Primate Taxonomy and Conservation

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Introduction

“Only what we know, we can appreciate and protect.” This short version of a famous quote by *Baba Dioum*, a Senegalese environmentalist, nicely depicts the relationship between conservation and taxonomy. We have to name and classify things and organisms in order to know them and hence appreciate and preserve them. Taxonomy, as the science of classification, usually refers to the theory and practice of describing, naming, and classifying organisms, whereby classifying refers to “the ordering of [organisms] into groups (or sets) on the basis of their relationships” (Simpson 1961, p. 9). A taxonomic classification is the basis for most other biological disciplines, such as ecology, phylogeny, and evolution, and it is essential for an understanding of biodiversity and its conservation. The basic unit of taxonomy is the taxon (plural taxa) which is according to Simpson (1961, p. 19) “a group of real organisms recognized as a formal unit at any level of a hierarchic classification.” For instance, the species *Papio hamadryas* (hamadryas baboon) is a taxon, but also the genus *Papio* (baboons) and the family Cercopithecidae (Old World monkeys) are taxa.

The taxon “species” is of particular importance in taxonomy and species are also the fundamental units of evolutionary biology, macroecology, biogeography, and conservation. Many conservation issues are concerned with the protection and preservation of species (e.g., Endangered Species Act in the United States 1973) and the diversity, abundance, and distribution of species is used to prioritize conservation

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areas. Species are crucial to conservationists and also to policy-makers, who use them as units for formulating national and international conservation laws. It is understandable that these people rather prefer stable taxonomies. On the other hand, taxonomy is a biological hypothesis and is open to changes if new data become available. Progress in biological research and conservation is often hampered by widespread taxonomic uncertainty and, in particular, the delimitation of species is thus crucial for conservation biology. In our contribution we will briefly sum up the history of taxonomic research with a focus on primates, touch on the problems of species concepts, and delve into the impacts on primate taxonomy and conservation. Comprehensive introductions into primate taxonomy can be found in, e.g., Groves (2001, 2004, 2011, 2012, 2014).

Extinction of Species and the Biodiversity Crisis

Biodiversity is a term used to describe the variety of life on Earth and an essential proportion of this variety is the diversity among species (Wilson 1988). Within the last decades we witnessed an escalating loss of species due to human activities and thus a decline in species diversity, so that some authors already speak about a sixth mass extinction, after five earlier events in geological times, as suggested by fossil evidence (Casetta and Marques da Silva 2015). The human-caused increase of extinction risk also affects nonhuman primates. Currently (August 2015) the IUCN lists 430 extant primate species of which 259 (60.2 %) are Vulnerable, Endangered, or Critically Endangered (IUCN 2015). Several of these threatened species are already down to less than a few hundred individuals (Schwitzer et al. 2014). Due to various reasons, species differ in respect to their extinction risk and, because of the scarcity of time and financial resources, not all threatened species can be protected and managed at the same time. Conservationists have to set priorities and for decision-making they use, among others, data on population sizes, distribution, and threats, which all rely on information on the taxonomic status of respective populations under consideration. If conservation legislation and conservation work is focused on the preservation of species, a classification of a threatened population as a subspecies or species can make a critical difference.

Consider the case of the Hainan gibbon (*Nomascus hainanus*). With less than 30 individuals it is close to extinction and is regarded as Critically Endangered by IUCN. This species has been recently elevated from subspecies *N. nasutus hainanus* to species (Roos et al. 2007) and a species-specific conservation action plan was implemented. This measure most likely would not have been employed if the status would have remained at the subspecies rank. Another example is orangutans (*Pongo* spp.). Previously Sumatran (*P. abelii*) and Bornean orangutans (*P. pygmaeus*) have been considered as one species and animals from both provenances have been kept and bred together in captivity. Genetic studies however showed that Sumatran and Bornean orangutans are genetically so distinct that they qualify as separate species (Xu and Arnason 1996; Steiper 2006). A moratorium was placed on producing hybrid orangutans and each species has now its own species survival plan (SSP) to prevent genetic admixture.

Genetic admixture of populations or closely related species that are adapted to different local conditions can result in outbreeding depression, which leads to a reduction in fitness caused by the breakdown of coadapted gene complexes (Templeton 1986). Outbreeding depression is now recognized to be a problem in wildlife conservation and captive breeding programs similar to inbreeding depression (Storfer 1999; Waller 2015). On the other hand, if closely related but genetically impoverished populations were not elevated to species rank, genetic exchange between these populations as a management tool to improve genetic diversity (genetic rescue, Frankham 2015) would be an option to prevent possible negative effects of inbreeding.

Anyhow, for conservation decisions, reliable information on the taxonomic status of populations are therefore relevant and the demarcation of species becomes an important prerequisite for species conservation. It is thus comprehensible that the application of specific species concepts is one of the most hotly debated issues not only in taxonomic research but also in conservation biology (Rojas 1992; Cracraft 1997; Dubois 2003; Isaac et al. 2004; Mace 2004; Zink 2004; Gippoliti 2007; Morrison et al. 2009; Blair et al. 2011; Frankham et al. 2012, Gutiérrez and Helgen 2013, Zachos et al. 2013a, b; Melville et al. 2014; Shirley et al. 2014; Rylands and Mittermeier 2014).

Taxonomy

People at all times and in all places most likely ordered living things in a hierarchical system based on how organisms appear, that is, on similarities and dissimilarities in how they look, smell, taste, sound, or behave (Yoon 2011). Such classifications are often organized by particular interests for particular uses, e.g., beneficial versus noxious, edible versus inedible, harmless or dangerous (Atran 1998). In some cases taxonomic sophistry was employed to make animals useful. In medieval times the Catholic Church declared, among others, the beaver (*Castor fiber*) as “fish” so that its meat could be eaten even during Lenten seasons. In most cases, however, classifications are much more detailed, constituting a vernacular naming system also referred to as “folk-taxonomy”. Comparisons of folk-taxonomies of indigenous people from various parts of the globe with respective scientific taxonomies of the same regions revealed that both classifications come up with strikingly similar numbers of species and even higher taxonomic groupings (e.g., birds on New Guinea: Diamond 1966; Diamond and Bishop 1999, in the Philippines: van der Ploeg and van Weerd 2010, fish in the Amazon: Begossi et al. 2008). Furthermore, the indigenous knowledge of vertebrates and plants is most often not limited to economically important species, but represent in depth knowledge of the alpha diversity of the respective groups. But there are exceptions. For example, the Kalam of New Guinea deny that cassowaries fall under the bird category, not only because flightless cassowaries are physically unlike other birds, but also because they are ritually prized objects of the hunt (Bulmer 1967).

Humans everywhere classify animals and plants into species-like groups as obvious to a modern scientist as to a Maya Indian (Atran 1999). This apparently ubiquitous tendency of people to classify the organic world into "species" is often considered as an indication for the reality of species, independent of elaborate species definitions by western taxonomists (e.g., Mayr 1969).

Similarly, nonhuman primates were also named and classified in a system and one can imagine that their obvious similarity with humans qualified them into special classes. Primates have been often seen as distant relatives, ancestors or fallen ancestors and they became part of the local mythology and were often protected by taboos (e.g., Fuentes 2012; Zinner et al. 2013a). Two prominent examples of primates becoming important figures in mythology or religion are the hamadryas baboons of ancient Egypt and the Hanuman langurs (*Semnopithecus* spp.) of India. In ancient Egyptian the baboon held several positions in mythology. The name of the baboon god Babi or Baba, who was worshipped in Pre-Dynastic times for its intelligence and sexual lustfulness, may be the origin of the animal's common name (English baboon, French babouin). Later the baboon was closely associated with Thoth the god of wisdom, science, and measurement and it was often depicted on temples and monoliths. The Hanuman langur's common name originated from the Hindu deity Hanuman, who is sometimes considered a reincarnation of Lord Shiva. Traditional Hindus belief that each individual langur represents the living embodiment of this god and therefore is warranted protection. How local folklore affects the protection of monkeys in Africa is illustrated by the treatment of the white-thighed colobus (*Colobus vellerosus*) and Mona monkeys (*Cercopithecus mona*) by villagers in the Boabeng-Fiema Monkey Sanctuary in central Ghana. Local hunting taboos, based on an association of these monkeys with their gods, resulted in their protection since the nineteenth century.

The history of scientific taxonomy began in the eighteenth century with *Carl Linnæus* (Carl von Linné). He developed a hierarchical and nested system, in which animals, plants, and even minerals have been ordered according to their similarities (Table 1). With his "Systema Naturæ" he laid the foundations for the biological nomenclature scheme of binomial names, where the first name refers to the genus and the second, the specific epithet, to the species, e.g., *Homo sapiens* (modern humans) or *Papio hamadryas*. He also provided rules on how to name species, e.g., which language to use (Latin or Latinized Greek). The first edition of the "Systema Naturæ" was published in 1735 and already classified humans as members of the primate order. Of particular importance for zoology was the 10th edition from 1758 in which all listed animal species were given binomial names. The primate order in this edition contained four genera, namely *Homo* (humans), *Simia* (monkeys & apes), *Lemur* (lemurs & colugos) and *Vespertilio* (bats). Linnæus listed more than 20 species of primates, among them the ring-tailed lemur, the Philippine tarsier, the cotton-top tamarin, the lion-tailed macaque, and the mandrill, but he also wrongly included the colugo or Philippine flying lemur (*Cynocephalus volans*) and

Table 1 The descending ranks of the Linnaean hierarchy

Kingdom	Animalia	Animals
Phylum	Chordata	Vertebrates and relatives
Class	Mammalia	Mammals
Order	Primates	Primates
Family	Cercopithecidae	Old World monkeys
Genus	*Papio*	Baboons
Species	*Papio hamadryas*	Hamadryas baboon

The hierarchy starts with the kingdom and goes down to the species

The position of the hamadryas baboon within the system is shown here as an example. Additional (intermediate) ranks can be added, e.g., suborder, superfamily, subfamily, tribe, superspecies, subspecies. In case of hamadryas baboons additional ranks are Haplorrhini (Suborder), Cercopithecoidea (Superfamily), Cercopithecinae (Subfamily), Papionini (Tribe) and Papionina (Subtribe)

the bats, which are given their own mammalian orders today. Nevertheless, the work of Linnæus was a major progress in ordering and naming the living world and the binomial system is still in use. The use of Linnaean taxonomy is governed by the International Code of Zoological Nomenclature (ICZN).

During Linnæus' time, species were regarded as immutable and the idea that the perceived hierarchical and nested structure of the classification could be a result of common descent and hence of evolution was not yet conceivable. However, this changed in the nineteenth century with the work of *Charles R. Darwin* and *Alfred R. Wallace*. Within the evolutionary framework a hierarchical nested order made sense and graded similarities among groups of organisms could be explained by their descent from a common ancestor, thus by their phylogenetic relationships. After the recognition that species are not immutable but change over time and by adopting an evolutionary view, it became clear that a "natural order" of organisms has to be based on their phylogenetic relationship and not just on "similarities".

In many cases, similarity is indeed the result of a common heritage. For instance, members of two species of sportive lemurs (genus *Lepilemur*) are more similar to each other (e.g., genetically, morphologically, behaviorally) than either of them are to sifakas (genus *Propithecus*). Because they are closer related to each other than to the sifaka, their common ancestor lived not as long time ago as the common ancestor of *Lepilemur* and *Propithecus*. In other cases similarity is not due to common descent, but is a result of convergent evolution. Adaptation to certain environments or ecological niches produces traits that appear similar because they have the same function. For instance the multi-chambered stomachs of colobine monkeys and ruminants, only distantly related mammals, are both adaptations to digest leaves and grass with the help of microbes (Chivers and Hladik 1980). Therefore, not every similarity can be used to infer relationships and are not always useful in grouping

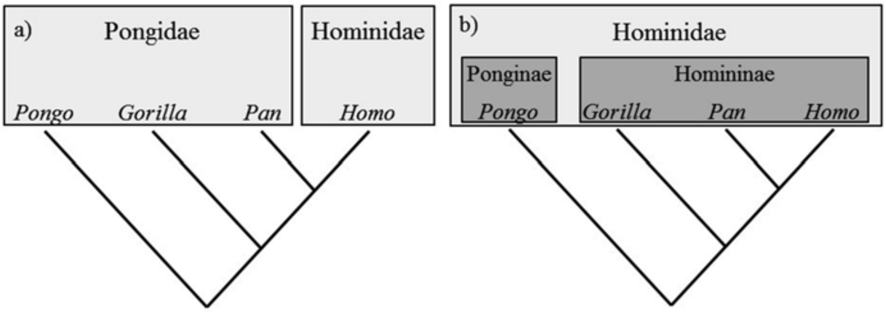

Fig. 1 Cladograms of great apes and humans. (**a**) The traditional paraphyletic taxonomy, where autapomorphic human traits, such as bipedalism, "naked skin," or large brain size, have been used to separate humans (family Hominidae) from great apes (family Pongidae), resulting in paraphyletic relationships. (**b**) Evolutionary-based taxonomy, where genomic synapomorphies have been applied, resulting in the monophyly of the African great apes and humans (subfamily Homininae) separated from the sister subfamily Ponginae (modified from Groves 2004)

organisms in an evolutionary taxonomic framework. Along with traits shaped by convergent evolution, traits that occur in a number of groups are not usually useful to differentiate among groups. Taillessness is a character of all apes and humans (Hominoidea) and can thus not be used to group humans into the tribe Hominini (including, e.g., *Australopithecus*, *Homo*). Taillessness is a trait which was most likely already present in the common ancestor of the Hominoidea and as such is a "primitive" or symplesiomorphic character. To designate Hominini, we have to look for an evolutionary novelty, a derived or synapomorphic character only shared by the members of the Hominini, e.g., bipedalism, which most likely first occurred in their common ancestor. Groups defined by synapomorphies are called monophyletic (Hennig 1950, 1966). A monophyletic group of organisms, or a clade, contains an ancestral species and all its descendants (Fig. 1b). If a group does not include all the descendants of a common ancestor, i.e., one or a subset of its descendants is not included, the group is paraphyletic (Fig. 1a).

Within the hierarchical system each rank can be regarded as a monophyletic group containing one or more smaller monophyletic groups. Among Mammalia (mammals) the Placentalia (mammals with placenta) constitute a monophyletic group. Furthermore, within Placentalia the Archonta (primates, colugos, and tree-shrews), within the Archonta, the order Primates, within Primates the Haplorrhini (primates with dry noses), within Haplorrhini the Catarrhini (Old World monkeys and apes), within Catarrhini the family Cercopithecidae (Old World monkeys), within Cercopithecidae the genus *Papio*, and within *Papio* the species *Papio hamadryas* all form monophyletic groups or clades nested within the respective higher level group. Although the species is the central unit in taxonomy and in biodiversity conservation, finding an all-encompassing definition of species is difficult and thus, the delimitation of units as species often remains controversial.

Species Concepts

Ever since Linnæus (1758) instructed taxonomists to use a hierarchical species classification, researchers have been unable to define a single all-inclusive species concept. More than 20 species concepts have been proposed (e.g., Mayden 1997; Mallet 2006; Wilkins 2009) and discussions about these concepts have filled volumes. For primates, the species concepts most frequently invoked in recent years are the Biological Species Concept (BSC, Mayr 1942), the Recognition Species Concept (RSC, Paterson 1986), and the Phylogenetic Species Concept (PSC, Eldredge and Cracraft 1980; Cracraft 1997). Essentially, the BSC tends to lump groups into few species, whereas the PSC tends to split groups into more species. For instance, the number of recognized primate species increased from 180 in 1967 (Napier and Napier 1967) to 480 in 2013 (Mittermeier et al. 2013) partly due to more thorough surveys, but mainly due to the application of the PSC. This increase invoked the question whether it is real or just "taxonomic inflation" (Isaac et al. 2004; Tattersall 2007; Markolf et al. 2011). Fierce controversy emerged and subsists on the higher or lower numbers of species that are delineated by the application of different species concepts and on the incidence that such numbers have on the practice of conservation biology (Morrison et al. 2009; Dubois 2010; Frankham et al. 2012; Gippoliti and Groves 2013; Groves 2013; Gutiérrez and Helgen 2013; Zachos and Lovari 2013; Zachos et al. 2013a, b; Cotterill et al. 2014; Frankham et al. 2014; Russello and Amato 2014; Wilmet et al. 2014; Zachos 2015).

Given that evolution and speciation is a process in time, placing cut-offs somewhere along the transition from populations to species, remains somehow arbitrary and discrepancies between species concepts may arise because they look at different stages of the speciation process. For instance, the sequence of events for two recently separated lineages may begin with the appearance of diagnostic differences (criterion of the PSC), then reciprocal monophyly will occur and finally the two lineages become reproductively isolated (criterion of the BSC) (de Queiroz 2007; Tobias et al. 2010) (Fig. 2).

Therefore, no species concept can fully capture what a species is (Hendry et al. 2000; Hey 2006; Wiens 2007; Tobias et al. 2010). In principle, we are still at the same point as Darwin 1859 (Chap. 2, p. 25) when he wrote about the pointless exercise of defining the nature of species: "No one definition has satisfied all naturalists, yet every naturalist knows vaguely what he means when he speaks of a species." Darwin simply preferred not to address the issue of species concepts at all, but instead referred to varieties.

Species can be regarded as taxonomic hypotheses and depending on the applied species concept and available data, units or taxa are split or lumped together. The dynamics in taxonomic knowledge affects biodiversity assessment and conservation strategies and decision makers in conservation politics may be alienated. Usually they prefer to work with more static taxonomies and species lists when setting conservation priorities, but there is no agreed-on official species list and there may never be.

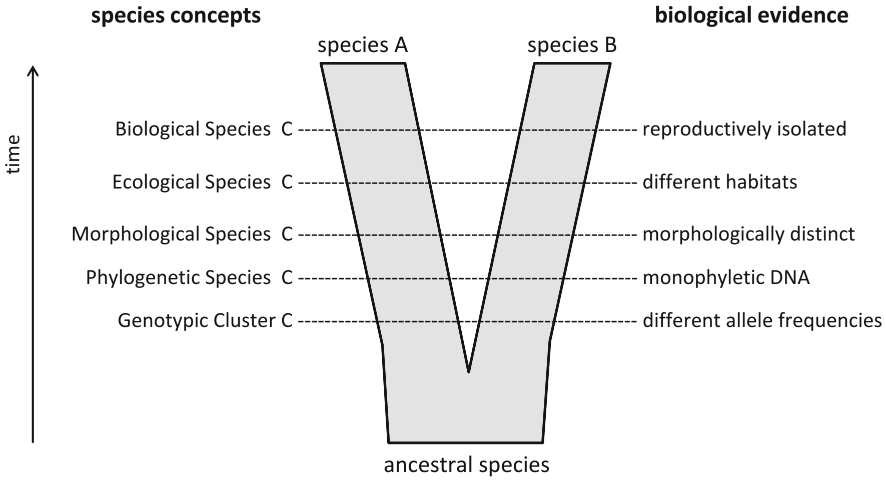

Fig. 2 Highly simplified diagram of speciation, possible sequence of species concepts, and corresponding biological properties of species (modified from de Queiroz 2007)

Species Delimitation

Since finding an all-encompassing definition of species is difficult, the delimitation of species remains controversial. However, we assume that species are real and that it is indeed possible to delimit them, because the process of speciation is most likely short compared to the long existence of the species, and that brief transitions between long-lasting and discrete entities (species) do not make those entities unreal (Coyne and Orr 2004). Christoffersen (1995), based on the PSC, provided some directions of how to delimit species on a more operational level. A species is "an irreducible cluster of sexual organisms within which there is a parental pattern of ancestry and descent and that is diagnosably distinct from other such clusters by a unique combination of fixed characters" (Christoffersen 1995, p. 448). Diagnosably distinct here means that they are 100 % diagnosable (given age/sex variation), they have fixed heritable differences between them, they are genetically isolated, though not necessarily reproductively isolated. A good example is the case of Northern and Southern white-cheeked gibbons (*Nomascus leucogenys* and *N. siki*). Both species are phylogenetically closely related (Thinh et al. 2010b) and females of both species are morphologically indistinguishable. However, males show a clear diagnosable character: while in *N. siki* the white cheeks extend just to the ears, in *N. leucogenys* they go well beyond the ears. Accordingly, both are classified as species and not just as subspecies of a single species.

Recently, molecular genetic methods have been applied to assist species delimitation. Molecular data can reveal the historical descent of lineages and the extent of gene flow between them. Such findings are relatively easy to interpret in the case of genera and families (Tobias et al. 2010), and phylogenetic analyses are therefore changing higher-level systematics in primates and other groups and improve the reliability of phylogenetic inferences. On the species level such approaches are not as easy to interpret, in particular since different genetic markers may provide different and contradicting phylogenies. When using molecular data, phenomena such as incomplete lineage sorting or (introgressive) hybridization can affect some genetic markers but not others, making groups diagnosable and reciprocally monophyletic for one set of markers and para- or polyphyletic for others.

For many taxa, differences in the mitochondrial genome have been used to diagnose species status (e.g., barcoding, http://www.barcodeoflife.org/). The barcoding approach is based on the assumption that by analyzing and comparing parts of the mitochondrial genome, taxon differences will be revealed, which can subsequently be used to delimit species (Tautz et al. 2003; Forsdyke 2013). This approach has been successfully applied to different taxonomic groups, including primates, and in many cases provided results that are congruent with results obtained by using other methods to delimit species (e.g., dissimilarities in morphology, behavior, or ecology). For instance, in several lemur groups many cryptic species have been discovered by the analysis of mitochondrial markers (e.g., *Microcebus*, Louis et al. 2006; Olivieri et al. 2007). Subsequently, for most taxa identified as potential species on mitochondrial differences species status was confirmed by using nuclear genetic data (Weisrock et al. 2010).

In other taxonomic groups the mitochondrial genetic approach failed to identity potential species. In baboons (*Papio*), mitochondrial clades mostly reflect the geographic provenance of the respective individual but not its taxonomic affiliation. No congruence was found between morphological characters used to delimit baboon taxa and their mitochondrial relationships (Zinner et al. 2009b, 2013b) (Fig. 3). Even more striking is the close relationship between the mitochondrial lineage of the southern yellow baboons and a population of kipunjis (*Rungwecebus kipunji*). If only the mitochondrial marker had been used, the kipunji would have been clearly delineated as a baboon. Zinner et al. (2009a), however, interpreted the close relationship as a result of introgressive hybridization.

The baboon example clearly shows that species delimitation based solely on one genetic marker (here mitochondrial sequence data) can result in a complete mess. Several authors have pointed to potential problems when using just one genetic marker to delineate species (Markolf et al. 2011, 2013; Stoeckle and Thaler 2014; Ermakov et al. 2015). We therefore agree that taxonomic decisions should be based on a number of characters. An ideal scenario would be an integrative approach involving a combination of genetic or even genomic, phenotypic, behavioral, and ecological data (e.g., Yoder et al. 2005; Padial et al. 2010; Wielstra et al. 2013; Dowton et al. 2014; Leaché et al. 2014).

The problem might even become more complicated if DNA information alone does not help to differentiate among species. In a population genomics study on carrion crows it was recently shown that small differences in gene expression (<1 %) is sufficient to maintain the phenotypic differences of carrion and hooded crows, although there is some gene flow between the two taxa (Poelstra et al. 2014). The results of the crow study stress the importance of using RNA-based information in addition to DNA, an approach, which most likely will also have to be applied in phylogenetic and phylogeographic studies on primate groups such as baboons.

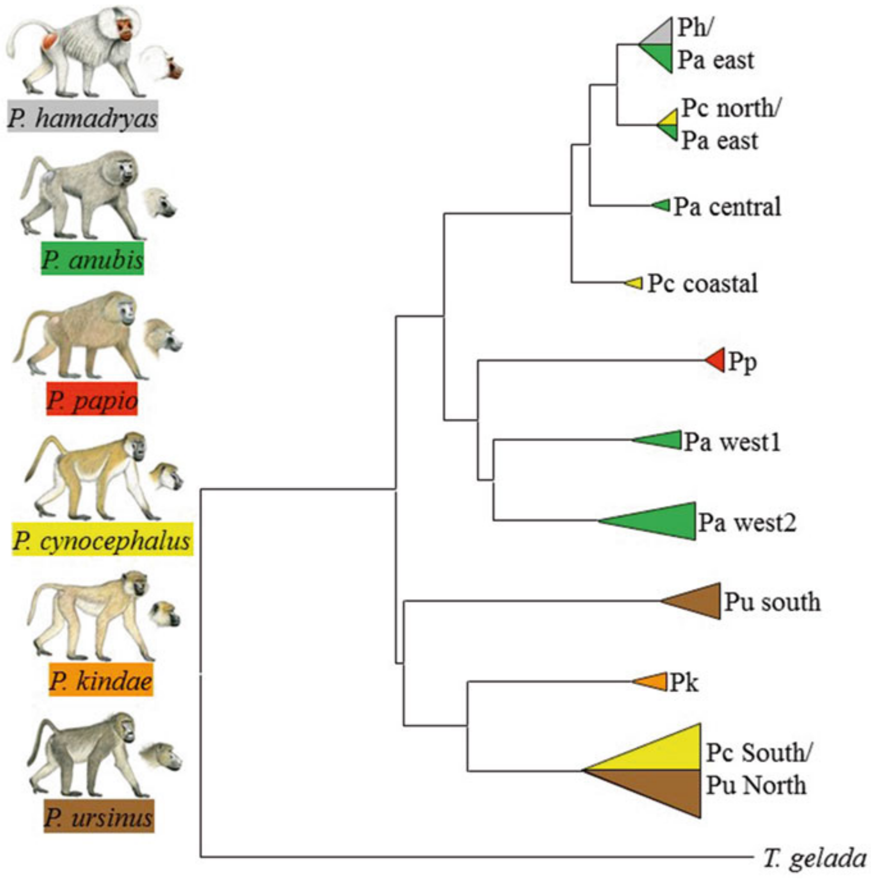

Fig. 3 Baboon phylogeny based on mitochondrial sequence data (Zinner et al. 2009b, 2013b). Para- and polyphyletic relationships are obvious among baboon species and almost no congruence between mitochondrial clades and morphologically classified species is indicated. Mitochondrial clades instead reflect the geographical provenance of the respective lineages. Introgressive hybridization was discussed here as a possible cause for the observed para- and polyphyletic relationships (baboon drawings by S. Nash)

Ranking of Taxa

Beside species delimitation, the ranking of taxa (assigning a taxon a rank in the hierarchical system) is another major problem in taxonomy. Even if species could be unambiguously delineated, the cut-offs for higher taxa would remain problematic (Fig. 4). One possible solution is to use genetic distance between sister taxa to delimit higher ranks and given that genetic differences accumulate by time, genetic distance correlates somehow with divergence ages (Goodman et al. 1998). By applying molecular clocks, divergence ages can be determined, but since molecular clocks run differently in different taxa a simple rule of thumb, such as if the

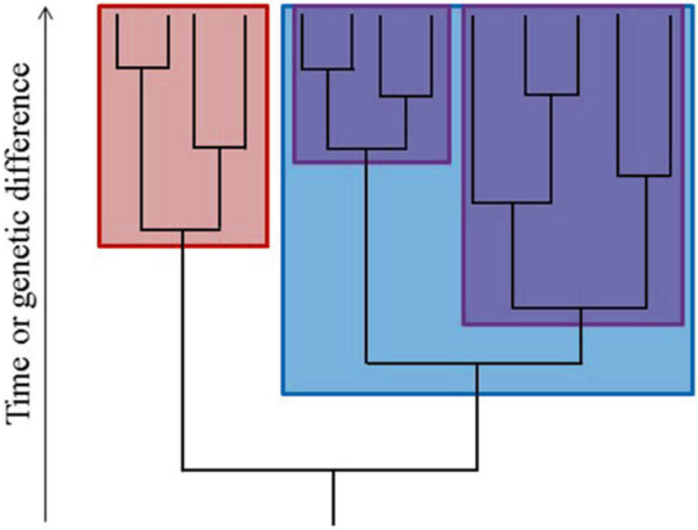

Fig. 4 A nested hierarchy and monophyly as species criteria. Hypothetical phylogenetic reconstruction with several alternative possibilities to delimit species according to monophyletic relationships. Since monophyletic clades are nested within monophyletic clades (e.g., *purple* nested within *blue*) the problem of how to decide at which level we will make the cut-off to delimit species and how to rank the monophyletic groups (taxa) arises. Should we delineate two *purple* and one *red* species or one *red* and one *blue* species or should we rank the *red* clade as a monotypic genus and the blue clade as a genus with two (*purple*) species?

divergence age between two taxa is two million years, we have two species, if it is four million years, we have two genera, and so on, is thus not applicable. Groves (2012) argues that ranking processes based on genetic distances are highly subjective and the same is true when evaluating the time of divergence (Alström and Mild 2003).

Primate Taxonomy

As mentioned the number of primate species increased dramatically over the last decades, mainly due to the application of the PSC (Groves 2011, 2012) and by routinely implementing molecular methods, but also due to surveys in remote areas and an increase in knowledge about species' ecology and behavior. Although several recently described primate species were indeed newly discovered in previously unexplored areas including the kipunji (*Rungwecebus kipunji*, Jones et al. 2005; Davenport et al. 2006), the lesula (*Cercopithecus lomamiensis*, Hart et al. 2012), and the Myanmar snub-nosed monkey (*Rhinopithecus strykeri*, Geissmann et al. 2011), most other recent species descriptions, however, rely on splitting a geographically widespread species into various locally restricted species or raising subspecies to species (e.g., *Microcebus*, *Lepilemur*, *Avahi*, *Callicebus*, *Piliocolobus*).

Molecular analyses provided fundamental insights into the evolutionary history of primates on all taxonomic levels and the taxonomic classification of primates on family or genus level changed accordingly. For example, New World monkeys originally contained only two families (Callithrichidae, Cebidae) (Napier and Napier 1967). Today we know that the original Cebidae family (comprising all non-callitrichid New World monkeys) is a paraphyletic group and thus should be divided into four families. This division is now widely accepted and there is consensus that the Pitheciidae split off first, followed by the Atelidae, before finally Cebidae (now containing only capuchin and squirrel monkeys), Aotidae and Callithrichidae diverged, while the relationships among the latter three families are still unresolved (e.g., Osterholz et al. 2009; Perelman et al. 2011; Finstermeier et al. 2013). Another good example for a misclassification of primates at the family level is provided above with the case of great apes and humans.

At the genus level, various changes and shifts occurred as well. For tarsiers it was recently shown that the lineages from the Philippines, the western Sundaland, and from Sulawesi diverged in the Miocene (Shekelle et al. 2010) and hence, these three are now classified as three genera (*Carlito*, *Cephalopachus*, *Tarsius*) (Groves and Shekelle 2010). Galagos originally contained only two genera (*Galago* and *Euoticus*) (Schwarz 1931), but today five genera are recognized (Mittermeier et al. 2013). For dwarf galagos (*Galagoides*) polyphyly was confirmed with the species from the African Eastern Arc forming a sister clade to *Galago*, while the more western species fall into a clade that is basal to *Otolemur*, *Sciurocheirus*, *Galago*, and the dwarf galagos from forests of the Indian Ocean catchment area in Africa (Pozzi et al. 2014, 2015). Accordingly, the dwarf galagos from the African Eastern Arc need a new genus name. Likewise, the African papionin clade originally contained only two genera, *Papio* subsuming the more robust morphotypes (baboons, gelada, drill, mandrill) and *Cercocebus* consisting of the more slender mangabeys (Napier and Napier 1967). Morphological and genetic investigations, however, have shown that the drill and mandrill cluster together with white-eyelid mangabeys, that the kipunji is the closest relative of baboons, and that the three lineages, the kipunji-baboon clade, the gelada, and the crested mangabeys diverged within a relatively short time period, although their phylogenetic relationships remain unresolved so far (Harris and Disotell 1998; Fleagle and McGraw 1999; Page and Goodman 2001; Finstermeier et al. 2013; Liedigk et al. 2014). Accordingly, the African papionins were divided into six genera: *Papio* (now containing only baboons), *Rungwecebus* (kipunji), *Theropithecus* (gelada), *Lophocebus* (crested mangabeys), *Mandrillus* (drill, mandrill), and *Cercocebus* (now containing only white-eyelid mangabeys) (Mittermeier et al. 2013). Similarly, the African genus *Cercopithecus* contained until recently the arboreal guenons, green monkeys, and terrestrial guenons, but it was shown that the latter two are closely related with patas monkeys (*Erythrocebus*) (Tosi et al. 2004), and hence, both were separated from *Cercopithecus* and classified in their own genera *Chlorocebus* (green monkeys) and *Allochrocebus* (terrestrial guenons) (Mittermeier et al. 2013). The lesser apes were originally divided into only two genera, *Symphalangus* with the siamang and *Hylobates* subsuming the remaining gibbon species (Napier and Napier 1967). However, today four major gibbon lineages are recognized which exhibit distinct diploid chromosome numbers and which diverged from each other roughly at the same time (Carbone et al. 2014). Accordingly, these four lineages are today recognized as four genera (*Symphalangus*, *Hylobates*, *Hoolock*, *Nomascus*) (Mittermeier et al. 2013). An example for shifting species from one into another genus is that of two langur species from the Indian subcontinent. While originally placed in the genus *Trachypithecus* (Napier and Napier 1967) the Nilgiri langur (*T. johnii*) and the purple-faced langur (*T. vetulus*) are today recognized as members of the genus *Semnopithecus* (Osterholz et al. 2008; Mittermeier et al. 2013). In other cases, new evidence suggests a return to an older classification, e.g., in the case of the woolly monkeys of the Neotropics. Groves (2001) separated the yellow-tailed woolly monkey *flavicauda* in its own genus *Oreonax* from other woolly monkey species (genus *Lagothrix*), but recent molecular investigations clearly showed that *flavicauda* and the other woolly monkey species are closely related thus suggesting the presence of only a single genus (*Lagothrix*) (Di Fiore et al. 2015).

The most extensive taxonomic changes in primates apply to the species level, with a general trend of an increasing number of species (from 180 in 1967 to >480 in 2013) in all families due to the application of the PSC and molecular techniques. A few examples are provided here. Most prominent are the nocturnal lemurs of Madagascar. Until the beginning of the 1990s, only two species of mouse lemurs have been recognized (*Microcebus murinus*, *M. rufus*). Today we list more than 15 *Microcebus* species (Mittermeier et al. 2013). Is this taxonomic inflation? Or does it reflect the evolutionary history and the existing number of cryptic species (Tattersall 2007)? Most of the recent mouse lemur species descriptions relied solely on sequence data of a mitochondrial DNA fragment, but multi-locus nuclear sequence data subsequently confirmed that most of these newly described species are indeed genetically distinct from each other (Weisrock et al. 2010). Further, with increasing knowledge of the behavioral ecology of these species, we see that they are indeed distinct from each other, in their ecological niche, behavior, vocalization, etc. Accordingly, despite being phenotypically cryptic species, they are likely valid species and the species richness of the genus *Microcebus* was underestimated. The same is true for most other Malagasy lemurs, e.g., the dwarf lemurs (*Cheirogaleus*), sportive lemurs (*Lepilemur*), or woolly lemurs (*Avahi*) for which numerous new species have been described in recent years (e.g., Rasoloarison et al. 2000; Andriaholinirina et al. 2006; Zaramody et al. 2006; Lei et al. 2014), or the sifakas (*Propithecus*) or "true" lemurs (*Eulemur*) for which many subspecies have been elevated to species (Mittermeier et al. 2013).

In the African and Asian cousins of the lemurs, the galagos, pottos, and lorises, the number of species increased due to new species descriptions and ranking subspecies as species (e.g., Grubb et al. 2003; Roos et al. 2007; Munds et al. 2013). This is mainly the result of improved knowledge about their biology and evolutionary history and with further information additional splitting can be expected for these primates. Tarsiers were recently not only divided into three genera, but also the number of species increased to a total of 11 (Mittermeier et al. 2013). For both, New World and Old World monkeys, the number of species increased dramatically over the last decades, mainly because taxa formally ranked as subspecies are now listed as species. This has occurred in howler monkeys (*Alouatta*), spider monkeys (*Ateles*), capuchin monkeys (*Cebus*, *Sapajus*), tamarins (*Saguinus*), baboons (*Papio*), green monkeys (*Chlorocebus*), red colobus monkeys (*Piliocolobus*), hanuman langurs (*Semnopithecus*), and doucs (*Pygathrix*). However, some New and Old World monkey species recognized today are indeed new to science. These include the Rondon's marmoset (*Mico rondoni*, Ferrari et al. 2010), the Hernández-Camacho's night monkey (*Aotus jorgehernandezi*, Defler and Bueno 2007), the Vieira's titi (*Callicebus vieirai*, Gualda-Barros et al. 2012), the kipunji (*Rungwecebus kipunji*, Jones et al. 2005; Davenport et al. 2006), the lesula (*Cercopithecus lomamiensis*, Hart et al. 2012), the Myanmar snub-nosed monkey (*Rhinopithecus strykeri*, Geissmann et al. 2011), or the white-cheeked macaque (*Macaca leucogenys*, Li et al. 2015). Finally, taxonomic changes in apes have also occurred, most prominently in the gibbons, where today 19 species are recognized (Mittermeier et al. 2013). One of these—*Nomascus annamensis*—was newly described in 2010 (Thinh et al. 2010a). The great ape genera *Pongo* (orangutans) and *Gorilla* (gorillas) formally contained only a single species with two and four subspecies, respectively, but today both orangutan subspecies were elevated to species and gorillas were divided into an eastern (*G. beringei*) and a western species (*G. gorilla*), each with two subspecies (Mittermeier et al. 2013).

Conclusion

Classifying and naming things seems to be a human universal, making communication about the environment possible which most likely had fitness advantages. In particular with respect to living things, humans everywhere think about plants and animals in highly structured ways, and rank organisms into lower- and higher-order groups. Interestingly, such folk-taxonomies show strong congruence with the Linnaean taxonomy, at least for vertebrates and higher plants. The basic entity of the indigenous classification systems is most often equivalent to species in the scientific taxonomy, providing additional arguments that biological species are real and not only a construct of taxonomists' imagination (Mayr 1982). Nevertheless, species definition and species delimitation remain controversial with subsequent consequences for biodiversity assessment and species preservation.

In our view, conservation biology, including primate conservation, is informed by taxonomy in two fields, and in light of limited resources for conservation, both are related to the "agony of choice" (Vane-Wright et al. 1991). (1) Assessing species diversity (How many species occur in a certain area?) and (2) in conservation priority setting (Which areas or species should be prioritized for conservation?). In both fields, the question of whether a taxon qualifies as species is essential. Beside the problem of species delimitation, the impact of taxonomy on primate conservation and conservation in general is affected by insufficient knowledge about diversity on inter- and intraspecific level and data deficiencies in species distribution. The identification and description of further primate taxa, either due to the discovery of truly new species in geographically so far unexplored areas or because of the application of molecular methods resulting in the splitting of formally widespread "species," would dramatically alter the vulnerability of these taxa to extinction, making an understanding of their taxonomy an area of urgent conservation action.

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