Abstract
As for all biodiversity, society requires an accurate taxonomy of the Bovidae. We need to know what the different antelopes really are, and where these occur. Sound scientific, economic and aesthetic arguments underpin this rationale. This paper highlights some of the costs that result from the misconstrual of the real nature of species. Controversy reigns over which species concepts are most applicable to characterize biodiversity; a controversy magnified by how different species concepts create taxonomies of differing accuracy and precision. The contemporary taxonomy of the Mammalia continues to be based on the Biological Species Concept (BSC). Its deficiencies are too rarely acknowledged, and afflict apparently well known taxa of large mammals, notably the Bovidae. Errors in the BSC misconstrue natural patterns of diversity: recognizing too many (Type I errors), or too few species (Type II errors). Most insidious are Type III errors; where evolutionary relationships are misconstrued because the BSC cannot conceptualize, and thus ignores phylogenetic uniqueness. The general trend in current taxonomies of antelopes is to under represent true diversity - exemplified in the dikdiks (Type II errors). Misconstrual of phylogenetic relationships among species (Type III errors) appear rampant in these same taxonomies (the Cephalophini for example). This paper presents a solution to these problems and the species debate. Termed the Consilient Solution, it consists of disparately derived knowledge of species’ properties. The Consilient Solution is structured by the historical philosophy that has replaced a non-historical philosophy in systematics. Examples from the Bovidae emphasize why accurate and precise taxonomies underpin conservation initiatives and policy. Furthermore, there are practical ways whereby all those interested and working on antelopes can contribute toward elucidation of an objective taxonomy of the Bovidae - especially the small antelopes.

“All true classification is genealogical; that community of descent is the hidden bond which naturalists have been unconsciously seeking, and not some unknown plan of creation, or enunciation of general propositions, and the mere putting together and separating of objects more or less alike” (Darwin, 1859:420)

Introduction
The small bodied (or dwarf) antelopes are a significant component of the diversity of African antelopes; having radiated alongside their larger relatives within forests, savannas and deserts. The Bovidae have great economic and aesthetic importance. Admired worldwide, their diversity is commonly perceived as well known. As for all biodiversity, taxonomy underpins reliable identity and conservation of these antelopes; such that their real diversity needs to be characterized accurately and precisely in terms of its actual species. Species are the fundamental units employed to understand the patterns and processes of evolution; they are central subjects of biologists’ studies. The species category is crucial in biological explanation; it interlinks the great fields of micro- and macroevolutionary biology (Adams, 1998; Brooks & McLennan, 1991, 1999).
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For decades, there has been great debate within biology as to what species really are. Through the 1970s, contributions to this “species debate” increasingly exhibited influences of the parallel development of phylogenetic systematics. These deliberations over species had been confined largely to within evolutionary biology; then more recently, reactions to the biodiversity crisis intensified the species debate and also widened its scope and audience. This has been catalyzed by cognisance of the critical influences held by systematics in conservation and indeed all biology; because conservationists’ decisions focus on the extinctions and integrity of species. How we characterize species has particularly important impacts on failure or success of these decisions (Claridge, et al. 1997; Cracraft, 2000).

These problems and challenges encountered in the species problem of contemporary biology are important when we consider the Bovidae, and especially smaller antelopes. As with all biodiversity, disparate opinions among biologists, over what species are, has been a major reason why taxonomists have classified antelopes differently. The prevailing approach has been to use overall resemblance (phenetic measures) and inference of reproductive isolation. The time honoured tool of taxonomists has been the BSC (Biological Species Concept) or the even vaguer notion of morpho-species1 (or a combination of these two). This situation typifies all mammalogy; such that Corbet (1997) concluded the BSC to be the optimal solution in mammalian taxonomy. It has structured recent taxonomic reviews of the Bovidae (Grubb, 1993, 1999, 2000); with the BSC, as the conceptual capsule, packaging bovid diversity at the microtaxonomic level. This central reliance on the BSC has also employed the satellite concepts of the subspecies and superspecies (following Amadon, 1968; Amadon & Short, 1976) to pigeonhole populations. As argued below, scientific authenticity of these contemporary taxonomies of bovids leaves much to be desired. These African mammals exemplify critical issues at stake in the species debate, with respect to taxonomic precision and accuracy.

Indeed, the precision and accuracy of contemporary bovid taxonomies require critical scrutiny. Here, precision (degree of detail) denotes exactly what species are characterized; while accuracy (correctness) refers to whether or not one classifies species correctly with respect to their evolutionary relationships. For example, Ansell (1972), followed by Grubb (1993), treated all tiangs, topi, tsessebes and korrigum as just one polytypic species, Damaliscus lunatus (Burchell, 1823): containing six subspecies distributed across Africa’s southern, eastern and northern savannas. Yet, a recent morphometric analysis of this species complex of alcelaphine antelopes employed the Evolutionary Species Concept (ESC) to conclude that the taxon, D. lunatus, is artificial. The taxa lumped into one polytypic species actually are parts of two divergent clades; true D. lunatus only occurs west and south of the Zambezi river. The taxonomic status of the other populations awaits elucidation (Cotterill, in press).

Before we get too carried away discussing just species, some attention is due to overall goals and relevance of the twinned disciplines of systematics and taxonomy. Systematists discover and classify evolutionary patterns, while the science of the naming and classification of biological entities is the focus of taxonomists. Research by evolutionary biologists elucidates the origins and processes underlying these patterns. In practice, systematist, taxonomist, and evolutionary biologist are often one and the same person. Significant scientific benefits follow when we integrate phylogenetic systematics, biogeography and evolutionary biology as closely as possible to accurately explore and characterize biodiversity. The species category is the keystone concept in this research (Wiley & Mayden, 2000). As highly organized knowledge, correct taxonomies structure, whilst simultaneously improving, the scientific operations in which biodiversity is explored and characterized, and hopefully conserved.

And it is here that one’s choice of species concept is critical. Credible taxonomies are not only constructed using stable names for species, but require that these names refer to real entities. Very different classifications of the same biodiversity can and do exist; but false taxonomic information can have far reaching consequences. Certain of the taxa classified are often not real; unfortunately, such artificial taxa, erroneously created by inappropriate species concepts, hamstring the scientific objectivity and truth of taxonomies (Cracraft, 2000). The far reaching values of correct taxonomies cannot be over emphasized. Benefits from this knowledge extend throughout biology, notably in conservation, to benefit society overall. Agriculture, biotechnology, engineering, medicine, and tourism are examples of just a few mainstream

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1The morpho-species concept is also termed the Linnaean or typological species concept (Mayr 1963); and an extension of this idea, the Phenetic Species Concept (PSC) uses overall similarity of organisms to try and distinguish between species (Mayden 1997)
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humanitarian, economic and social arenas in which taxonomic knowledge of biodiversity is indispensable: to solve problems; create wealth; and maintain human livelihoods.

Obviously, the debate raging among evolutionary biologists over what species are (and how they are best recognized) is no trite issue - even if it appears to be some esoteric academic debate. Any deeper consideration of taxonomic accuracy and precision demands that we consider certain philosophical issues simultaneously. In fact, an understanding of key philosophical concepts and arguments predates any attempt to resolve the species problem. A theoretically sound, yet practicable, solution to this wide ranging controversy over species has huge influences on all biology and any applications of its knowledge. In fact, their resolution is not only fundamental to what life is; for it prescribes how we biologists can and cannot go about characterizing biodiversity; whether we study insects, duikers, microbes or any other organisms.

This paper is structured into three sections. The first is a philosophical review of species’ properties, and how species are best characterized. This begins with an overview of the species problem and highlights some important properties of species ontology - what species are. The core aims of this first section are:

"... to achieve a clear conception of what it means to assert that entities such as species exist independently of human perception..... to develop at least one species definition compatible with the notion of independent existence.....and to develop the epistemological tools" (Baum, 1998: 641) to discern these real species

This first section provides the platform and context to present a solution to the species problem. This I term the “Consilient Solution”. It has been forged of independently derived theory and data about species. It not just solves the species problem, but empowers biology to classify organisms with an hitherto unavailable objectivity. Following this overview of the Consilient Solution (and pernicious errors it avoids), the third and final section extends the taxonomic argument of this paper, employing examples of the actual diversity of African antelopes. I focus especially on the smaller bodied antelopes: including the duikers (Cephalophus and Sylvicapra), the Beira antelope (Dorcotragus) and all other neotragines (Madoqua, Oreotragus, and Raphicerus) and oribis Ourebia. Comparisons of these dwarf antelopes, and also the Reduncini, illustrate the priority need to research bovid diversity objectively.

It is indeed remarkable that considerable research is still required to elucidate the real diversity of what many consider to be well known vertebrates. Overall, the synthesis of theory and data in this review emphasizes the far reaching consequences of employing different species concepts to characterize biodiversity. This paper argues that sound knowledge of phylogenetic relationships is quintessential; for accuracy, and not just precision, is critical to scientifically credible taxonomies. Based on this approach, this paper highlights key issues critical to an improved, and scientific, taxonomy of African antelopes. Although its focus and examples are on antelopes, this extends to any consideration of all biodiversity. Taxonomy of species concepts and acronyms in this review follows Mayden (1997) and Brooks and McLennan (1999).

THE DEBATE ABOUT THE “SPECIES PROBLEM”

"This seemingly timeless debate has generated a heterogeneous proliferation of concepts, most hoping to capture the operational and/or theoretical qualities of a good concept. The search has been for a concept – definition that is biologically relevant and meaningful, one that is easily applied, and one that encompasses natural bio-diversity. That is, a concept of real species assisting in and ensuring their recognition and our understanding of them in nature.” (Mayden, 1997:382)

In actual fact, the “species problem” entails several complex controversies (Kluge, 1990). Its history will not be covered in detail here, given several recent scholarly reviews of the subject and its scope (Claridge, Dawah & Wilson, 1997; Ghiselin, 1997; Adams, 1998; Howard & Berlocher, 1998; Wilson, 1999; and Wheeler and Meier, 2000). As Mayden’s explanation, quoted above, emphasizes: the nux of the species debate is the unfulfilled search for a species concept that objectively describes the real heterogeneity of all biodiversity with respect to its real diversity (Mayden, 1997; Cracraft, 2000). Dozens of species concepts have been proposed; these differ in important ways (Mayden, 1997). Many attempts have been made to sift “good” concepts from the “bad” (e.g. Kitcher, 1984). None such classification has been successful; and some authorities have drawn the extreme conclusion that this search for a universal species concept is an impossibility (Hull, 1997).

With respect to antelopes, the central question that focuses discussion in this paper is ‘which species concept best characterizes the diversity of African Bovidae with requisite accuracy and precision?’ Many problems complicate and
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Dichopatric (Cracraft 1984) is the appropriate term to describe geographically isolated populations that have evolved vicariantly.

Figure 1. Three models of speciation depicting the evolutionary relationships between three evolutionary species: A, B and C. Note how species C does not persist after events of cladogenetic speciation that bifurcate lineages. Many biologists believe that species only form by cladogenesis.

invariably foil attempts to unequivocally define what species are. One such issue is whether a species can only be monophyletic (Rosen 1979), or whether paraphyletic and indeed polyphyletic species exist (De Queiroz 1998, 1999). Often the fuzzy boundaries between species routinely foil attempts at neat classifications. Have species formed through anagenesis or blastogenesis, or have they evolved through cladogenesis only (Fig. 1)? A pertinent case in question are the red duikers of the Cephalophus natalensis complex, including adersi, harveyi, nigrifrons, rubidus, rufiliatus, and weynsi. Are all these allopatric species each one species; collectively just one polytypic species, or do they comprise a complex of evolutionary species? Or are only certain of these red duiker populations “good” species? Different solutions have been employed to try and classify such organisms objectively with disparate success.

Species are real entities
A tenet of this paper is that species are real entities; they actually exist out there in nature; they are not mere figments of taxonomists’ imaginations. Species have also evolved in different ways. But even so, can all organismal biodiversity actually be classified, and thus understood, in terms of just one species category? Is there a universal category within which all species - whether microbial, plant or animal - can be naturally classified without injecting huge disarray,

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2Dichopatric (Cracraft 1984) is the appropriate term to describe geographically isolated populations that have evolved vicariantly.
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conceptual and epistemological, into biology? Scientific success in overcoming this challenge entails several problems, which are best grouped into these three categories:

1. If species are real entities in nature (see Frost & Kluge, 1994 for a detailed defense), then how can they be most clearly conceptualized?

2. Given appropriate conceptual tools, what exactly is represented by the term ‘species’? In other words, what natural entities in the hierarchical patterns of living complexity do we call species?

3. Should biologists be empowered with a species concept that accurately describes what species are; then how can we best characterize living organisms and classify them?

Clearly, we are challenged by multifaceted problems. The next section reviews species’ properties toward answering these three questions, structured around five topics. This discussion sets the stage and presents an overview of a solution to the species ‘problem’ - the Consilient Solution.

3. THE STRUCTURE OF LIVING VARIETY

“The recognition of the uniqueness of every individual and the role of individuality in evolution is not only one of the utmost importance for an understanding of the history of biology, but it is one of the most drastic conceptual revolutions in western thought...” (Mayr, 1991:80).

3.1 The Variety of Life

Charles Darwin introduced a revolutionary concept to philosophy in 1859 - unprecedented in human thought; he recognized that biological populations vary because they are comprised of unique individuals (Mayr 1988). The nature of this variation was compared by Dobzhansky (1937: 4), who distinguished continuous from discontinuous variation in the organization of the earth’s biota; he emphasized the discontinuous patterns whereby evolution has sorted continuous variation into distinctly discrete clusters of populations and larger taxa. Variation has been sorted hierarchically across these clusters; each cluster a population of closely related organisms that exhibit continuous variation. Besides entomologist Karl Jordan in 1905 (see Mayr, 1976), Dobzhansky’s is one of the first explicit, and also widely read, articulations of this phenomenon. Equally importantly, the scientific endeavour to describe and understand these complementary patterns (exhibited in continuous and discontinuous variation) have had a fundamental influence on the growth of biological thought since 1859; this recognition, albeit not often explicitly articulated, has implicitly structured the development of the life sciences and resultant knowledge (Mayr, 1982).

Although the variation of populations was first recognized by Darwin (Lewontin, 1974; Montalenti, 1974), biologists rarely consider the overall ontology of the variety manifested in the hierarchical organization of biodiversity. This deficiency is unfortunate, as explicit understanding of life’s variety predates elucidation of what biologists seek to understand, and taxonomists to classify. If we are to meaningfully understand the species category, we must first understand how and why living organisms differ; and how these phenomena are structured in time and space. I use variety to conceptualize any differences among two or more entities that are part of biodiversity; with the term variation restricted to describe differences within the parts of an organism or its lineage (or population or species). Diversity is the term that encapsulates discontinuous variation between two or more populations or species, and the larger phyla inclusive of species. Although we commonly use these terms interchangeably, demands for conceptual rigour dictates a pedantic stance if we are to understand exactly what living novelties evolution has created. So, “variety” describes manifestations of uniqueness in its broadest sense. It encompasses both variation and diversity, which describe manifestations of uniqueness within and across populations and lineages respectively. Obviously, ‘variation’ and ‘diversity’ are complementary terms for the continuous and discontinuous variation which make up the living variety that is biodiversity. These crucial properties of species are summarized in Figure 2.

3.2 Uniqueness and Variation

The occurrence of unique biological entities that manifests in variation (Darwin 1859; Lewontin, 1974) is an emergent property among two or more unique living entities. The fact cannot be overemphasized that any two living entities, no matter how identical, have only to differ in one respect to be unique. Levins and Lewontin (1985), Rose (1997) and
Lewontin (2000) have emphasized this property of life. If anything, this universal occurrence of biological uniqueness - in its ubiquity across all levels of hierarchical organisation - constitutes a law in biology. The hierarchical structuring of uniqueness has a fundamental influence on how variety is conceptualized and characterized in biology (Fig 2).

The obvious manifestation of uniqueness is exemplified in an organism’s ontogeny. Its cell lineages develop and diverge; they differentiate into different organs and other tissues and morphologies (Fig. 2). Thus, variety is created through the lifeline of an organism (Rose, 1997). The differences between biological entities tends to increase when two or more organisms are compared. This is true even of siblings with identical genotypes, because their phenotypes differ. The term ‘population-thinking’ conceptualizes continuous variation; “We call the concept which emphasizes uniqueness of each individual population thinking” (Mayr, 1988: 224, italics his). Mayr (1976:12) concluded that “The replacement of typological (essentialistic) thinking by population thinking was perhaps the most important conceptual revolution in the history of biology”. Nevertheless, it is still not widely appreciated nor practiced, as typological thinking persists in some theatres of systematics. Most unfortunately, it continues to hamstring progress in understanding species.

**Figure 2.** A hypothetical representation of the patterns of variation exhibited at different levels of biological organization: the organism, the population, and species of which organisms are parts. This illustrates the hierarchical manifestation of uniqueness in living complexes. The realms of biological investigation that approximate these great fields of inquiry into biological variety are life history theory, population-thinking and tree-thinking, respectively. This example depicts the pattern of discontinuous variation between the red duiker species *Cephalophus natalensis* and *C. nigrifrons* that have evolved from a hypothetical common ancestor.
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As emphasized further below, a population is an individual (sensu Ghiselin, 1997); its intrinsic variation results from dissimilarities among its unique parts. This variation recognized by population thinkers is an historical product, with the organisms comprising a population united by their relatively recent history of reticulate descent (tokogeny, sensu Hennig, 1966). Singularities of uniqueness among organisms imparts a real and dynamic variation to a population:

“This uniqueness is true not only for individuals but even for stages in the life cycle of any individual, and for aggregations of individuals whether they be demes, species, or plant and animal associations. Considering the large number of genes that are either turned on or off in a given cell, it is quite possible that not even any two cells in the body are completely identical. This uniqueness of biological individuals means that we must approach groups of biological entities in a very different spirit from the way we deal with groups of identical inorganic entities. This is the basic meaning of population thinking.” (Mayr, 1982:46).

3.3 The Diversity of Life

Similarly, uniqueness in living systems has manifested in larger domains of space and time. This variety is represented in the diversity of species and higher phyla. Patterns of discontinuous variation dominate living variety at this hierarchical level. Complementing population-thinking, the term ‘tree-thinking’ (O’Hara, 1988, 1997) aptly encapsulates this diversity among species and larger, more inclusive phyla. Tree-thinking underlies the philosophies and methods of phylogenetic systematics. Tree-thinkers see each species and phylum as one unique part of the singular Tree of Life. This variety of life is a complex assemblage of all the historical products of evolution. Dobzhansky (1973: 125) did not go far enough when he stated that “Nothing in biology makes sense except in the light of evolution”; for more accurately, “Nothing in biology makes sense except in the light of history” (Rose, 1997). What lesson can we glean from the hierarchical organization of the uniqueness of living organisms? This ubiquitous uniqueness of living entities, with recurrent structuring of living variety into variable populations and diverse species and taxa, is a fundamental property of life. The accuracy and precision of our knowledge about biodiversity hinges on exactly how we dissect its living variety according to intrinsic natural patterns. Our cognisance of these phenomena frames and underpins any serious attempt to conceptualize and characterize species (Cotterill 2002a; Fig. 2).

4. SPECIES ARE INDIVIDUALS; NOT CLASSES NOR SETS

A logical consequence of uniqueness of biological entities acknowledges each species to be an individual, not a class. A tenet of tree-thinking (complementing population-thinking) is that each species is a unique individual. Although not articulated sufficiently by its principal proponent (Ghiselin 1974, 1984, 1997), uniqueness underpins this individuality. It is surprising that this axiom - of the uniqueness of living entities - has not been explicitly articulated by its large band of protagonists. Still, Ghiselin’s individuality thesis has become central to understand not just what species are, but equally proscribes how species can and cannot be characterized (Eldredge & Cracraft, 1980; Frost & Kluge, 1994; Baum, 1998; Brooks & McLennan, 1991, 1999, 2002).

The individuality thesis explains why an organism is a part and not a member of a species. This metaphysical foundation of the species category leads to some interesting and perplexing caveats. Notably, the identity of a species lineage persists despite the turnover (or flux) of organisms through time; while episodes of hybridization do not alter its identity. The persistence of a species’ individuality is analogous to that of an organism. Its individuality persists through the turnover of its cell lineages. Organ transplants do not change the recipient’s nor the donor’s identity. Overall, it is the historical legacy of an individual’s history - in terms of its intrinsic lineages - which overrides such sporadic events.

More accurately, Kluge (1990) emphasized that species are historical individuals, which have originated through ancestor-descendant relations among organisms. Here, we need to distinguish contemporaneous individuals (organisms) from historical individuals (species and larger monophyletic taxa). Organisms are the more familiar individuals we encounter. So, an insect maintains its individuality from the formation of the zygote to adulthood. This is despite the very different morphology this organism exhibits through its life history, from egg, through larva and pupa, and also through more than one “adult-like” instar. Calling an organism’s lifeline a ‘life cycle’ is a misnomer, because its events are irreversible, even though life histories of organisms in the same lineage exhibit broad similarities. The key to an organism’s individuality is the persistence of unbroken cell lineages through the insect’s life. Quite simply, a species persists because its population lineage has (De Queiroz, 1999). To reiterate, nothing in biology makes sense except in the light of history. The problem faced by investigators seeking a refined ontology of species “…is, therefore, given the individuals, to decide what the classes are.” (Ghiselin, 1985: 34). As individuals, species are historical entities with spatial and temporal properties.
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Recognizing that species and phyla are historical individuals is a prerequisite - fundamental to understanding what tree-thinking conceptualizes.

ARE SPECIES POPULATIONS, METAPOPULATIONS, OR TIME-EXTENDED LINEAGES?
5.1 Populational Lineages and Divergence
There is consensus across biology that species comprise populations of closely related organisms (Darwin, 1859; Dobzhansky, 1937; Mayr, 1942, 1997; Hennig, 1966; Masters and Rayner, 1996). De Queiroz (1998, 1999) has demonstrated that all species concepts describe certain properties implicitly acknowledged to be common to all species. All species concepts focus on either the population or lineage as the unit of understanding. A critical defining property of any such populational-lineage is the nature of relationships among its member organisms; all share recent ancestry through tokogeny (at least for sexually reproducing organisms). Tokogenic relationships within a variable population contrast with the divergence between lineages - the model of biodiversity firmly articulated by Hennig (1966) which complements that of Dobzhansky (1937). Here, again, we see the distinction between variation and diversity.

Many species exhibit internal branching, represented in the spatial segregation of its populations. The concept of the metapopulation allows us to imagine and quantify the structure of populations of closely related organisms that have become heterogeneously distributed in space and time. The metapopulation concept is closely focused on patterns of spatial variation only, and typically at ecological scales. These spatially segregated parts of a population are avatars (sensu Damuth, 1985) and are ephemeral in that they split and then merge into more widely distributed species with no permanent, and thus discernable, persistence. This occurs such that no persistence of any lineage can be perceived within the larger, and thus more inclusive species.

5.2 All Species are Lineages
All species are lineages. This idea was first emphasized by Hennig (1966). Species, whether comprised of asexual or sexual organisms, are segments of populational lineages. The trajectory of each of these lineages has traced a unique topology through space and time. The properties of a species are emergent; in that they are derived from organisms’ characters. Characteristically, these characters vary, like all a lineage’s properties. Simply stated, species are segments of lineages and cognisance of this phenomenon is implicit in all species concepts (De Queiroz 1998, 1999). We can build on this understanding to dissect additional issues of species ontology. Thus, through evolution, time-extended lineages formed through organisinal descent have manifested in the finer-scaled structure of organisinal biodiversity. With respect to speciation, it is important to note that “The analogy from organisms to lineages is not gestation and birth; it is mitosis or schizogony” (Frost & Kluge, 1994: 272).

5. LINEAGES AND SPECIES EXHIBIT LIFE HISTORIES
Variation within a species is often only acknowledged in spatial terms. This acknowledgment reaches its extremes with neontologists in the infatuations with populations in so much of the literature published under the auspices of the Neo-Darwinian Synthesis. So many ideas and studies in this era failed to consider the temporal dimension of populations. Considered in retrospect, this blinkered focus on contemporary populations eclipsed cognition of history from biology; for decades it has hampered progress toward understanding the historically derived nature of biodiversity (Brooks & McLennan, 1999).

As an individual, a species experiences a history from its origin until its extinction; the concept of a species’ life-history dovetails nicely, and is in fact a logical consequence of Ghiselin’s Individuality Thesis (see above). Acknowledging that a species has a life history brings to the taxonomist’s mental toolkit a device to help reconcile with a frustrating state of affairs. Its properties change irreversibly through its existence. Critical events in a lineage’s history change the species’ properties; these are emergent in that they result from changes in characters of its integral organisms.

Quite logically, we are not always going to encounter species that are fully mature; with their maturity manifest in explicitly divergent lineages. Many species are young; we may encounter neospecies that have only recently diverged from the parent lineage. The boundaries around such species are fuzzy, and often overlap. This complicates our attempts to determine precisely the membership of some of their parts (organisms). So we should not be surprised to encounter great

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3Unless otherwise emphasized, reference to lineages from here on refers to populational lineages as opposed to genetic, cell or organelle lineages.
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variation within certain species; this is logical when we acknowledge it to be a natural property of individuality. It is analogous to how organisms differ greatly in differentiation of their molecules and tissues (the result of divergence between cell lineages). Widely distributed species are especially likely to exhibit high variation. This is exemplified by the Grey Duiker, *Sylvicapra grimmia*; which appears to exhibit clinal variation (perhaps as a morphocline, Grubb, 2000) across its extensive range through southern and eastern Africa; similarly, Oribi, *O. ourebia*, and Steenbuck, *R. campestris* appear to exhibit clinal variation (at least in parts of their ranges). This continuous variation means that we should not be surprised to discover species which vary more among their parts (organisms) than might be intuitively expected. We can view such variable species as a metapopulation. The null hypothesis is that their constituent populations have not diverged, and thus individuated into more than one species. Most likely reticulation, and thus gene flow, persisted within avatars of these widely dispersed species. Viewed collectively, the variety of avatars in such species exhibits variation, not diversity.

Explicit cognisance that species are lineages with a history greatly refines our understanding of all their properties. Most importantly, it empowers us to reconcile with the complex patterns exhibited through the dynamic life of a species (De Queiroz, 1998; Harrison, 1998, Figure 3). All told, we can expect species to exhibit great variation, especially through the temporal trajectory of their existence.

**Figure 3.** Schematic depiction of the analogous stages in the life histories of organisms and species (modified from De Queiroz, 1998). Stages in the evolutionary history of two sister species are depicted in the context of complementary properties of their lineages - discernable by apposite species criteria. The Distinguishability Criterion (employing a Phylogenetic Species Concept, PSC) can discover “younger” species that have diverged, and may or may not have evolved exclusivity. Note that early divergence is discovered by the Coalescent criterion employing the Genealogical Species Concept (GSC). With complementary discovery power, the cohesion criterion is applicable to those mature lineage segments in which different Specific Mate Recognition Systems (SMRS) have evolved. Here, only the Reproductive Species Criterion (RSC) can discover such “adult” species - discerning cohesive segments. Obviously, this situation is hypothetical; it would rare (given the patchy fossil record) to be able to discern all the contiguous stages in a species’ life history illustrated in this example. Invariably, biologists can only study populations that are “slices” of such lineages in more localized scales of ecological space and time; so only one stage can be discerned in a lineage.
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6. PRIMARY AND SECONDARY CONCEPTS OF THE SPECIES CATEGORY, AND SPECIES CRITERIA

The explanatory scope of the species category encompasses all those individuals called species; while a species concept is the definition that accounts for properties common to this category: one being that all species are individuals. And a thesis of this paper is that these individuals cannot be defined, but they can be discovered (Mayr, 1988). Mayr (1957) distinguished between theoretical (primary or non-operational) and operational (secondary or practicable) properties of species concepts. Subsequent contributors to the species debate (notably Mayr himself) then ignored this distinction. It was resurrected and emphasized by Mayden (1997) only recently. It is important to note that if a species concept is to be universally applicable to all biodiversity; it has to account for an immense variety of properties.

In actual fact, there is only one candidate for a primary species concept - as based on a classification of 22 species concepts; and all other concepts are secondary to it in conceptual scope. This is Simpson’s (1951) Evolutionary Species Concept (ESC) amended by Wiley (1978). It is the only species concept that comes anywhere near accounting for all properties of the species category. Mayden’s conclusion is reinforced by a widening consensus; his conclusion was preceded by Brothers (1985), who first concluded that only the ESC - as refined by Wiley (1978) - could fulfill all the demands for a universal species concept. This conceptual supremacy of the ESC has been concluded independently by several reviewers (Brooks & McLennan, 1991, 1999, 2002; Frost & Kluge, 1994; Mayden & Wood, 1995; Adams 1998; Wiens & Servedio 2000; and Wiley & Mayden 2000). The ESC is the only definition that comes anywhere near accommodating all that heterogeneity that has manifested in the species category. “The ESC is maximally applicable because everything we currently understand about descent, speciation, and species are compatible with the intent of the ESC” (Mayden, 1997: 419). This is because a species is:

“...... 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: 18).

The ESC is not operational, but certain secondary concepts are; so we can use the latter to reveal certain properties of species, such as divergence and lineage cohesion (see below). De Queiroz’s (1998, 1999) ontology of the species category (termed the General Lineage Concept, GLC⁴) highlights the properties of species discussed above as segments of populational lineages, with emphasis on the heterogeneous properties of lineages. Moreover, De Queiroz’s explication (1998, 1999) went further by emphasizing that operational species concepts are better termed species criteria, especially as they distinguish complementary properties of lineages. These criteria allow us to evaluate certain properties of a species as conceptualized by the ESC. It is important to note that these secondary concepts are not in conflict; in fact so much of the species debate has wasted considerable energy defending each concept’s apparent superiority.

Biologists have routinely conflated species concepts with species criteria; a common mistake has been to try and force the explanatory scope of a concept (such as the PSC) in the mistaken belief it would account for all heterogeneous properties of a species lineage. The obvious reason for these ensuing failures, in fact an allied mistake, has been to underestimate the heterogeneity of species’ properties. The articulation of this problem by De Queiroz (1998, 1999) has removed significant constraints that had preempted solutions to understand and discern complex properties of species. All species are evolutionary species; given their histories of origin, through persistence in time and space to extinction. Now exactly what properties of lineages can biologists conceptualize and discern? It is time to evaluate what these are, and how concepts (or rather criteria) of the species category can discover them.

7. KEY PROPERTIES OF EVOLUTIONARY SPECIES AND THEIR DISCOVERY

As individuals, species can only be discovered. They cannot be defined. Species criteria enable us to evaluate properties of lineages, and so discover evolutionary species. This is not merely because species are real entities out there in nature (Kluge, 1990). Neither is this some semantic issue. The strength of this distinction between discovery and definition parallels the radical dichotomy between an historical and non-historical philosophy of biology; indeed this philosophical dichotomy directly underpins this distinction. Species can only be reliably known in terms of their history. We can try and

⁴There is no discernable difference between the GLC and ESC; and the Evolutionary Species Concept (Simpson 1951, 1961) holds nomenclatural priority. As noted by De Querioz (1999: 77) notable ontological issues explicated in recent contributions to the Consilient Solution were first identified by Simpson (1951).
predict that two species will remain divergent lineages, but this is a prospective exercise fraught in uncertainty (O’Hara, 1993; Zink & McKitrick, 1995). Prospective guesses at the futures of species have all the credibility of crystal ball gazing; only retrospective investigations into species’ histories lie within the mandate of science. Frost and Kluge (1994) as well as Adams (1998) and Brooks and McLennan (1999) have dealt with these epistemological aspects of species discovery in detail. Nonetheless, they focused discovery operations on the PSC and divergence only. The ability to evaluate properties of lineages, with improved understanding of species’ properties, is significantly enhanced if other species criteria are brought to bear to evaluate pertinent properties of a populational lineage complementary to its divergence. For, example, the Recognition Species Concept (RSC, Paterson, 1985) can discern cohesiveness in a lineage (Fig. 3).

8.1 Coalescence
The existence of some young species (or neospecies) may be very hard to diagnose. This is especially where their initial divergence has manifested only at the molecular level. This is one good reason why we often struggle to diagnose species in terms of a preconceived conspicuousness. A pertinent example is the Nearctic Timberline Sparrow, *Spizella taverneri*, diagnosed as a recently evolved species (Klicka et al, 2001). The Genealogical Species Concept (GSC) (Avise & Ball, 1990) appears to be the appropriate criterion to discover neospecies; or more practically, molecular techniques in phylogenetic systematics allow coalescence and concordance to be measured. The latter are refined phylogenetic signals that can be detected within the noise of discordant gene trees. Indeed, Baum and Shaw (1995) proposed that what they termed “genealogical species” occupy the nexus where two lineages diverge. Here, genetic coalescence might well be (and indeed logically should be) the diagnosable property of a recently budded species. Emergence of genetic coalescence in a budding lineage would logically precede the evolution of unequivocal morphological divergence and exclusivity in the same lineage, before it has matured.

Coalescence is a less tangible property of lineages, because it typically manifests only in molecular characters. It is a property amply accommodated within the conceptual scope of the ESC. Some might argue that a coalescent lineage is not any part of a species, or is a “subspecies” (this last error is discussed in detail below). This argument boils down to which events we decide have been critical in a species’ individuation. Just because a lineage is hard to find, does not mean it does not exist, or is not a real evolutionary product. “The evolutionary species concept does not demand that there be morphological or phenetic differences between species, nor does it preclude such differences” (Wiley, 1978: 20).

8.2 Divergence
Incidence of lineage divergence is testable against the distinguishability criterion (de Queiroz, 1998) employing one of several Phylogenetic Species Concepts (PSC). A PSC can result in a Type I Error - too many species are recognised (Vrba, 1995; Adams, 1998, see below). The impetus for adoption of PSCs has been the growth of phylogenetic systematics emphasizing the temporal dimension of taxa: exemplified in the spread of tree-thinking through biology. The different phylogenetic species concepts differ profoundly, being based on either a pattern cladistic or phylogenetic (history-based) philosophy of systematics (Baum & Donoghue, 1995). Behavioural, molecular, or morphological characters, when evaluated in the context of the PSC, confirm whether two or more lineages have or have not diverged. PSCs contribute little to explanations of what species are (ontology of the species category), but their operational strength is better exploited as the distinguishability criterion: using diagnostic characters to discover evolutionary species.

Brooks and McLennan (1999) concluded that their PSC-1 is the best solution to detect divergent lineages that are segments of species. This is because it is couched in historical terms, and allows for the maximum possibility of different processes of speciation. Compared to the somewhat similar PSC-2, and Composite Species Concept (the CSC of Brooks & McLennan, 1999 is the Internodal Species Concept, ISC, in Mayden 1997), the PSC-1 requires evidence for both lineage divergence and character fixation to discover species. It is therefore the most scientifically robust criterion to detect lineages which have diverged unequivocally (Brooks & McLennan, 1999).

8.3 Exclusivity
Through its life history, a lineage may diverge and become exclusive. Again, the PSC-1 can discover such exclusive lineage segments that are part of a comparatively mature species (Fig. 3). “Where an exclusive group of organisms is one whose members are more closely related to each other than they are to organisms outside the group.” (Baum & Donoghue, 1995: 565; and see Baum & Donoghue, 1995, and Zink & McKitrick, 1995 for detailed discussion of exclusivity).
8.4 Cohesion
The RSC characterizes the cohesiveness of a species in terms of its Specific Mate Recognition System (SMRS). Compared to the BSC, the RSC is a subtle, but explicitly different criterion. Reproductive isolation is an incidental effect of interbreeding organisms’ adaptations for effective syngamy. The SMRS is an historical product, and it is a species level property that manifests in lineage cohesion. For example, the different pelage patterns of forest duikers; together with their scent glands, calls, and behaviours can be interpreted as parts of each species’ SMRS. These are adaptations that likely evolved directly to achieve mate recognition and syngamy. Exercising the criterion of cohesion, the RSC distinguishes between such populations as evolutionary species.

The superiority of history in structuring taxonomies moves beyond the “resemblance - descent dichotomy” that has persistently plagued the species debate. The BSC is centred on the notion of resemblance, and thus degree of difference between organisms which are treated as members of different sets; this typological view contrasts with the strength of the Paterson’s (1985) RSC. In actual fact, the RSC, when properly conceptualized, can only be construed in terms of organismal descent. The RSC see such resemblances as an historical product; more specifically it sees organisms’ characters as co-evolved adaptations that collectively form the co-evolved SMRS in a cohesive lineage. Such resemblances among the closely related organisms making up this lineage may well prove useful to discover species, but tells us little, if anything, about what species really are.

The RSC complements the distinguishability criterion of PSCs. It allows one to evaluate the comparative maturity of a lineage segment of a species that exhibits divergence and/or exclusivity; newly divergent species may indeed be distinguished by their divergence, yet distinct cohesion will only be discernable in a matured lineage (Fig. 3). Again, our cognisance of history underwrites this construal of the radical difference between the BSC and RSC. As applied to cryptic species of Afrotropical horseshoe bats (*Rhinolophus*) the combination of the PSC and RSC provided insightful tools to discover evolutionary species (Cotterill, 2002b). Behavioural, molecular and morphological characters can be compared to discern whether one or more individual lineages exist (Fig. 3).

8.5 Applications of the Evolutionary Species Concept
The scientific power of the Evolutionary Species Concept has been demonstrated for fishes (Mayden and Wood, 1995), herpetofauna (Collins, 1991; Frost, Kluge & Hillis, 1992) and nematodes (Adams, 1998). Contemplation of the well known arguments over the PSC versus BSC (e.g. Zink 1996) reveal that what is at stake is a non historical versus historical philosophy of biology. Considered in the light of previous discussion, avian species characterized by the PSC are actually evolutionary species (subject to no Type I errors). It is interesting that mammalogy is one of the last bastions of the BSC; mammalogists are conspicuous in ignoring the debate and revolution (grounded in tree-thinking) in evolutionary biology, which began to permeate herpetology and ornithology in the 1980s! Nevertheless, the forthcoming 3rd edition of *Mammals of the World* is adopting “a more phylogenetic viewpoint” (D. E. Wilson pers. comm.); and the taxonomy of Chiroptera (*Simmons, in press*) distinguishes many more species over those classified using the BSC by Koopman (1993). Groves (2001) also acknowledged that the PSC is the operational analogue of the ESC; but remarkably, he proceeded to use trinomials in revising the world’s extant primates! The ESC (with PSC and RSC as operational criteria) has been applied to certain Afrotropical bovids and bats (Cotterill 2001a,b; 2002b, *in press*). So while expurgation of the BSC from mammalian taxonomy has begun, much work is still required. The most positive attribute of this revolution is the replacement of a non-historically based taxonomy with that grounded intrinsically in the philosophies and methods of historical biology - in short tree-thinking.

In conclusion, species criteria reveal to us the existence of historically derived properties of lineages; this enables systematists to characterize evolutionary species. Deeper explanation of this operationalism centres on the observation that species criteria can quantify complementary facets in a variable species lineage; such pertinent facets include coalescence, divergence and exclusivity, and cohesion (Fig. 3). Now that we can see that all species concepts are secondary to the ESC (and can discern complementary attributes of lineages), we can expand on this valuable solution to the species debate.

9 THE CONSILENT SOLUTION TO THE SPECIES DEBATE
What could be labeled the “ESC-criteria solution” to the species problem, I call the “Consilient Solution”. This is a more succinct and descriptive label for a theoretical structure built of disparately derived knowledge. Independent findings by different authorities converged to create a mutually supporting solution. This was arrived at from different starting points in independent research and reviews of species’ properties. Perhaps even more significantly, several of these papers have
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tackled very different parts of biodiversity (several phyla of eukaryotic parasites, nematodes and different vertebrate phyla). The Consilient Solution is consolidated by the ontology of species (see previous section) that construes them as lineages (De Queiroz 1998, 1999). Explicit reference to consilience follows Whewell (1834–1858, in Butts 1989) and Ruse (1979). It refers to the jumping together of independent findings into an expanded synthesis of improved understanding. Consilient knowledge is formed from mutual reinforcement of disparately derived discoveries about the properties of the natural world. This coming together of results of several independent discovery operations provide global explanations. In this respect, the explanatory power of the ESC has been set up from the consilient integration of separate theories about populations and phylogenetics (Frost & Kluge, 1994).

A commonality of key contributions (Wiley, 1978; Brothers, 1985; Frost & Kluge, 1994; Mayden, 1997; Adams, 1998; Brooks and McLennan, 1999; Wiley, and Mayden 2000) to the Consilient Solution recognized that questions centred on “What is a Species?” differ fundamentally from those to do with discerning actual species in nature. All these key contributions agree on a universal species concept - the ESC. This shared focus on the ESC arises from agreement that, as individuals, species are time-extended lineages, formed by the more-making activities of organisms. The ontological basis to the finer scaled patterns structured as discrete variation among species is most objectively understood in terms of time-extended lineages being historical individuals (Kluge 1990; Baum 1998). An admixture of constraint and benefit followed from a consensus among evolutionary biologists of species’ individuality, with cognisance of its revolutionary implications. Systematists came to reconcile with critical epistemological limits that constrain attempts to understand and characterize species. Yet, these constraints actually fostered solutions. Here, the species-are-individuals thesis, in permeating evolutionary biology, has come to underpin a scientific methodology to characterize species.

9.1 The Distinction between Theoretical and Practical Concepts

This key idea, originally recognized by Mayr (1957), belatedly influenced the species debate only toward the close of the 20th century. This distinction is however implicit in no less than three contributions. One was an overview of the definitions and discovery of species (Eldredge & Cracraft 1980) - understandable given that their definition of the species category was explicitly based in a construal of species as individuals. Two, it underpinned Ridley’s (1989) proposal of the Hennigian Species Concept (HSC) being operationalized by the BSC and Ecological Species Concept (EsSC). (Considered in retrospect, Ridley’s solution was misleading, principally in employing the wrong concepts.) Third, Templeton (1994, 1998) emphasized that species are lineages, and testable hypotheses allow us to discover these entities. Other authors, in elucidating the primacy of the ESC, tacitly distinguished between theoretical and practical concepts. Kluge (1990), for example, concluded that his definition of the species category was monistic in allowing it to be operationalized in more than one way. Yet these operational, and thus practicable, instruments were still seen in the main as concepts, albeit in a secondary role; then De Queiroz (1998, 1999) explicitly distinguished between concept and criterion. Whether labeled a species criterion or secondary concept, these mental constructs quantify both a pattern common to the species category, and also a property discernable in an historical individual - namely a particular segment of a unique populational lineage. This property of the Consilient Solution reveals how difficult it is to separate ontological explication from epistemological procedure. A species criterion highlights a common pattern in the species category, such as cohesion; as it simultaneously quantifies characters associated with instances of that pattern in a specific lineage. With respect to cohesion, an example of a particular lineage segment would be that cohesive segment resplendent in the SMRS of *Cephalophus hooki*. The latter insight is obtained directly from studying the natural history of representative duikers of this particular historical individual, namely *C. hooki*. One function of a species criterion is clearly ontological, the other is patently epistemological. The ESC allows us to conceptualize (but no more than conceptualize) the entirety of a lineage, while criteria (as secondary concepts) visualize lineage segments (and only segments) because their conceptual scope is circumscribed; but most importantly each can quantify this delimited property only (divergence or cohesion for example).

9.2 Conclusions

These solutions are all focused on recognizing and characterizing time-extended lineages; a development formalized in the ontological explication of the ESC. The latter is based in turn on accommodating species’ individualities in all their heterogeneity. As an emergent strength of the Consilient Solution, this pattern is instructive; for it illustrates how a robust theory has been forged through independent yet mutually supporting pathways of resolution. This has been achieved by stitching together many different philosophical and empirical insights into the properties of organismal biodiversity; each was etched out in an individual contribution in resolving a certain aspect of species’ biology. These independent discoveries frequently employed empirical evidence to reach their particular solution. Subsequently, in novel combination, they have then solved more challenging problems about the species category. So considered in retrospect, different solutions (each
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enunciating primacy of the ESC) converged on one solution; independent discoveries repeatedly converged to mutually reinforce a global solution.

Through the latter half of the 20th century, the NeoDarwinian Synthesis eclipsed considerations of history from biology (Brooks & McLennan, 1999, 2002). Latterly, founded on population-thinking and structured by tree-thinking (O’Hara 1988, 1997), the Consilient Solution is founded firmly in acknowledging that each living entity is unique; and in cognisance that nothing in biology makes sense except in the light of history. Furthermore, the ESC has provided a conceptual platform of sufficient breadth to incorporate all those independent contributions that have revealed the disparate, yet complementary, properties of the species category. The corroborative progress in forging the Consilient Solution enabled theoreticians to make forays into previously inaccessible conceptual terrain. To reiterate a noteworthy example, the construal of the notion of species criteria was contingent on the realization that only one species concept (the ESC) is the primary concept, and operationalized by certain secondary concepts. This refinement in theory enabled biologists to bootstrap their understanding to overcome several entangled issues that had previously proved intractable. Overall, structured by tree-thinking and founded on the ESC, the synthesis of many facets of independently derived understanding into the Consilient Solution overcame knotty challenges in understanding biodiversity.

ERRORS IN CHARACTERIZATION OF SPECIES

Taxonomic Errors: Types I, II and III

So far, risks of Type I and Type II errors in taxonomy were mentioned without explication. We can now lean on the Consilient Solution to review this critical topic. This section follows Frost and Hillis (1990) and Adams (1998) to emphasize far reaching consequences of erroneous taxonomies. Three categories of mistakes hover over the deliberations of taxonomists as they search for and classify species. Not only may we characterize either too many or too few species, but the evolutionary history among species can be misconstrued (Adams, 1998). Recall, precision (degree of detail) denotes exactly what, or how many, species are characterized; while accuracy (correctness) refers to whether or not one classifies species with respect to their evolutionary relationships. Selected taxa of duikers exemplify and illustrate these major differences in classifications of biodiversity:

! Type I Errors. Too many species are characterized, compared to reality, to reduce taxonomic precision. Type I errors occur when uncritical use of the distinguishability criterion splits two or more populations of a heterogeneous species into different lineages. Such a Type I error would result from inappropriate use of a PSC, and equally from inadequate sampling of populational variation Here, despite what contemporary knowledge suggests is just one species of red duiker (Fig. 4a), natalensis and robertsi are treated as distinct species (Fig. 4b);

! Type II Errors. Too few species are characterized, and again taxonomic precision suffers; this often happens in the case of cryptic species, especially using the BSC. Here, for example, Cephalophus harveyi is treated as conspecific with C. natalensis, despite these species being distinct lineages (Fig. 4c);

! Type III Errors. Evolutionary histories of species are wrongly represented at the cost of taxonomic precision. Type III errors can be especially serious in creating false knowledge of biodiversity. Treating Peters’ Duiker, C. callipygus as part of a superspecies, together with east African red duikers, is a pertinent example (Figs 4c & 4d). Another example is classifying Ruwenzori Red Duiker, C. rubidus with the east African red duikers. An analogous, and common, mistake in typological taxonomies is to lump divergent lineages into polytypic species in ignorance of phylogenetic uniqueness (here rubidus and harveyi are considered subspecies of C. natalensis - Figs 4c & 4d). Such erroneous taxonomies enfeebled by Type III errors have far reaching consequences - especially in conservation - because the correct topology of evolutionary relationships is not merely misconstrued, but ignored.

Weaknesses in the Biological Species Concept (BSC)

A serious weakness of the BSC is that it misses real species, and invariably lumps lineages into non historical groups (Frost et al. 1992; Zink & McKitrick 1995; Adams, 1998). A combination of the PSC (notably the PSC-1) and RSC minimizes the risk of injecting these Type II errors into taxonomies ( Cotterill 2002b). Type III errors are insidious in their failure to characterize phylogenetic uniqueness accurately. Contrary to popular belief, the superspecies concept (whether trying to employ the vague concepts of semispecies, allospecies, or megasubspecies) does not overcome inadequacies of the BSC;
it magnifies Type III errors. Worse, these concepts confer a false sense of “taxonomic security” (see below). Type III errors afflict many taxonomies, particularly of vertebrates; and these problems are rife in mammalogy - notably in incorrect taxonomies of antelopes. Use of the PSC-1 as a criterion minimizes Type III errors (as well as Type I errors), to maximize accurate representation of evolutionary history (Brooks & McLennan, 1999). In practice, the existence of biological species has been divined from appraisals of overall similarity. And this criticism can be equally applied to whether these antelopes are labeled subspecies, allospecies, semispecies, or actual biological species. The BSC’s ability to characterize the real diversity of antelopes is confounded by the prescription for unambiguous evidence of reproductive isolation (see following section). Patterns of reproductive compatibility (assuming they could even be tested in these natural populations) are at odds with the goal of systematics to discern patterns in evolutionary history - testing which extant populations represent evolutionary species. It ignores the topological patterns traced out among evolving lineages. In fact, it appears that the time honoured classification of antelopes as polytypic species rarely considered reproductive isolation; because these were structured on notions of morphospecies. To conclude on the scientific inadequacies of the BSC (see Cotterill 2001a,b, 2002a,b for additional argument) the BSC cannot begin to account for the evolutionary history of divergent lineages, and especially falls down in trying to characterize allopatric lineages. For further details on these problems and criticisms of the BSC: see Paterson (1982, 1985); Templeton (1989); Cracraft (1983, 1989, 1997, 2000); Zink & McKitrick (1995); Klicka et al. (2002); and Avise and Wollenberg (1997) and Mayr (2000) for defenses.

To conclude on these examples, and reiterate an earlier conclusion; only the ESC comes anywhere near characterizing the real diversity of biodiversity precisely and accurately. Remarkable as it may seem, many biological species are fictional entities (see Jolly 1993 for examples of African primates). Examples include certain red duikers, notably the polyphyletic and polytypic C. [natalensis] (Fig. 5, see above) the “Red lechwe” Kobus leche (Cotterill, 2002c), and the polytypic D. lunatus (Cotterill, 2002a). In contrast, evolutionary species are conceptual renditions of lineages that actually exist. The major potential error facing taxonomists’ deliberations in diagnosing evolutionary species is a Type I error - recognizing more species than actually exist (but use of the PSC-1 minimizes these errors). This overview of the three categories of errors in taxonomy leads us on to lay to rest three serious weaknesses in taxonomic theory and practice.

11. THREE COMMON MISCONSTRUALS OF SPECIES’ PROPERTIES

11.1 Ephemerol Lineages and Fuzzy Boundaries between Lineages: Are Subspecies\(^5\) Real?

“If they [i.e. subspecies] are discoverable, then they clearly are elements of evolutionary biology; if they are invented they are an impediment to the formulation of historical hypotheses. Within the context of phylogenetic inference the use of subspecies (= temporarily isolated sublineages; not “incipient” lineages) is severely restricted. This is because identifying a sublineage requires the same kind of evidence for recognizing a lineage, not less, and also requires the additional assumption that the sublineages will reconstitute in the future to reconstitute the lineage....no theoretical justification exists for such predictions.” (Frost, et al. 1992:48).

Through over two centuries of taxonomic history, biology has struggled to account for the heterogeneity of populations. In clear cut cases, where two or more lineages exhibit unequivocal divergence (the obvious divergence between Oreotragus oreotragus and Raphicerus campestris is an example) uncertainty is minimal, if not absent in the resulting characterization (Table 1). Uncertainties, in fact major problems, creep in, once we consider more closely related or highly convergent lineages. For example, how does one objectively classify the many populations of klipspringers across subSaharan Africa? These challenges bedevil taxonomy no matter the organisms studied. Its problems are construed as those of classification “below the species level”.

The subspecies concept entered taxonomic usage in the late 19th century in the guise of trinomial naming of organisms. Organisms perceived to be races, forms or varieties were given subspecific names. Subspecies have become a popular, and indeed entrenched concept in contemporary taxonomy, and especially in taxonomies of vertebrates. Mayr and Ashlock (1991: 43) described a subspecies as “…an aggregation of phenotypically similar populations of a species inhabiting a geographic subdivision of the range of that species and differing taxonomically from other populations of that species”. The subspecies category has been applied in several different roles. It is very difficult to pin down exactly what a subspecies really is in nature. The limits imposed are only arbitrary, human-constructed boundaries; such that a widely

\(^5\)Comments and arguments in this section also apply to the concept of an “Evolutionary Significant Unit (ESU)”.

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Figure 4. The three main categories of errors in taxonomies (modified from Adams, 1998 with graphics derived from Kingdon, 1997) 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*.

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.
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Figure 4. Cont.  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.
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used application is to use subspecies to sort museum specimens of one species into cabinet drawers. Much of what is concluded about the subspecies concept here is based on Frost, et al. (1992).

Jolly (1993) concluded that, compared to species, subspecies are more ephemeral lineages. The key difference being that subspecies disappear either through extinction or through merging into neighbouring populations. “it is a subspecies’ failure to attain complete independence, not its origin, that defines its difference from species” (Jolly, 1993: 90). Conversely, according to Jolly (1993), species only disappear by going extinct. All such arguments that attempt to distinguish subspecies from species fall down on their ontological wooliness. If they are indeed distinct discoverable entities, these more ephemeral lineages that Jolly and others term subspecies should have discrete trajectories as distinct lineages. If discoverable, such lineages are merely young evolutionary species (or neospecies); and divergence in their lineages may only be detectable using molecular characters applying the coalescent criterion. Even though indistinguishable in morphology, the existence of a neospecies, that has recently diverged from a parent lineage, can be diagnosed by the GSC.

As argued by Frost et al. (1992), we can dismiss the argument that subspecies are “incipient species”. This runs counter to an axiom of species ontology and epistemology in this paper; a species can be discovered because it exists as a lineage with a unique history. For example, if one encounters two lineages (Fig. 3) that have undergone recent and initial divergence, then we might quibble over whether they are treated as one or two species. One can arbitrarily decide what criteria (coalescence, divergence or cohesion) delimit the species category. Some might argue that a species only comes into being when the lineage exhibits cohesion manifested in a distinct SMRS. Yet, as argued by De Queiroz (1999), it is wrong to argue that an embryo, neonate or juvenile are not the same individual organism. Equally a larva or pupa are all the same individual insect. Thus, analogously, a lineage is a species at its stages of coalescence and initial divergence, and not just in its cohesion (Fig. 3). It is unique particulars of a lineage’s individuation that determines its ‘species-ness’. It is important to acknowledge that we often need to see through and around the heterogeneous variation of lineages to diagnose those instances of authentic diversity that represent real species. Again, nothing in biology makes sense except in the light of history.

It has proved impossible to develop an objective definition of what subspecies are, yet alone objective protocols for their characterization. This is not surprising when one acknowledges that species are individuals, and may often exhibit great heterogeneity in their properties; which are especially likely in widespread species. The modern treatment of subspecies has been either to discount their existence entirely (Cracraft, 1983; Frost et al, 1992; Mayden & Wood, 1995), or try and utilize them as labels for recognizable taxonomic units (Groves, 2001). Groves’ defense of subspecies is bizarre - considering he used the PSC as superior to the BSC. Subspecies are nothing more than anthropogenic inventions, with no place in a scientific taxonomy. Similarly, the defense of subspecies of avifauna (Ball & Avise, 1992) merely reiterated typologically based arguments that ignore key facets of the ontology of biodiversity, and the goals and operations of systematics that underpin the Consilient Solution.

The Consilient Solution obviates these problems. One, refined ontology of the species category acknowledges that any species (as a time extended lineage) exhibits a life history. Thus, species are implicitly heterogeneous in their properties. Second, understanding these contributions of the Consilient Solution, and their application to taxonomic problems, obviates any need to employ subjective concepts (notably that of subspecies) in taxonomy. Most importantly, the grounding of the Consilient Solution in an historical philosophy of biology gets us over the subjectivity of the subspecies category. It is simply unnecessary to employ a subspecies concept. Evolutionary biology and systematics awaits a credible explanation of the subspecies category. A scientifically robust explication - as to what subspecies are - has so far defeated its protagonists. Until this happens (an impossibility given the ontology of life’s variety presented above), I conclude that its use in taxonomy (including mammalogy) creates more problems than it solves.

11.2 What about Reproductive Isolation?

"Rather than getting over the species problem, we need to get over the inclination to obliterate history by changing the names of historical entities whenever reticulation or, as is more often the case, limited exchange or donation of parts has been detected or inferred." (Zink & McKitrick, 1995: 711)

There is a widespread belief that a species is defined by its reproductive isolation. Organisms breed true within their species. Evidence that organisms belonging to two apparently distinct species hybridize is held up as evidence for their conspecificity. Not necessarily. Schilthuizen (2000) has distinguished (note italics for emphasis) between the species
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A concept that sees a species as a cohesive population of co-evolved genes⁶, and the species definition that emphasizes reproductive isolation of the population. It is worth noting that these populations recognized as biological species are simply segments of a lineage; a lineage segment that is conceptualized amply well by the ESC. Again, our earlier example of organ transplants between donor and recipients (see Section 4.0) emphasizes why hybridization (especially along peripheries of species’ ranges) does not change the individuality of the two species.

Much more attention needs to be paid to an explicit understanding of how reproduction isolation evolves. Here, the historical origin of cohesion in species lineages is instructive. Cohesion arises as an incidental effect of selection acting on more-making activities of organisms. This point has already been made in arguing for the practicable relevance of the RSC to discern cohesiveness. As argued emphatically (initially by Paterson, 1982, 1985, and belatedly by Schilthuizen 2000), reproductive isolation is an incidental byproduct of evolutionary processes acted out among organisms. It cannot be overemphasized that reproductive isolation is an effect (but an important effect nonetheless) that manifests in the cohesiveness of a lineage.

The belief that species breed true, and that reproductive purity is the singular, defining property of the species category, smacks of thinly disguised typological thinking. This antiquated, and unfortunately entrenched, belief about nature is closely linked to the idea that species have essences. Obsession with reproductive isolation greatly distorts and ignores understanding of the complex properties of species. Costs to scientific understanding are acute. A objective cognisance of the heterogeneity of the properties of the species category has to consider at least coalescence, divergence, exclusivity: and thus not just cohesion in lineages. In the same vein (contra the assertion that the PSC is the operational analogue of the ESC, Frost & Kluge 1994; Groves 2001), much more evidence besides divergence reveals species. Above all, one has to structure these ideas and allied research into an historical framework, given that species exhibit complex life histories.

11.3 The superspecies concept compounds deficiencies of the BSC

Some systematists have tried to characterize what appear to be closely related populations as superspecies. The superspecies concept "... a monophyletic group of closely related and largely or entirely allopatric species" (Mayr & Ashlock, 1991: 53) was introduced in attempts to characterize populations of morphologically similar organisms with scientific objectivity. Grubb (1978, 2000) concluded that much of the extant diversity of African mammals includes a preponderance of superspecies: each comprised of two or more allopatric and/or parapatric populations. Exemplified by certain Cephalophini⁷ (Fig. 5), Ansell (1972) employed the superspecies concept to try and solve several problems in bovid taxonomy.

This treatment of complexes of geographically disjunct populations attempts to overcome intractable inadequacies in the BSC. Although superspecies are purported to be objectively characterized groups of closely related species, use of this concept perpetuates the typological mistake of lumping divergent lineages into one unit comprised of “allospecific” or “semispecific” sets. Morphological resemblance is used to group these taxa. It is a matter of subjective opinion whether these populations are subspecies, allospecies, paraspecies or “good” biological species. The superspecies concept is not only inherently phenetic, it is typological and non-historical. If divergence within what is (apparently) one monophyletic clade of lineages is to be objectively characterized, then superspecies nomenclature (as with trinomials) is challenged to describe real patterns of divergence between constituent lineages accurately. Structured by the underlying concept (the BSC to be precise), the names placed on such taxa should constitute monickers that characterize these lineages (real biological entities) as evolutionary products accurately and precisely.

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⁶Such a cohesive lineage segment would likely possess a distinct SMRS; that can be conceptualized and discerned if we employ the Recognition Species Concept (RSC) of Paterson (1985) as a criterion.

⁷Grubb and Groves (2001) recently published a phylogeny of the Cephalophini. This employed 41 morphological characters for 17 taxa in a cladistic analysis. Although their cladogram broadly agrees with Jansen Van Vuuren and Robinson (2001), the two phylogenies differ in important aspects.
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Whether we like or not, cognisance of how evolutionary processes have structured properties of living variety are fundamental to understand, discover and classify the historical products that are parts of biodiversity. Considered in this vein, the recent argument that the BSC outdoes the operational capabilities of the PSC (Avise & Wollenberg, 1997) is fundamentally flawed by its typological view of taxonomy as a pigeon-holing operation to organize sets of populations divided by patterns of discontinuous variation. Unfortunately (but not surprisingly given that it is merely a rehash of the BSC), the superspecies concept cannot account for historical properties of taxa. This obviates its scientific relevance. In practice, only a PSC can discover those monophyletic clusters of lineages that are allopatric species; in phylogenetic systematics these natural groups are known as clades.

If taxonomy does seek authentic knowledge of biodiversity, then the superspecies concept is a perilous panacea; principally because it lumps together apparently morphologically similar taxa into non-historical groups. Taxa implicitly construed as closely related may well turn out to be highly divergent. Despite its definition, the criterion of monophyly is not just ignored but intrinsically misconstrued. The undesirability of such Type III errors in taxonomies, already criticized above, cannot be overemphasized. The examples illustrated in Fig. 4 provide a pertinent example where evolutionary relationships of forest duikers have been utterly misconstrued by the superspecies concept. So, insidiously, far from classifying biodiversity correctly, the superspecies concept magnifies Type III errors in taxonomy.

12. FINAL REMARKS ABOUT THE SPECIES DEBATE AND CONSILENT SOLUTION

12.1 Conclusions to Conceptual Review

It is impossible to understand anything about biodiversity (including species) unless an historical philosophy is brought to bear on the complexities of nature; whether one seeks to discover species or any other entities. This necessarily involves cognisance of biological variety, especially its manifestation in the variation of populational lineages and diversification of lineages into species and higher taxa. The understanding that each species is unique is antithetical to entrenched typological views of biodiversity (typological thinking that can be traced back to Plato, and is implicit in folk taxonomies, Atran, 1990). A historical perspective of life’s complexities is essential to reveal what species actually are. In fact, this understanding is only a facet, albeit a central facet, of an encompassing ontology of life; the keystone of this ontology recognizes the hierarchical organization of uniqueness, across the levels of organization of organisms, populational lineages and larger clades; species are important entities as they are central and dynamic products of diversification, forged at the nexus where variable populations have diversified (Figs 1-4).

"Thus, the key issue is not the number of kinds of species admitted but whether we stress unitary perceptual individuals or the parallel individuation of groups of organisms by multiple biological processes." (Baum, 1998:647). It is likely that debate will continue to rage among philosophers of biology and systematists as to how many kinds of individuals actually exist; and perhaps how many kinds of species exist. And we may at some future date come to reconcile with a state of affairs where what we construe to be the species category contains some very different entities indeed. One might hypothesize that this state of affairs could prevail when the nature of microbial diversity becomes much better known. It might indeed differ utterly from eukaryotic biodiversity. This fascinating possibility need detain us no longer, given the focus of this paper on antelopes.

At the bottom line, it is unprofessional to allow society to infer (through published information or other media) that things like subspecies and superspecies are conceptual constructs of real biodiversity when they are not. It is questionable for a professional biologist to try and blatantly defend those ideas that have no philosophical let alone material credibility. Such debates fall outside the sphere of scientific rationality. This endorses a professional responsibility to present and defend scientific concepts and knowledge about biodiversity, given societal demands for accurate and precise information. The ideas of subspecies and superspecies are not heuristic guides, because they misconstrue properties of biodiversity severely. Defense of such concepts and their persistent popularity is strange considering that taxonomy and systematics are the fundamental sciences uniting all biology. The persistence of these ideas is stranger still, given that we have the Consilient Solution; where the ESC eclipses concepts of the species category that are subjective and of inferior explanatory power. The time is long overdue for systematists and indeed all biologists to rid science of the subjective notions of the subspecies and superspecies, and especially the Biological Species Concept.

A convergent solution to the species problem has provided biologists with a credible research programme; species are historical individuals whose existence can be discovered by sifting the empirical evidence obtained from studied organisms; species criteria are our key tools in these operations. The ontological foundations of the ESC, explicated in terms of De Queiroz’s General Lineage Concept of species and Ghiselin’s individuality thesis, provide the conceptually sound
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... explanation for us to evaluate populational lineages, in terms of their divergence, exclusivity, or cohesiveness. The ESC further accommodates all organisms of disparate phylogenetic affinities. It can conceptualize species that are geographically cosmopolitan or locally endemic, and those lineages whose constituent organisms exhibit great or minimal variation. It is the history of their lineages that matters, and the biologist of the new millennium now has powerful methodology (including cladistics) and tools (including molecular techniques) to discover these historical entities. We can indeed classify organisms in many different ways; but the overarching axiom of this paper's argument is that systematics aims to discover and describe evolutionary history. This forecloses all other options for taxonomists; for nothing but deciphered historical patterns can build authentic taxonomies - of all biodiversity, not just antelopes.

13. CHALLENGES IN ELUCIDATING THE REAL TAXONOMY OF THE BOVIDAE

It is premature to survey all the Bovidae to try and determine their real diversity in the currency of evolutionary species. We first need an unprecedented investment in basic research to quantify variation within lineages; for only then will we be able to appraise the overall patterns of antelope variety comprehensively. This is the logical, albeit lengthy, procedure to diagnose those lineages that represent real species. While we need to employ the ESC to evaluate the diversity of these antelopes more objectively, this is a task beyond the scope of this paper. Still, certain examples illustrate deficiencies, research opportunities, and the way forward.

Table 1 surveys some of the antelopes believed to have evolved within certain genera. It is important to acknowledge that these taxa have been characterized in terms of the morphospecies and Biological Species Concepts. This raises risks of Type II errors, when we consider published phylogenies of selected African antelopes. Sampling of populational variation has been sparse; especially in the case of molecular characters. Biological species are the stolid units of analysis in bovid phylogenies, in which the BSC has framed interpretations. Examples include Jansen Van Vuuren & Robinson (2001) and Vrba, Vaisnys, Gatesy, Desalle & Wei (1994). Nonetheless, these microtaxonomic deficiencies aside, these phylogenies present interesting puzzles. For example, *Ourebia* has traditionally been classified in the Neotragini (Ansell, 1972; Meester, et al., 1986; Gentry, 1990, 1992). It was presumed to be closely related to *Raphicerus* (Grubb, 1993); a recent phylogenetic analysis by Vrba, et al. (1994) included it in the Reduncini on the basis of cranial characters and the morphology of scent glands (Hofmann, 1972). Most recently, a comprehensive cladistic analysis (Vrba & Schaller, 2000) concluded oribi to be most closely related to gazelles - an interesting result.

Many examples of clinal variation have been described in African bovids (Grubb, 2000). Obviously, any serious attempts to get to grips with the evolutionary species of these antelopes will have to evaluate the patterns of this variation as objectively as data permit and theory dictates. One example is the *Damaliscus lunatus* complex. Reevaluation of museum specimens has revealed that the real diversity of these alcelaphine antelopes had been seriously misconstrued; it is anything but clinal (Cotterill, in press). Recently, Grubb (1999) presented a scholarly review of the incidence of cladogenesis in African mammals, but couched in terms of the BSC. In consequence this weakened an otherwise robust dataset, and rendered the conclusions equivocal. As with a recent taxonomy of Primata (Groves, 2001), one cannot go halfway in applying an historical perspective to try and understand the diversity and taxonomy of these mammals. One can no longer justify taxonomy which “pigeon-holes” artificial taxa imprecisely into inaccurate taxonomies. Both Vrba (1995) and Grubb (1999) are right in stating that not all allopatric populations are automatically species in terms of the PSC (their criticism of Cracraft, 1983). This deficiency was discussed above; it can be obviated by using the PSC-1 (Brooks & McLennan, 1999) to apply the distinguishability criterion.

The deficiencies of museum collections are a serious impediment to progress in establishing the true diversity of African antelopes (Box 1). This impediment to taxonomic progress has scarcely been rectified over the past half century; since discussed by Ansell (1958) in a paper which deserves to be more widely read, especially today. The fundamental importance of natural science specimens in systematics, taxonomy; and indeed all biology cannot be overemphasized (Box 1). All biologists working with antelopes and concerned with their conservation can make immense contributions to rectifying inadequate representation in museum collections. This is especially true of those in the position to collect material from the hunting and bushmeat industries (Boxes 1-3).

13.1 Reduncines (Lechwes and Waterbucks)

Aspects of the recent diversification of reduncine antelopes in south-central Africa (with a focus on the Zambezi Basin) has been reviewed in detail (Cotterill, 2000, 2003). This will not be repeated, except to emphasize that *Kobus leche* is not a polytypic species. As for many antelopes, this treatment can be traced back to Lydekker and Blaine (1914) and Ellerman, et al. (1953), and in this case Barclay (1933). Nevertheless, Ansell & Banfield (1979) used multivariate analyses...
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of representative samples of the four populations to demonstrate that the described populations exhibited unequivocal divergence; but they still recognized four subspecies, despite unequivocal dichopatry and morphological differences between these four species lineages.

The lechwes actually comprise no less than four evolutionary species. These are: the Black lechwe, *K. smithemani*; Kafue lechwe, *K. kafuensis*; the apparently extinct Robert’s lechwe, *K. robertsi*; and topotypical Red lechwe, *K. leche sensu stricto*. These four taxa are not only dichopatric, but exhibit significant divergence in morphology and behaviour. The latter characters likely represent distinct SMRSs. Elucidation of the true diversity of these lechwes is the subject of current research (Cotterill, unpublished data). The diversity of waterbucks also requires objective review. The many described populations have been suggested to comprise one superspecies: *Kobus [ellipsiprymnus]* (W. F. H. Ansell, in Meester, et al. 1986: 223); but this is very unlikely, given the patchy distributions, and evidence for clear divergence between the *defassa* and *ellipsiprymnus* lineages. Resolution of the true patterns of variation and diversity in these widely distributed reducines will entail challenging research. It will require exhaustive review of existing museum material, and likely necessitate analysis of molecular characters.

### 13.2 Dikdiks

The true diversity of the arid adapted dikdiks appears to have been misconstrued. *Madoqua damarensis* is dichopatrically isolated in southwest Africa from *M. kirkii* in northeast Africa (Tinley, 1969; Smithers, 1983). The dichopatric *M. damarensis* lacks pedal glands and has padded hooves (Tinley, 1969), compared to *M. kirkii* (Pocock, 1910); the four populations are considered subspecies in the polytypic biological species *kirkii* (Grubb, 1993). Nevertheless, they have distinct karyotypes (Ryder, et al., 1989). This karyotypic evidence for their distinguishability strongly suggests that, in addition to *damarensis*, *kirkii* comprises no less than three evolutionary species. Should these characters represent distinct SMRS's, then the speciation between these distinguishable lineages is comparatively mature; the different crowns (and other pelage characters) and scent glands of *M. damarensis* and *M. kirkii* support this hypothesis.

The complex of *Madoqua* in the arid regions of northeast Africa is thought to comprise at least four biological species (Yalden, 1978; Grubb, 1993). Initial perusal of the dichopatric and peripatric distributions of these populations suggest that at least nine evolutionary species are likely involved. Diversification of *Madoqua* in Africa’s arid landscapes approaches that of *Cephalophus* in the continent’s forests (Table 1). Some of these species, especially the Silver Dik dik, *M. piancentinii, are acutely endangered. The latter is confined to an unusual strip of coastal scrub in Ottia on the northeast African littoral zone (Kingdon, 1997).

### 13.3 Forest Duikers

The forest duikers represent a great and still poorly understood component of the variety of dwarf antelopes. A high proportion of these bovid include some of the most poorly known Mammalia, whose continued existence is greatly threatened by humans. The recently elucidated phylogeny of the Cephalophini (Jansen Van Vuuren & Robinson, 2001) is a useful starting point (see Fig. 4 above). Unfortunately, its analysis and interpretation is weakened by dependence on the BSC and satellite concepts. The data need to be re-analyzed in the context of the Consilient Solution to diagnose evolutionary species.

Examples of evolutionary species of duikers include: Pemba Blue Duiker, *Philantomba pmbae* Kershaw, 1922 (endemic to Pemba Island); Foster’s duiker, *C. fosteri* St. Leger, 1934 (endemic to Mount Elgon, Kenya and treated as a subspecies of *C. nigrifrons* by Ansell, 1972). To these may be added *Philantomba melanorheus* Gray, 1846 (endemic to Bioko Island, Equatorial Guinea, and treated as a subspecies of *C. monticola* by Ansell, 1972). As with many small antelopes, there are several polytypic species of duikers which need to be scrutinized in the context of the Consilient Solution. An obvious example is “Ogilby’s Duiker” which clearly consists of three evolutionary species. These are: Brooke’s Duiker, *C. brookei* Thomas, 1903; White-legged Duiker, *C. crusalbum* Grubb, 1978; and Oligby’s Duiker, *C. ogilbyi* (Waterhouse, 1838) as mapped in Kingdon (1997).

The ecologically ubiquitous *Sylvicapra* occurs throughout the southern and Guinean savannas of Africa, and also occurs in arid landscapes (Smithers, 1983). At least 36 forms and races have been described: all considered synonyms of *S. grimmia* (Grubb, 1993). It remains to be established whether these are all parts of one heterogeneous lineage (and thus a single evolutionary species); or whether there are two or more evolutionary species in *Sylvicapra*. Such widely distributed
duikers, exemplified by *S. grimmia* and *C. sylvicultor*, require rigorous reappraisal, employing the Consilient Solution to discern exactly what evolutionary species are hidden in what are artificial polytypic species.

### 13.4 Neotragines and Allies

This loosely affiliated group appear closely related to the gazelles (Tribe Antilopini), such that current classifications of Artiodactyla (Grubb, 1993) have not recognized the Neotragini as a real clade; and the most recent phylogenetic studies support this (Groves & Schaller, 2000; Vrba & Schaller, 2000). This reclassification suggests the strong possibility that many of the “dwarf neotragines” may in reality be gazelles (Gentry, 1992; Groves, 2000). The genera of interest are *Dorcotragus* (Beira Antelope) *Neotragus* (Suni, *N. nostragus* and Dwarf and Royal Antelopes, *N. batesi* and *N. pygmaeus*, respectively), *Oreotragus* (Klipspringers) and *Raphicerus* (*Rap. campestris, R. melanotis* and *R. sharpei*). The unresolved status of *Ourebia* was mentioned earlier. There is Haggard’s Oribi, *Ourebia haggardi* (Thomas, 1895), morphologically distinct and restricted to southern Somalia (East, 1998); and also Peters’ Oribi, *Ourebia hastata* (Peters, 1852) in southwest Tanzania. Another important example is the endangered Western Klipspringer, *Oreotragus porteousi* Lydekker, 1911 (endemic to west Nigeria). In fact, there are several dichopatric populations of klipspringers in west Africa (East, 1999) that require taxonomic appraisal urgently. Interestingly, females of the Tanzanian *Oreotragus schillingsi* Neumann, 1902 are nearly always possessing horns (Ansell, 1972).

Considerable microtaxonomic research is required to diagnose the evolutionary species in and among these genera. In this respect, several small antelopes can be singled out as obvious evolutionary species, based on distinct morphological characters and dichopatric distributions. Contemporary taxonomies have missed their taxonomic significance (Table 1). It is likely that many more such evolutionary species of small antelopes await discovery. All told, these examples emphasize the immaturity of bovid taxonomy when viewed in the context of the goals and structure of phylogenetic systematics. A sustained subscription to the BSC and morpho-species concepts continues to exact huge costs on objective knowledge of bovid diversity. Contemporary taxonomies are clearly rife in Type II errors: with the likelihood of more Type III errors quite possible (similar and additional to those mapped in Fig. 4). All in all, contemporary knowledge of the taxonomy of these antelopes is woefully inadequate. The implications of this situation, especially for conservation decisions, are alarming, to say the least.

### 14. CONCLUSIONS

#### 14.1 Taxonomic Implications and Future Research

Many may be comfortable in believing we know all the antelope species. Unfortunately, our knowledge of antelope taxonomy is messy, and very immature; the actual magnitude of its deficiencies has yet to be determined clearly. Recent and continuing discoveries of new large mammals have evoked great surprise and publicity (MacKinnon, 2000); but actually, nearly all Mammalia remain incompletely known taxonomically (Patterson, 2001) - exemplified by recent discoveries of new bats in the well known mammal fauna of western Europe (Mayer, & Van Helversen, 2001). This review has marshaled theory and data to argue that the African Bovidae, especially the smaller bodied antelopes, present rich opportunities for taxonomic research. Clearly, future research into antelope diversity faces many challenges in both the micro- and macrotaxonomic theatres of enquiry. This creates a wealth of opportunity; conservation crises emphasize that taxonomic study of the Bovidae deserves urgent and priority support. This review has focused on microtaxonomic patterns of biodiversity, by asking what are the real species of African antelopes. Only a great deal of basic research will actually characterize this diversity. This is the first step to elucidate a comprehensive taxonomy built on the philosophies and methods of phylogenetic systematics. It is indeed a remarkably humbling circumstance for humanity and science to reconcile with the state of affairs that the taxonomy of nearly all African antelopes has yet to be explored scientifically.

It is pertinent to acknowledge that our understanding of the macroevolutionary history of the Bovidae (as with all mammals) continues to undergo radical revision, with surprising discoveries (Groves, 2000; Vrba & Schaller, 2000). The higher classification of antelopes most certainly demands elucidation; but some taxonomists have analyzed the wrong units (through blind adherence to the BSC) - as exemplified in the Cephalophini (Jansen Van Vuuren & Robinson 2001) and Reduncini (Vrba et al 1994).

An interesting phenomenon that challenges systematists’ conceptual understanding of species (and equally demands thorough evidence) are the morphoclines exhibited among some African bovids. Our unclear taxonomic knowledge of *Oreotragus, Ourebia, R. campestris* and *S. grimmia* has been emphasized. Fine-grained sampling of organisinal variation within and across these lineages (and other lineages) of antelopes is required before we can evaluate the evolutionary
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history of these taxa with requisite objectivity and insight. Molecular evidence is likely to provide valuable insights. In this respect, all available character evidence needs to be incorporated into phylogenetic analyses. These will must include molecular, behavioural and morphological characters; and hopefully allow us to discern the histories of these variable lineages.

14.2 Conservation and Utilization of Antelopes
The pervasive biodiversity crisis places urgent and brutal reality on the species problem. The discovery of species, and their formal naming is the first quintessential step that permits humans to know and conserve, or destroy biodiversity. Human activities continue to drastically impinge on nearly all populations of extant antelopes throughout Africa. It is a reality magnified by the sweeping extirpations in the ranges and numbers of nearly all antelopes in the past two centuries, and especially by the unsustainable mining of African forest antelopes (and other biodiversity) for bushmeat. The need to improve our patchy and inadequate knowledge of bovid systematics (at micro and macrotaxonomic levels) places a precedent on all researchers working with bovids to collaborate and improve the primary foundations of knowledge (Boxes 1 & 3). Not least, any one researching and publishing on antelopes needs to understand and adhere to critical tenets of scientific procedure (Boxes 1-2).

14.3 Science and Species Discovery
The problems entailed in the species debate and our poor knowledge of bovid diversity prescribe at least two responsibilities on the professional biologist. One is how we inform society about taxonomy and taxonomic findings. The second has to do with responsibilities and opportunities to make original contributions to improve our knowledge of small antelopes and indeed all biodiversity. The species problem places critical prescriptions on how professional biologists go about their work. These prescriptions are reinforced by the demands from science and society for accurate and authentic knowledge about biodiversity. There is an individual responsibility to reliably identify exactly what species you have worked on; it is not sufficient just to label organisms according to literature sources. Not only does a professional responsibility endorse accurate and correct information; but emphasizes verifiable identification of any organisms you report on - verifiable on tentelic evidence (Box 2); identifications should employ a credible species concept; thus any reporting about antelope diversity must state how identified species are conceptualized. Those continuing to employ the obsolete Biological Species Concept, need to justify why. This places an onus on editors and peer reviewers to tighten up taxonomic procedures in scientific reporting. There is no longer any excuse to perpetuate taxonomy as an art at high costs to the quality and relevance of published knowledge. So, editors and peer reviewers should consider whether data can be justifiably published about antelopes whose taxonomic identify cannot be independently established and verified; this prescription for scientific veracity based on voucher specimens cannot be overemphasized (Boxes 1-3).

14.4 Phylogenetic Uniqueness Really Matters
The philosophical and taxonomic argument presented above has nothing to do with a semantic battle between subspecies versus species, or any other concepts. “The goals of systematic biology are to discover the various forms of life that exist and have existed, to reconstruct as far as possible the relationships among these forms, and to create a system of classification that reflects these relationships” (Davis & Nixon, 1992:434). It is indeed possible to classify organisms in many different ways. Prescriptions and demands for scientific taxonomies have underwritten an overarching axiom in this paper; systematics aims to discover and describe evolutionary history. This forecloses all other options potentially open to taxonomists; for a scientific knowledge of historical patterns is quintessential to build authentic taxonomies. It endorses why only accurate taxonomies, that classify evolutionary species which have been precisely diagnosed, meet scientific rigour in systematics. This applies to all biodiversity, and not just African bovids.

One of two strengths of the Consilient Solution is its knitting together of disparately derived nuggets of knowledge about organisal biodiversity. Second, grounded in this knowledge, it is structured by population-thinking and tree-thinking (O’Hara 1988, 1997). The Consilient Solution is founded firmly in acknowledging the uniqueness of living entities; and the cognisance that nothing in biology makes sense except in the light of history. Most importantly, this welding together of disparately derived theories and procedures empowers biologists to discover evolutionary species precisely: accurately elucidating their phylogenetic uniqueness.

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BOX 1. PROFESSIONAL RESPONSIBILITIES: THE NEED FOR NEW SPECIMENS

There are severe practical constraints that thwart scientific progress in taxonomy. One major constraint are the gaps in representation of biodiversity in natural science collections. This especially applies to antelope taxonomy. This situation has not improved markedly since Ansell (1958) reviewed the magnitude of the problem and its impacts on African biology and wildlife management. Ansell used the example of Hippotragus to emphasize that there are few, if any, specimens of sable antelope from eastern Angola. The deficiency is still there today. It preempts any scientific assessment of variation in *Hippotragus*; and prohibits comparisons of Giant Sable (*variani* for which there are adequate museum specimens from central Angola) with *kirkii* and populations further east in south-central Africa.

Many small antelopes are poorly represented (if at all) in museum collections. The conservation crisis, from which few wild African vertebrates are exempt, emphasizes the criticality of the opportunity for biologists, conservation agencies, and naturalists to collect and preserve scientific specimens of antelopes. Such scientific collecting will aid taxonomy and conservation immensely especially where poorly known organisms and regions become better known. Obviously, excessive collecting of threatened populations is undesirable, but by default dead animals (from poaching, and natural deaths) should be routinely preserved. Where possible field workers should collect and preserve specimens they encounter:

! Given the imperative need to preserve voucher specimens for a scientific study (Box 2), then skulls and postcranial skeletons of dead individuals fortuitously encountered in one’s study area are adequate. Tissue vouchers can obviously be obtained from freshly killed animals, and even dried out skeletons.

! Ecological and behavioural studies of wild populations of dwarf antelopes invariably involve handling and marking of live individuals. Collection of tissues for molecular analysis should be routine; blood samples are not sufficient. Muscle tissue (preferably collected by an “ear nick”) is the optimal sample. Postmortems are endorsed for any studied animals, that die during handling or in captivity. There is an equal precedent to collect these animals for ultimate preservation in a museum collection (Box 3).

! Antelope prey remains, even if damaged by predators, are valuable specimens. A useful source of “picked up” specimens of small antelopes are the kills of large raptors, especially under and in nests of the Crowned eagle, *Stephanocaetus coronatus*. Possibly, routine monitoring of crowned eagle nests by field workers could corroborate orthodox methods of assessment of small antelope populations.

! Those researchers with access to the bushmeat industry should avail museums of specimens; this especially applies to poorly known regions and taxa.

! All specimens must have the minimum attribute data, especially locality and date of collection (Box 3). Any additional field data and natural history observations are of immense value. Specimens lacking the minimal information are of scant relevance to science. Where you collected each of your specimens, and when, are these most critical data.

As judged by the growth of museum collections, little if any collecting of new small antelopes is being carried out, except by museum professionals. This is a disturbing situation considering the biodiversity crisis, and the inadequacies of existing collections and scientific knowledge. Even more significantly, many of the growing number of mammal researchers in Africa are not contributing to collections despite the plethora of opportunities. It is envisaged that several years of such collaborative effort will greatly augment and improve the overall representation of dwarf antelopes in museums. A greatly improved representation of small antelopes in museum collections and tissue banks is essential if we are to understand what species occur where. Conservation decisions based on poor, or no, scientific evidence will continue to create and exacerbate more problems than are solved.

The typical repository for specimens, for their preservation into perpetuity, is a world recognized natural science collection (typically maintained in an herbarium or natural history museum). This requirement is underwritten by the explicit distinctions between the properties, uses, and values of specimens in creating and maintaining tentelic knowledge of biodiversity (Box 2). Deposit your specimens in a reputable natural history museum where they can be professionally maintained to benefit all biology. I single out the Chicago Field Museum of Natural History (FMNH) and the United States National Museum of Natural History, Smithsonian Institution, Washington DC (USNM) for deposits of African bovids. These mammal departments maintain the world’s best curated and representative collections of recent African Bovidae. It is important to reconcile with the unfortunate circumstances where many museums now lack the resources and corporate support to expand their collections.
BOX 2. THE PROPERTIES, USES, AND VALUES OF NATURAL SCIENCE SPECIMENS.

The authenticity of the data about biodiversity which are built into reliable taxonomic and biogeographic knowledge is often not considered. Here, reliable refers to the authenticity of the point data: especially occurrences, identities and properties of organisms reported and analysed. Names for organisms must refer to unique lineages; and these referrals must be open to independent assessment in science. It is here that voucher specimens hold a pivotal and fundamental role in maintaining biological knowledge (Lloyd & Walker, 1967; Cotterill, 1995, 1999; Winker, 1996). This summary follows Cotterill (1999, 2002a) closely.

It is critical to distinguish the properties of a specimen from its uses. The properties of a specimen are based on the entirety of the preserved organism’s genotypic (=genome) and phenotypic constitution. Current and future uses of a specimen hinge on these properties. The many and varied uses of specimens determine in turn their existing and potential values. These collective properties, uses and values potentially influence the economic and scientific values assigned to collections of specimens. In practice, the contemporary values perceived of specimens tend to determine decisions over their integrity. At the centre of this argument, and whether occurring in the past, present or future, each use of a specimen involves derivation and application of its preserved information. This operation = whereby a specimen is used = involves an epistemology unique to biology:

1. Specimens preserve complex information. --Each organism is unique (Mayr, 1997) and each biological specimen is an original sample from its variable population. In its preserved form, a specimen is the best known means to preserve the complex information represented in its genetic and phenotypic characters (Cotterill, 1995, 1997). New opportunities to study previously inaccessible properties of specimens (notably molecule characters) permit unprecedented insights into the nature of biological variety. These continue to be facilitated by technological developments. Given rapid and novel accessibility to specimens’ properties, we can only hazard guesses at possible uses of specimens in the future. So it is unwise to categorize specimens’ values solely on the basis of current uses.

2. Historical information preserved in collections ramifies through biology. --The individual constitution, together with a singular origin in time and space, confers a unique historicity on each specimen and makes its replacement impossible. Different groups of specimens, originally studied within their respective subdisciplines, are equally essential in many other life sciences. For example, uses of mammal specimens originally collected primarily for a biogeographic survey (summarized in Smithers, 1971 for example) extend beyond these published compendiums. The specimens continue to operate as sources (in the form of refutable vouchers) for biogeographical, taxonomic, ecological and biochemical information which interrelate with numerous other domains of biological knowledge.

3. Information derived from natural science specimens maintains biological knowledge. --In addition to their myriad uses throughout the life sciences, specimen preservation maintains data quality. This is critical. For biologists to disseminate knowledge about organisms, such as specific plants, taxonomies allow disparate facts to be collated, compared, synthesized, and also refuted. In epistemological terms, taxonomies maintain consensibility (see Ziman, 1978) across the life sciences, and wherever else biological knowledge is applied. Type specimens vouch for Linnaean binomials to allow universal communication of disparately derived data. Underpinning the construction and maintenance of taxonomies, preserved specimens are fundamental to authenticate independently derived facets of information -- whether an identity, relationship or other property published about an organism and circumstances of its existence. These epistemological functions, where specimens are sources of historical information and underpin a web of consensible knowledge about the living world, firmly establishes the unique role of specimens in science.

Continued existence of specimens confers reliability to information communicated through electronic and printed media. Further explication of the role of preserved specimens is in order. The information preserved in specimens I term tentelic; such that a preserved, correctly documented specimen preserves tokens of tentelic information; and so contributes a unique detail of reliable information to a web of knowledge assembled by biologists about life. Such tokens include its occurrence, identity, and age. The neologism, scientela, describes this composite web of authentic knowledge about biodiversity, built of tentelic information. Singular properties of the scientela are consensibility and authenticity, where authenticity is built from reliable and representative tokens of tentelic information. Literally, the scientela is the “web of knowledge”, while the verb, tentela means “to hold together the web of knowledge”. The most critical epistemological contribution in biology of preserved specimens is their operation as tentelic tokens of reliable information (Cotterill, 2002a).

BOX 3. BRIEF GUIDELINES FOR THE COLLECTION AND PRESERVATION OF MUSEUM SPECIMENS OF MAMMALS, WITH EMPHASIS ON SMALL ANTELOPES

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This section focuses on the practicable procedures and techniques to preserve small antelope specimens. The goal of preservation is to ensure storage of an organism’s molecules and tissues into perpetuity so that they can be independently studied. An organism should be preserved such that the maximum authentic information is kept available for independent studies. Remember that many such uses by future scientists can only be guessed at. Preservation of those parts and organs of an organism of key interest to taxonomists is the priority. Taxonomists need to study a suite of morphological and molecular characters.

Ideally, the most complete natural history specimen is the entire organism pickled in liquid preservative such that any organs and tissues can be studied at some future date. Unfortunately, this is not practically possible. No such fluid exists to preserve all cells, molecules and tissues optimally. So, a collector and/or researchers have to prioritize what tissues and organs they preserve of an antelope. We invariably are limited by field conditions, available materials, and the state of the organism we are about to preserve. In practice in the field, it is not always feasible to preserve a specimen adequately. The minimum specimen of a mammal is the cranium (or portion thereof) and if possible, the full skeleton and skin. Under extreme duress, a skull or even just the frontlet with horns is better than nothing - provided it is of reliable provenance. Obviously, it is better to have one horn of a rare duiker than no voucher at all! This is best achieved by pickling the entire animal in 10% formalin with a separate, appropriately preserved, tissue voucher. (This is feasible for dwarf antelopes up to red duiker size, and is valuable for poorly known taxa.) The next best scientific specimen is the complete skeleton with cranium, entire skin, entire reproductive tract, scent glands, and of course tissue vouchers. Any other information revealing morphology of other organs and tissues is especially valuable; the latter data are virtually impossible to obtain from older museum specimens. The more data the better, and this need especially applies to scent glands. Equally, the more information collected from the fresh animal the better; including measurements and undigested food (rumen contents in 70% ethanol or 10% formalin).

An increasingly important aspect of specimen preservation is to ensure that relevant molecular characters (especially nucleic acid sequences) remain practicably accessible for future analysis. The value of molecular characters places a precedent on preservation of voucher tissue. The preservation of certain characters and allied data requires careful planning and investment in the appropriate equipment and preservatives. This is especially true of gamete morphology (including spermatozoa), parasites and karyotypes (consult specialized literature for details of these techniques). Many decades of antelope systematics have resulted in the vast majority of bovid specimens being preserved as cleaned crania and tanned skins; and only a frontlet with attached horns is quite common is some older collections. Inadequate (and equally poor curation) in some contemporary collections of bovids restricts research opportunities for comparative biologists, and not just systematists and taxonomists.

The first step is to tie a small specimen tag to the whole animal (around a hindleg) which records the minimum data (collector’s number, who collected it where and when, sex, and what it is). The next procedure is to record the organism’s body mass and standard measurements. The latter are measured - in the case of a small antelope - with a flexible metal tape measure: Total Length (TL) from tip of nose to end of the last caudal vertebrae in the unskinned mammal; Tail (TL) from last caudal vertebrae to mid-anus; Hindfoot (HF) from tip of the hoof to the base of the hock; Ear (E) from the outermost margin of the ear tissue to the internal notch. Record these data on a larger specimen label, and in your data catalogue. Preserve ectoparasites and endoparasites in separate vials. 70% ethanol is also the standard preservative for invertebrates, but nematodes may require different fixatives. If possible obtain blood samples and smears.

Record the GPS coordinates and altitude (if possible) for the locality. All these data must be written in soft lead pencil (or Indelible Indian ink) on a label of suitable paper (200gm) of a high rag content (synthetic tracing paper is also suitable). All data of invaluable scientific worth can fit on both sides of a label 50 by 100mm. Tie your labels securely to each separate part of the specimen (skeleton, skull, reproductive tract and tissue vouchers). Use a tough polyester thread; a thin gauge galvanised wire of mild steel is preferable to nylon string, which is useless as it invariably works loose. Never use wire on fluid preserved specimens, because it corrodes and also damages the specimens. Two labels are best (the smaller tag with the catalogue number, sex, date and locality) and the larger more complete one. The more data the better; but never leave off the critical tentelic information of the specimen’s provenance in time and space!

The skull should be defleshed, and salted. One can often allow the skull, after removal of flesh, to be cleaned by insects in a safe place (especially beware of damage or theft by carnivores); then boil it briefly to kill these insects, and their eggs and pupa. Seal the thoroughly dried skull in a plastic bag with a sprinkling of salt (NaCl). Remember to write the minimum scientific data on both cleaned, dry cranium and mandible with an indelible ink marker (a 0.5mm mapping pen with Indian ink is ideal) in small, printed lettering. Deflesh the skeleton, including the ribcage and salt.
liberally. Leave the vertebral column intact. The skeleton is best tied into a bundle with thin string and allowed to dry (preferably biltong) before storage in an suitable container safe from physical damage. Where ever possible keep skeletal material separately from dry skins to minimize damage from insects.

Skin the entire animal but leave the hooves on the skeleton if the latter is to be preserved. Keep the skin cool, and process it promptly to prevent hair slip; process it in the shade, away from hot surfaces. Clean the skin of flesh, and salt it liberally. Then, fold the skin into a square parcel, hair side out. It is a very good idea to soak the skin before salting in a 5% solution of sodium silicofluoride and sodium chloride for 12 hours; once dried it will be surprisingly immune to insect attack. Store skins, once completely dry, in a completely sealed, robust container safe from damage by insects and carnivores. Be careful that the skin does not go moldy in humid, tropical conditions. Ultimately, tanning is vital to maintain the quality of the pelt, especially against microbial degradation, but destroys nucleic acids and proteins.

Small mammals can be preserved whole in 10% formaldehyde solution; the tough, opaque, airtight plastic drums (100 to 200l capacity) used to distribute corrosive chemicals are ideal containers for larger specimens. The stomach cavity (and rumen) must be opened with small incisions (5 - 10cm long). Inject 10% formalin liberally into the base of the skull and major muscles. Keep the mouth open with a small stick or wad of cottonwool. It is vital to monitor the condition of such pickled specimens, and fortify the fixative as it becomes diluted by body fluid. Internal organs can be preserved in a similar way; don’t forget those labels.

Remember to preserve separately small pieces of muscle or segments of ear tissue (approximately 1-4mm²) for DNA analysis in solution (the ideal are vials containing 5mls of DMSO in 5M NaCl solution, but 70% ethanol is suitable and often easier to obtain). Deep frozen tissue vouchers are difficult to maintain in a cannister of liquid nitrogen, but these are optimal for mtDNA extraction, and essential for cell cultures. And never forget to label ALL your specimens carefully with the minimum data; enter these data into a separate catalogue (a robust, waterproof field notebook is ideal) such that they are materially backed up as a hardcopy (especially if entered originally into a computer). Additional information on the preservation of mammal specimens is available in De Blase & Martin (1981). It is also important to note that preservation techniques continue to be refined, especially in the case of tissues used by molecular systematists; obtain up to date advice from a recognized laboratory with seasoned experience in preparing tissues for mammalian systematics. Investigators of particular laboratories and museums differ in procedures and priorities used to preserve scientific specimens. These may also be tailored to local health and collecting legislation.
Table 1. Overview of the diversity of extant Afrotropical dwarf antelopes to illustrate how applications of disparate species concepts generate different classifications, and knowledge of their diversity. Contemporary classification, using the Biological Species Concept (BSC), follows Ansell (1972) and Grubb (1993). Evaluation of the Cephalophini is incomplete, and other geographically widespread species in other genera (exemplified by Oreotragus oreotragus, Raphicerus campestris and Sylvicapra grimmia) require rigorous evaluation. This summary is not an attempt to exhaustively reclassify these Bovidae, but serves to emphasize the message of this paper.

<table>
<thead>
<tr>
<th>Genus</th>
<th>Biological Species</th>
<th>Evolutionary Species</th>
<th>Comments</th>
</tr>
</thead>
<tbody>
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<td>adersi</td>
<td>unknown</td>
<td>The dichopatric population on the east African coast requires investigation</td>
</tr>
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<td></td>
<td>callipygus</td>
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<td>apparently monotypic</td>
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<td>dorsalis</td>
<td>dorsalis</td>
<td></td>
</tr>
<tr>
<td></td>
<td>castaneus</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>harveyi</td>
<td>harveyi</td>
<td>apparently monotypic</td>
</tr>
<tr>
<td></td>
<td>jentinki</td>
<td>jentinki</td>
<td>apparently monotypic</td>
</tr>
<tr>
<td></td>
<td>leucogaster</td>
<td>unclear</td>
<td></td>
</tr>
<tr>
<td></td>
<td>maxwelli</td>
<td>unclear</td>
<td>Dichopatric populations of maxwelli, monticola, and natalensis require evaluation with respect to what appears to be clinal variation in these three species</td>
</tr>
<tr>
<td></td>
<td>monticola</td>
<td>unclear</td>
<td></td>
</tr>
<tr>
<td></td>
<td>natalensis</td>
<td>unclear</td>
<td></td>
</tr>
<tr>
<td></td>
<td>niger</td>
<td>unknown</td>
<td>apparently monotypic</td>
</tr>
<tr>
<td></td>
<td>nigrifrons</td>
<td>nigrifrons</td>
<td>The Black-fronted duiker consists of at least three evolutionary species; and their correct relationships to other Cephalophini awaits analysis</td>
</tr>
<tr>
<td></td>
<td>fosteri</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>hooki</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>ogilbyi</td>
<td>ogilbyi</td>
<td>The polytypic Ogilby’s Duiker lumps together three evolutionary species</td>
</tr>
<tr>
<td></td>
<td>brookei</td>
<td></td>
<td></td>
</tr>
<tr>
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<td></td>
<td>rubidus</td>
<td>rubidus</td>
<td>not a subspecies of natalensis</td>
</tr>
<tr>
<td></td>
<td>rafilatus</td>
<td>unclear</td>
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</tr>
<tr>
<td></td>
<td>silviculter</td>
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<td>requires review</td>
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<tr>
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<td>spadix</td>
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<td>not a “subspecies” of silviculter</td>
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<tr>
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<td>weynsi</td>
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<td>requires review</td>
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<td>zebra</td>
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<td>requires review</td>
</tr>
<tr>
<td>Sylvicapra</td>
<td>grimmia</td>
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<td>requires review</td>
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<tr>
<td>Dorcotragus</td>
<td>megalotis</td>
<td>unknown</td>
<td>requires review</td>
</tr>
<tr>
<td>Madoqua</td>
<td>guentheri</td>
<td>unclear</td>
<td>requires review</td>
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Species concepts and antelope diversity

<table>
<thead>
<tr>
<th>Neotragus</th>
<th>Oreotragus</th>
<th>Ourebia</th>
<th>Raphicerus</th>
</tr>
</thead>
<tbody>
<tr>
<td>kirkii</td>
<td>kirkii</td>
<td>saltiana</td>
<td></td>
</tr>
<tr>
<td>cavendishi</td>
<td>thomasi</td>
<td>thomasi</td>
<td></td>
</tr>
<tr>
<td>damarensis</td>
<td>SW arid endemic</td>
<td>thomasi</td>
<td></td>
</tr>
<tr>
<td>piancentinii</td>
<td>piancentinii</td>
<td>saltiana</td>
<td></td>
</tr>
<tr>
<td>saltiana</td>
<td>highly endangered</td>
<td>saltiana</td>
<td></td>
</tr>
<tr>
<td>hararensis</td>
<td>SW arid endemic</td>
<td>saltiana</td>
<td></td>
</tr>
<tr>
<td>lawrancei</td>
<td>karyotypically distinct</td>
<td>saltiana</td>
<td></td>
</tr>
<tr>
<td>philipsi</td>
<td>SW arid endemic</td>
<td>saltiana</td>
<td></td>
</tr>
<tr>
<td>swaynei</td>
<td>SW arid endemic</td>
<td>saltiana</td>
<td></td>
</tr>
<tr>
<td>batesi</td>
<td>batesi</td>
<td>batesi</td>
<td></td>
</tr>
<tr>
<td>harrisoni</td>
<td>batesi</td>
<td>batesi</td>
<td></td>
</tr>
<tr>
<td>“ogoouensis”</td>
<td>harrisoni</td>
<td>batesi</td>
<td></td>
</tr>
<tr>
<td>moschatus</td>
<td>moschatus</td>
<td>moschatus</td>
<td></td>
</tr>
<tr>
<td>livingstonianus</td>
<td>moschatus</td>
<td>moschatus</td>
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</tr>
<tr>
<td>zanzibaricus</td>
<td>moschatus</td>
<td>moschatus</td>
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</tr>
<tr>
<td>oreotragus</td>
<td>oreotragus</td>
<td>oreotragus</td>
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</tr>
<tr>
<td>oreotragus</td>
<td>oreotragus</td>
<td>oreotragus</td>
<td></td>
</tr>
<tr>
<td>ourebi</td>
<td>ourebi</td>
<td>ourebi</td>
<td></td>
</tr>
<tr>
<td>campestris</td>
<td>campestris</td>
<td>campestris</td>
<td></td>
</tr>
</tbody>
</table>

Traditionally believed to be polytypic biological species. All these taxa, especially the vicariantly distributed *O. oreotragus* and *R. campestris*, require rigorous revision with respect to their true variation and evolutionary history.

For example, the status of Peters’ Oribi, *O. hastata* (Peters, 1852) requires clarification; and *O. haggardi* (Thomas, 1895) appears to be an evolutionary species

The precise status of the 23 synonyms of “stenbucks” awaits appraisal.

*melanotis*

*sharpei*