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Commentary

Taxonomic inflation and the poverty of the Phylogenetic Species Concept – a reply to Gippoliti and Groves

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Abstract

There has been an ongoing debate over mammalian taxonomy, species splitting and the Phylogenetic Species Concept (PSC). As a reply to a recent commentary in this journal, we characterise the PSC in its two most widely used versions (based on diagnosability and monophyly, respectively) and highlight both its theoretical flaws and practical shortcomings for taxonomy, evolutionary biology and conservation.

Introduction

Mammalian taxonomy (and taxonomy in general) has seen its fair share of debates recently whose main cause, along with a hitherto unseen wealth of molecular data, is a paradigmatic shift from the Biological Species Concept (BSC) to the Phylogenetic Species Concept (PSC). The BSC became widely accepted in the wake of the Modern Synthesis of the mid-20th century and particularly so through the mediation of the highly influential Ernst Mayr. It holds that species are reproductively isolated units in that, by definition, only conspecific matings yield fertile offspring. The BSC shows several shortcomings, e.g. when the criterion of reproductive isolation is difficult to assess because populations are allopatric or when there is a number of morphologically/ecologically/behaviourally and genetically (to some extent) different – but closely related – “species” which will generate fertile (at different levels) hybrids (Sika *Cervus nippon* and Red deer *Cervus elaphus*, McDevitt et al. 2009; White-tailed *Odocoileus virginianus* and Mule deer *Odocoileus hemionus*, Stubblefield et al. 1986; sheep and goat species, *Ovis* and *Capra*, that are notorious for hybridisation, e.g. Giacometti et al. 2004 and Loehr et al. 2006). The infinite variability of options provided by aeons of evolution and natural selection militates against fully objective criteria to define species as discrete entities. Some level of subjectivity is unavoidable because evolution is a continuous process, while taxonomic names are discrete (species or not, there is nothing in between). The PSC is a pattern-based species concept (as opposed to the process-based BSC) that exists in different variants. In its original version, species are defined as unequivocally diagnosable units, but often species are defined on the basis of monophyly (Cracraft 1983; Zachos et al. 2013a and references therein; see also below). The widespread acceptance of the PSC has recently led to a huge number of species splittings in mammals (and other taxa) – most notably the doubling of bovid species according to a recent monograph (Groves and Grubb, 2011) – that many consider to be unwarranted and detrimental to conservation (Frankham et al., 2012; Heller et al., 2013; Zachos et al., 2013a,b). In a recent commentary paper published in *Hystrix*, Gippoliti and Groves (2012, hereafter abbreviated as G&G)

defend the huge number of newly erected mammal species against critics (see also Groves 2012, 2013), specifically criticising views published in one of our previous articles (Zachos et al., 2013a). In this brief rejoinder, we will comment on their criticisms and explicate where in our opinion their arguments are erroneous. The PSC – whether based on diagnosability or monophyly – results in taxonomic artefacts because it is theoretically flawed and based on a naive and oversimplified view of the evolutionary biology of speciation.

The poverty of the Phylogenetic Species Concept

First of all, we wish to emphasise that we are not against species splitting *per se*. Taxonomic stability can be just as ill-founded as splitting, and it has rightly been stated that the low profile often accorded to taxonomy may have led to an artificial stability in many taxa (Gippoliti and Groves, 2012). Baker and Bradley (2006) hypothesised that there are more than 2000 unrecognised mammal species, and this may well be true. But this is no justification to base species splittings on superficial data sets, small sample sizes and (what we consider) a misguided species concept. The main reason for what we have recently called “splitting frenzy” (no offence meant!) (Zachos et al., 2013a) is the adoption of the PSC, and the main argument of its adherents is its (alleged) testability. We shall now outline briefly why we think that the PSC is theoretically and practically flawed. There are two main versions of the PSC, and we are aware that G&G only advance one of them (the diagnosability concept). We nonetheless address both versions as they are both popular and because they share analogous shortcomings. The PSC in its original form defines species as diagnosable units: “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, our italics). This does *not* involve monophyly or apomorphy, just 100% diagnosability (i.e. no overlap) due to fixed genetic differences – which, incidentally, have often been hypothesised or assumed, but not corroborated. It is indeed a theoretically testable concept: samples can be analysed (morphologically, genetically, behaviourally etc.), and if there is no overlap, then you have two or more species. The problem with this concept, however, is that the biological reality has been sacrificed on the altar of testability. Diagnosability, and consequently what exactly the *smallest* cluster is (see above), critically hinges on the resol-

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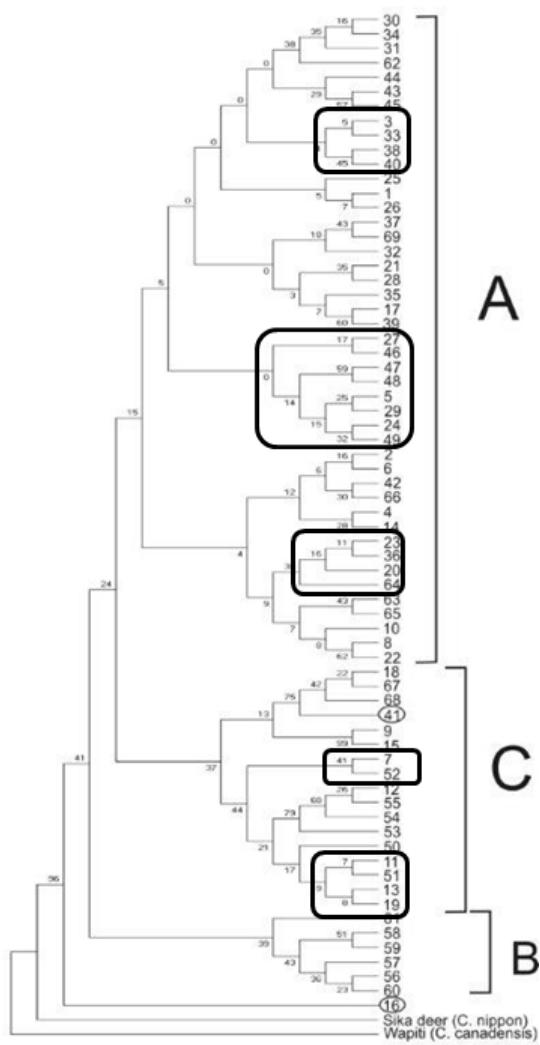


Figure 1 – Monophyly and species delineation. mtDNA phylogeny of European red deer (*Cervus elaphus*) with outgroups taken from Niedziałkowska et al. (2011). A (western), B (African-Sardinian) and C (eastern) denote the main mitochondrial lineages that have been assigned species status by Groves and Grubb (2011). The rounded squares show arbitrarily chosen monophyletic groups at different hierarchical levels. A multitude of other such monophyla are also present. For details, see text.

ution power of the characters analysed. The usual answer of adherents of the diagnosability concept is that this is the whole point: “the world is far richer in biodiversity than we had conceived” (Groves 2012, p. 687). Agreed, but is biological diversity the same as species diversity? Does every level of biological diversity correspond to natural units that are separately evolving lineages (the common ground that all species concepts can agree upon, de Queiroz 2007)? With whole-genome analyses any two individuals (with the possible exception of monozygous twins) become diagnosably different. Family groups sharing *de novo* mutations are the next inclusive level of diagnosable clusters. As a result, every and any population of every and any species will contain dozens or hundreds of diagnosable units or, under the diagnosability PSC logic: species... While diagnosability in itself is testable and thus objective, it will always be a matter of convention where to draw the actual line between species unless one is willing to accept that there is not one species of, say, ardvark (or grey wolf or muskrat or, for that matter, human) but hundreds or thousands. The PSC, if applied to *Homo sapiens*, would generate a multitude of “species”, with quite viable hybrids! The same argument is applicable to the monophyly version of the PSC. Again, monophyly is testable and thus objective. However, it has long been known that character trees (e.g. gene trees) and organismal trees are not the same, that taxa can be monophyletic for a given character, but non-monophyletic for another and that cladograms are really “cloudograms” (see Zachos 2009 and references therein). But for the sake of the argument, let us assume that the phylogeny for a

taxon that we have arrived at correctly represents the true organismal evolutionary history. Then, surely, monophyly is an unequivocal arbiter of species delimitation, isn’t it? Unfortunately, the answer to this question again is no because monophyly, just like diagnosability, can be found at any given level in the hierarchy of living things. So, where should we draw the line? Fig. 1 shows a phylogeny of European red deer (*Cervus elaphus*, we will neglect here that it is only a mitochondrial phylogeny). The monophyletic groups designated A, B and C denote the major lineages indicative of different glacial refugia, and they coincide with the three different European red deer “species” recently advanced by Groves and Grubb (2011) based on diagnosability, *C. elaphus*, *C. pannonicus* and *C. corsicanus*. Monophyly, one could argue, supports the same three “species” because A, B and C are all monophyletic. But so are dozens of other groupings at different levels of the tree (five of which are denoted by the rounded squares in Fig. 1). So, why are there only three species and not many, many more? Just like diagnosability, monophyly – while purportedly objective (because testable) – is a poor guide to species delimitation because it offers no criterion as to where (i.e. at which level of nested monophyla) the line between species should be drawn. Apart from that, monophyly is a concept that can only be applied around the species level with great caution because evolution at this hierarchical level is reticulate, and monophyly is indeed a function of time and (effective) population size (see Zachos 2009 and references therein). It is only at higher levels (that is with time and through isolation and divergence) that the complex population biological (horizontal!) processes become dissolved into the simple vertical dichotomous pattern of cladistic phylogenetics. Monophyly as a species criterion misrepresents and oversimplifies the biological processes that are involved in differentiation, divergence and, ultimately, speciation.

There is yet another line of argumentation that clearly shows the shortcomings of both diagnosability and monophyly as yardsticks for species delimitation and that we believe is another coup de grâce for the PSC. Diagnosability (just like reciprocal monophyly) can and often does occur as a consequence of extinction of intermediate forms, which is shown in Fig. 2. A sundering event splits a panmictic population with two different character states (e.g. two different alleles at a locus determining coat colour) into two smaller populations isolated from one another. Genetic drift in smaller populations is higher than in large ones, so over time, one of the two alleles may get lost in both populations by pure chance. If it is the black one in one population and the white in the other, both populations will be 100% diagnosable. Thus, the death of the last carrier of one of these alleles in one population marks the exact point in time (to the minute!) that speciation occurs. If this is to be taken seriously, then the extinction crisis will produce millions of new species as more and more populations will be disrupted into small isolates. Tigers, for instance, are a highly endangered spe-

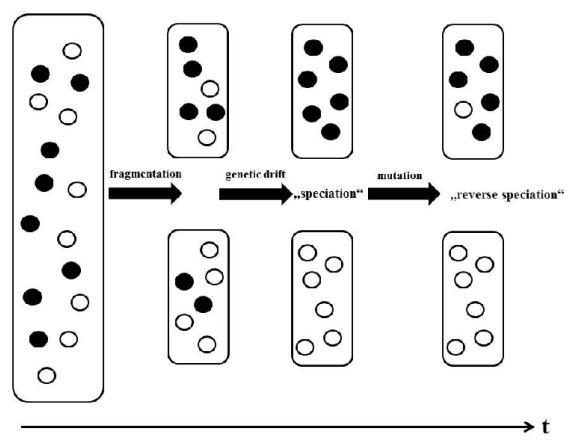


Figure 2 – Absurd consequences of diagnosability as arbiter of species delimitation. Rounded squares denote populations, black and white circles different character states (e.g. coat colour alleles), t is time. For explanations, see text. Similar reasoning applies to monophyly.

cies, and even in India, which harbours about 60% of the global population, tigers are only found in isolated remnant populations that are undergoing rapid genetic drift (see Fig. 3 in Sharma et al. 2011). Tigers may well go extinct in the near future, but not, according to the logic of the PSC, before splitting into a multitude of “new” tiger species. This line of reasoning goes even further: in case of a novel mutation again introducing the white allele into the “black” population (or vice versa, of course), diagnosability gets lost, and species boundaries get blurred. According to the logic of the diagnosability PSC, this is equivalent to reverse speciation. As a consequence, speciation producing two species and reverse speciation uniting them into a single species again may occur in each generation. In our view, this is a bizarre and unacceptable contortion of biological reality.

Taxonomic inflation and conservation

Both unwarranted lumping and splitting hampers well-informed conservation efforts aiming at preserving as much biological diversity as possible (Frankham et al., 2012; Gutiérrez and Helgen, 2013; Heller et al., 2013; Zachos et al., 2013a,b). A sound taxonomic knowledge based on the evolutionary history of a group is key to its conservation. Ill-informed lumping of different taxa may dilute the genetic integrity of both and be particularly harmful if one or both are threatened. However, while there is indeed no reason to believe that cryptic species in mammals are rare, the PSC is, as shown above, a very poor guide to identifying and delineating them. Unwarranted splitting, as discussed elsewhere (Frankham et al., 2012; Zachos et al., 2013a,b), has a number of deleterious consequences because it reduces the population size of each species with concomitant legal and regulatory ramifications. Genetic rescue may not be allowed (because it would require the crossing of two different acknowledged species!), and as a result, the increase in genetic drift and inbreeding and the decrease in fitness may not be counteracted. Even more, since inflation causes devaluation, an inflationary use of the term “species” may well lead to its devaluation in the public as well as the scientific community. ☺

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