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Geospecies and Superspecies in the African Primate Fauna

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Abstract: Primate taxa in Africa (and elsewhere) are not randomly distributed. Most are dispersed in monophyletic groups of allopatric taxa, termed superspecies, but some species cannot be allocated to superspecies because any allopatric sister species that once existed are now extinct. These two categories — superspecies and species not assignable to superspecies — are together termed geospecies. African primates belong in 33 geospecies. The number of geospecies is an index of the continent's faunal diversity and in that sense is the highest of all primate faunas, with implications for conservation strategy.
Key Words: African primates; geospecies; species; superspecies.

Introduction

Species of many kinds of animal are distributed in an ordered fashion — they tend to be represented by vicarious taxa as their phylogenetically nearest allies. The largest monophyletic lineages of allopatric species are called superspecies, a category familiar to ornithologists (Amadon 1966) and cited in the Code of Zoological Nomenclature (ICZN 1999: Article 6.2). The name of a superspecies is based on the oldest name among its included species, following the principle of priority (ICZN 1999). Mayr (1963, p.499) defined the superspecies as "a monophyletic group of entirely or essentially allopatric species that are morphologically too different to be included in a single species."

Not all species are parts of superspecies. Species that are not parts of superspecies, together with superspecies, nevertheless represent similar zoogeographical entities; each of them contributes no more than one taxon to a local fauna, no matter how little or how much they may have proliferated by cladogenesis. They were given the collective term "zoogeographical species" by Mayr and Short (1970, p.3), who stated (their emphasis) that "When several species comprise a superspecies, they are counted as *one* zoogeographical species just as is each individual species not forming part of a superspecies." The term "zoogeographical species" has now been shortened to "geospecies" (Eck 1996). A superspecies is no more than a variety of geospecies.

This paper considers the allocation of African primates (and others) to superspecies and geospecies. Illustrating how a primate superspecies is named, the example including moustached and lesser spot-nosed monkeys (#27 in Table 1) is the *Cercopithecus cephus* superspecies because *cephus* dates from 1758 and the other names of included species date from 1774 to 1904 (Groves 2001). The Code of Zoological Nomenclature (ICZN 1999) recommends that this naming should be formalized as "*Cercopithecus* (superspecies *cephus*)," and a species in this superspecies — for example, *C. erythrotis* — can be termed "*Cercopithecus (cephus) erythrotis*," but I am not sure how popular these practices would be among primatologists, and they are not mandatory. A geospecies can be named from its unique genus or sole constituent species (e.g., *Allenopithecus* geospecies or *A. nigroviridis* geospecies) or from its oldest included species name (e.g., *Cercopithecus cephus* geospecies).

Methods

The taxonomy of the African primates, including the number of species and subspecies (Table 1), follows that of Grubb *et al*. (2003). Additional genera and species recognised by Groves (2001, 2005) and Cotterill (2003) as well as the genus *Allochrocebus* (discussed in Grubb *et al*. 2003) are listed in parentheses (Table 1). Grubb *et al*. (2003) did not agree on how to allocate taxa to species in the genus *Procolobus* [*sensu lato*] from Central and East-Central Africa, and they are here provisionally allocated to *P. tholloni*. An unnamed species of *Otolemur* is no longer included in the list (S. K. Bearder, pers. comm.), while *Pan troglogytes*

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marungensis (Groves in press) is added to the list. A new species has recently been named as *Lophocebus kipunji* Ehardt, Butynski, Jones and Davenport, 2005 (in Jones *et al*. 2005), raising the total of species and subspecies to 175.

For the purposes of discussion, I use the classification of Groves (2001, 2005) and Brandon-Jones *et al.* (2004) for non-African primates, augmented by additional genera recognized by Rylands *et al*. (2000). In lists of genera, the dagger—†—indicates those in which all species or (in parentheses) only some became extinct in the Holocene within the Malagasy and Caribbean faunas.

By inspecting distribution maps (reviewed by Grubb in prep.) and the systematic literature (Groves 2001) it is possible to identify superspecies (as defined above) and those species that cannot be allocated to superspecies, both in Africa and in other continents. There appears to be no serious controversy about the relationships of African primates that could lead to changes in the categorization in this paper, but further systematic studies, particularly of galagos and *Cercopithecus dryas*, will possibly require some careful reconsideration.

Superspecies are lineages whose limits are determined by phylogeny and geography, not by species definitions or concepts, or by age. Students of primatology, therefore, may not wish to regard them as part of conventional taxonomy and classification. Indeed, there are indications that some superspecies outside Africa include more than one genus, so the category is not necessarily part of the hierarchy of classification.

Results and Conclusions

There are 20 to 22 primate superspecies in Africa, depending upon the species list adopted (Table 1). Therefore, 152 to 160 out of 175 species and subspecies are allocated to superspecies and only 15 to 23 taxa are not so allocated. Some superspecies have been recognized as such or have been called "species groups" (Grubb 1990) or simply "groups" (Grubb *et al*. 2003), though not all species groups are superspecies. The categorization of superspecies does not disturb the taxonomy of Grubb *et al*. (2003) except in the case of East African *Galagoides* species. Here I follow Groves' (2005) species-groups and allocate these to two superspecies—#3, the smaller galagos of the *G. orinus* superspecies; and #4, the somewhat larger galagos of the *G. zanzibaricus* superspecies, formerly included in a single species (Table 1).

Apart from the superspecies of African primates, there are three polytypic species with subspecies that have not so far been elevated to species rank, and eight monotypic species. None of these 11 species have allopatric sister taxa. They cannot be included in any superspecies, but nevertheless can be ranked with them as geospecies. Altogether there are 33 geospecies of African primates (Table 1). References to geospecies are most likely to be made when the whole primate fauna is being considered. Use of the term superspecies rather than geospecies depends on context.

Seventeen genera (Table 1, in bold) are coextensive with African primate geospecies and the figure is raised to 21 out of a total of 24 if *Chlorocebus*, *Allochrocebus*, and *Piliocolobus* are ranked as genera and *Procolobus* hence becomes restricted to *P. verus*. *Galagoides* and *Cercopithecus* are the only other genera including more than one African geospecies. *Macaca* includes non-African geospecies. There is apparently a tendency for both genera and geospecies to evolve over the same time span and to be of equivalent age. Genera such as *Cercopithecus* with several geospecies may have evolved differently from other genera, perhaps relatively more rapidly.

Like their constituent superspecies, geospecies are parts of lineages the limits of which are not determined by species definitions or species concepts, but by geography. Geospecies are lineages passing through an evolutionary history from the stage when they have lost allopatric sister-taxa through extinction, to the stage when they have proliferated by cladogenesis, but not so far that daughter taxa have yet become sympatric.

The "species group" (e.g., in Groves 2001; Grubb *et al*. 2003) may seem to be a similar category to the geospecies. Indeed, designated species groups include not only some superspecies but also single species lacking allopatric sister-taxa (e.g., the single species in the *Cercopithecus neglectus* species group). Species groups of African primates recognized by Grubb (1990) were effectively geospecies. Nevertheless, designated species groups are usually divisions of genera and the term is not generally used where genera are monospecific, or where there is no apparent need to recognize subdivisions among a series of congeneric species. Thus, systematists would not allocate all primate species to species groups. Species groups have not been defined, do not necessarily correspond with geospecies, have not clearly been distinguished from subgenera, and may include sympatric species—at least among non-primates. Perhaps the species group can be identified as a monophyletic division of a genus, part of conventional systematics, though Mayr (1963, p.501) preferred to restrict the term to monophyletic aggregates of species that were not all allopatric.

Primate geospecies can be recognized outside Africa. The 29 genera *Alouatta, Aotus,* †*Archaeolemur*, *Ateles*, *Avahi, Brachyteles, Cacajao, Callithrix, Chiropotes,* (†)*Daubentonia, Hylobates, Lagothrix*, *Leontopithecus*, *Lepilemur*, *Loris*, †*Megaladapis*, †*Mesopropithecus*, *Mico*, *Mirza*, *Nomascus*, *Phaner*, *Pithecia*, *Pongo*, *Propithecus*, *Pygathrix*, *Rhinopithecus*, *Saimiri*, *Semnopithecus*, and (†)*Varecia* are superspecies and therefore also geospecies. Some subgenera or groups of species designated within the seven genera *Callicebus*, *Cebus*, *Cheirogaleus*, *Macaca*, *Saguinus*, *Tarsius,* and *Trachypithecus* are superspecies. *Allocebus*, †*Antillothrix*, †*Archaeoindris*, †*Babakotia*, *Callibella*, *Callimico*, *Cebuella*, †*Hadropithecus*, *Hoolock*, *Indri*, *Lemur*, *Nasalis*, *Oreonax*, †*Palaeopropithecus*, *Prolemur*, *Simias*, *Symphalangus,* and †*Xenothrix* are 18 monospecific genera whose species hence lack vicarious representatives and are therefore also geospecies. This leaves the five genera *Eulemur*, *Hapalemur*, *Microcebus*, *Nycticebus,* and *Presbytis* for which species groups or superspecies have not been identified and for which new sys-

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Table 1. List of African primate species allocated to 33 geospecies. Genera in bold are coextensive with geospecies. "Number of taxa" is the number of species and subspecies in each geospecies.

Senior species names in 33 geospecies	Other species included in geospecies	Number of taxa
1. *Galagoides demidovii*		1
2. *G. thomasi*		1
3. *G. orinus*	*G. rondoensis*	2
4. *G. zanzibaricus (G. udzungwensis)*	*G. cocos*, *G. granti*, *G. nyasae*, *G*. sp. nov 1., *G.* sp. nov. 2, *G*. sp. nov. 3	7
5. ***Galago*** *senegalensis*	*G. gallarum*, *G. matschiei*, *G. moholi*	8
6. ***Euoticus*** *elegantulus*	*E. pallidus*	3
7. ***Sciurocheirus*** *alleni (S. cameronensis)*	*S. gabonensis*, *S.* sp. nov.	4
8. ***Otolemur*** *crassicaudatus*	*O. garnettii*, *O. monteiri*	8
9. ***Arctocebus*** *calabarensis*	*A. aureus*	2
10. ***Perodicticus*** *potto*		3
11. *Macaca sylvanus*		1
12. ***Cercocebus*** *torquatus*	*C. atys*, *C. galeritus (C. agilis*, *C. chrysogaster*, *C. sanjei)*	7
13. ***Mandrillus*** *sphinx*	*M. leucophaeus*	3
14. ***Lophocebus*** *albigena*	*L. aterrimus (L. opdenboschi)*, *L. kipunji*	4
15. ***Papio*** *cynocephalus (P. kindae)*	*P. anubis*, *P. hamadryas*, *P. papio*, *P. ursinus (P. griseipes)*	8
16. ***Theropithecus*** *gelada*		2
17. ***Allenopithecus*** *nigroviridis*		1
18. ***Miopithecus*** *talapoin*	*M. ogouensis*	2
19. ***Erythrocebus*** *patas*		1
20. *Cercopithecus* (or ***Chlorocebus***) *aethiops (C. cynosuros*, *C. djamdjamensis*, *C. pygerythrus*, *C. sabaeus*, *C. tantalus)*		6
21. *Cercopithecus* (or ***Allochrocebus***) *preussi*	*C. lhoestii*, *C. solatus*	4
22. *Cercopithecus diana (C. roloway)*		2
23. *C. dryas*		1
24. *C. neglectus*		1
25. *C. mona*	*C. campbelli (C. lowei)*, *C. pogonias (C. denti*, *C. wolfi)*	10
26. *C. hamlyni*		2
27. *C. cephus*	*C. ascanius*, *C. erythrogaster*, *C. erythrotis*, *C. petaurista*, *C. sclateri*	15
28. *C. nictitans*	*C. mitis (C. albogularis*, *C. doggetti*, *C. kandti*, *C. moloneyi*, *C. opisthostictus)*	18
29. *Procolobus* (or ***Procolobus*** *sensu stricto*) *verus*		1
30. *Procolobus* (or ***Piliocolobus***) *badius*	*P. gordonorum*, *P. kirkii*, *P. pennantii (P. preussi)*, *P. rufomitratus*, *P. tholloni (P. foai*, *P. tephrosceles)*	18
31. ***Colobus*** *polykomos*	*C. angolensis*, *C. guereza*, *C. satanas*, *C. vellerosus*	19
32. ***Gorilla*** *gorilla*	*G. beringei*	4
33. ***Pan*** *troglodytes*	*P. paniscus*	6

tematic information is probably needed to decide how they can be partitioned into geospecies. Up to 68 (82%) of the 83 primate genera listed in this paper correspond with geospecies. However, these figures are provisional and some genera are allopatric sister taxa (e.g., *Cacajao* and *Chiropotes*, or *Nasalis* and *Simias*) and could be combined as members of single geospecies.

Of the four regional primate faunas, the neotropical fauna is the richest, with 210 species and subspecies (Rylands *et al*. 2000; Van Roosmalen *et al*. 2002) plus Caribbean taxa surviving into the Holocene. Asia with 187 taxa (183 recognized by Brandon-Jones *et al*. 2004; and an additional four cited by Groves 2005) is the next richest, followed by Africa with 175. Including species that became extinct in the Holocene; 81 taxa are found in Madagascar (updated from Groves 2005, and Tattersall 1982). These figures are subject to revision, and to additions from newly described taxa reported to be in press.

The approximate numbers of geospecies are in a different sequence and though provisional, validly indicate orders of magnitude. Africa leads with 33 geospecies followed by Madagascar with about 25, then the neotropics with perhaps as few as 18, and Asia, possibly with only 15. With respect to its number of geospecies, Africa has the most diverse fauna and implicitly the greater variety of ecological niches. Occurrence in non-forest habitats, and variety of body size are factors that possibly contribute to this diversity. The age of the fauna may also have contributed to it achieving its scale of ecological diversity. While there are many taxa in neotropical and Asian superspecies, their faunas have relatively few geospecies and fewer distinct niches are occupied.

The terms superspecies and geospecies name phenomena observed in nature and illuminate the geographic structure of evolutionary lineages. Recognition of superspecies and geospecies highlights an aspect of diversity that suggests that conservation has different needs in different continents;

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in Africa putative refuges or centers of endemism differ in ecology, abundance, and richness from conditions in Asia and the neotropics. When areas of Africa were examined where certain geospecies had not previously been recorded, new and distinctive species and subspecies were discovered. In the last 20 years such taxa were named in 1986 (*Cercocebus [galeritus] sanjei*), 1987 (*Cercopithecus hamlyni kahuziensis*, *C. mitis heymansi*, *Procolobus tholloni parmentieri*), 1988 (*Cercopithecus solatus*), 1996 (*Galagoides rondoensis*), 1999 (*Cercopithecus cephus ngottoensis*, *C. erythrogaster pococki*, *Procolobus badius epieni*), and 2005 (*Lophocebus kipunji*). Others were described but their status has been disputed. Several have been recognized but have yet to be named (Table 1; Groves 2001; Grubb *et al*. 2003). The newly described taxa are representatives of already-known geospecies. It may be productive to carefully examine the potential habitat of each geospecies to determine whether still more primate taxa are to be discovered. This applies particularly to galagos of montane forest in East Africa.

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