

So What is a Species Anyway? A Primatological Perspective

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Since Darwin's time, the question "what a species" has provoked fierce disputes and a tremendous number of publications, from short opinion papers to thick volumes.¹ The debates covered fundamental philosophical questions, such as: Do species exist at all independently of a human observer or are they just a construct of the human mind to categorize nature's organismic diversity and serve as a semantic tool in human communication about biodiversity?^{2–4} or: Are species natural kinds (classes) or individuals that are "born" by speciation, change in course of time, and finally "die" when they go extinct or diverge into new species?^{5–8} Also included was the problem of species as taxa (taxonomic) versus species as products of the speciation process (evolutionary).⁹ More pragmatic issues arose, such as: How can we reliably delineate and delimitate species?^{10,11} The great interest in what a species is reflects the importance of "species" as fundamental units in most fields of biology, especially evolutionary biology, ecology, and conservation.^{2,12–14}

More than twenty species concepts have been proposed to answer the question of what a species is. How-

ever, a generally accepted concept is not available.¹⁵ In principle, we are still at the same point that Darwin was 1859, when he wrote: "No one definition has satisfied all naturalists; yet every naturalist knows vaguely what he means when he speaks of a species."^{16:44} Given that biologists have spent decades trying to find a universal definition of "species" and have not achieved it, it has become obvious that there is no single correct definition. As an alternative, a pluralistic, approach was proposed, where different species concepts are equally legitimate and useful in classifying organisms and understanding the history of life, although many people find this unsatisfying.^{17–19} Another question is whether species, particularly as a taxonomic rank, means the same in different groups, such as prokaryotes, plants, invertebrates, and mammals.^{20,21} For instance, we have to ask whether a macaque species and a baboon species are really the same rank, given that most macaque species constitute phylogenetically much older lineages than do baboon species, and thus are genetically more heterogeneous.²²

In primatology, the number of species has increased tremendously within recent years. Rowe,²³ in 1996, listed 230 species; Groves,²⁴ in 2001, listed >350 species; and in the third volume of the *Handbook of the Mammals of the World*,²⁵ published in 2013, the number of species exceeds 480. This increase is partly a result of discoveries of formerly unknown primates in the wild, among them *Rungwecebus kipunji*²⁶ and *Rhinopithecus strykeri*²⁷ or *Cercopithecus lomamiensis*,²⁸ but it is more strongly a consequence of the use of molecular methods in phylogenetic studies and the use of differences in DNA sequences to delimit species. This, combined with the application of a Phylogenetic Species Concept³¹ has caused the increase in species numbers in primates as in most other studied taxonomic groups, such as birds³² or bovids.³³ This led Ian Tattersall³⁴ to pose the question, "Madagascar's lemurs: cryptic diversity or taxonomic inflation?" This question can be generalized for all primate and nonprimate lineages.³⁵

The increase in species, the splitting of genera, and the constantly changing primate species list have recently created uncertainty about primate taxonomy and fueled a controversy about the usefulness of particular species concepts and the criteria that should be applied to delineate and delimit species.^{36–42} In our previous work, we have contributed to this species increase (e.g. 43–48) by applying an integrative approach⁴⁹ using information from mitochondrial DNA, chromosomes, morphology, behavior, acoustics, and biogeography to delimit new taxa. Based on this information, the

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identification of phylogenetic clades or evolutionary units was relatively easy, and conservatively, we ranked the detected biological entities or clades as subspecies or species. We did this with hesitation because whether such units should be given species rank in a Linnean classification was a question we were, in fact, unable to decide.

Here, our aim is not to provide a solution to the species problem or present another “new species concept” because we think that a general species concept, according to which species are classes in a classification scheme (*sensu* Linné) and not biological entities is an unattainable solution. We see a species as a group of individuals that are vertically connected by descent and/or horizontally by sexual gene exchange.^{50–52} Our main problem is not identifying or distinguishing such entities, but whether it is justified to give them a rank (genus, species, subspecies) in the classification scheme.⁵³ For us, it also remains questionable whether giving a species, as a product of speciation, a rank at all. We also wonder whether the Linnean hierarchical taxonomy should be abandoned and a rank-independent nomenclature used instead (for example, “species” in a non-Linnean sense, “taxon,” or “evolutionary significant unit”).

When delimitating “species,” we face two challenges: how to identify phylogenetic clusters, groups, or evolutionary entities when regarding species as products of the speciation process (vertical gene flow) and how to determine the degree of horizontal gene flow among such entities, given that pre- and postzygotic barriers are not complete and occasional sexual contacts occur between entities. The first challenge can be addressed by applying cladistic methods⁵⁴ to either molecular or other characters to define exclusive (monophyletic) entities. The second challenge is more difficult. In many cases, genealogical discordances caused by both historical and ongoing gene flow between entities are detectable with molecular methods.^{55–57} This makes delimitation of exclusive entities based on only one or a few genetic

markers questionable.^{39–58} An extreme example is the case of *Rungwecebus kipunji*. If this species had been delimited just on the basis of mitochondrial sequence information, the introgressed population in the Southern Highlands of Tanzania, would have been classified as a baboon and the second, the non-

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troggressed population at Ndundulu, Tanzania carrying the original *Rungwecebus* mitochondria, would have been delineated as *Rungwecebus*.^{59–61}

To obtain an estimate of gene flow between closely related species, such as in brown lemurs or tarsiers, population genetic approaches are indicated.^{62,63} In such analyses, it often becomes obvious that a certain degree of gene flow occurs. Most importantly, some genes might be affected whereas others might not.⁶⁴ Interestingly, occasional horizontal exchange of genes does not, *per se*, break the exclusivity or identity of species. It might become more important to identify particular genes that hinder complete fusion of entities or genes that cause reproductive incompatibilities.⁶⁵ An approach that will become increasingly applicable as genetic data on nonmodel organisms

accumulates is a multi-locus coalescent-based method that specifically links patterns of lineage divergence to speciation and demographic processes.^{64,66,67} Such large population genomic datasets have the potential to investigate the role of gene exchange in the speciation process.

Our approach is based on a Phylogenetic Species Concept,⁶⁸ but adds, if possible, information on horizontal gene flow, which is part of the Biological Species Concept.⁶⁹ However, we think, as explained earlier, that the Linnean system is not suitable for the classification of species, although, its nomenclature is still important for practical reasons. Without question, a universal taxonomic communication system is needed.

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