Species Concept in Primates

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COMMENTARY

Species Concept in Primates

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The way we view the Species category in Primates, as in other animals, especially other vertebrates, has been going through a revolution over the past 20 years or so. Much is wrong with the idea that we can define species according to whether or not they are "reproductively isolated": this concept, the so-called Biological Species Concept, has never offered any guidelines in the case of allopatric populations; this has now been shown to be simply wrong. Although other ways of looking at species – the Evolutionary, Recognition, Cohesion and Genetic Species Concepts – have all provided particular insights, the only proposal to offer a repeatable, falsifiable definition of species is the Phylogenetic Species Concept. This has been criticised for increasing the number of species to be recognised, although it is not clear why this should be a problem: indeed, it tells us that the world is far richer in biodiversity than we had conceived. Am. J. Primatol. 00:1–5, 2012.   © 2012 Wiley Periodicals, Inc.

INTRODUCTION

The importance of what we mean by the word "species" goes way beyond taxonomy and systematics as such: it affects such diverse fields as genetics, biogeography, population biology, ecology, and ethology, in the present-day sphere; paleontology and paleoanthropology; and, in an era in which threats to the natural world and its biodiversity are ubiquitous and accelerating, it affects conservation strategies [Rojas, 1992].

How many "species concepts" one distinguishes is a matter of how finely one is prepared to seek out the fine distinctions between different authors' manner of phrasing. Thus, Harrison [1998] distinguishes only 7; Mayden [1997] as many as 24. Broadly, we may divide them into those that emphasize the absence of interbreeding, and those that do not: "theoretical" and "operational," in the terminology of Groves [2011].

To some extent, disagreement as to what precisely constitutes a species is to be expected, given that the concept serves so many functions [Vane-Wright, 1992]. Endler [1989] listed some of the different aims of different species concepts: purely taxonomic, or evolutionary; theoretical (what the nature of a species should be, versus how one recognizes one on the ground); instantaneous or cladistic; and reproductive or cohesive. This "pluralism" has been used by Ereshevsky [1999] and Mishler [1999] to junk the concept of species altogether, making the terminal taxon merely the lowest level in a rankless hierarchy. This is in fact a logical endpoint if one adopts the rank-free "Phylogenetic Taxonomy," and

its nomenclatural correlate, the Phylocode: most biologists reject such a drastic step as it entails a reduction of information content, and depends on a (probably unobtainable) 100% complete knowledge of phylogeny.

Yet, there is a sense in which species concepts are all trying to say the same thing, and that the differences between them are just the criteria employed [De Queiroz, 1998], or at what point in the divergence of two lineages one wishes to start calling them "species" [De Queiroz, 2007]; but the results of applying these different criteria can be startlingly different. It is a pity if specialists in different fields must be forever talking past each other.

THE BIOLOGICAL SPECIES CONCEPT (BSC)

Under the BSC, species are defined as "groups of actually or potentially interbreeding natural populations, which are reproductively isolated from other such groups" [Mayr, 1940: 256]. Hence for Mayr, as for Dobzhansky [1937] before him, what distinguishes a species (read: a sexually reproducing

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species!) is its reproductive isolation. The history of this concept was summarized by Ayala and Fitch [1997], who discussed the roles of pre- and postmating isolation.

The BSC works very well in cases of sympatry. If two taxa are sympatric, yet maintain their own separate identities, then they are reproductively isolated: they are distinct species, and no further discussion is possible. If they are parapatric, then equally they have the chance to interbreed, and do not. But what if they are allopatric?

In cases of complete allopatry, the BSC offers no criteria at all to decide species status [Cracraft, 1989]. Mayr et al. [1963; see also Mayr, 1969] suggested that the amount of difference between allopatric taxa should be compared to that between sympatric taxa in the same group, or between the most divergent intergrading subspecies. But when all is said and done, "amount of difference" is a very slippery concept, and whether morphological sources of evidence, or vocalizations or other behaviors, or molecules are being considered, what "amount of difference" is adopted seems arbitrary, and the status of the differences, especially whether they are fixed or only average, is usually left unstated or somehow taken for granted [*pace* Mallet, 1995]. Under the BSC, the interpretation of allopatric pairs, whether they are species or just subspecies within a species, depends entirely on a taxonomist's personal assessment [Cracraft, 1989]: his/her intuition, one might say. The same criticism could also be applied in the case of Specific Mate Recognition Systems, on which the Recognition Species Concept of Paterson [1978, 1980, 1982] relies—though this concept has been productive as far as primatology is concerned (e.g., Bearder et al., 1995).

This subjective nature of the BSC in cases of allopatry is a very serious drawback, because it makes the species concept unrepeatable and unfalsifiable, and so is not strictly scientific.

But this is not all. Sympatric species, as I noted above, are the very foundation stone of the BSC. If two species maintain their separate identities when existing in sympatry, then clearly they are not interbreeding—right? Not right. The molecular revolution has arrived, and with it the rather startling discovery that sympatric species may indeed interbreed—and often. When, nearly 40 years ago, Dunbar and Dunbar [1974] recorded *Papio anubis* and *Theropithecus gelada* interbreeding in the wild in Ethiopia, it seemed possible to interpret this as a mere isolated instance of the violation of the BSC. The spread of intensive fieldwork began to suggest that the baboon/gelada case might not after all be so isolated; in particular, Detwiler [2002] found that hybridization between two species of *Cercopithecus* occurs in many forests bordering the eastern side of the Western Rift Lakes in East Africa,

and that in some forests, notably in Gombe National Park, hybrids are found in frequency comparable to or exceeding that of the parent species. Yet more startling, De Jong and Butynski (2010) reported hybridization between representatives of two genera, *Cercopithecus* and *Chlorocebus*. But what has really shown the invalidity of the "sympatric, so not interbreeding" assumption has been the increasing ability to sequence large samples of both mtDNA and nDNA from wild populations, with the astonishing discovery that some populations of some species all too often contain the mtDNA not of their own species but of a related sympatric species, indicating that they have been interbreeding. Some striking examples: One of the two known populations of the recently discovered *Rungwecebus kipunji* (the kipunji or highland mangabey) contains mtDNA from the local population of the Yellow Baboon, *P. cynocephalus* (Roberts et al., 2010). Two morphologically distinctive South Asian langur species, *Semnopithecus johnii* of southwestern India and *S. vetulus* of Sri Lanka, contain mtDNA of the respective local representatives of the *S. entellus* group (Karanth et al., 2008). Quite a number of species of Old World monkeys have actually arisen as the products of hybridization (Osterholz et al., 2008; Ting et al., 2008; Tosi et al., 2000).

As a rather startling (non-Primate) addendum: possibly the two largest animals ever to have existed, the Blue Whale *Balaenoptera musculus* and the Fin whale *Balaenoptera physalus*, appear to hybridize at a nontrivial frequency (Bérubé & Aguilar, 1998).

THE EVOLUTIONARY SPECIES CONCEPT (ESC)

The ESC was proposed by Simpson [1961: 153]: "A lineage . . . evolving separately from others and with its own evolutionary role and tendencies." Subsequent authors have modified this, or drawn it out, in different ways: as far as sexually reproducing organisms are concerned, a species is "a single lineage . . . genetically integrated by historically contingent events of interbreeding" [Christofferson, 1995: 447]. There is of course considerable value in this concept, and it in some way summarizes what a species should be, and why it is important theoretically; nonetheless, it is hardly an operational definition, hence it is not objectively falsifiable.

THE GENETIC SPECIES CONCEPT

Under the Genetic Species Concept, the amount of genetic difference necessary for potential reproductive isolation can be measured [Mayden, 1997; and see especially Baker & Bradley, 2006; Bradley & Baker, 2001]. The idea that species ought to be more differentiated genetically [or phenetically:

Mallet, 1995] than infraspecific groups has a long history. In a classic paper, Ayala [1975] compared values for Identity (Nei's I) and Distance (Nei's D) for various animal groups. Looking at his Table 1, which compares genetic differentiation between (what they deem to be) local populations, subspecies, sibling and sister species, and nonsister species (in *Drosophila* and other invertebrates, fish, salamanders, lizards, and rodents), it appears that there does tend to be increasing differentiation up the scale, but it is also true that there is a good deal of overlap between levels, and one would be foolhardy to insist that, for example, below a certain level of genetic distance two taxa are merely subspecies, but above it they are species. Thorpe [1983] collected an even larger amount of data, again using Nei's D; he too concluded that there is an average difference between the amount of genetic differentiation to be expected between species and that to be expected between samples at infraspecific levels, but that there is an enormous overlap between levels.

Nei's I and D are calculated from allele frequency differences; today, DNA sequencing has opened up the possibility of elucidating the genetics of species differences in a direct way, rather than indirectly as was the case until the 1990s, and there have been several attempts to organize the flood of molecular data in a way that contributes to an understanding of the nature of species. Bradley and Baker [2001] compared cytochrome-b sequences for a number of bat and rodent genera in much the same way as Ayala (1975) and Thorpe (1983) had compared the allele frequencies, and found that, although the average species pair differs more than does the average intraspecific (including subspecies) pair, it is simply not possible to draw a line at some level of sequence divergence and say that above this level they are species, below it they are not. We must simply adjust to the fact that well-differentiated species pairs may show extraordinarily little sequence divergence in a given DNA region.

THE PHYLOGENETIC SPECIES CONCEPT (PSC)

Under the Phylogenetic Species Concept or PSC [Baum, 1992; Cracraft, 1983, 1989], species are populations (or groups of populations) that are 100% diagnosable: they have fixed heritable differences between them (though these may in fact be expressed only in one sex or at one stage in the life cycle); equivalently, they are genetically isolated, though not necessarily reproductively isolated. As summarized by Nixon and Wheeler [1990: 218], under the PSC a species is "the smallest aggregation of populations... diagnosable by a unique combination of character states in comparable individuals."

Note that under the PSC, the diagnostic characters of a species need not be evolutionarily derived (autapomorphic). It is perfectly possible to have a species that is defined only by primitive retentions, a "living fossil" in the broad sense. There is nonetheless a good deal of misunderstanding about this: Mallet [1995] and Harrison [1998], for example, misquote Cracraft [1989] as specifying that a species must be defined by apomorphies. Let us be clear about this: the PSC does not demand that each species be diagnosed by apomorphies. The "phylogenetic" in the concept simply records the roles of species as the terminals in a cladogram (on the—erroneous, we now know—supposition that it is at this point that reticulation takes over from divergence). Many people have misunderstood the concept in this way, and it should probably have been originally called something like the Diagnosability Species Concept.

Kimbel and Martin [1993] refer to species under both the PSC and the Recognition Species Concept as being "units of reproductive cohesion" as opposed to units of isolation as in the BSC, and opine that this is why they often identify the same units. Because the ability to interbreed is a plesiomorphic condition, not an inherent one, this is not strictly true of the PSC. One might modify their characterization by saying that under the PSC species are units of genetic cohesion.

WHAT ARE DIFFERENT SPECIES CONCEPTS TRYING TO SAY?

The BSC was the first to define species in the population-genetic terms of the New Evolutionary Synthesis of the 1930s: species do not exchange genes. As discussed above, the BSC leaves plenty of gaps that render it less than scientific, most glaringly the problem of what to do with allopatric populations; and, ironically, it has been the advances in genetics of the past 20 years that have pointed up shortcomings even in the sort of situation for which the BSC was designed—populations coexisting in sympatry.

The general unease with the BSC since about 1970 generated a number of alternatives that are essentially modifications (endoheresies), notably the Recognition Concept (see above) and the Cohesion Species Concept of Templeton [1989], seemingly saying that the BSC is what species ought to mean, but that there is this or that problem that needs to be addressed. The PSC, when proposed, was a very radical departure (exoheresy), based as it was on pattern rather than on process. Nonetheless, in the light of some recent comparative surveys (most notably those of Christofferson [1995], Mayden [1997] and De Queiroz [1998]) it appears after all to have much in common with more process-based concepts,

because the essence of a species is the separation of evolutionary lineages. As De Queiroz (2007, see especially his Figure 1) has argued, what the different concepts are doing is to take different points along the divergence trajectories of two sister populations and to say "it is at this point that we can define them as being different species." I have argued above that the only objective point at which we can define them as species is when they are 100% differentiated (i.e., by fixed heritable character state differences).

SUBSPECIES

The founder of the PSC rejected the idea of subspecies [Cracraft, 1983], but other PSC supporters do not [Nixon & Wheeler, 1990]. For Avise and Ball [1990], some geographic concordance between molecular lineages is necessary before subspecies can be recognized. Any way we look at it, subspecies are not really objective concepts, certainly they are not entities in the way in which species are, and should not be reified. The plethora of subspecies which have been erected in mammals can be divided into the Good, the Bad, and the Ugly [Groves & Grubb, 2011]. It is not, *contra* the sometimes stated assertions of those shocked by the PSC, simply a matter of raising subspecies to species rank, but it takes a good deal of solid research to discover which "subspecies" are Good, and should be reranked as species, which are Bad, and should be reduced to synonymy, and what to do with the Ugly residue.

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