

1 **Running head: IS DIAGNOSABILITY AN INDICATOR OF SPECIATION?**

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3 **Is Diagnosability an Indicator of Speciation? Response to ‘Why One Century of**
4 **Phenetics is Enough’**

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1 Recently (Heller et al. 2013; H&A), we commented on a revision of the bovid
2 taxonomy, which proposes a doubling in the number of recognized species (Groves and
3 Grubb 2011; G&G). The subsequent response by Cotterill et al. (2014; C&A) contains a
4 number of misunderstandings and leaves much of the critique voiced in our paper
5 unanswered, focusing instead on species ontologies and taxonomic history. C&A argue
6 strongly against phenetics, morphospecies and taxonomic conservatism, ascribing us views
7 that we do not hold and hence confusing the substance of our disagreement. These
8 misconceptions oblige us to clarify our views on certain key issues to avoid being
9 misrepresented.

10 More seriously, however, the authors fail to respond to, or acknowledge, some of our
11 crucial practical concerns, notably the risk of taxonomic inflation (Isaac & Mace 2004) posed
12 by their diagnostic phylogenetic species concept (dPSC). Here we restate a number of our
13 concerns regarding the proposed bovid taxonomy of G&G and discuss their treatment in
14 C&A.

15 16 MISCONCEPTIONS IN C&A

17 C&A misrepresent our views on several topics and attack notions and concepts to which
18 we never subscribed. To help distinguish real disagreements from artificial ones, we discuss
19 the misrepresentations here.

20 In our original critique, we made it clear (p490) that the object of our criticism is not the
21 phylogenetic species concept *per se*, but rather the diagnostic version used by G&G. The
22 distinction is important since we agree with the authors that species are evolutionary or
23 phylogenetic entities. However, we do not agree that the dPSC does a good job of
24 operationalizing the ontological evolutionary species concept. C&A seem to overlook this

1 distinction, and consequently go to great lengths to defend their ontological notion of a
2 species (pp4-8), which is unnecessary given the concordance on most aspects of this issue.

3 The title of C&A “*Why one century of phenetics is enough*” and a considerable part of
4 the text portray G&G as an overdue liberation from phenetics, which the authors believe has
5 permeated bovid taxonomy until now. C&A claim (from p19 onwards) that previous bovid
6 taxonomies—including the reference volume of Wilson and Reeder (2005)—are based on
7 phenetics and the notion of morphospecies. The reader is led to believe that our own
8 skepticism towards G&G is driven mainly by our support of these concepts and by taxonomic
9 conservatism. This allegation is not supported by any of our statements; as population
10 geneticists we explicitly analyze data in the context of evolutionary processes, recognizing
11 that DNA or other characters evolve along the branches of evolutionary trees. We clearly
12 stated our preference for phylogenetic and genealogical methods (p491), which is also evident
13 from even a cursory glance at our collective work. Hence we find the allegation and the
14 general attack on phenetics wide off the mark. Furthermore, it is difficult to reconcile C&A’s
15 criticism of phenetics and the use of morphological (dis)similarity to diagnose species (e.g.
16 p1L56, p5L21, p18L30, p20L14) with their own defense of the dPSC. The dPSC clearly uses
17 discontinuities in morphological measures to delimit species, causing C&A’s denigration of
18 morphospecies to appear misplaced.

19 We do not believe that the current bovid taxonomy is the absolute truth, nor do we
20 claim that 143 is the correct number of bovid species. Bovid diversity is certainly an
21 understudied topic and many new discoveries are yet to be made. However, this does not
22 mean that we should accept a taxonomic revision if we find its methodology questionable. It
23 is not clear what justification C&A have for claiming that our criticism is driven by
24 taxonomic conservatism (pp17-19), or for claiming that G&G “unnerves” us in any way

(p1L58- p2L3). Our criticism of G&G does not relate to the novelty of the species list, nor directly to the magnitude of the taxonomic revision, although it stands to reason that any extensive scientific revision should be subject to thorough scrutiny. Rather, our criticism is practical and founded in our disagreement with the operational principles of dPSC.

Another unsupported claim in C&A concerns the labeling of all critics as proponents of the biological species concept or “its surrogates”, allegedly including the genealogical and the genetic species concepts; we have never stated a preference for any of these species definitions. In contrast to C&A, we are less convinced that any one of the traditional species concepts captures the true and singular ontology of species. For example, we believe the biological species concept encompasses some rational elements with regard to describing how evolutionary divergence occurs and is maintained. It is not unreasonable to assume that reproductive isolation and reduced hybrid fertility plays a role in speciation or that they are indicators of separate evolutionary trajectories. However, it is true that the biological species concept is not very useful for diagnosing species, at least not allopatric populations; we never claimed it was. Neither do we support the traditional genealogical or genetic species concepts. For example, requiring a certain level of genetic differentiation to diagnose species is an oversimplification and neglects the processes that affect genetic diversity. Rather, we support using genetic data in coalescent approaches that specifically aim to infer the parameters of evolutionary processes within a modeling framework, i.e. divergence times, genetic drift, gene flow, selection etc. (Bryant et al. 2012; Fujita et al. 2012; Satler et al. 2013).

UNRESOLVED ISSUES

In order to evaluate the revised taxonomy of G&G, it is necessary to understand how the evolutionary species concept is operationalized by the dPSC. G&G are not clear on this point;

page 1 in G&G defines a species as “the smallest population or aggregation of populations which has *fixed heritable differences* [our italics] from other such populations or aggregations”, followed on page 2 by “If the evidence before us indicates that, in some character state or other, two operational taxonomic units (OTUs) are discrete (i.e. *non-overlapping* [our italics]), then the two OTUs are to be classified as distinct species”. Elsewhere, in the Morphometrics section (page 5) G&G state that “The ideal multivariate method is *discriminant analysis*. This is a method that requires specimens to be assigned to groups, and it then minimizes intragroup variation while maximizing intergroup variation.” On the same page, G&G write “...the ideal is to compare different samples of restricted geographic origin with each other, aggregating those which turn out not to be *discrete* [our italics]. Eventually, a picture is arrived at in which two or more of these aggregations may remain, and, if they are discrete and *there is morphometric space between them* [our italics], they then answer to the requirement of the PSC”. Note that there are many statistical concerns regarding the use of discriminant analysis with morphometrics (Kovarovic et al. 2011), notably sample size concerns: it is prone to false positives unless the sample size in each OTU is considerably higher than the number of measured traits, which is often not the case in G&G.

Based on the above excerpts we conclude that univariate or multivariate non-overlap are both used as valid criteria for delimiting species in G&G. The two are in fact not interchangeable, since multivariate non-overlap can be found even when all univariate traits overlap. However, G&G do not mention which criterion takes precedence or why—and when—it is necessary to supplement the simpler univariate non-overlap with a multivariate criterion. Furthermore, very few of the species accounts state which criterion was used to delimit species, making it difficult to assess the evidence in favor of splitting. In the following

we use the term ‘diagnostic’ or ‘diagnosability’ as shorthand for univariate or multivariate non-overlap to distinguish them from the fixed differences criterion, and we note that both diagnosability criteria are subject to criticism regarding whether they define meaningful taxonomic entities (see below). Diagnosability is used far more in G&G than fixed differences for obvious reasons; G&G mainly use morphometric data in their analyses.

In our original critique of G&G we raised two main concerns: (i) dPSC will tend to split species into individual populations and (ii) the presented data in G&G do not support the decision to split species in many cases. Although we clearly stated these concerns, C&A’s responses given on pages 9-12 do not put our concerns to rest.

i. dPSC will tend to split species into individual populations

C&A claim that “ontologically speaking” species are individuals, not groups (C&A, p5L3-5). However, they do acknowledge that species must at least be populations. We agree with C&A that the most appropriate notion of a species is an assemblage of individuals that share a common evolutionary history. The challenge of operational taxonomy—which really is the substance of this discussion, rather than species ontologies—is how to identify such units. This has two components: which characteristics to use and how to ensure that the ensuing OTUs are non-trivial, i.e. that they are distinguished by “critical [our italics] events of individuation” (C&A, p5L50-52) and hence on separate evolutionary trajectories. The latter is important because individuation in a tree-thinking context has no lower limit and progresses all the way to the individual. G&G and C&A mitigate this resolution issue by requiring that species must at least be populations, but this just means that as the number of traits accumulate each population will almost always be a diagnosable species. Both G&G and C&A fail to argue why diagnosability is a reliable indicator of critical events of

1 individuation, i.e. that it cannot occur in the early phases of population divergence. Here we
2 discuss how evolutionary history can be inferred from the two most commonly used traits,
3 morphometrics and genetics.

4 **Morphometrics** There is, to our knowledge, no unified theoretical framework for the
5 progression of morphometric differentiation under different evolutionary scenarios, e.g. under
6 the effect of gene flow, selection, drift and mutation. In the absence of a quantitative link
7 between evolutionary processes and morphometric variation, the dPSC seems entirely
8 descriptive. There are many cases where populations that differ in some morphological trait
9 interbreed in overlap zones forming viable admixed populations, e.g. waterbuck (Table 1,
10 Appendix 1; Dryad doi:10.5061/dryad.82vr1) and Uganda/white-eared kob (Lorenzen et al.
11 2007). Morphological variation can accumulate rapidly during vicariance or through isolation
12 by distance, e.g. in plains zebra (Lorenzen et al. 2008). Hence, while we acknowledge that
13 morphometric diagnosability may reflect local, heritable population-specific processes
14 (barring environmental factors and phenotypic plasticity), it does not necessarily signify
15 critical events of evolutionary individuation. We fail to see why such diagnosable populations
16 lacking separate evolutionary trajectories should be distinguished in taxonomy.

17 **Genetics** In contrast to morphometrics, genetic data can be linked to evolutionary
18 processes using quantitative models. These models are based on the coalescent, which
19 specifically considers genetic data in the context of evolutionary trees (Kingman 1982a,b).
20 From coalescent and population genetic theory we know that diagnostic variation extends far
21 into the intraspecific realm (see examples in Appendix 2 and Frankham et al. 2012). Although
22 coalescent theory cannot determine the threshold of uniqueness in evolutionary history that
23 justifies splitting populations into species, it is clear that as the number of genetic markers
24 grows by orders of magnitude, the dPSC is not useful for defining meaningful species.

1 As genetic data show, any reasonable species concept must accommodate intraspecific
2 variation, which C&A call polytypy and reject as “fictitious” (C&A footnote p7) and part of
3 the “obsolete” biological species concept. The authors seem to ignore that speciation, and
4 evolution in general, are gradual processes; populations can be at any stage in the speciation
5 process and hence have varying levels of trait differentiation ranging from complete overlap
6 to fixed differentiation (Padial et al. 2010). The stage at which it is possible to detect
7 diagnostic differences depends on which traits, samples and diagnostic criterion one applies.
8 Much of our disagreement with G&G and C&A seems to derive from this single point:
9 establishing when critical events of individuation have occurred and whether polytypic
10 species—as in the case of differentiated populations within species—should be accepted or
11 not.

12 It concerns us that C&A do not acknowledge the predicament of taxonomic inflation
13 and argue that inflated species lists are “... a small price to pay for exactitude” (G&G, p2).
14 We do not see any reason why exactitude and biological relevance should be mutually
15 exclusive requirements for operational taxonomy. A taxonomic method that partitions
16 diversity into arbitrary and meaningless categories with a high accuracy is not useful in
17 biology.

18 C&A cite the “Precautionary Principle” in preferring taxonomic type I errors (false
19 positives; splitting species that are not significantly different) to type II errors (false
20 negatives; failing to split distinct species), a preference that is also explicit in G&G (p2). The
21 logic is that type II errors lead to the risk of losing biodiversity by overlooking it. While this
22 is true, it should not be used to support precautionary over-splitting. In fact, we find a
23 proliferation of type I errors just as damaging for conservation efforts as type II errors, as it
24 can lead to the loss of genetic diversity when populations are managed as separate

conservation units, preventing translocation or other management initiatives that promote gene flow. Furthermore, the increased species numbers under type I errors will stretch conservation resources simply because each species requires a separate census and management effort (see Frankham et al. (2012) for a detailed discussion on how over-splitting can be harmful to conservation). Cotterill himself has previously warned that “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 [phylogenetic species concept], and equally from inadequate sampling of populational variation” (Cotterill 2003). We maintain that G&G suffers from both uncritical use of the phylogenetic species concept and, in some cases, inadequate sampling.

ii. Lack of Support for Species Splits in G&G

Even if we accept the dPSC as a sensible operational approach, there are numerous cases in G&G where the reported data are not diagnostic among species. We previously exemplified this with the klipspringer, which G&G split into eleven allopatric species (the same case was independently criticized by Zachos et al. (2013)). While it is possible that in such cases the decision to split species was based on multivariate rather than univariate non-overlap (as explicitly stated for the buffalo species group), G&G do not present any diagnostic data or analyses. Although C&A comment (p9L40-53; p12L8-28) on this element of our previous critique, they evade the real issue by failing to clarify which diagnosability criterion was used and to explain why no diagnostic analyses are accessible to the reader. We have listed additional examples where the presented data contradict the decision to split in Table 1 and Appendix 1. Assuming that all these species splits are based on discriminant analysis it is questionable whether the sample sizes warrant this approach. In Table 1 we mark species

groups where the sample sizes are certainly questionable for this approach (sample size \leq number of variables for at least one OTU). We also highlight three cases where morphological and genetic data disagree; G&G do not discuss how these discrepancies should be solved. For example, the authors adhere to morphology only in kob, ignoring genetic data (Appendix 1), and for impala and waterbuck, the available genetic data are misinterpreted (Appendix 1). Although these cases may represent oversights, they highlight the overall bias towards unwarranted species splits in G&G.

MOVING FORWARD

In the interest of a constructive debate, we want to point out several aspects on which we agree with C&A. First, we agree with many of the authors' theoretical notions of species, i.e. we support the concept of species as evolutionary entities. Second, we sympathize with the overarching goal of identifying cryptic diversity and agree that there is likely a lot of it within bovids, as in other taxa. Third, we consider it crucial to move away from descriptive taxonomy based on casual observations to data-driven taxonomy, acknowledging the considerable work carried out by G&G in describing morphometric variation in the bovids. Their data provide a unique resource for future studies on the adaptive evolution of wild ungulates, ideally in combination with genetic data. It should also be acknowledged that G&G and C&A try to incorporate genetic results when available, to supplement their morphometric analyses, although we do not always agree with the way the data are reconciled.

We follow Hey (2006), de Queiroz (2007) and Padial et al. (2010) in noting that all or most species concepts—including the evolutionary species concept outlined in C&A—agree that a species represents “a separately evolving metapopulation lineage” (de Queiroz 2007). The disagreement lies in how to operationalize this idea, and this is the essence of our critique

1 of G&G. Rather than separating the operational from the theoretical species concept by
2 ignoring the underlying processes and focusing on trait patterns as the dPSC does, we
3 recommend that taxonomy should become more concerned with inferring phylogenetic and
4 population genetic parameters. Assuming that speciation represents discontinuities or ‘jumps’
5 in the evolutionary process, these will be easily inferred when the actual parameters of the
6 evolutionary history are estimated. In this regard, taxonomy today is in a fortunate position
7 due to two recent developments. First, nucleotide sequence data can be generated—even for
8 non-model organisms—at a steadily decreasing cost. Second, models based on the coalescent
9 are being developed for species delimitation (Bryant et al. 2012; Fujita et al. 2012; Satler et
10 al. 2013). Although multilocus data are not yet available for the majority of bovid species, it
11 is becoming more feasible to obtain them. We therefore foresee a great leap forward for the
12 field of taxonomy in the years to come, but we also acknowledge that a large-scale taxonomic
13 revision of the bovids using multilocus coalescent approaches is not feasible yet. Hence we
14 advocate an integrative taxonomy that draws on as many lines of evidence as possible,
15 realizing that different types of traits reveal different aspects of the evolutionary history of
16 OTUs (Padial et al. 2010) and exercising pragmatism when there is a large discrepancy
17 between the species list emerging under different species concepts or operational criteria
18 (Seifert 2014). We do not expect that taxonomy based mainly on morphological data will be
19 replaced by coalescent-based approaches, as morphological traits are easily the most
20 accessible proxies of biodiversity, caveats aside. Also, variability in morphological traits is
21 likely to be linked to evolutionary and ecological processes in many cases, even though the
22 mechanism of this relation is presently elusive. We envision that morphological characters
23 will supplement process-oriented and model-based methods merging morphological,

1 ecological, biogeographical and genetic data in an integrative approach to resolving the tree of
2 life.

4 SUPPLEMENTARY MATERIAL

5 Supplementary material, consisting of two appendices, can be found in the Dryad data
6 repository at <http://datadryad.org>, doi:10.5061/dryad.82vr1.

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1 TABLE 1

2 List of taxa where the postulated morphometric diagnosability is not supported by the data
 3 presented in G&G, or where genetic data contradicts the morphometric species splits.
 4 Comparisons are based mainly on measured morphometric data, not on more subjective
 5 measures such as differences in coat color. See Appendix 1 for details.

Species group	Reason for lack of support
Impala: <i>Aepycerus melampus</i> , <i>A. petersi</i>	Genetics contradicts split
*Wildebeest: <i>Connochaetes taurinus</i> , <i>C. albojubatus</i> , <i>C. johnstoni</i> , <i>C. mearnsi</i>	Overlapping morphometrics in G&G
*Topi: <i>Damaliscus eurys</i> , <i>D. jimala</i> , <i>D. ugandae</i> , <i>D. topi</i>	Overlapping morphometrics in G&G
*Topi: <i>Damaliscus korrigum</i> and <i>D. tiang</i>	Overlapping morphometrics in G&G
Dik-dik: <i>Madoqua guentheri</i> , <i>M. smithii</i>	Overlapping morphometrics in G&G
*Klipspringer: <i>Oreotragus oreotragus</i> , <i>O. aceratos</i> , <i>O. aureus</i> , <i>O. centralis</i> , <i>O. porteousi</i> , <i>O. saltatrixoides</i> , <i>O. schillingsi</i> , <i>O. somalicus</i> , <i>O. stevensoni</i> , <i>O. transvaalensis</i> , <i>O. tyleri</i>	Overlapping morphometrics in G&G
*Oribi: <i>Ourebia ourebi</i> , <i>O. hastata</i> , <i>O. montana</i> , <i>O. quadriscopa</i>	Overlapping morphometrics in G&G
*Sable antelope: <i>Hippotragis niger</i> , <i>H. roosevelti</i>	Overlapping morphometrics in G&G
Waterbuck: <i>Kobus ellipsiprymnus</i> , <i>K. defassa</i>	Genetics contradicts split

*Kob: *Kobus thomasi*, *K. leucotis*

Genetics contradicts split

Lechwe: *Kobus kafuensis*, *K. smithemani*, *K. robertsi*

Overlapping morphometrics in G&G

*Forest duikers: *Cephalophus fosteri*, *C. hooki*

Overlapping morphometrics in G&G

1 *: species group contains at least one OTU with fewer samples than morphometric variables.