

## Are There Really Twice as Many Bovid Species as We Thought?

RASMUS HELLER<sup>1,2,\*</sup>, PETER FRANDBSEN<sup>1</sup>, ELINE D. LORENZEN<sup>3,4</sup>, AND HANS R. SIEGISMUND<sup>1</sup>

<sup>1</sup>Department of Biology, University of Copenhagen, Ole Maaløes Vej 5, DK-2200 Copenhagen N, Denmark; <sup>2</sup>Instituto Gulbenkian de Ciência, Rua da Quinta Grande 6, P-2780-156 Oeiras, Portugal; <sup>3</sup>Department of Integrative Biology, University of California Berkeley, 1005 Valley Life Sciences Building, Berkeley, CA 94720, USA; and <sup>4</sup>Centre for GeoGenetics, Natural History Museum, University of Copenhagen, Øster Voldgade 5–7, DK-1350 Copenhagen K, Denmark

\*Correspondence to be sent to: Department of Biology, University of Copenhagen, Ole Maaløes Vej 5, DK-2200 Copenhagen N, Denmark; E-mail: rheller@bio.ku.dk, rathmuth@gmail.com.

R. Heller and P. Frandsen contributed equally to this article.

Received 3 December 2012; reviews returned 7 January 2013; accepted 18 January 2013  
Associate Editor: Frank (Andy) Anderson

A major reappraisal of the taxonomy of ungulates (hoofed mammals) was presented in 2011 (Groves and Grubb 2011; G&G henceforth). The reappraisal presents a drastic revision of the taxonomic diversity of the group. It nearly doubles the number of bovid species—a group comprising cattle, bison, buffalo, goats, sheep, and antelopes—currently recognized (IUCN 2012), raising the number of species from 143 to 279. In our opinion, this represents taxonomic inflation; ecotypes or subspecies have been raised to the level of full species based not on new data, but solely on a change in the species concept used (Isaac et al. 2004). As we argue below, the excessive splitting of species is unconvincing in many cases. Furthermore, we warn that such taxonomic inflation in the bovinds may impede management and conservation efforts (Isaac et al. 2004; Mace 2004; Frankham et al. 2012).

The revised bovid species list of G&G was incorporated into the recently published “*Handbook of the Mammals of the World—Volume 2*” (Wilson and Mittermeier 2011; HMW henceforth) published in collaboration with the IUCN and Conservation International, 2 of the leading international authorities involved in the conservation of global biodiversity. Whereas G&G is a scientific revision intended for experts in the field, HMW is a multiauthored book series presenting the most up-to-date taxonomy of mammals for a broader readership. Collectively, these two volumes are likely to be highly influential and serve as a guideline for a wide-ranging audience including taxonomists, conservationists, ecologists, biodiversity managers, and policy makers.

Any taxonomic revision that doubles the number of species within a family must anticipate critical evaluation, not least when it occurs in a prominent group such as the bovinds. Here, we discuss the revision and its potential consequences, which we believe may be detrimental in many respects. The critiques we are raising are two-fold. First, we call into question the scientific grounds for the species splitting in G&G. Second, we criticize HMW for singularly adopting the

bovid species list of G&G without subjecting it to critical evaluation. We discuss some of the practical downstream consequences of these actions.

### ISSUES REGARDING THE CRITERIA USED TO DEFINE NEW SPECIES

The term “species” has many interpretations, and a multitude of species concepts and species delimitation criteria have been proposed (Hey 2006; Frankham et al. 2012). Although we acknowledge that no consensus exists, we argue that in order to define a species, some nontrivial level of biologically relevant differentiation must have taken place. G&G interpret the phylogenetic species concept to delimit species as “the smallest population or aggregation of populations which has fixed heritable differences from other such populations or aggregations” (G&G, p. 1; we refer to this interpretation as “PSC”). Such differences can be based on phenotype, behavior, physiology, or genetic data; traits are not evaluated but are used as long as they are diagnosable (and are presumed heritable). It has been shown that such approaches lead to taxonomic inflation, as there is no lower limit to the resolution of the variability used to partition populations (Avice 2000; Isaac et al. 2004; Zachos et al. 2013). Under PSC, humans could be partitioned into any number of distinct species (subject to the definition of human populations) by allowing behavioral, morphological, or genetic characters to define species boundaries (Zachos et al. 2013). Hence, the number of diagnostic PSC species within any given taxon depends only on the amount of data considered and on how populations are defined. For example, the marked increase in the availability of genetic data during recent years has led to a point where a single individual can be distinguished from others (Frankham et al. 2012). This serves as an illustration that PSC is unsuitable and causes taxonomic inflation. G&G assume that a fixed difference in any given character is a valid ground for species designation. The authors

explicitly state that fixed differences should not be evaluated in the context of their biological significance or the underlying divergence process (“the decision [to split species]...never [depends] on extrapolation or hypothesis”; G&G, p. 2). Although we support data-driven species delimitation, we do not see the biological justification of using diagnosability as a proxy in itself without a conceptual or quantitative framework linking it to speciation processes (Padial et al. 2010).

In addition to our concerns regarding the theoretical foundation of PSC, we find that the diagnosability criterion (G&G, p. 4) is not consistently applied in G&G. The authors include morphometric tables for most species complexes, but measurements from species often overlap. Although multivariate analyses are in many cases quoted as the basis of species delimitation, these are not presented and hence impossible to assess. Furthermore, species sample sizes are often low (<5 and in certain cases limited to a single individual), which raises the concern of sampling effects on the measured metrics. One example illustrates these issues: The klipspringer (*Oreotragus oreotragus*) is currently considered one species (Wilson and Reeder 2005; IUCN 2012), but G&G have split it into 11 new species. The account for *Oreotragus porteousi* states: “Closely resembling *O. saltraxoides* and *O. schillingsi* in pelage; variation within each of these species greater than between them. Distinguished by the particularly long horns.” However, the horn length ranges given for the three species are 89–109 mm ( $n=2$ ), 72.5–100.0 mm ( $n=7$ ), and 82.5–87.0 mm ( $n=4$ ). Although the means differ, the overlap makes horn length unusable as a diagnostic character. No other justification for splitting the three species is provided. Another case from the klipspringers: “*O. aceratos* is very similar to *O. centralis*, from which it differs in the smaller size of females, and (on average) slightly larger teeth.” Of the three measures reported in Table 69 (G&G, p. 276), two overlap and one is adjoining, again excluding diagnosability. Overall, the accounts and data for this “species complex” cannot be used as an identification tool, nor can the accompanying species illustrations (G&G; HMW plate 54). Similar examples of taxonomic inflation in G&G include the splitting of many of the duikers, the hartebeest, topi, and serow. Many of the new species proposed by G&G have been elevated from their current status as subspecies or ecotypes (IUCN 2012), to full species—purely because a different species delimitation criterion has been used (Isaac et al. 2004; Mace 2004).

All species show a degree of intraspecific variability (De Queiroz 2007), which is acknowledged in many species concepts (Frankham et al. 2012). To systematically describe biodiversity, we need criteria to assess what level of character variability merits species designation (De Queiroz 2007; Padial et al. 2010). We suggest the use of an integrative taxonomy drawing on diverse types of data (e.g., ecological, behavioral, morphological, or DNA) that are deemed informative regarding the speciation process (Padial et al. 2010; Schlick-Steiner et al. 2010). An approach that will become

increasingly applicable as genetic data on nonmodel organisms accumulates is a multilocus coalescent-based methodology that specifically links patterns of lineage divergence to speciation and demographic processes (Bryant et al. 2012; Fujita et al. 2012). Although appropriate data are only available for a few species, such a probabilistic model-based approach will offer a replicable and quantitative supplement to morphometrics. However, for now, where primarily morphological data are available and a quantitative model linking character variability to speciation processes is lacking, it is vital that characters used for species delimitation are otherwise evaluated to ensure that the term *species* is reserved to describe a certain level of biologically meaningful diversity (Padial et al. 2010).

#### PROPAGATING TAXONOMIC INFLATION IN A REFERENCE VOLUME

HMW have adopted G&G’s revision of the bovid species list, sanctioning it for a much wider audience. We find this surprising for a number of reasons. By basing the bovid section on only one primary source, HMW have disregarded a vast number of experts in the field (including the current assessment of the bovid species list by the IUCN). In addition, as we argue above, the species delimitation criteria of G&G are questionable, as is the application of the criteria in a number of cases. Finally, the magnitude of the increase in the species list (which is acknowledged by HMW, p. 14) should have prompted careful scrutiny of the scientific basis for the revision. For an influential reference volume with a wide readership, the task of seeing through different taxonomic paradigms and presenting the best available knowledge is crucial due to the impact such volumes have and the importance of species lists as the main currency of biodiversity.

Of note, HMW has not adopted the PSC in the other ungulate families: The giraffe, for example, is treated as a single species, although differences in morphology and genetic evidence suggest otherwise, even under less discriminate species concepts (Brown et al. 2007). This inconsistency introduces a bias in the taxonomic diversity of the families presented in HMW. It is difficult to grasp the editorial decision to explicitly follow a controversial species concept in the bovids, yet not in other families.

#### PRACTICAL IMPACTS OF AN INFLATED SPECIES LIST

Taxonomy and biodiversity metrics are intimately connected, and taxonomic inflation has consequences for the many fields of work that depend on such metrics. Species have become the main currency in conservation practices (Mace 2004) and when biodiversity is assessed, every entry on a species list is often given equal weight (Chaitra et al. 2004). The editors of HWM justify their acceptance of the G&G bovid species list

with: "...this expanded species concept [PSC] better enables us to explore the conservation status of each [taxon or species]" (HMW, p 15) However, if species do not represent a standardized and meaningful level of biodiversity, this decision can have several undesirable consequences. As an example, a reader consulting HMW would be led to believe that the southern Tanzanian klipspringer carries the same biological significance as all giraffes. Such biological imbalance makes it impossible to make informed conservation decisions.

Intensive species splitting also affects the management and conservation of species. An example, which encompasses many of the practical issues, is species translocations, where individuals are moved from one area to another. At times, the procedure may be the only viable solution to human-wildlife conflicts or in the conservation of small populations (Fischer and Lindenmayer 2000; Frankham et al. 2012). If populations are designated as belonging to different species, management efforts will be severely hampered by legal obstructions (Frankham et al. 2012). Another downstream effect of taxonomic inflation is the suboptimization of conservation priorities. As the number of species increases, the census population size of each decreases; this will lead to a rise in the number of narrow-range endemic species (Isaac et al. 2004) and hence the conservation requirements of each taxon will increase. Conservation funding is unlikely to increase apace with the extra requirements caused by taxonomic inflation, contradicting the justification of PSC from a conservation perspective.

Species delimitations using PSC have been demonstrated as unstable and unsuitable for the long-term assessment of biodiversity, as temporal shifts in diversity cannot be adequately monitored when species are continually split as data accumulate (for a discussion of issues with shifting species lists, see Agapow et al. 2004). Conveying the message to the public that global biodiversity is on the decrease, with few mitigating exceptions to this trend, is unnecessarily confounded when the number of bovid species has just doubled without sufficient justification. Inflating species lists may give policy makers the pretext for restricting conservation funds and efforts.

#### PERSPECTIVES

Diversity within species has long been recognized (e.g., Moritz 1994; De Queiroz 2007; Zachos et al. 2013) and species concepts should not dismiss this by splitting taxa into the smallest diagnosable entities. Taxonomy is an evolving field and species lists are bound to be transient; we do not advocate static species lists, but argue that dramatic taxonomic reappraisals should involve careful weighing of the evidence at hand. The taxonomic inflation in the bovids in G&G is problematic, and its adoption in HMW is likely to further propagate a distorted perception of bovid diversity. This may have profound consequences for

policy, biodiversity assessment, species management, conservation measures, and other disciplines that rely on species lists.

The question remains whether the IUCN will choose to adopt this new taxonomy, which we strongly advise against. We urge the IUCN to consider other opinions on bovid taxonomy before making any changes to their species list. Similarly, we encourage the HMW readership to consult previous works or other sources presenting alternative and more widely accepted species delimitations.

#### FUNDING

This research was supported by The Danish Council for Independent Research | Natural Sciences and a Marie Curie International Outgoing Fellowship within the 7th European Community Framework Programme.

#### ACKNOWLEDGMENTS

We thank Colin Groves, an anonymous reviewer, and Associate Editor Frank Anderson for constructive comments that improved this manuscript significantly.

#### REFERENCES

- Agapow P.-M., Bininda-Emonds O.R.P., Crandall K.A., Gittleman J.L., Mace G.M., Marshall J.C., Purvis A. 2004. The impact of species concept on biodiversity studies. *Q. Rev. Biol.* 79:161–179.
- Avisé J.C. 2000. Cladists in wonderland. Review of: "Species Concepts and Phylogenetic Theory" by Quentin D. Wheeler; Rudolf Meier. *Evolution* 54:1828–1832.
- Brown D.M., Brenneiman R.A., Koepfli K.-P., Pollinger J.P., Milá B., Georgiadis N.J., Louis E.E. Jr., Grether G.F., Jacobs D.K., Wayne R.K. 2007. Extensive population genetic structure in the giraffe. *BMC Biol.* 5:57.
- Bryant D., Bouckaert R., Felsenstein J., Rosenberg N.A., RoyChoudhury A. 2012. Inferring species trees directly from biallelic genetic markers: bypassing gene trees in a full coalescent analysis. *Mol. Biol. Evol.* 29:1917–1932.
- Chaitra M.S., Vasudevan K., Shanker K. 2004. The biodiversity bandwagon: The splitters have it. *Curr. Sci.* 86:897–899.
- De Queiroz K. 2007. Species concepts and species delimitation. *Syst. Biol.* 56:879–886.
- Fischer J., Lindenmayer D.B. 2000. An assessment of the published results of animal relocations. *Biol. Conserv.* 96:1–11.
- Frankham R., Ballou J.D., Dudash M.R., Eldridge M.D.B., Fenster C.B., Lacy R.C., Mendelson J.R. III, Porton I.J., Ralls K., Ryder O.A. 2012. Implications of different species concepts for conserving biodiversity. *Biol. Conserv.* 153:25–31.
- Fujita M.K., Leaché A.D., Burbrink F.T., McGuire J.A., Moritz C. 2012. Coalescent-based species delimitation in an integrative taxonomy. *Trends Ecol. Evol.* 27:480–488.
- Groves C., Grubb P. 2011. *Ungulate taxonomy*. Baltimore (MD): The Johns Hopkins University Press.
- Hey J. 2006. On the failure of modern species concepts. *Trends Ecol. Evol.* 21:447–450.
- Isaac N.J.B., Mallet J., Mace G.M. 2004. Taxonomic inflation: its influence on macroecology and conservation. *Trends Ecol. Evol.* 19:464–469.
- IUCN. 2012. IUCN red list of threatened species. Version 2012.2 [Internet]. Available from: URL [www.iucnredlist.org](http://www.iucnredlist.org).
- Mace G. 2004. The role of taxonomy in species conservation. *Phil. Trans. R. Soc. B Biol. Sci.* 359:711–719.

- Moritz C. 1994. Defining “Evolutionarily Significant Units” for conservation. *Trends Ecol. Evol.* 9:373–375.
- Padial J.M., Miralles A., De la Riva I., Vences M. 2010. The integrative future of taxonomy. *Front. Zool.* 7:16.
- Schlick-Steiner B.C., Steiner F.M., Seifert B., Stauffer C., Christian E., Crozier R.H. 2010. Integrative taxonomy: a multisource approach to exploring biodiversity. *Annu. Rev. Entomol.* 55:421–438.
- Wilson D.E., Mittermeier R.A. 2011. *Handbook of the mammals of the world. Vol. 2 Hoofed mammals.* Bellaterra (Spain): Lynx Edicions.
- Wilson D.E., Reeder D.M. 2005. *Mammal species of the world. A taxonomic and geographic reference.* 3rd ed. Baltimore (MD): The Johns Hopkins University Press.
- Zachos F.E., Apollonio M., Bärmann E.V., Festa-Bianchet M., Göhlich U., Habel J.C., Haring E., Kruckenhauser L., Lovari S., McDevitt A.D., Pertoldi C., Rössner G.E., Sánchez-Villagra M.R., Scandura M., Suchentrunk F. 2013. Species inflation and taxonomic artefacts—a critical comment on recent trends in mammalian classification. *Mamm. Biol.* 78:1–6.