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Point of View

Species inflation and taxonomic artefacts—A critical comment on recent trends in mammalian classification

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ABSTRACT

Recently, many new (extant) mammal species have been named, mostly by raising subspecies to species rank. This is primarily a consequence of the phylogenetic species concept (PSC) that has become very popular over the last few decades. We highlight several cases of splitting and argue that much of this taxonomic inflation is artificial due to shortcomings of the PSC and unjustified reliance on insufficient morphological and/or genetic data. We particularly discourage species splitting based on gene trees inferred from mitochondrial DNA only and phenetic analyses aimed at diagnosability. Uncritical acceptance of new species creates an unnecessary burden on the conservation of biodiversity.

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Introduction

In the wake of the “molecular revolution” in biology, systematics and taxonomy have experienced an exciting and fruitful renaissance, from molecular phylogenetics and, recently, phylogenomics to barcoding and DNA taxonomy. Apart from some astonishing and long-awaited breakthroughs with respect to the relationships of higher taxa (e.g. Ecdysozoa and placental mammals), perhaps the most important impact of these new techniques has been the detection of hidden (genetic) diversity and the identification of cryptic species: morphologically very similar taxa formerly believed to represent a single species have been shown to comprise more than one evolutionarily distinct lineage or species. There are countless

recent examples; perhaps one of the most spectacular (and contentious) being the case of two species of African elephant (see below). While doubtless many of these splitting events are justified, others are not, and doubts have been raised whether taxonomic splitting might in fact tell us more about taxonomists than about the taxa under study. Indeed, one of the driving forces of splitting seems to be a paradigmatic shift in much of the taxonomic community from the biological to the phylogenetic species concept (Isaac et al., 2004; Groves and Grubb, 2011). Therefore, the increase in species numbers, or taxonomic inflation, is due mainly to subspecies being raised to full species, rather than to new discoveries (Isaac et al., 2004).

Schaller (1977) wrote that “ecological and behavioural analyses require sound systematics”. We think that conservation requires it, too. In fact, conservation-oriented agencies, e.g. the IUCN (International Union for Conservation of Nature) and the WWF (Worldwide Fund for Nature), need reliable nomenclature criteria to indicate

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taxa at risk. The naming of taxa is also important to trophy collectors, who will face enormous costs up to 60,000 USD to buy the permit and hunt a species missing in their collections. Thus, a questionable approach at taxonomical classification may elicit concern for conservational purposes, e.g. when a threatened taxon is lumped together with a non-threatened one, or when splitting species will provide a catalogue of “new” trophies to hunters.

Here, we argue that many recently named mammalian species are taxonomic artefacts, resulting from (i) the inappropriate application of the phylogenetic species concept and/or (ii) a naive interpretation of inconclusive available data sets. This paper exclusively deals with extant mammals. In principle, extinct and living species do not differ with respect to their status, so in theory what is said below also holds for fossil mammals. However, palaeontology is much more restricted methodologically since usually only skeletons remain, and sample sizes only rarely match the requirements of population-level analyses. Therefore, morphological data (and differences) are paramount in palaeontological taxonomy. Species splitting as outlined below is doubtful also in palaeontology, but the fact that with fossils more time horizons than just the present can be analysed gives more weight to diagnosability as a criterion of species delineation if the temporal (“vertical”) dimension is added (chronospecies). Besides, the limited information that can be drawn from fossil compared to extant organisms makes many hypotheses that are testable in the latter untestable in the former (most obviously the possibility of reproduction, but there are many more). This must not result in neglecting information where it is obtainable (extant species).

A short note on species concepts in mammalian taxonomy

Evolution is a continuous (although not necessarily gradual) process, and so are genetic divergence and speciation. Taxonomic designations (including species names), on the other hand, are static. Either a group of populations is recognised as a distinct species or it is not. Thus, a complete reflection of the evolutionary process in taxonomy is a priori impossible, and species *in statu nascendi* are difficult to address taxonomically. If all living species were fully distinct without varying degrees of intergradation, this would be a serious challenge to the theory of evolution by common descent with modification (Zachos, 2002). Even if species are natural entities and independent of our ordering minds, species designation must follow conventions which, ideally, are based on criteria that help us to successfully discern these entities and thus uncover the natural structuring of living beings. This is what species concepts are for (and there are notoriously many), and we will not discuss them here in detail. It may suffice to briefly outline the three concepts most relevant to the classification of mammals. The biological species concept (BSC) as advanced most famously by Ernst Mayr (e.g. Mayr, 1942) holds that species are groups of interbreeding populations that are reproductively isolated (i.e. no fertile hybrids) from other such groups. This concept obviously only applies to sexually reproducing taxa, and allopatric populations are difficult to evaluate. The genetic species concept (GSC), going back to W. Bateson at the beginning of the 20th century (see Baker and Bradley, 2006), defines species as “a group of genetically compatible interbreeding natural populations that is genetically isolated from other such groups”; instead of reproductive isolation (BSC) the focus is on “genetic isolation and protection of the integrity of the 2 respective gene pools that have independent evolutionary fates” (Baker and Bradley, 2006, p. 645). It is noteworthy that the GSC in its present form (Bradley and Baker, 2001; Baker and Bradley, 2006) was developed with explicit reference to mammalian taxonomy. The third and recently very influential concept is the phylogenetic species concept (PSC), of which

there are many different versions. These share an emphasis on common descent coupled with diagnosability (all individuals of a species are always unequivocally identifiable as a consequence of fixed genetic differences) such that “A species is the smallest diagnosable cluster of individual organisms within which there is a parental pattern of ancestry and descent” (Cracraft, 1983, p. 170). There are many variants on this theme (see Wheeler and Meier, 2000), some stipulating that species be defined on at least one apomorphic character state or requiring monophyly, and indeed it is monophyly of groups that is often taken as evidence of their species status or non-monophyly that is believed to indicate the need for splitting (see below). Hence, it is the PSC that most often leads to the splitting of one mammal species into two or more, and recently model-based approaches have been developed for species delimitation (Pons et al., 2006). The question arising from this is twofold: is the PSC a good choice, and if – for the sake of the argument – we accept the PSC, are the many newly erected mammal species supported by “hard” data or merely by inconclusive evidence?

The PSC, just like any other species concept, has been criticised extensively, and indeed it has serious shortcomings that make its application inappropriate on theoretical and practical grounds. First of all, diagnosability, whether based on apomorphic characters or not, and monophyly extend far into the intraspecific realm: “thousands of de novo mutations arise and spread relentlessly in populations. Given limited organismal dispersal (and sufficient resolution in the molecular assays), one or more of these synapomorphs often will differentiate regional populations, local demes, extended kin groups, and even nuclear family units” (Avice, 2000a,b, p. 1830; this paper is a critical book review on Wheeler and Meier, 2000). It would be nonsensical, however, to assign species status to each such diagnosable cluster. Also, whether a cluster is diagnosable or not, depends on the combination of characters under study, and different combinations will inevitably yield different diagnosable units. Fixed differences among populations as the defining criterion for species status also have another bizarre corollary: “as natural populations of many species are extirpated or reduced to small inbred units, intraspecific polymorphisms increasingly will be converted to fixed allele differences between allopatric demes. Under PSC logic, by definition, this will result in a great proliferation of new species” (Avice, 2000a,b, p. 1828; see below for an example in red deer).

Furthermore, it has long been known that gene trees and organismal (here: species) trees are not the same, but that different markers (be they molecular or not) will often yield different tree topologies, not due to erroneous reconstruction of relationships but because an organismal phylogeny comprises many different gene trees. Each of these is correct in its own right but only a fraction of them will correctly represent the true organismal history, in effect transforming a cladogram into a “cloudogram” with a variance (Avice and Robinson, 2008; Zachos, 2009 and references therein). This may be considered the coup de grâce for some versions of the PSC. Monophyly in general is not a good criterion for species delimitation because evolution below and at the species level is often reticulate, making many “good” species (i.e. those acknowledged universally by all or most species concepts) para- or polyphyletic (see Funk and Omland, 2003 for a review). This is hardly surprising, given that after population sundering a chronological sequence of polyphyly, paraphyly and eventually – for neutral markers after $4N_e$ generations (N_e being the effective population size) – monophyly is expected from population genetic theory (e.g. Avice, 2000a,b, particularly Figure 2.14 on p. 65). Monophyly may thus be decoupled from geographic or reproductive isolation or other ecological aspects that may result in independent evolutionary trajectories of newly established populations.

“Splitting frenzy”, cryptic species, or both?

Mammal taxonomy is experiencing a dramatic increase in named species, mainly through the splitting of existing species based on the PSC rather than through new discoveries. Primates and terrestrial Cetartiodactyla, in particular, contain many taxa that only recently have been raised to species status. To our knowledge, the primates are the first mammal group (“order”) to have entirely been revised as a whole under the philosophy of the PSC (Groves, 2001), and it was the steady increase in primate species numbers during the last decades (from 150–200 to >350) that triggered the term “taxonomic inflation” (Isaac et al., 2004). A similar recent analysis of terrestrial cetartiodactyls has also dramatically increased species numbers. The number of bovids has more than doubled according to Groves and Grubb (2011) and Groves and Leslie (2011) compared with Grubb’s (2005) chapter in the taxonomic reference by Wilson and Reeder. We shall now look critically at select cases of recent species splittings (see also Table 1).

Taking the PSC to a molecular extreme, Cracraft et al. (1998) raised Sumatran tigers to species status (*Panthera sumatrae* instead of *P. tigris sumatrae*) based on three diagnostic sites in the mitochondrial cytochrome b gene. Using discriminant analysis of craniometric data and qualitative skull characters, Mazák and Groves (2006) even distinguished three tiger species: *P. tigris*, *P. sumatrae* and the Javan tiger (*P. sondaica*), because these taxa differed absolutely (100%) in their analyses and were thus diagnosable. Fortunately (in our view), this distinction has largely been neglected by mammalogists, and we are not aware of any subsequent publication listing more than one tiger species. The genetic data set has a small sample size and no nuclear markers. To automatically interpret diagnosable populations with no phenetic overlap in the characters studied as distinct species results in an unwarranted explosion of species numbers because even the tiniest fragments of a species can be made diagnosable if the markers have enough resolution power. How many “species” would exist, if this rationale were applied to, say, domestic dogs or even humans? Domestic forms are particularly revealing as many races are completely different morphologically (100% diagnosability!), and yet they readily and freely interbreed.

A second unwarranted splitting is that of red deer (*Cervus elaphus*). There has been a long-standing debate of whether European, Asian and North-American populations should be united into a single (*C. elaphus*) or two species, i.e. red deer and wapiti or “elk” (*C. elaphus* and *C. canadensis*). Recent molecular phylogenies have shown this assemblage to be non-monophyletic with respect to sika (*C. nippon*) and white-lipped or Thorold’s deer (*C. albirostris*) and even some *Rusa* and *Axis* species (Pitra et al., 2004), although the latter (*Rusa* and *Axis*) was not confirmed when nuclear markers were included (Gilbert et al., 2006) or when a larger mtDNA data set was used (Hassanin et al., 2012). Whether the non-monophyly with respect to sika and Thorold’s deer holds cannot be judged from the latter two cited studies as intraspecific red deer sampling was very limited. Groves and Grubb (2011), however, based on mtDNA and their morphological diagnosability analysis, distinguish three European red deer species (and 12 (!) for the entire red deer/wapiti complex): *C. elaphus* (West European red deer), *C. pannoniensis* (East European red deer) and *Cervus corsicanus* (Corsico-Sardinian and North-African red deer). The latter is usually acknowledged as two different endangered subspecies (*C. e. corsicanus* and *C. e. barbarus*), and indeed, they are differentiated at nuclear markers (Hajji et al., 2008), a finding ignored by Groves and Grubb. Both subspecies are probably the descendants of only a small number of founders introduced by humans (only a few thousand years ago!) and have since diverged from their source populations by genetic drift. The nuclear study has shown closer relationships of Corsico-Sardinian deer with the last autochthonous Italian red deer from

Mesola in the Po delta (Hajji et al., 2008). Although the Mesola red deer are mentioned by Groves and Grubb, they did not include recent data which show them to exhibit a single but unique mitochondrial haplotype (Hmwe et al., 2006) somewhat intermediate between the two major mtDNA lineages (eastern and western) of European red deer (Niedziałkowska et al., 2011 and references therein). This monomorphism and uniqueness is almost certainly due to their long isolation which resulted in a fixed difference that, following the logic of the PSC, should make the Mesola red deer a fourth species in Europe. This again, along with free interbreeding among all these “species”, highlights the problems of phenetics and diagnosability as defining criteria of species, particularly if decisions rely only on mtDNA data. Also, distinct and comprehensive phenotypic differences are not necessarily reflected by genetic divergence among individuals and populations (and vice versa): for instance, clear differences in metric and non-metric skull and dental characters together with chorological data stimulated Palacios et al. (2008) to provisionally split South African cape hares (*Lepus capensis*) into *L. capensis* and *L. centralis*, a distinction not confirmed by mitochondrial and multilocus nuclear DNA (Suchentrunk et al., 2009).

One of the most spectacular recent incidents of taxonomic inflation pertains to klipspringers, a small bovid of rocky habitats from southern to eastern Africa. The single species *Oreotragus oreotragus* has been split into 11 species by Groves and Grubb (2011) based on phenetics only: size differences and different sexual dimorphism believed to be correlated to territory size. There are no genetic data and no phylogenetic analyses, and sample sizes are very small (in most cases < 10 and often < 5). In our view, this is a prime example of rash taxonomic conclusions derived from an inappropriate data set.

Another example of premature splitting is the case of the mainland serows. Formerly, just one species was acknowledged: *Capricornis sumatraensis*, with 11 subspecies (cf. Schaller, 1977). Grubb (2005) already listed four species, *C. milneedwardsii*, *C. rubidus*, *C. sumatraensis* and *C. thar*, all of them “Threatened” or “Near-threatened” (WWW: iucnredlist.org, accessed 07.06.2012). Recently, Groves and Grubb (2011) increased the number of species to six (one of them still undescribed). Very little is known on the behaviour, ecology and intersexual, as well as interpopulation, morphologic and genetic variability of these goat-antelopes of South Asia. We think it quite unconvincing to separate four species of mainland serows primarily based on pelage characteristics and on very small sample sizes (for one species, only four skins were analysed).

These examples (of which there are many more), however, do not preclude the existence of cryptic species within taxa that are usually considered a single species. The long-standing debate about the African forest elephant (*Loxodonta cyclotis*) as a species separate from the African savanna elephant (*Loxodonta africana*) has produced different lines of evidence, both morphological and genetic (mitochondrial and nuclear) that there may indeed be more than one species of African elephant (Rohland et al., 2010 and references therein). There are more cases where there is good reason to consider more than one species. Brown et al. (2007) present mitochondrial and nuclear genetic data of giraffe (*Giraffa camelopardalis*) that fit with differences in pelage pattern and suggest that there may be reproductive isolation, possibly through assortative mating based on pelage patterns or differences in timing of reproduction, in the absence of extrinsic barriers to gene flow. The authors cautiously conclude that there might actually be six or more distinct species of giraffe. In this case, the morphological data analysed by Groves and Grubb (2011) are in good accordance with the genetics, and consequently, they list eight giraffe species.

Two more examples reveal that diversity at the species level is at times underestimated. Del Cerro et al. (2010) present extensive and

Table 1
Select examples of recently erected or resurrected mammal species as a consequence of splitting of a formerly single species into two or more. We have chosen examples with good and insufficient arguments for splitting as well as those in need of further data. This selection and its proportions are not representative, and on the whole we fear that in most cases splitting is rash. For details, see text.

Single species	Number of species after splitting	Reference	Sufficient evidence
African elephant (<i>Loxodonta africana</i>)	2	Rohland et al. (2010) and references therein	Probably
Clouded leopard (<i>Neofelis nebulosa</i>)	2	Buckley-Beason et al. (2006) Kitchener et al. (2006) Wilting et al. (2007) Christiansen (2008)	Yes
Tiger (<i>Panthera tigris</i>)	2	Cracraft et al. (1998)	No
	3	Mazák and Groves (2006)	
Eurasian badger (<i>Meles meles</i>)	3–4	Del Cerro et al. (2010)	Yes
Giraffe (<i>Giraffa camelopardalis</i>)	≥6	Brown et al. (2007) Groves and Grubb (2011)	Perhaps
European red deer (<i>Cervus elaphus</i>) ^a	3	Pitra et al. (2004) Groves and Grubb (2011)	No
Klipspringer (<i>Oreotragus oreotragus</i>)	11	Groves and Grubb (2011)	No
Serow (<i>Capricornis sumatraensis</i>)	4	Grubb (2005)	No
	6	Groves and Grubb (2011)	

^a We only consider the European and North-African red deer here (i.e. neglecting also the maral). Asian red deer and North-American wapiti (“elk”) have also been split into various species recently. The whole red deer/wapiti complex is considered to comprise no less than 12 different species by Groves and Grubb (2011).

conclusive data that Eurasian badgers (*Meles meles*) actually include three to four different species: *M. meles* (Europe to the Volga River), *M. leucurus* (north-west and central Asia), *M. anakuma* (Japan), and possibly *M. canescens* (south-west Asia and Crete). Their conclusion is based on mtDNA and six nuclear loci and is in accordance with earlier morphological findings such as baculum shape, a good taxonomic diagnostic in carnivores (see references in Del Cerro et al., 2010) and geographic distribution suggesting reproductive isolation among the different taxa. Recent studies of the taxonomic status of clouded leopards (*Neofelis nebulosa*) produced convincing morphological, karyological and genetic (mitochondrial and nuclear) data that support the recognition of two species: *N. nebulosa* on the south-east Asian mainland and *N. diardi* in Indonesia (Borneo and Sumatra including the Batu islands) (Buckley-Beason et al., 2006; Kitchener et al., 2006; Wilting et al., 2007; Christiansen, 2008).

Potential guidelines and concluding remarks

New species of mammals are constantly described and introduced to the taxonomic literature (González-Ruiz et al., 2011; Moratelli and Wilson, 2011; Moratelli et al., 2011; Puechmaile et al., 2012; and references above). So, how many mammal species are there? The answer obviously hinges on the underlying species concept one selects, but it is probably fair to say that all modern concepts share the view that species are “separately evolving metapopulation lineages” or segments thereof (De Queiroz, 2005). Just when the status of separate evolution is reached and how this is to be inferred, or what data are sufficient to conclude that lineages evolve separately, is a matter of contention. It is important to recall that all organisms – whether different species or not – are part of an ancestor-descendant continuum (“common descent”), and over (geological) time, the tokogenetic relationships among individuals are replaced by phylogenetic relationships among species and higher taxa (cf. the by now classic figure in Hennig, 1966, p. 31). Consider the two species of clouded leopard. Since they are strictly allopatric, hybridisation does not occur in the wild. Whether potential hybridisation would be viewed as evidence against species status (strict application of the BSC), is a theoretical or perhaps philosophical question. As mentioned above, the existence of species *in statu nascendi* is a direct consequence of evolution, and exactly when or where the static taxonomic line should be drawn and a species name should be given, is a question of convention.

Based on their genetic species concept (GSC), Baker and Bradley (2006) hypothesise that there are >2000 hitherto unrecognised mammal species. Whether or not this number is correct and whether or not one is an adherent of the GSC, recent studies making use of new molecular techniques have shown that there is much hidden diversity in mammal species and many cryptic species. However, since speciation is ultimately a genetic process, *before* species are split the minimum required evidence is data showing more than one integral gene pool. Those gene pools must have been evolving separately for a sufficient amount of time (what “sufficient” means is again a convention, but without demanding a certain timer after divergence every single island or otherwise spatially isolated population would be a distinct species). To achieve this, it is *not* sufficient to present diagnosability based on a selection of morphometric traits or fixed differences at single sites in a small stretch of DNA. Such findings can only define species boundaries between *sympatric* populations (because then they are conclusive evidence of genetic isolation).

When only limited data are available, a fruitful approach is to compare them to data from the same marker in better-studied closely related pairs of sister species. Kryštufek et al. (2012), in an analysis of voles (*Microtus*) based on cytochrome b sequences, found divergence levels within two acknowledged species that exceeded the threshold of 4.3%, a conservative cut-off criterion between sibling species in *Microtus*. A similar line of reasoning led Osmer et al. (2012) to support the separation of southern and eastern oryx antelopes (*Oryx gazella* and *O. beisa*). The divergence at the single locus itself, however, is not conclusive evidence that there are two species. It just confirms hypotheses that have been arrived at based on different data. If no such data exist, then the single genetic finding may be formulated as a two-species hypothesis that needs further testing. This approach is in accordance with Bradley and Baker (2001) who carried out an in-depth study on intra- vs. interspecific divergence in select taxa of rodents and bats. They found that for cytochrome b sequences “values <2% would equal intraspecific variation; values between 2% and 11% would merit additional study concerning specific status, and values >11% would be indicative of specific recognition” (p. 972). The same authors also point out one important pitfall of using mitochondrial DNA only. It has repeatedly been found that introgression has blurred phylogenetic relationships up to the point that in some populations most or even all animals carry mtDNA from a closely related but different species (“mitochondrial capture”). Examples include hares (*Lepus* spp., Melo-Ferreira et al., 2012 and references therein),

bovids (where the obvious sister species American and European bison, *Bison bison* and *B. bonasus*, are found in different parts of mtDNA trees, Ward et al., 1999; Verkaar et al., 2004) and polecats (*Mustela putorius* and *M. eversmannii*, Suchentrunk and Zachos, unpublished data).

We acknowledge the underestimation of species diversity in mammals and appreciate the need for further taxonomic research, particularly in less well-studied groups, but we strongly discourage the splitting of existing species based on non-conclusive genetic (especially mtDNA) and/or morphological as well as behavioural data sets, particularly so if these data are derived from small sample numbers, heterogeneous for age and sex. Evolution below and at the species level is a population biological process, and its analysis therefore requires sound sample sizes covering the whole intraspecific realm to avoid artificial phylogenetic gaps in the outcome. Many recent splittings where intraspecific taxa have been raised to species level do not meet these criteria. If an independent evolutionary history, i.e. largely separate gene pools, is what ultimately makes a species, then conclusive nuclear genetic or mitochondrial and nuclear genetic data is what should be required from geneticists before splitting a species. Similarly, morphological data (preferably qualitative character state divergence) that goes beyond simple quantitative differences is what is needed in anatomy and palaeontology to accept a species. Ideally, different data sets are combined: "Importantly, the empirical evidence for genealogical distinction must come, in principle, from concordant genetic partitions across multiple independent, genetically based molecular (or phenotypic) traits" (Avice, 2004, p. 363). In sympatry, the thresholds will be lower than for allopatric populations because even subtle divergence can be indicative of isolated sympatric gene pools.

There are also practical issues that have to be taken into account. Taxonomy has important consequences for conservation. The number of species is often used to assess the conservation value of protected areas, and many laws and international conventions are based on the identification of species. Just as it is crucial to identify cryptic species, it is counterproductive to name species based on insufficient data. Development of conservation plans and legal listings of non-existent species is a waste of resources. Acceptance of invalid species may hinder conservation and management plans, or lead to inappropriate translocation or captive breeding decisions. Besides, there are concepts that highlight intraspecific diversity that avoid taxonomic inflation and the somewhat arbitrary subspecies concept, e.g. evolutionarily significant units (ESUs, Ryder, 1986; Moritz, 1994; Crandall et al., 2000). Ultimately, there will probably never be a definitive arbiter of what is a species and what is not, but this is a direct consequence of the continuous process of evolution and nothing taxonomists should worry about.

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