochondrial DNA data reveals non-monophyly in the bushbuck (*Tragelaphus scriptus*) complex. *Mammal. Biol.* 74:418–422. doi:10.1016/j.mambio.2008.05.003

Nadler S.A. 2002. Species delimitation and nematode biodiversity: phylogenies rule. Nematology 4:615-625.

Naomi S.-I. 2011. On the integrated frameworks of species concepts: Mayden's hierarchy of species concepts and de Queiroz's unified concept of species. J. Zool. Syst. Evol. Res. 49:177–184. doi:10.1111/j.1439-0469.2011.00618.x

Navarro-Siguenza A.G., Peterson, A.T. 2004. An alternative species taxonomy of the birds of Mexico. Biota Neotropica 4:1-32.

Nee S. 2005. The great chain of being. Nature 435:429.

Norris R.D., Hull P.M. 2011.The temporal dimension of marine speciation. Evol. Ecol. 26:393–415. doi:10.1007/s10682-011-9488-4

O'Hara R.J. 1988. Homage to Clio, or, toward an historical philosophy for evolutionary biology. Syst. Zool. 37:142-155.

O'Hara R.J. 1997. Population thinking and tree thinking in systematics. Zool. Script. 26:323-329.

Padial J.M., De la Riva I. 2006. Taxonomic inflation and the stability of species lists: the perils of ostrich's behavior. Syst. Biol. 55:859–867. doi:10.1080/1063515060081588

Padial J.M., De La Riva I. 2010. A response to recent proposals for integrative taxonomy. Biol. J. Linn. Soc. 101:747-756.

Padial J.M., Castroviejo-Fisher S., Köhler J., Vilà C., Chaparro J.C., De la Riva I. 2009. Deciphering the products of evolution at the species level: the need for an integrative taxonomy. Zool. Script. 38:431-447.

Padial J.M., Miralles A., De la Riva I., Vences M. 2010. The integrative future of taxonomy. Front. Zool. 7:16.

Pastorini J., Forstner M.R.J., Martin R.D. 2001. Phylogenetic history of sifakas (*Propithecus*: Lemuriformes) derived from mtDNA sequences. Amer. J. Primat. 53:1-17.

Pavlinov I.Y. 2013. The Species Problem, why again? In: The Species Problem - Ongoing Issues. I. Ya. Pavlinov (Ed.), InTech. p. 2-37.

Peterson A.T. 2006. Taxonomy is important in conservation: a preliminary reassessment of Philippine species-level bird taxonomy. Bird Conservation International 16:155-173.

Rohland N., Reich D., Mallick S., Meyer M., Green R.E., Georgiadis N.J., Roca A.L., et al. 2010. Genomic DNA sequences from mastodon and woolly mammoth reveal deep speciation of forest and savanna elephants. PLoS Biol. 8(12), e1000564. doi:10.1371/journal.pbio.1000564

Rookmaaker K. 2011. A review of black rhino systematics proposed in *Ungulate Taxonomy* by Groves and Grubb (2011) and its implications for rhino conservation. Pachyderm 50:72–76.

Rosauer D.F., Mooers A.O. 2013. Nurturing the use of evolutionary diversity in nature conservation. Trends Ecol. Evol. 28:322-323.

Rosenberger A.L. 2012. New World Monkey nightmares: science, art, use, and abuse (?) in Platyrrhine taxonomic nomenclature. Amer. J. Primat. 695:692–695. doi:10.1002/ajp.22037

Sangster G. 2009. Increasing numbers of bird species result from taxonomic progress, not taxonomic inflation. Proc. Biol. Sci. Roy. Soc. 276(1670):3185–3191. doi:10.1098/rspb.2009.0582

Shetty N.R., Vidya T.N.C. 2011. To split or not to split: the case of the African elephant. Curr. Sci. 100:810–812.

Simpson G.G. 1940. Types in modern taxonomy. Amer. J. Sci. 238:413-431.

Simpson G.G. 1961. Principles of Animal Taxonomy. New York: Columbia University Press.

Smithers R.H.N. 1971. The Mammals of Botswana. Museum Memoir No 1. Salisbury: National Museums and Monuments. p. 1-340.

Stoffberg S., Schoeman M.C., Matthee C.A. 2012. Correlated genetic and ecological diversification in a widespread southern African horseshoe bat. *PloS one*, *7*(2), e31946. doi:10.1371/journal.pone.0031946

Taylor P.J., Lavrenchenko L.A. Carleton M.D., Verheyen E., Bennett N.C., Oosthuizen C.J., Maree S. 2011. Specific limits and emerging diversity patterns in East African populations of laminatetoothed rats, genus *Otomys* (Muridae: Murinae: Otomyini): Revision of the *Otomys typus* complex. Zootaxa 3024:1-66.

Taylor P.J., Stoffberg S., Monadjem A., Schoeman M.C., Bayliss J., Cotterill F.P.D. 2012. Four new bat species (*Rhinolophus hildebrandtii* complex) reflect Plio-Pleistocene divergence of dwarfs and giants across an Afromontane archipelago. PloS ONE *7*(9), e41744. doi:10.1371/journal.pone.0041744

Trontelj P., Fišer C. 2009. Cryptic species diversity should not be trivialised. Systematics and Biodiversity 7:1-3.

Van Daele P.A., Blondé P., Stjernstedt R., Adriaens D. 2013. A new species of African mole-rat (*Fukomys*, Bathyergidae, Rodentia) from the Zaire-Zambezi watershed. Zootaxa 3636:171-189.

Wheeler Q.D., Platnick N.I. 2000. The phylogenetic species concept (sensu Wheeler & Platnick). In Wheeler, Q. D. & R. Meier (eds). Species Concepts and Phylogenetic Theory: A Debate. New York: Columbia University Press. p. 55-69.

Wiens J.J. 2007. Species delimitation: new approaches for discovering diversity. Syst. Biol. 56:875–878. doi:10.1080/10635150701748506

Wiley E.O., Lieberman B.S. 2011. *Phylogenetics: theory and practice of phylogenetic systematics*. Second Edition. New York: Wiley-Blackwell.

Wiley E.O., Mayden R.L. 2000. A defense of the evolutionary species concept. In: Wheeler, Q. D. & R. Meier (eds). Species Concepts and Phylogenetic Theory: A Debate. New York: Columbia University Press. p. 198-208.

Willows-Munro S., Robinson T. J., & Matthee C.A. 2005. Utility of nuclear DNA intron markers at lower taxonomic levels: phylogenetic resolution among nine *Tragelaphus* spp. Mol. Phylogenet. Evol. 35:624–636. doi:10.1016/j.ympev.2005.01.018

Winston J. 1999. Describing Species: Practical taxonomic procedure for biologists. New York: Columbia University Press.

Yeates D. K., Seago A., Nelson L., Cameron S. L., Joseph L., &Trueman J. W. H. 2011. Integrative taxonomy, or iterative taxonomy? Syst. Entomol. 36:209–217. doi:10.1111/j.1365-3113.2010.00558.x

Yoon C.K. 2011. Naming Nature: The Clash between Instinct and Science. New York: W.W. Norton.

Zachos F. E. 2012. Book Review. D.E. Wilson, R.A. Mittermeier (Eds.) 2011. Handbook of the Mammals of the World, vol. 2. Hoofed Mammals. Lynx Edicions. Mammalian Biology 77:74. doi:10.1016/j.mambio.2011.10.002

Zachos F.E., Lovari S. 2013. Taxonomic inflation and the poverty of the Phylogenetic Species Concept - a reply to Gippoliti and Groves. Hystrix It. J. Mamm. 24:3. doi: 10.4404/hystrix-24.1-8849.

Zachos F.E., Apollonio M., Bärmann E.V., Festa-Bianchet M., Göhlich U., Habel J.C., Haring E., Kruckenhauser L., Lovari S., McDevitt A.D., Pertoldi C., Rössner G.E., Sánchez-Villagra M.R., Scandura M., Suchentrunk F. 2013a. Species inflation and taxonomic artefacts – A critical comment on recent trends in mammalian classification. Mamm. Biol. 78:1-6.

Zachos F.E., Clutton-Brock T.H., Festa-Bianchet M., Lovari S., Macdonald D.W., Schaller G.B. 2013b. Species splitting puts conservation at risk. Nature 494:35.

Ziman J. 1978. Reliable Knowledge. Cambridge: Cambridge University Press

Figure 1. The three main categories of errors in taxonomies – modified from Cotterill (2003a) with graphics derived from Kingdon (1997); and see Adams (1998) and Bernardo (2011) for detailed discussion of errors that afflict characterizations of biodiversity where species are wrongly described and classified. Differing classifications of selected taxa of duikers (*Cephalophus* spp.) illustrate three categories of taxonomic error:

a) Based on available information, the correct taxonomy depicting - from left to right - seven evolutionary species of forest duikers: Ader's *adersi* (ade), Black-fronted *nigrifron*s (ni) and Hook's *hooki* (ho), Harvey's *harveyi* (ha), Natal red *natalensis* (na) including Robert's *robertsi* (ro) as a synonym, Peters' *callipygus* (cal), and Ruwenzori red *rubidus* (rub), applying phylogenetic relationships from Jansen Van Vuuren & Robinson (2001). The Mt Kenya duiker *C. hooki* is added to this classification on the assumption that it is a sister species of *C. nigrifrons*, but the distinct Mt Elgon red duiker *C. fosteri* is not shown (Groves and Grubb 2011).

b) Type I error (Too many species), with *robertsi* and *natalensis* split into artificial species. An error most likely when a Phylogenetic Species Concept (PSC) is used as a criterion to discover evolutionary species; but in this case, it wrongly splits one heterogeneous species into two. Taxonomic precision suffers.

c) Two examples of Type II error (Too few species): one polytypic species "natalensis" lumps *natalensis*, *robertsi*, *harveyi*, and *rubidus*; the second biological species "nigrifrons" comprises *hooki* and *nigrifrons*. Taxonomic precision is reduced radically in this case. Evolutionary relationships are arbitrary, as they are tacitly assumed to reflect overall resemblance. This incorrect taxonomy further risks creating chimeras, as when one author obtains a mtDNA sequence from *nigrifrons*, another obtains a nDNA sample from *hooki*, and both get incorporated into GenBank under the rubric "nigrifrons".

d) Type III errors (Incorrect depiction of evolutionary histories). The evolutionary relationships of these duikers is not only ignored, but misconstrued by the BSC, which obviates insights into phylogenetic relationships among taxa, which are lumped into species groups, or superspecies. The superspecies illustrated here, proposed by Ansell (1972), lumps together [*adersi*-*callipygus*-"natalensis"] to compound Type II errors. Adherence to the superspecies concept perpetuates the mistaken belief that *adersi*, *callipygus*, and "natalensis" are closely related allospecies. The taxonomic errors in this example are exceeded in the lumping of all bushbucks into a single polytypic species *Tragelaphus scriptus*, which comprises at least eight species in the *scriptus* and *sylvaticus* clades (Groves and Grubb 2011).

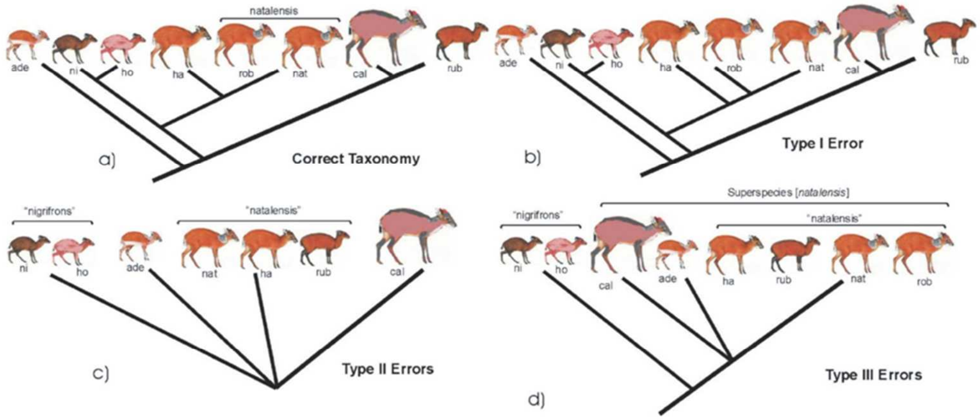

Figure 1. The three main categories of errors in taxonomies – modified from Cotterill (2003a) with graphics derived from Kingdon (1997); and see Adams (1998) and Bernardo (2011) for detailed discussion of errors that afflict characterizations of biodiversity where species are wrongly described and classified. Differing classifications of selected taxa of duikers (Cephalophus spp.) illustrate three categories of taxonomic error:

a) Based on the best information available, the correct taxonomy depicting - from left to right - seven evolutionary species of forest duikers: Ader's adersi (ade), Black-fronted nigrifrons (ni) and Hook's hooki (ho), Harvey's harveyi (ha), Natal red natalensis (na) including Robert's robertsi (ro) as a synonym, Peter's callipygus (cal), and Ruwenzori red rubidus (rub). These phylogenetic relationships are based on Jansen Van Vuuren & Robinson (2001). C. hooki is added to this classification on the assumption that it is a sister species of C. nigrifrons (Groves and Grubb 2011).

b) Type I error (Too many species), with robertsi and natalensis split into artificial species. An error most likely when a Phylogenetic Species Concept (PSC) is used as a criterion to discover evolutionary species; but in this case, it wrongly splits one heterogeneous species into two. Taxonomic precision suffers.

c) Two examples of Type II error (Too few species): one polytypic species "natalensis" lumps natalensis, robertsi, harveyi, and rubidus; the second biological species "nigrifrons" comprises hooki and nigrifrons. Taxonomic precision is reduced radically in this case. Evolutionary relationships are arbitrary, as they are tacitly assumed on overall resemblance; so this taxonomy is also incorrect.

d) Type III errors (Incorrect depiction of evolutionary histories). The evolutionary relationships of these duikers is not only ignored, but misconstrued by the BSC. This figure and also Fig. 4c illustrate how adherence to the BSC obviates any insights into phylogenetic relationships among taxa, which are lumped into species groups, or superspecies. The superspecies illustrated here, proposed by Ansell (1972), lumps together [adersi-callipygus-"natalensis"]. Here, the superspecies concept compounds Type II errors. Adherence to the superspecies concept perpetuates the mistaken belief that adersi, callipygus, and "natalensis" are closely related allospecies. This taxonomy is highly incorrect, but is exceeded in the lumping of all bushbucks into a single polytypic species Tragelaphus scriptus, which comprises at least eight species in the scriptus and sylvaticus clades (Groves and Grubb 2011).

252x116mm (96 x 96 DPI)