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An Overview of the Primates

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Abstract

The order Primates, to which humans belong, is one of the best-known mammalian orders, but there is still much to be learned about its phylogeny and taxonomy. It is clear by now that there are two suborders, Strepsirrhini and Haplorrhini, but beyond that there is still a lot of controversy and misunderstanding including how to operationalise the evolutionary species. The example of the Old World Monkey tribe Cercopithecini is treated in some detail.

Keywords: primates, taxonomy, phylogeny

1. Introduction

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The order Primates, constituting one of about 20 orders of placental mammals, is most closely related to the orders Scandentia (treeshrews) and Dermoptera (colugos). The order consists of lemurs, lorises, bushbabies, tarsiers, New World monkeys, Old World monkeys, apes and humans.

It is hard to diagnose the order Primates, because evolution is an ongoing process, and those features which characterised the ancestors of any group of organisms may well have changed in their descendants; as the order Primates originated some 65 million years ago, there has been ample time for change. This was pointed out in detail by Szalay et al. [1], who suggested a number of conditions that probably constituted the Primate morphotype (i.e., the ancestral state of primates); if we select just those features which are diagnostic of modern primates, we can list the following:

1. Auditory bulla formed by the petrosal (in other mammals with an ossified auditory bulla, the bulla is formed from the alisphenoid, or from the tympanic, or from one or more of a group of special bones, the entotympanic complex).

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- **2.** The underside of the ends of the digits has a specialised nerve ending, Meissner's corpuscles (this is convergent on some of the arboreal marsupials).
- **3.** Hallux is divergent from other toes, and is supplied with a flat nail instead of claws (this, obviously, is modified in humans). This results in a grasping foot, and is, again, convergent on some arboreal marsupials. In some primates, the hand has specialised grasping abilities as well, and in most but not all primates all the digits, not just the hallux, have flat nails.
- **4.** Penis hangs free from the body wall (this is convergent on the order Chiroptera, the bats; in other mammals, it is enclosed within a prepuce).

We, when thinking about primates, automatically tend to think of convergent and frontated orbits, and of binocular vision, but these are in fact fairly widespread among other mammals, both in placentals and marsupials.

It is much easier to define the subgroups of Primates, as follows:

1.1. Suborder Strepsirrhini

They are characterised by the possession of a rhinarium (moist nasal tip, continuous, via a split upper lip, with the gums); by having a tapetum lucidum (reflective layer) behind the retina in the eye; and by having an epitheliochorial placenta (maternal and foetal vascular systems well separated, and the embryo/foetus is nourished largely by uterine glands). They are the lemurs, lorises and galagos (bushbabies).

1.2. Suborder Haplorrhini

They lack a rhinarium; they lack a tapetum, but have a fovea and macula in the retina; they have a haemochorial placenta (embryonic/foetal tissue invades the maternal bloodstream). They are the tarsiers, monkeys, apes and humans.

It is not easy to say which of these diagnostic features may be derived, and which of them may be primitive. Almost certainly, the possession of a rhinarium is a primitive retention, but there are arguments for each of the others being evolutionarily derived features.

The two suborders separated well back in the Cenozoic, probably in the Palaeocene, although some estimates place their split even as far back as the Middle Cretaceous (see [2]). The point to emphasise is that they are clades — that is to say, each is monophyletic. Monophyly (descent from an exclusive common ancestor) is the essential basis for systematics above the species level. Some older Primate classifications, widely adopted up until the 1980s and still sometimes seen in textbooks even as late as the early 2000's, were recognised, as the two suborders, Prosimii (strepsirrhines plus tarsiers) and Anthropoidea (monkeys, apes and humans); but this tells us nothing about relationships, which is what systematics is all about, as the group called Prosimii is defined by nothing except retention of some primitive characters (mostly, relatively small brains).

2. The Strepsirrhini

The Strepsirrhini are the lemurs, lorises and galagos. They divide into two monophyletic clades, which, conveniently, are geographically separated: one in Madagascar, one in mainland Africa and tropical Asia. These separated from each other in the Palaeocene or Eocene (the TTOL calculates a median time of separation at 58.5MA). Many classifications place the Malagasy lemurs into one infraorder, Lemuriformes, and the non-Malagasy lorises and galagos into another, Lorisiformes; but the evidence indicates that the Malagasy group divided again very early on, one of the clades containing just a single living species, the aye-aye, *Daubentonia madagascariensis*, the other containing all the other Madagascar lemurs. The TTOL gives a median separation time of 54 MA, which is very close to the time of separation of the Malagasy group as a whole from the Lorisiformes, and so much earlier than the other groups of Malagasy lemurs started to diversify (see below) that the aye-aye is now generally removed from the Lemuriformes and placed in a third infraorder, Chiromyiformes. Thus, we split the Strepsirrhini into three infraorders: Lorisiformes, Lemuriformes and Chiromyiformes.

There is, in fact, some suggestion that *Daubentonia* may be the sister-group of the Late Eocene genus *Plesiopithecus*, which would imply that the Lemuriformes and Chiromyiformes dispersed separately to Madagascar from the African mainland [3]. This would actually make a great deal of sense, because the Lemuriformes started to separate into families in Madagascar around the Middle-Late Oligocene, at the same time as the families of the other endemic Malagasy mammals (euplerid carnivores, tenrecs and nesomyine rodents), which might suggest that they had all arrived together in a new, mammal-free island and began to diversify into vacant niches.

The families of Lemuriformes are Lemuridae, Cheirogaleidae, Indriidae and Lepilemuridae (**Figure 1**).



Figure 1. Giant Bamboo Lemur, Prolemur simus.



Figure 2. Bengal Slow Loris, Nycticebus bengalensis.

There is only one family in the Chiromyiformes: Daubentoniidae. Within the Lorisiformes, division into two families, Lorisidae and Galagidae, is usual; but the two African genera ascribed to Lorisidae (*Perodicticus* and *Arctocebus*), stubbornly refuse to align with the two Asian genera (*Loris* and *Nycticebus*) (**Figure 2**) in most molecular studies [3], and there is probably a case for recognising them as a separate family, Perodicticidae, implying that they acquired their 'slow climbing' adaptations quite independently of each other.

3. The Haplorrhini

The Haplorrhini, like the Strepsirrhini, divide into two clades, classified as infraorders: Tarsiiformes and Simiiformes. The latter infraorder is more usually called Anthropoidea, a term which has in the past been used confusingly, so is better avoided (whereas, there are rules for the nomenclature of species, genera and families, there are none for taxonomic ranks above the family-group level).

It was the Tarsiiformes which caused all the angst over the Primate suborder question in the latter half of the twentieth century. From the point of view of that most solipsistic of primates, *Homo sapiens*, the Tarsiiformes are irredeemably primitive because they have small brains — hence, so the argument went, they should be bundled into the Prosimii along with those

other small brained primates, the lemurs, lorises and galagos. A taxonomic philosophy that emphasises relatedness, however, puts them into the Haplorrhini, because there is absolutely no doubt that they share derived conditions with monkeys and apes. Molecular phylogenies amply confirm that this is where they truly belong [4, 5].

There is only a single family, Tarsiidae, of Tarsiiformes, but this divides into three genera [6]. So far, only the genus *Tarsius* (the Eastern Tarsiers, from Sulawesi and offshore islands) has been studied taxonomically, and there turn out to be quite a large number of species; the other two genera, *Cephalopachus* (Western Tarsiers, from Borneo, Sumatra and intermediate islands) and *Carlito* (Philippine Tarsiers), are assigned a single species each, but this is only because there have been no detailed taxonomic surveys of them (**Figure 3**).

The Simiiformes again divide into two clades, Platyrrhini and Catarrhini, alternatively classified as parvorders or, sometimes, left unranked (there is much dissension about unranked



Figure 3. Maros tarsier, Tarsius fuscus.

taxonomic systems; in the opinion of most taxonomists, ranks are useful, especially if tied to some time-depth scheme). The Catarrhini are distinguished in particular by the reduction of the premolars in both jaws from three to two, and the 'deflation' of the auditory bulla, with the tympanic ring extended into a tube. The Platyrrhini retain the primitive three premolars, inflated bulla and ring-like tympanic, and it has proved difficult to find any derived character states which they share, although molecular research confirms their monophyly; most recently, however, it has been shown that contact between parietal and zygomatic (malar) bones is a truly derived platyrrhine condition [7].

The Platyrrhini are the New World monkeys; all of them occur in South America, some of them extending north into Central America, even as far as southern Mexico. There are three families of Platyrrhini: Cebidae (including the marmosets and tamarins, at one time assigned to their own family), Atelidae and Pitheciidae (**Figures 4–6**).

The Catarrhini all live in the Old World. There are three families of Catarrhini: Cercopithecidae, belonging to the superfamily Cercopithecoidea (the Old World monkeys) (**Figure 7**), and the Hylobatidae (gibbons, of Southeast Asia) (**Figure 8**) and Hominidae (great apes and humans) (**Figures 9** and **10**), these latter two belonging to the superfamily Hominoidea. Molecular calculations of the separation time of the two families of Hominoidea tend to fall in the late Early Miocene, well below the criterion laid down by Goodman et al. [8] and Groves [9], that families should have separated around the Oligocene-Miocene boundary, and it is probable that the two hominoid families should be reduced to a subfamily rank within a single family, as indeed proposed by Goodman et al. [8].



Figure 4. Colombian night monkey, Aotus griseimembra, a member of the Cebidae.



Figure 5. Pied Tamarin, Saguinus bicolor, a member of the Cebidae.



Figure 6. Northern red howler monkey, *Alouatta seniculus*, a member of the Atelidae.



Figure 7. A female olive baboon, *Papio anubis*, from Kenya (a member of the Cercopithecidae), filling her cheek pouches with food.



Figure 8. Kloss gibbon, Hylobates klossii.



Figure 9. Sumatran orangutan, Pongo abeli.



Figure 10. Western Gorilla, Gorilla gorilla.

4. The species of primates

There are many more species of lemurs that had previously been appreciated [10], and the list is still growing. Similarly, the number of species in some platyrrhine genera is growing (see, for example, [11]), and there are many more species of Asian primates than had previously been recognised [12]. This is much more that simply recognising supposedly 'trivial' differences as diagnostic of species: where we have knowledge of them, all the species have ecological and/or physiological significance. This brings us to ask the important question: what actually is a species?

There has been a lot of discussion about 'the species question' over the past 20–30 years, and several surveys have converged on the essence of what we mean by species: they are evolutionary lineages [9, 13, 14]. Species thus have a real existence. This settles the ontological status of the species concept, but it does not necessarily solve the question of how to recognise them; the most logical way of defining species operationally is by the so-called Phylogenetic Species Concept: 'A species is the smallest population or aggregation of populations which has fixed heritable differences from other such populations or aggregations' [15]. This definition has three strands:

- **1.** Species are populations (or aggregations of populations). They are not, for example, segments of populations. This can generally be observed in the field, though in the museum or on the laboratory bench it must be inferred.
- **2.** The differences are heritable. They may thus be differences observable in the genome; or they may be differences in morphological characters or in behavioural characters, in which case a heritable (genetic) basis is only inferential, although such a basis tends to be very strongly implied.
- **3.** The differences are fixed. This is a geneticists' term meaning that one allele, or even just one base-pair, occurs in 100% of one population, but in 0% of another. That is to say, the two populations are absolutely (diagnosably) different.

Many people have found difficulty coming to terms with the evolutionary species itself, let alone with the phylogenetic/diagnosability species criterion, feeling that a species is not a 'real' species unless, for example, it does not or cannot interbreed with other species (the notion which some of us were brought up with, and which unfortunately is still taught in many schools, even in university courses). The work of Christian Roos and his colleagues has shown that, in fact, there has been very widespread interbreeding and gene exchange between different species during their evolution (see, for example, [16]).

5. The case of the Cercopithecini

The strepsirrhines, the tarsiers and the platyrrhines have been subjected to critical taxonomic revision over the past 15 years or so. What of the catarrhines?

The Asian catarrhines (gibbons, the orangutan, colobines and the genus *Macaca*) have in most cases been carefully examined taxonomically, and work on them continues [12]. The macaques and langurs, especially, both need further attention. New species of macaques have been described, and the question of the gene flow between the long-tailed macaque *Macaca fascicularis* and the rhesus macaque *Macaca mulatta*, where their ranges meet (in mainland Southeast Asia) is an ongoing focus of research.

This leaves the African catarrhines, particularly the Old World Monkeys (superfamily Cercopithecoidea, family Cercopithecidae). The Cercopithecidae are divided into two subfamilies. The African members of the subfamily Colobinae (the leaf eating monkeys) need further attention, both genetically and morphologically. Within the other subfamily, Cercopithecinae (omnivorous monkeys with cheek pouches), the taxonomy of the baboons (*Papio*), of the tribe Papionini, is receiving continual attention and has already yielded unexpected insights [17]. The related genera *Cercocebus, Lophocebus, Rungwecebus, Theropithecus* and *Mandrillus* (mangabeys, geladas and mandrills) remain to be investigated in depth. But, the outstanding case of a group that requires attention is the genus *Cercopithecus* and its relatives, which together form the tribe Cercopithecini.

Traditionally, the Cercopithecini have been divided into four genera, *Cercopithecus* (the rain forest living guenons and their relatives), *Erythrocebus* (the patas monkey), *Miopithecus* (the talapoin monkey) and *Allenopithecus* (the swamp monkey); while over the past quarter century, the further separation of *Chlorocebus* (savanna monkeys, the vervet group) and *Allochrocebus* (terrestrial forest monkeys: the former *Cercopithecus lhoesti, preussi* and *solatus*) has been increasingly recognised. This six-genus scheme is adopted in the latest compendium [18], and we may summarise them as follows:

- 1. *Cercopithecus*. These are colourful, mostly rainforest, monkeys. The *C. nictitans/mitis* group, the *C. mona/campbelli/pogonias/wolfi* group and the *C. petaurista/cephus/ascanius* group are widespread from West Africa through central Africa into at least Uganda, with some 'subspecies' of the *C. mitis* group extending into Ethiopia, and even South Africa (Figures 11–13). *C. diana* and its sister species *C. roloway* are confined to West Africa. *C. neglectus* is found in central Africa and extends into Kenya and Ethiopia. *C. hamlyni* and its sister species *C. lomamiensis* are confined to the east of the Democratic Republic of Congo. The enigmatic *C. dryas* is found in small areas in the DRC.
- **2.** *Allochrocebus*. These are terrestrial rain forest monkeys. There are three species: *A. lhoesti* from the eastern DRC, *A. preussi* from Cameroon and *A. solatus* from south-eastern Gabon.
- **3.** *Chlorocebus*. Several Savanna woodland species, including *C. sabaeus* (the Green monkey of West Africa), *C. aethiops* (the Grivet monkey of Ethiopia) and *C. pygerythrus* (the Vervet monkey of eastern and southern Africa).
- **4.** *Erythrocebus*. The Patas monkey of the grasslands of mainly West Africa, all belonging to a single species, *E. patas*.
- **5.** *Miopithecus*. Two very small species known as Talapoin monkeys, from West-central Africa (Cameroon, upon, Congo Republic and Angola). Unlike the previous genera, talapoins

have periodic sexual swellings in females, a link to the Papionini which also have sexual swellings.

6. *Allenopithecus*. The Swamp monkey of the lower Congo River; this also has periodic sexual swellings, and in other morphological characters it recalls the Papionini.

Until just a few years ago, everybody seems to have settled down with this six-genus scheme, a few authors suggesting particular links between some of the genera. Groves [19] noted cranial characters shared between *Chlorocebus* and *Erythrocebus*, suggesting that these two genera form a clade: their similarities could perhaps relate to their general non-forest adaptations, which might suggest convergence as much as sister-group status. Within *Cercopithecus*, sister-group relationship between the *C. mona* and *C. cephus* groups and between *C. hamlyni* and the *C. lhoesti* group (the latter now recognised as the genus *Allochrocebus*) was postulated by Groves [19], who also drew special attention to the mystery species *C. dryas* and *C. salongo*, although it was not recognised at the time that they are in fact, respectively, the juvenile and adult of one and the same species (interestingly, the skull of the juvenile type specimen of *C. dryas* has vervet-like resemblances, whereas the available adult skulls seem not to). Further complications in the Cercopithecini were noted by Groves [9].



Figure 11. Putty nosed monkey, *Cercopithecus nictitans*, a member of the *C. mitis* group.



Figure 12. Wolf's Mona, Cercopithecus wolfi.



Figure 13. Red-tailed monkey, Cercopithecus ascanius.

Most recently, a remarkable study by Guschanski et al. [20] used museum samples to collect mtDNA, and incorporated carefully chosen samples from GenBank, including nDNA as well as mtDNA. This has clarified some relationships, but at the same time added quite unexpected complexity to others.

In the phylogeny of Guschanski et al. [20], there are four major 'speciation event' time periods. The initial split within the Cercopithecini is between *Miopithecus* and the rest, and a second split between *Allenopithecus* and the rest comes very quickly afterwards; both are around 9.5 Ma, and this near-trifurcation constitutes the first speciation event. That these two genera are the most divergent of the Cercopithecini is certainly not unexpected, although the order of branching perhaps is.

The second speciation event, between about 6.5 and 7.5 Ma, sees four branches separate, and these separations are most unexpected:

- 1. *Chlorocebus* plus *Cercopithecus hamlyni*. Within the *Chlorocebus* cluster, in the third-speciation event, three lineages diverge: *Allochrocebus solatus*, *C. sabaeus*, and a clade containing not only the other species of *Chlorocebus*, but also *Cercopithecus dryas*. These relationships were totally unsuspected, and raise several questions: is *C. hamlyni* not a member of the genus *Cercopithecus* after all? Is the genus *Allochrocebus* non-monophyletic? Is *C. dryas* likewise not a member of the genus *Cercopithecus*, but is it instead a 'vervet' that has recolonised a rainforest niche, and has it somehow undergone hypermorphosis, in that the juvenile skull reveals its affinities, whereas adult skulls have changed?
- **2.** A clade consisting of the *C. mona*, *C. neglectus* and *C. diana* groups; in this, *C. diana* and *C. roloway* do not cluster together, but are the first and second to separate within the clade. Is the *C. diana* group, therefore, non-monophyletic?
- 3. *Erythrocebus*. Patas monkeys are uncontroversial.
- **4.** A *C. cephus* plus *Allochrocebus preussi/lhoesti* subclade, and the *C. nictitans/mitis* group as the other. This raises further questions about the phylogenetic position and the monophyly of the genus *Allochrocebus*.

The third-speciation event sees the major branchings within these groups. There is nothing surprising about these (given the unexpected composition of some of the major clades), but we can notice that, within clade 2, *C. mona* and *C. campbelli* separate strongly (at or before the third-speciation event) from the *C. pogonias* cluster; and, within clade 4, the third-speciation event splits are *C. mitis opisthostictus*, *C. mitis mitis* plus *C. nictitans*, and the rest of *C. mitis*, i.e., the presumed species *C. mitis* is non-monophyletic.

But, remarkably, there is some noteworthy discrepancy between the new mtDNA data and the nDNA. Most notably, *C. hamlyni* associates with *Chlorocebus* in mtDNA but is part of *Cercopithecus*, although the most distinct branch, in nDNA; and it is the *A. lhoesti* group which is associated with *Chlorocebus* in nDNA. Again, *Erythrocebus* is associated with *Chlorocebus* in nDNA but is nested within *Cercopithecus* in mtDNA. These discrepancies are noted by the authors who suggest periods of hybridisation with nuclear swamping as a possible explanation.

How would this work? An example might be as follows. A population of very early *Chlorocebus* (proto-vervets) was invaded by males from a population of proto-*Cercopithecus*. The invading males were dominant over the indigenous males, and so mated with all the indigenous (proto-vervet) females. The male hybrids were again dominated by the proto-*Cercopithecus* males, which therefore were able to mate with the female hybrids, generating backcrosses which were 75:25 in nuclear DNA; in the next generation, it happened again. In the end, we have a population which in essence is proto-*Cercopithecus*, but retains the (matrilineally inherited) mtDNA of *Chlorocebus*, which, over the course of time, developed its own characteristic features and became *Cercopithecus hamlyni* (presumably also *C. lomamiensis*), and so on.

And then there is the taxonomy. If we accept the Miocene/Pliocene boundary as the cut-off point for genera, then (apart from the uncontroversial *Erythrocebus, Miopithecus* and *Allenopithecus*) there are, according to the mtDNA scenario, at least five genera involved: *Chlorocebus* (including *C. solatus* and *C. dryas*), one for *C. hamlyni*, one for clade 2, and one each for the two subclades of clade 4. In addition, the relationships within clade 2 are so unexpected that more genera might be involved. But the discrepancies noted by the authors, between nDNA and mtDNA (noted above), dictates caution before we start to revise the taxonomy wholesale.

6. Where to now?

The old taxonomic certainties with which we have been comfortable for so many years have been shaken to the core. Species that do not interbreed are somewhat of a rarity. Taxonomy, at least above the species level, is based severely on monophyly. Inter-relationships between families, between genera, and between species are often not at all as we thought they were.

Taxonomy is a dynamic science. There is no excuse for a conservative attitude: disagreeable as it may seem, we have to constantly be prepared for new revelations, overturning the old certainties.

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References

- [1] Szalay FS, Rosenberger AL, Dagosto M. Diagnosis and differentiation of the order primates. Yearbook of Physical Anthropology. 1987;**30**:75-105
- [2] TTOL (TimeTree of Life). 2016. http://www.timetree.org/

- [3] Chatterjee HJ, Ho SYW, Barnes I, Groves C. Estimating the phylogeny and divergence times of primates using a supermatrix approach. BMC Biology. 2009;9:259. DOI: 10.1186/ 1471-2148-9-259
- [4] Hartig G, Churakov G, Warren WC, Brosius J, Makałowski W, Schmitz J. Retrophylogenomics place tarsiers on the evolutionary branch of anthropoids. Scientific Reports. 2013;3:1756. DOI: 10.1038/srep01756
- [5] Ziętkiewicz E, Richer C, Labuda D. Phylogenetic affinities of tarsier in the context of primate Alu repeats. Molecular Phylogenetics and Evolution. 1999;11:77-83
- [6] Groves C, Shekelle M. The genera and species of *Tarsiidae*. International Journal of Primatology. 2010;31:1071-1082
- [7] Fulwood EL, Boyer DM, Kay RF. Stem members of Platyrrhini are distinct from catarrhines in at least one derived cranial feature. Journal of Human Evolution. 2016;**100**:16-24
- [8] Goodman M, Porter CA, Czelusniak J, Page SL, Schneider H, Shoshani J, Gunnell G, Groves CP. Toward a phylogenetic classification of primates based on DNA evidence complemented by fossil evidence. Molecular Phylogenetics and Evolution. 1998;9:585-598
- [9] Groves C. Primate Taxonomy. Washington: Smithsonian Institution Press; 2001
- [10] Mittermeier RA, Louis EE, Richardson M, Schwitzer C, et al. Lemurs of Madagascar. Illustrated by Nash SD. 3rd ed. Conservation International; 2010 ISBN: 978-1-934151-23-5
- [11] Marsh LK. A taxonomic revision of the Saki monkeys, *Pithecia* Desmarest, 1804. Neotropical Primates. 2014;21(1):1-163
- [12] Roos C, Boonratana R, Supriatna J, Fellowes JR, Groves CP, Nash SD, Rylands AB, Mittermeier RA. An updated taxonomy and conservation status review of Asian primates. Asian Primates Journal. 2014;4(1):2-38
- [13] De Queiroz K. Species concepts and species delimitation. Systematic Biology. 2007; 56:879-886
- [14] Mayden RL. A hierarchy of species concepts: The denoument in the saga of the species problem. In: Claridge MF, Dawah HA, Wilson MR, editors. Species: The Units of Diversity. London: Chapman and Hall; 1997. pp. 381-423
- [15] Groves C, Grubb P. Ungulate Taxonomy. Baltimore: The Johns Hopkins University Press; 2011
- [16] Wang B, Zhou X, Shi F, Liu Z, Roos C, Garber PA, Li M, Pan H. Full-length numt analysis provides evidence for hybridization between the Asian colobine genera *Trachypithecus* and *Semnopithecus*. American Journal of Primatology. 2015;77:901-910
- [17] Zinner D, Wertheimer J, Liedigk R, Groeneveld LF, Roos C. Baboon phylogeny as inferred from complete mitochondrial genomes. American Journal of Physical Anthropology. 2013;150:133-140

- [18] Butynski TM, Kingdon J, Kalina J. Mammals of Africa, II: Primates. London: Bloomsbury Publishing; 2013
- [19] Groves CP. A Theory of Human and Primate Evolution. Oxford: Clarendon Press; 1989
- [20] Guschanski K, Krause J, Sawyer S, et al. Next-generation museomics disentangles one of the largest Primate radiations. Systematic Biology. 2013;**62**:539-554







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