

GORILLAS

What, if Anything, Is Taxonomy?

Taxonomy and classification, two words that have come to mean much the same thing, are "the ordering of organisms into groups, on the basis of their relationships" (modified after Simpson, 1961).

It is important to realize that taxonomy is a part of biological science, like ecology, behaviour, physiology or evolution. So a classification is a scientific hypothesis, subject to modification if new evidence comes to light, or if new understandings are brought to bear. In this sense, a classification is never finalized, there is no "official taxonomy". There can only be a statement of the present position, as seen by a particular taxonomist, taking (one hopes) all relevant information into account.

Nowadays, nearly all taxonomists agree that common ancestry is the most objective criterion for orders, families and genera (and suborders, subfamilies ... and so on); so, the lemurs, tarsiers, monkeys, apes and humans are classified in the order Primates because they share a common ancestor not shared by other mammals. In older books, humans are usually classified alone in the family Hominidae, whereas orangutans, gorillas and chimpanzees are placed in a

different family, Pongidae; but it is now clear that humans, chimpanzees and gorillas share a common ancestor not shared by the orangutan, so we should classify them together in a group that excludes the orangutan. As all four are rather closely related, it is now almost universal to place them in a single family, for which the correct name is Hominidae, with two subfamilies: Ponginae for *Pongo* (the orangutan) alone, and Homininae combining *Homo* (humans), *Pan* (chimpanzees) and *Gorilla* (gorillas).

A Word about Names

I referred to "the correct name" because, unlike taxonomy, nomenclature is objective. Once one has decided what the most appropriate taxonomy is, the question of what names to call the resulting taxonomic groups is decided by the rules of naming, laid down in the *International Code of Zoological Nomenclature*. In the main, one must use the earliest available name given to a species (or subspecies, or a genus, or a family).

A species name is a binomial. The first word is the generic name, the second is the specific name. So in the genus *Macaca* we have the species *Macaca mulatta*, *Macaca fuscata* and others. In the genus *Pan* we have *Pan troglodytes* (common chimpanzee) and *Pan paniscus* (pygmy chimpanzee or bonobo).

Always begin the generic name with a capital letter; always begin the specific name with a small letter.

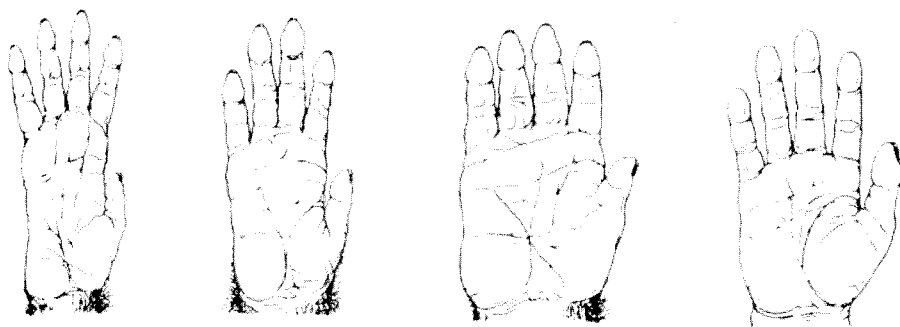
What Are Species?

The category "species" needs to be discussed separately, for reasons that will become clear. The great taxonomist Ernst Mayr defined a species as being "reproductively isolated"; his fullest discussion of what this would mean was published nearly 40 years ago (Mayr, 1963), but is still well worth reading. The concept of reproductive isolation has been much misunderstood. It actually means that two species do not, "under natural conditions" (meaning, more or less, in the wild) interbreed with each other. What it does not mean is that they do not interbreed with each under any circumstances. Thus, horses and mules interbreed, though their hybrids (mules and hinnies) are almost invariably sterile; and lions and tigers can be persuaded to interbreed in zoos, and their hybrids are fertile – yet nobody, as far as I know, has ever suggested that they should be included in one species. This is known as the Biological Species Concept (BSC).

But what if two animal populations live in different geographic areas (are allopatric), so do not have the opportunity to interbreed? Consider the following three levels of separation:

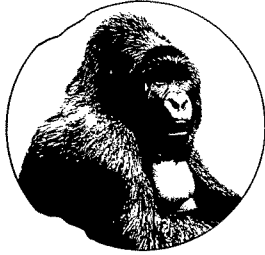
– Japanese macaques (on all the Japanese islands) differ strongly and consistently from rhesus macaques, which live on the Asian mainland. Japanese and rhesus macaques are customarily separated into different species, *Macaca fuscata* and *Macaca mulatta* respectively.

– Within Japan, the macaques of Yakushima (=Yaku island) differ on average from those of the three main islands, but not absolutely. The Japanese macaques are customarily divided into two subspecies, *Macaca*

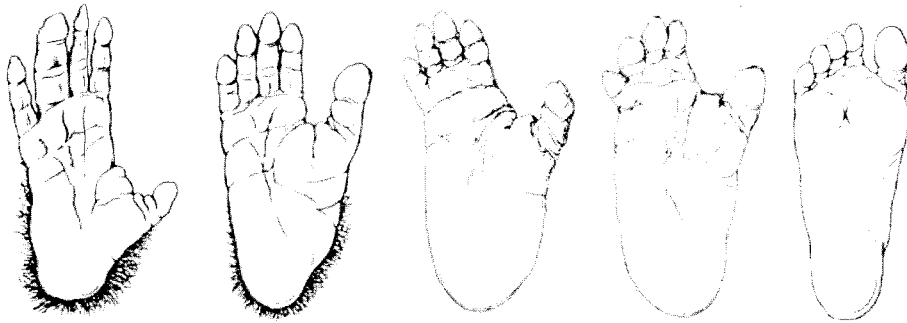


Hands of (from left to right) orangutan, chimpanzee, gorilla and man

Drawings from Schultz, 1956



GORILLAS



Feet of (from left to right) orangutan, chimpanzee, western gorilla, eastern gorilla and man

Drawings from Schultz, 1933 and 1956

fuscata fuscata (large islands) and *Macaca fuscata yakui* (Yakushima).

– Macaques on the three main Japanese islands of Honshu, Shikoku and Kyushu are indistinguishable morphologically from each other. Macaques of all three islands are regarded as belonging to one and the same subspecies, *Macaca fuscata fuscata*.

Could the essence of species, then, be that they are morphologically distinct, and if so, how much difference is required?

It is today possible to examine DNA sequences directly, and these, like morphological characters, may differ between two populations. Those sequences that have been analysed tend either to code for enzymes (haemoglobin, cytochrome oxidase) or not to code for anything (pseudogenes, introns) and so apparently are "silent". No sequences that code for morphological characters have yet been identified, let alone analysed, though clearly they exist, because such morphological (visible or metrical) differences as occur between individuals, and hence between populations, are, to a greater or lesser degree, heritable. So morphological differences are a special case of genetic differences. Let us then rephrase the question: Could the essence of species be that they are genetically dis-

tinct, and if so, how much difference is required?

The view promoted by the ornithologist Joel Cracraft nearly twenty years ago (Cracraft, 1983), and now widely adopted, is that species should be "diagnosable", or 100% distinct; that is to say, that every member of a species should be distinguishable from every member of all other species. This is known as the Phylogenetic Species Concept (PSC). Some of the DNA sequences of pseudogenes could likewise be identified infallibly though, interestingly, in their mitochondrial DNA some rhesus macaques are much more similar to Japanese macaques than to other Rhesus – so not all genes give the same results.

In the Japanese vs. Rhesus macaque example, there is not the slightest possibility of determining whether they are separate species or not using the BSC. (These drawbacks apply, quite frankly, to most comparisons between pairs of populations.) But the PSC can be applied, and we find that the two are genetically distinct: there are some genes which are universal (fixed) in the one, absent from the other. Each can be *diagnosed*. By contrast, Yakushima and larger-island macaques differ on average only: no gene (including morphological charac-

ter) has been discovered which is universal in the one, absent in the other.

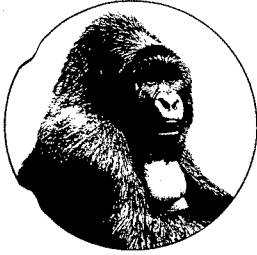
Although species theory is very controversial, there is a growing consensus that the BSC has outlived its usefulness as a criterion. It is still a touchstone, in that it illustrates in some important way what a species is all about, but it is simply inapplicable in most cases. The PSC, however, always offers objective criteria, and it is likely that a majority of taxonomists now adopt some version of it, consciously or subconsciously.

A species, then, is a population (or group of populations) which differs diagnostically (i.e. absolutely) from others. Put another way, it has fixed genetic differences from others. Put another way, there are gaps between different species. Below the species level, relationships between populations are reticulate (shared genes, shared characters). In cladistic jargon, the species is the terminal on the cladogram.

What Are Subspecies?

Subspecies are geographic segments of a species. They are populations which differ from one another as a whole, but not absolutely. In this case it is relevant to ask how much they should differ to merit being called different subspecies – what proportion of individuals should be recognizable? The decision is somewhat arbitrary, but a good rule of thumb is the "seventy-five percent rule" (Mayr, 1963): three-quarters of individuals in a population should differ from all individuals in other populations of the species.

Subspecific names are trinomials. The first two words denote the species; the third denotes the subspecies itself. Note that there is never just one subspecies, there are none or there are two or more: a species is divided into subspecies. As mentioned, *Macaca fuscata* is divided into two subspecies. One, the mainland Japa-



GORILLAS

nese macaque, is called the nominotypical subspecies, and its subspecific name repeats the specific name: *Macaca fuscata fuscata*. It is the one that occurs at the type locality (the locality from which the species was first described). The other has its own subspecific name, peculiar to it: *Macaca fuscata yakui*.

Applying the Criteria to Gorillas

Gorillas are found in two widely separate parts of Africa. Western gorillas live in the West-Central African region: southwestern Central African Republic, Congo, Mayombe, Luanda, Gabon, Río Muni, southern Cameroon, southeastern Nigeria, and the Djabbir region of the Democratic Republic of Congo. Eastern gorillas live in the East-Central African region: eastern D.R. Congo, southwestern Uganda, northern Rwanda. Eastern and Western gorillas are somewhat different. How to classify them?

In my experience, every gorilla is at once distinguishable as an Eastern or a Western gorilla. They are diagnosable. They differ 100% in their external characters, and in the skull and teeth. Their mitochondrial DNA (mtDNA) sequences are absolutely different; note that what is important, in deciding whether they are different species or not, is not the fact that their sequence differences show that they diverged over a million years ago (Garner & Ryder, 1996), but that they have fixed genetic differences between them. Even if we knew nothing of their mtDNA, we would still be justified in concluding that they have fixed genetic differences, because their morphological differences are absolute, and are heritable. So, under the PSC, they rate as distinct species.

Note that, because their distributions are entirely separate, we have not a hope of applying the BSC to them – just as in the rhesus and Japanese macaque example. Unless we

apply the PSC, we will have no objective means of deciding whether to call them different species or not. Some biologists do not accept the PSC; but for myself, I do not see how else we are to arrive at anything like a repeatable, falsifiable hypothesis for their classification.

The first gorillas to be described were from the Gabon estuary and were Western gorillas. The Reverend Savage, who first made gorillas known to science (Savage & Wyman, 1847), gave the name *Troglodytes gorilla*.

About the generic name: The name then in common use for the chimpanzee was *Troglodytes niger*, which had been given to it by the great French zoologist, Etienne Geoffroy St. Hilaire, in 1812; Savage thought that the gorilla was a giant species of chimpanzee, which is why he called it *Troglodytes gorilla*. But the chimpanzee's generic name had to be changed, because the same name, *Troglodytes*, had earlier been applied (by Vieillot in 1806) to the wren! So the next available name, *Pan* Oken, 1816, is now used for the chimpanzee. But the gorilla is in any case no longer considered to belong to the same genus as the chimpanzee, and in fact as early as 1852 Isidore Geoffroy St. Hilaire, son of Etienne, gave it its own generic name, *Gorilla*. And that is

why the correct scientific name for the Western gorilla is *Gorilla gorilla*.

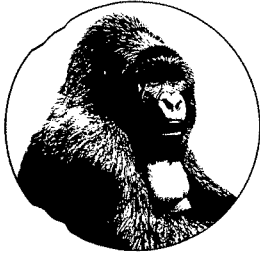
In 1902, Captain Oskar von Beringe discovered the Eastern gorilla (he "discovered" it by shooting one), and it was described the following year (Matschie, 1903), and named after him: *Gorilla beringei*. Von Beringe's gorilla was from Mt. Sabinyo in the Virunga Volcanoes, so this is the type locality of *G. beringei*. I have argued, above, that Eastern and Western gorillas are distinct species, so both Savage's and Matschie's names are valid.

Paul Matschie, describer of *Gorilla beringei*, was by modern standards a great "splitter" of species: where we today see a single species, he saw two, three or more. Between 1905 and 1914 he described several more supposed new species of gorilla from different regions of Cameroon: *Gorilla diehli*, *jacobi*, *schwarzi*, *hansmeyerii* and *zenkeri* (and the Hon. Walter Rothschild even named one after him: *Gorilla matschiei*!). In 1914, too, he described a supposed new species, *Gorilla graueri*, from the Itombwe Mountains, in the D.R. Congo west of Lake Tanganyika. Other people described supposedly new subspecies of *Gorilla gorilla*: *G. g. halli* from Río Muni, *G. g. uellensis* from Djabbir, and *G. g. rex-pygmaeorum* from Mt. Tshiberimu.



Gorillas from the Virungas, Kahuzi-Biega and the western lowlands

Artwork: Chisato Abe



GORILLAS

Two of Matschie's "species" do actually denote different subspecies. It does not matter that he described them as species; we can also use the names for the subspecies they really are.

(1) The so-called Eastern Lowland gorilla, from the Itombwe Mountains, Kahuzi-Biega, Mt. Tshiaberimu and the D.R. Congo lowlands east of the Lualaba, is different from the true Mountain gorilla of the Virunga Volcanoes; but the morphological characters overlap slightly, and although there is no difficulty in distinguishing the two as a whole, I do not believe that every single individual could be allocated to one or the other. So I do not think that they are different species; instead, I class them as subspecies of *Gorilla beringei*. Because the Eastern Lowland gorilla occurs in the Itombwe Mountains, type locality of Matschie's *G. graueri*, its correct name is *Gorilla beringei graueri*. (In the days when I assumed that all gorillas belong to one single species, I called it *Gorilla gorilla graueri*; but, as explained above, I now conclude that all Eastern gorillas belong together in a species different from Western). The name *rex-pygmaeorum*, given to Mt. Tshiaberimu gorillas, denotes the same subspecies, so is a synonym of *graueri*; but if, at some future time, someone considers that Mt. Tshiaberimu gorillas are a different subspecies from Itombwe gorillas, the name will have to be resurrected. The true Mountain gorilla is *Gorilla beringei beringei*.

(2) It has recently been argued (Stumpf et al., 1998; Esteban Sarmiento, in preparation) that the gorillas of the Cross River district, on the Nigeria-Cameroon border, are somewhat different from other Western gorillas, and should be regarded as a separate subspecies. Matschie's name *diehli* was given to gorillas from this region. The Cross River gorilla

must therefore be known as *Gorilla gorilla diehli*, and other Western gorillas will be *Gorilla gorilla gorilla*.

I should add that long ago I studied and measured the three skulls on which the name *uellensis* was based and, unexpectedly (because the population is geographically so isolated), I could find no differences at all from any other Western gorillas. So I conclude that they are probably examples of *Gorilla gorilla gorilla*.

Sarmiento et al. (1996) consider that the gorillas of the Bwindi-Impenetrable Forest are different from all other Eastern gorillas, whether Mountain (Virunga) or Eastern Lowland. Should further specimens support this hypothesis, then a new subspecies of *G. beringei* will have to be described and named because curiously, despite the arrant splitting that went on in the early 20th century, no-one ever got around to looking at any Bwindi gorillas!

Colin Groves

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An Overview of Apes in Africa

All the great apes, except the orangutan, live in tropical Africa. They comprise two species of chimpanzee, the robust chimpanzee (also known as the common chimpanzee) and the gracile chimpanzee (also known as the bonobo or pygmy chimpanzee), and two species of gorilla, the western gorilla and the eastern gorilla. All four of Africa's great apes are found near the equator, primarily inhabiting tropical forest where they are essential components of the richest assemblage of species on the continent. Unfortunately, apes are also a source of food and cash for many people in West and Central Africa. Hunting, together with loss of habitat, has greatly reduced both the distribution and the abundance of all four species.

Chimpanzees

The robust chimpanzee lives in savanna woodlands, grassland-forest mosaic and tropical moist forest, and is found from sea level to an elevation of about 3,000 m. This species probably once spanned most of equatorial Africa from southern Senegal to southwestern Tanzania, ranging over all or part of at least 23 countries. Today, the robust chimpanzee is the most widely distributed of Africa's apes, occurring in 21 or 22 countries between 13° N and 7° S.

There are four subspecies of robust chimpanzee. The western chimpanzee once ranged over ten to twelve countries, but now an estimated 40,000 members of this subspecies are patchily distributed in eight or nine countries from southeastern Senegal eastwards, possibly to the Niger River in Nigeria. Recent genetic research supports the recognition of the robust chimpanzee in eastern Nigeria and western Cameroon as a distinct subspecies, the Nigeria chimpanzee. Its