

**COMPARATIVE SOFT TISSUE MORPHOLOGY OF THE
EXTANT HOMINOIDEA, INCLUDING MAN**

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by

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VOLUME I

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ABSTRACT

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This thesis collates existing morphological data for the Hominoidea from the anatomical and anthropological literature, and covers the gamut of soft tissue gross anatomy. From this anatomical database, characters are selected for cladistic analysis in order to test whether soft tissue data can be used to reconstruct evolutionary relationships.

The principle hypothesis tested was the ability of soft tissue anatomical characters to reconstruct the cladistic relationships between the extant hominoids, based on a comparison with the consensus molecular phylogenetic tree. Bootstrap analysis of a 200 character dataset supports the hypothesis that soft tissue anatomy can be used to reconstruct the cladistic relationships between the Hominoidea, based on the consensus molecular cladogram. Both *Homo-Pan* and *Homo-Gorilla-Pan* are significantly supported, with bootstrap values of 92% and 85% respectively. Neither *Gorilla-Homo* or *Gorilla-Pan*, the main alternative cladistic groupings, are significantly supported.

The second hypothesis tested was whether different regions of the body differ in their ability to reconstruct the cladistic relationships between the genera. The bootstrap analysis does show a difference in the clades reconstructed using two regional subsets, upper limb (A1) and lower limb (A2). Both subsets provide good support for the *Pan-Homo* clade, although A1 provides a bootstrap value slightly less than the

70% level required for strong support (69%). A2 shows a slightly higher bootstrap value (73%) than for A1. However, subset A1 also provides strong support for the African ape-*Homo* clade (74%), which is not the case for subset A2 (20%).

Additionally, subset A2 gives good support, although at less than 70%, to a *Pongo-Gorilla* clade (69%), which is not favoured by the consensus molecular cladogram.

Branch swapping, however, shows that the two alternative groupings within the African ape-*Homo* clade are not significantly less supported by the tree topology than the preferred *Pan-Homo* clade, although *Gorilla-Pan* appears to be less supported than *Gorilla-Homo*.

Synapomorphies for the African ape-*Homo* and *Pan-Homo* clades are discussed.

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CHAPTER 1.

INTRODUCTION

"Individual variations are by no means confined to adults, and are often fully as pronounced among fetuses. This marked and extensive variability causes taxonomic work...to be difficult, as it calls for a large series of individuals but also a consideration of as many characters as possible...No conclusion in regard to the exact relationships between various groups of primates can be accepted as absolutely final until they have taken into consideration all bodily parts and the physiological as well as the morphological conditions". Adolf Schultz, 1933.

At the end of the twentieth century; despite almost three hundred years of scientific investigation, we remain unsure of how the living species of hominoid primates are related to each other, to Man, and also to the extinct species of the fossil record.

Molecular biology has attempted to resolve the relationships between the living hominoids, with some degree of success. The consensus of these biomolecular studies is that of the great apes (the chimpanzee, gorilla and orangutan), it is the African apes, the gorilla (*Gorilla* sp.) and chimpanzee (*Pan* sp.), that are most closely related to our own species, *Homo sapiens*. The majority of these studies indicate a *HomolPan* sister relationship, with *Gorilla* more distantly related.

There has never been a systematic, regionally-based review of morphology to determine the expression of morphological characters within higher primates.

Continuing pressure on the habitats of the great apes is constantly eroding their numbers; this gives a study such as this a certain degree of urgency.

As the quotation from Schultz that opens this chapter states, the study of morphology is complicated by individual intraspecific variations. This demands large sample sizes, and suggests that as many characters as possible from all parts of the body should be studied. This sixty-five year old statement demonstrates that in many senses, little has changed. Investigations of comparative morphology are conducted piecemeal, with a sampling bias towards regions and structures that hold a particular interest for each investigator. Perhaps inevitably, given the intense interest in evolutionary history, researchers have tended to focus their comparative investigations on hard tissues.

This thesis collates existing morphological data for the Hominoidea from the anatomical and anthropological literature, and covers the gamut of soft tissue gross anatomy.

From this anatomical database, characters are selected for cladistic analysis in order to test whether soft tissue data can be used to reconstruct evolutionary relationships. Their reliability is assessed by comparing relationships derived in this way with those determined from molecular evidence. Comparison between molecular and morphology based cladistic analyses has previously been carried out for such diverse groups as brachiopods⁵⁴, insects³¹⁴, echinoderms^{171, 181}, salmon¹⁸⁹ and herons¹⁸⁵.

As morphological difference exaggerates genetic distance^{45, 79}, it would be expected to find far more difference between the hominoid species in their anatomy than in their molecular biology. The genetic changes resulting in morphological difference presumably occurred in the hominid lineage after divergence from the chimpanzee/human common ancestor.

Since soft tissue morphology has been largely ignored in favour of hard tissue data in the past, this thesis will examine whether soft tissue anatomy follows the "traditional" morphological reconstruction of phylogeny, or conforms with the majority of the molecular evidence, and the morphological study of Shoshani *et al.*²⁷².

This chapter will briefly introduce the genera covered by this thesis, set out the principles of cladistic analysis, and review the molecular biology of the Hominoidea. It will conclude with a discussion of how anatomy has been used in the past to support particular relationships between the hominoids.

1.1 TAXONOMY

Six extant genera are contained within the superfamily Hominoidea: *Homo*, *Pan*, *Gorilla*, *Pongo*, *Hylobates* and *Symphalangus*. *Homo*, *Gorilla*, *Pongo* and *Symphalangus* all contain single extant species, *Homo sapiens*, *Gorilla gorilla*, *Pongo pygmaeus* and *Symphalangus syndactylus* respectively. The genus *Pan* incorporates two species, *Pan troglodytes*, the common chimpanzee, and *Pan paniscus*, the bonobo, or pygmy, chimpanzee, while *Hylobates* contains eight living species, *H. concolor*, *H. hoolock*, *H. klossii*, *H. lar*, *H. agilis*, *H. pileatus*, *H. moloch* and *H. muelleri*⁹¹.

1.1.1 Hylobatidae

Hylobatids are the smallest apes, the large black siamang (*Symphalangus syndactylus*) being heavier than the gibbons (*Hylobates sp.*)⁹¹.

They are confined to the forests of South East Asia, from eastern India to southern China, as well as through the Indonesian islands to Borneo⁹¹. *Symphalangus* is found

on Sumatra and the Malay peninsula²¹². The habitat of gibbons is tropical rain forest, semi-deciduous forest and montane forest up to about 2000 metres²¹². They are predominantly frugivorous, with some folivory, although *H. (Nomascus)klossi* is predominantly folivorous with a small carnivorous component⁹¹.

The body weight of gibbons ranges from 4 to 8 kg in males, and 4 to 7 kg in females, while that of siamangs ranges from 10 to 13 kg in males, and 9 to 12 kg in females²¹². Hylobatids are monogamous, with little weight distinction between the sexes⁹¹, although the coat colour often differs. Because of their small size, their niche competitors are monkeys, rather than the orangutans, with which they overlap in range¹⁶⁸. Locomotion in hylobatids is almost entirely by brachiation, although arm swinging, climbing, bipedal walking on branches and downward leaping also occur. Terrestrial bipedal walking and occasional quadrupedalism are also noted, and siamangs walk bipedally on the ground in captivity²¹². Although the thumb of gibbons is opposable, used during climbing, manipulation of food and grooming²¹², it is reduced in size, and is distant from the other digits so that the hand is effectively a hook for brachiation¹⁶⁸. Because of this, gibbons lack both the power and precision grips; they use their hands for scooping rather than picking¹⁶⁸.

The word "gibbon" may be derived from an ancient Greek or Roman word, *keipon* or *cephus*, while *Hylobates* means "tree-walkers". *Symphalangus* means "the one with conjoined digits", referring to the webbing of the second and third toes which occurs in this species²¹².

1.1.2 Orangutan

The Bornean orangutan is *Pongo pygmaeus pygmaeus*, and the Sumatran, *Pongo pygmaeus abelii*. The two island races are separated both by distance and by genetics, and increasingly being regarded as separate species, for they are as different from each other as *Pan troglodytes* is from *Pan paniscus*^{39, 117, 143, 168, 240}. It has been suggested that orangutans from western and eastern Borneo should be given distinct subspecies status¹⁶⁸. The geographical range of the orangutan once covered much of South East Asia, but now they are confined to the island of Sumatra, southern Borneo (Kalimantan) in Indonesia and northern Borneo (Sabah) in Malaysia^{91, 168}.

The habitat of orangutans consists of tropical rain forest, peat swamp forest with little ground cover, and dipterocarp forest. Orangutans are predominantly frugivorous, but also consume leaves, bark and birds eggs²¹².

The average body weight of Bornean male orangutans is 189 kg, with Bornean females averaging 81 kg. The Sumatran form is much smaller, with males averaging 69 kg, and females 37 kg²¹².

Orangutans are almost entirely arboreal, using climbing, quadrupedal, or bipedal walking on branches, and occasional true brachiation. In captivity, terrestrial bipedalism is common, but normally orangutans are quadrupedal on the ground, the weight being borne by clenched fists and inverted clenched feet. Palmigrade quadrupedalism has been seen in captivity. The reduced thumb of orangutans remains fully opposable against the proximal phalanx of the first finger. The power grip is very strong for grasping slender branches, while the hook grip is the principal

grip used for locomotion, and the interdigital grip is employed for picking up small objects²¹².

Sumatran orangutans are lighter coloured and have thicker, longer hair than the Bornean orangutans. The Sumatran animals live at higher altitudes and these differences may be local cold-climate adaptations in the former. This may also account for the hairier face of Sumatran orangutans¹⁶⁸.

Orangutans were unknown to western science until the eighteenth century. The first live orangutan arrived in Europe in 1776, and both orangutan and chimpanzee were at this time called "Pongo", despite one animal being large-bodied and red, the other smaller and black. Chimpanzees had a shorter journey, and were more likely to survive¹⁶⁸. The local people have long known of orangutans, a word which translates from Malay as "man of the woods", while the Dayak people of Borneo call the animal a "mias". Other names for the orangutan have included *Homo sylvestris*⁷⁵, *Pithecus* or *Simia satyrus*³²⁶. Linnaeus originally believed that *Pan* and *Pongo* were the same species, giving them a collective name of *Simia satyrus*, the wild apeman²⁸⁰. Later, it was realized that they were two different animals, and in 1788 the orangutan was fully recognized by western science¹⁶⁸.

An increasing number of reports from central Sumatra identify a new ape, provisionally called the "orang-pendek", meaning "short man". Evidence is, however, confined to a few eye-witness accounts¹⁶⁸.

1.1.3 Gorilla

The western lowland gorilla, *Gorilla gorilla gorilla*, occurs in West Africa from the Cross River in south-east Nigeria, through Cameroon, Gabon and the former French

Congo to the Congo River. In East Africa, the mountain gorilla, *Gorilla gorilla beringei*, is known from the Virungas, and other high mountains to the north and east of Lake Kivu. The eastern lowland gorilla, *Gorilla gorilla graueri*, is known from the lowlands east of the Upper Congo (River Lualaba) to the mountains west of the northern tip of Lake Tanganyika^{116, 212}. Other populations in the lowlands west of the Upper Congo have been termed *Gorilla gorilla manyema*¹¹⁴. The distribution of present-day gorillas is apparently a fraction of their former area as reported, but just 150 years ago the apes would have been familiar in most of Africa's tropical forests. The habitat of gorillas ranges from lowland rain forest and montane rain forest up to around 2500 metres, to bamboo forest up to 3000 metres. In the Virungas gorillas are found in woodland with low trees and a dense undergrowth, and also on the open slopes above, up to around 4000 metres. The diet of the gorilla consists mainly of bulky foods such as stalks, bark and leaves²¹².

Body weight of gorillas averages 159 to 175 kg in males, and 71 to 98 kg in females⁹¹.

Gorillas move terrestrially by quadrupedal knuckle-walking, the weight being taken on the feet and dorsum of the middle phalanges of the fingers. Bipedal locomotion is rare, although bipedal standing occurs during display behaviours. Brachiation has not been noted, and tree climbing is observed only in juveniles and females. The thumb is opposable and the hand is capable of manipulation²¹².

Probably the first known written reference to gorillas is a passage from, "The voyage of Hanno the Carthaginian", from 470 BC³²⁶. The first accurate description was in a letter, along with a skull as proof, from the missionary Dr Savage²⁴⁸. Dr Savage was

living in the region now called Gabon, and came across the remains of a "new species of orang", which was then used as a blanket term for all known apes; chimpanzees were called black oranges¹⁶⁸.

Lowland gorillas were not scientifically recognized until well into the 20th century, but had been known by local Africans for many generations. Generally, although hunted by some societies⁶², gorillas were treated with respect and seen as near relatives who had decided to live in the forest, or as the souls of ancestors¹⁶⁸. Savage and Wyman²⁴⁸ put forward the idea of a second African ape species, confirmed as a separate genus from *Pan* after the investigation of skeletal material in the monographs of Geoffroy-Saint-Hilaire and Duvernoy³²⁶.

Scientific recognition of the mountain gorilla was made by Captain Oscar von Beringe. In 1902 he was leading an expedition to meet local chiefs on behalf of the German Empire, when he stopped to explore Mount Sabinio in the Virunga mountains. Von Beringe sent back a skeleton which was eventually labelled the 'mountain gorilla', and given the name *Gorilla gorilla beringei* in recognition of its collector¹⁶⁸. Mountain gorillas have been studied by many scientists since this time⁹⁵.

The term "gorilla" in the modern sense has been taken from a translation of the voyage of Hanno ("gorilloi"), but may originally have been related to the native African words "drill" or "mandrill", that have been applied chimpanzees. Other terms which have been used for the gorilla include *Engeco*, *Inchego*, *Jocko* (also used for orangutans and chimpanzees), and *Ingéna*. It is also sometimes referred to as a species of *Troglodytes*³²⁶.

1.1.4 Chimpanzees

There are three distinct subspecies of common chimpanzee, that do not overlap in geographical range. *Pan troglodytes troglodytes* (the western, or black-faced chimpanzee) is found in Guinea, Sierra Leone and several other West African countries. *Pan troglodytes verus* (the pale-faced chimpanzee) lives in Cameroon, Gabon, Congo and neighbouring states. The eastern chimpanzee, *Pan troglodytes schweinfurthii*, inhabits Zaire, Uganda and Tanzania¹⁶⁸.

Some researchers refer to a fourth race, the Koola-kamba, a more gorilla-like chimpanzee occupying the same area as *Pan troglodytes troglodytes*⁶². Reputedly these animals are jet black, with large feet and unusually thick hair¹⁶⁸, but may represent a rare variant rather than a separate subspecies²³³.

The habitat of chimpanzees ranges from tropical rain forest and forest savannah mosaic to deciduous woodland and montane forest up to around 3000 metres. Their diet is primarily vegetarian, although there is a carnivorous component²¹². Body mass averages around 49 kg for male, and 41 kg for female chimpanzees²¹².

Brachiation is quite common for short distances, while terrestrially quadrupedal knuckle-walking locomotion is normally used. Bipedal standing is frequent, but bipedal walking or running are rare, and normally used in long grass, when carrying a load in the hands, or for display purposes. The hands of chimpanzees are prehensile, with an opposable thumb, although the long fingers and short thumb prevent the precision grip between the tips of the thumb and first finger²¹².

Bonobos (*Pan paniscus*), also known as pygmy chimpanzees, inhabit the dense lowland rainforests south of the Zaïre River. They were not recognised as a separate species until 1933⁵⁵.

Bonobos are about the same height at the shoulder as *Pan troglodytes*, but their build is more slender, with longer hindlimbs relative to forelimbs, and they are up to 20% lighter in body weight. Their heads are more rounded, with flatter faces and smaller ears and teeth. Adult bonobos are generally blacker than *Pan troglodytes*, and often have hairy tufts on either side of the head^{56, 91}. The word "chimpanzee" may be derived from a native African word. Several different spellings have been used, including "quimpézé" and "japanzee". Due in part to past confusion between chimpanzees and orangutans, the chimpanzee has also variously been referred to as a *Pongo*, *Simia*, *Pithecus*, *Anthropopithecus* or *Troglodytes*³²⁶.

1.1.5 Humans

The single living species of hominid, *Homo sapiens*, is currently to be found across the world. Only Antarctica has no true permanent colonization⁹¹.

All habitats, including tropical rain forest, woodland, savannah, plains, deserts, mountains and arctic coastlines, support human populations. The human diet is omnivorous, with no particular specialization toward either a carnivorous or a vegetarian diet⁹¹. Body mass in *Homo sapiens* averages 68 kg in males, and 55 kg in females⁹¹.

The bipedal gait of *Homo* is unique in that it is habitual. As the most terrestrial of all primates, most adult humans will never have climbed a tree for the purposes of food or shelter⁹¹. The hands of humans are prehensile, with an opposable thumb, but an

opposable hallux is lacking, unlike the other apes¹⁶⁸. Dentally, the canines are smaller, the premolars broader and the third molars reduced or absent in *Homo* compared with the other hominoids. The presence of a protruding chin, the small, short face, large cranium, and the more centrally-placed foramen magnum are other defining features of *Homo sapiens*¹⁶⁸.

1.2 CLADISTIC CONCEPTS

1.2.1 Phylogeny

Today systematists agree that accurate phylogenies are essential for the process of classification. Classification involves relating biological groups according to their 'classical' phenotypes, and, with the scientific developments this century, also at the molecular level. In order to construct a phylogeny, the characters present in organisms must be evaluated and cladistic analysis, using algorithms such as Phylogenetic Analysis Using Parsimony (PAUP)²⁸⁹ is now considered the best method of producing these phylogenies.

A well-established phylogeny allows hypotheses about the relationships between particular characteristics to be tested¹⁹¹, and also enables the sequence of events in the evolution of character states to be evaluated²⁷.

1.2.2 Homology and homoplasy

Homologous characters are the result of common ancestry, and are also referred to as synapomorphies, or shared derived character states. Shared ancestral states are called symplesiomorphies. Features that are unique to a taxon are called autapomorphies.

Synapomorphies and symplesiomorphies are often distinguished by the assumption that the most common character-state in a related group of species is the character-state that was present in the common ancestor³.

Homoplasy refers to any similarity not attributable to common ancestry, such as analogy, parallelism, or convergence. Parallelism refers to the development of homoplastic features in animals with a relatively recent common ancestry.

Convergence refers to the parallel development of features in more distantly related animals. Analogy refers to homoplastic characters where the feature is not related to any common descent.

Only homologies reveal cladistic or monophyletic groups, and it is important to distinguish homologies from homoplasies. This can be difficult, particularly in genera with a similar structure and a recent common ancestry. Lieberman *et al.* argue that the most reliable way of distinguishing homoplastic similarity from homologous similarity is to study the ontogeny of the characters¹⁷⁸. Homologous characters, according to this theory, must arise by the same developmental mechanisms, whereas homoplastic characters can come about by the same or different mechanisms. A character shared by two or more taxa which has arisen by different developmental pathways must be a consequence of homoplasy¹⁷⁸.

1.2.3 Parsimony

Parsimony derives from the Latin word *parsimonia*, meaning frugality, and in the sense that it is used in this thesis, may be taken as meaning "economy of assumption in reasoning"¹⁵⁷. That is, that the simplest explanation is more likely to be true, and therefore most informative.

Parsimony analysis works best when there are large quantities of independent, evolutionarily informative characters, or homologies, evenly spread over all the branches of the true phylogeny. On this basis, parsimony analysis is suitable for the characters assembled in this thesis from the comprehensive anatomical review given in Chapter 3. When information is limited, functionally constrained or has a high rate of change, results of different methods tend to diverge, and are also affected differently by noise. As any one morphological system is influenced by constraints which will tend to bias phylogenetic reconstruction in one way or another, a combination of different characters; each with their own bias, can filter out the non-homological noise, allowing the historical phylogenetic relationships to come through^{18, 204}.

Cladistic analyses often reveals homoplasies in well established clades. This demonstrates the degree to which evolution is not parsimonious, and reinforces the true complexity of the evolutionary process.

1.2.4 Cladistic analysis

Cladistics is a method for reconstructing the phylogeny of a group of taxa utilizing the distribution among these taxa of evolutionarily original character states³¹⁵. The basic assumption of cladistics is that the splitting of lineages is marked by the sharing of discrete, heritable and independent characters, transformation of which occurs more slowly than the divergence of lineages. Reconstruction of the last common ancestor depends on inferences from the anatomies of the known hominoid taxa, living and extinct, and the phylogenetic relationships between those taxa. The goal of cladistic analysis is the representation of monophyletic clades, the cladogram. Monophyletic clades are lineages which include all the descendants from a single

ancestor. Paraphyletic clades, in contrast, exclude some descendants, or group together taxa some of which are more closely related to outside taxa than to others within the clade¹³⁰. Within the hominoids, for example, Pongidae is paraphyletic because it excludes *Homo*, even though *Homo* is more related to some pongids, the African apes, than this group is to other pongids, the orangutans.

Phylogenetic Analysis Using Parsimony (PAUP)²⁸⁹ infers phylogeny from discrete character data under the principle of maximum parsimony. Parsimony methods search for minimum length trees, minimizing the amount of evolutionary change needed to explain the available data, when constraints are made upon character changes.

A tree with a length less than or equal to other possible trees is most parsimonious. Depending on the data set, there may be a single most parsimonious tree, or two or more equally parsimonious trees. Exact methods guarantee to find the optimal tree(s). A cladogram is a rooted tree. Rooting a tree imparts polarity onto at least one character transformation, although often many or all the characters will be polarized. The usual method for rooting a cladogram is outgroup comparison. This method involves choosing the sister group, or other closely related taxon, of the group under study, to root the cladogram. Rooting determines the monophyletic groups, reveals paraphyly, and discovers relatively synapomorphic and symplesiomorphic characters²⁶⁴.

Character polarization determines the direction of transformation in a multistate character. For unordered characters, the change from a state to any other state is one step^{90, 121, 264}. If the direction of the transformation is determined, the characters are ordered. For ordered characters, the number of steps from a state to another state is

equal to the difference between their state numbers. Morphological characters in which one state is intermediate between the others, such as medium between small and large, might reasonably be considered ordered characters^{87, 290}. The state number determines the order, and can be recoded to try different orders. Irreversible characters are ordered characters, except that decreases are not allowed to occur⁴³. Dollo characters are also ordered, except that multiple losses are allowed, but multiple gains are not. Each state is allowed to originate only once, and all homoplasy takes the form of reversals⁸⁷.

1.2.4.1 Branch and bound

This method was first applied to evolutionary trees by Hendy and Penny¹²⁹. It resembles an exhaustive search, which evaluates every possible tree, except that it 'cuts off' portions of the search tree that exceed the length of a random tree, since the addition of further taxa cannot decrease the tree length. If a full tree is evaluated at less than, or equal to, the length of this random tree, it is a member of the set of optimal trees. Also, if the tree under evaluation has a length that is less than the current upper bound, the length of this tree becomes the new upper bound for tree length. This enables subsequent search paths to be terminated more quickly. When all possible paths have been evaluated, the minimum length tree or trees will have been found.

1.2.4.2 Measures of fit and confidence limits

1.2.4.2.1 Confidence in tree topologies

In PAUP, the bootstrap technique randomly samples the data set, which is then analysed to form a tree or trees. This procedure is then repeated, usually either 1000

or 10000 times, and the percentage of occurrences of a particular grouping can be considered as an index of support⁸⁹. A value of 70% or above can be considered as strong support for particular clade, especially if this clade is also supported by other sources, such as molecular or fossil evidence.

1.2.4.2.2 Consistency index (CI)

The CI for a character is m/s , where 'm' is the minimum amount of change possible for the character, and 's' is the actual number of changes observed in the character on the reconstructed tree. The CI for two or more characters, or ensemble CI, is calculated as M/S , where M and S are the summations of 'm' and 's' for the individual characters in the data set. In the event of homoplasy, 's' will exceed 'm', and so CI is a measure of homoplasy. The best explanation for the data, with no homoplasy, produces a CI of 1.0, while a CI of 0.5 indicates twice as many steps as necessary and so on²⁷⁶. The greater the homoplasy, the more the CI reduces. Uninformative characters in the dataset cause an inflation in the value of CI without providing support for the grouping of taxa²⁷⁶, and for this reason should be excluded before calculation of the ensemble CI for a tree.

1.2.4.2.3 Retention index (RI)

The retention index⁸⁸ expresses the amount of synapomorphy in a data set by examining the amount of actual homoplasy as a fraction of the maximum possible homoplasy.

For a single character:

$$RI = \frac{\text{Maximum conceivable steps (g)} - \text{actual number of steps on tree (s)}}{\text{Maximum conceivable steps (g)} - \text{minimum conceivable steps (m)}}$$

As with ensemble CI, the RI for two or more characters is calculated as $(G-S)/(G-M)$, where G, S and M are the sums of the g, s and m values for the individual characters.

If the characters are perfectly congruent with each other, and the tree, RI will be 1, while if maximally homoplastic, RI will be 0. So, for RI, the worst possible fit between the character and the tree produces an RI of 0. Unlike CI, RI is unaffected by uninformative characters. For these characters the minimum conceivable number of steps is equal to the maximum conceivable number of steps²⁸⁹.

1.2.5 Problems with cladistic analysis

The goal of parsimony is to find the shortest tree or trees for a given data set under a set of assumptions such as character polarization. Many of the problems associated with parsimony, such as homoplastic noise, can be minimized through character choice. However, parsimony may fail to find the shortest tree. This occurs for two reasons; too many taxa, or too few phylogenetically informative sites²⁸⁶. In addition, even if the dataset appears to contain abundant phylogenetically informative characters, and a single most parsimonious tree is found, that tree may not accurately reflect the true evolutionary history of the taxa. This is the result of homoplasy²⁸⁶.

Problems can also result from using highly adaptive characters to reconstruct phylogeny. However, partitioning of data may lead to weaker phylogenetic hypotheses and thus all characters should be included in any analysis¹⁸³. When cladistic data sets include taxa with abundant missing entries, as often occurs with fossil taxa, parsimony analysis may yield multiple equally optimal trees and necessitate the use of consensus methods to summarize relationships that are common to the multiple trees. Missing data may have an obfuscatory effect upon phylogenetic relationships³¹⁶.

1.3 MOLECULAR PHYLOGENY

Since the second half of the nineteenth century, the evolutionary relationships between humans and apes have been studied using anatomical variation^{25, 92, 132, 137, 298, 303}

The majority of morphological evidence supports the closer relationship of African apes to Man than to the orangutan, although some morphological characters group the orangutan with the African apes and others group orangutans with humans²⁶⁰.

Molecular evidence for hominoid relationships was first provided by the immunological reaction test published by Nuttall²¹⁴. Wide use of molecular evidence began in the 1950s and 1960s, and since this time progressively more sophisticated techniques have been developed to assess evolutionary relationships between species. Analysis at the protein level^{245, 246} has been supplemented more recently by nuclear and mitochondrial DNA (mtDNA) analysis. Studies of serum proteins¹⁰⁶, haemoglobin³²⁸, and chromosomes¹⁵⁵ among others has shown *Homo* and African apes to be more closely related to each other than to the Asian apes.

Molecular evidence that *Gorilla* and *Pan* are more closely related to each other than to *Pongo*, and more closely related to *Pongo* than to *Hylobates*^{9, 19, 21, 110, 111, 117}, has also established that humans should be included in the African ape clade. Most studies suggest that *Pan* is more closely related to *Homo* than *Gorilla*, including protein studies^{110, 143}, nuclear DNA sequencing^{19, 21, 105, 160, 161, 162, 205, 226, 306, 318}, single-copy DNA-DNA hybridisation^{39, 273, 274, 275} and mitochondrial DNA sequencing^{122, 123, 124, 133, 241, 242}. Other studies show slight differentiation between the hominoid species^{82, 98, 126, 147, 238}, yet still favour a *Pan-Homo* clade: a few have

supported a *Pan-Gorilla* clade^{72, 73, 74, 132, 195, 196, 275}; there has been little support for a *Homo-Gorilla* clade²³².

Rogers has argued that there are insufficient data to support any of these conclusions, and that a functional trichotomy is the best way of reconstructing the hominoid phylogeny. If multiple branching events occur close together in time, over less than about 0.8-1.2 million years, then reconstruction of the phylogenetic history will be difficult²³⁵. The aim of using molecular evidence to recover phylogeny is that it provides a basis for inferences about the last common ancestor and its descendant lineages. It is assumed that the branching order established from molecular evidence accurately reflects other characteristics such as morphology and behaviour.

1.3.1 Principles of molecular evolution

1.3.1.1 Proteins

Proteins are complex structures composed of subunits called polypeptides, which in turn consist of amino acids linked in long chains. A polypeptide chain may contain 200 or more amino acids, of which there are twenty naturally occurring kinds.

Protein synthesis occurs mostly in the cytoplasm of the cell on ribosomes, which contain ribonucleic acid (RNA).

The evolutionarily 'older' a protein is, the slower the rate of amino acid substitution should be because its class is closer to, or at, equilibrium. There should be certain regions that have a very high homology irrespective of the evolutionary distance between the organisms. Within a species, a protein should exhibit a degree of polymorphism that is a function of the length of time of the species' existence. For

proteins in a class at equilibrium, further evolution would be restricted to increasing their level of evolution or changing their reaction to effectors⁶⁶.

Protein analysis underestimates the real number of nucleotide substitutions, as changes in most third position nucleotides do not affect the amino acid produced. As an example, the amino acid sequences of corresponding C beta genes are identical in *Pan* and *Homo*, although synonymous substitutions are present at the nucleotide level¹⁴². In addition, functional genes comprise only a small part of the overall genome. Substantial parts of the genome are composed of apparently functionless repetitive DNA sequences.

Relationships have been established using molecular evidence on a variety of levels. These are discussed below.

1.3.1.2 Chromosomes

Each chromosome has, in most cases, a constriction called a centromere. This is a specialized portion of the chromosome that becomes attached to the spindle apparatus at cell division and to which the separating chromosomes remain joined at metaphase. The tip of each arm of a chromosome is called the telomere.

An acrocentric chromosome is one whose centromere is placed very close to one end, so that one chromosome arm is much shorter than the other. The long arm is designated 'q' and the short arm 'p'. A metacentric chromosome has a centrally located centromere and therefore has arms of approximately equal length, and a submetacentric chromosome has a centromere somewhere between central and almost terminal. Telocentric chromosomes have the centromere terminally located at the telomere and have no short arm at all.

Stains are used to distinguish chromosomes. Dark-staining genetic material, called heterochromatin, is more highly coiled and has more repetitive DNA sequences than the lighter-staining euchromatin. Long stretches of heterochromatin are present at the centromere and at the telomeres of chromosomes. Chromosome satellites are small appendages on the end of chromosomes connected to the main body by a thin, poorly staining "satellite stalk". In humans, satellites occur on the short arms of chromosomes 13 to 15 and 20 to 21.

Homologous chromosomes of the same species or closely-related species are structured in the same way, with the same proteins, and therefore they are likely to show the same bands when treated with denaturing agents. This is not necessarily evidence of an absolute homology between the chromosomes of different species, in spite of a similarity in their banding patterns⁵⁰.

1.3.1.3 Genes

A gene is a specific sequence of nucleotides in nuclear and mitochondrial DNA. This sequence is a code designating the sequence of amino acids in a polypeptide chain of a protein. The gene functions through the production of messenger RNA that transcribes the DNA strand. This messenger RNA communicates with the ribosomes, which carry out protein synthesis from the template. Templates specify polypeptide chains.

Many mutations are replacements of one nucleotide for another in the parent DNA chain. This altered codon may result in another amino acid being inserted in the polypeptide chain, resulting in a change in the protein structure. The mutation may

result in no change in the amino acid, or in a 'nonsense' triplet which will not code for any amino acid.

1.3.1.4 Nucleic acids

Deoxyribonucleic acid (DNA) and ribonucleic acid (RNA) are long molecules made up of subunits called nucleotides. Each nucleotide is composed of a linked phosphoric acid, sugar and nitrogen-containing ring compound. The sugar component is deoxyribose in DNA, and ribose in RNA.

The nitrogen-containing ring compounds are either purines or pyrimidines. The purines are adenine (A) and guanine (G) and the pyrimidines are cytosine (C) and thymine (T). RNA differs from DNA in containing uracil (U) instead of thymine.

DNA is a helical structure composed of two polynucleotide chains held together by hydrogen bonds between pairs of bases. Adenine is always paired with thymine and guanine with cytosine. The phosphate-sugar backbone forms the outside of the helix with the bases on the inside. A triplet of bases, called a codon, forms the DNA template for an amino acid. Sequencing involves determining the order of the four bases in a defined region of DNA.

Cells contain two DNA sources, the nucleus and the mitochondria. The nucleus contains about 5.8×10^9 base pairs, and the mitochondria contain about 1.6×10^4 base pairs. Whereas there is only one nucleus per cell, there are between a thousand and ten thousand mitochondria, depending on which type of cell is used.

Mitochondrial DNA (mtDNA) also evolves about ten times faster than nuclear DNA, and is therefore more suitable for studying the relationships between closely related species.

In the following discussion, HSA stands for *Homo sapiens*, PTR stands for *Pan troglodytes*, GGO is *Gorilla gorilla*, PPA is *Pan paniscus* and PPY is *Pongo pygmaeus*; the numbers correspond to the number of the chromosome.

1.3.2 Mechanisms of molecular change

1.3.2.1 Inversion and telomeric fusion

Inversion is a form of chromosome breakage consisting of two break-points within a single chromosome, the segment between them being turned 180 degrees before being reinserted. The inverted segment may include the centromere, pericentric inversion, or may not, paracentric inversion.

Chromosome banding has demonstrated that inversions, especially pericentric inversions, are characteristic for the hominoids and are thought to account for the majority of chromosomal changes in this group²⁸⁴. Some chromosomes that differ by a pericentric inversion show syntenic homologues, indicating a common origin. For example, HSA 4 and GGO 3 contain the gene PGM-2, and HSA 12 and PPY 9 contain the gene LDH-B which is also found in PTR 10 and GGO 10.

A small pericentric inversion distinguishes between the PPY 2 of the Bornean and Sumatran orangutans^{270, 271}, and a complex arrangement involving two inversions is a balanced polymorphism in both subspecies. Hybrid offspring are heterozygous carriers of both types of PPY 2²⁶⁹.

A paracentric inversion has been suggested to derive PPY 7 from its homologues in HSA 10 and PTR 8. There is as yet no evidence for similar gene loci on the presumed homologous chromosomes.

Telomeric fusion is a mechanism by which two chromosomes fuse by their telomeres to form a large metacentric chromosome. A telomeric fusion has been proposed to account for a large submetacentric human chromosome, HSA 2 which has no direct homologue in the great apes²⁸¹. This mechanism would involve the inactivation of one centromere to account for the existence of only one functional centromere in HSA 2. The inactivated centromeric region of HSA 2q must also have been transformed into a non-heterochromatic region, a process called euchromatization. Comparing the African ape homologues, the centromere region of GGO 11 (HSA 2q) is likewise not heterochromatic, but does not hybridize to any of the human satellite DNAs. The PTR 13 (HSA 2q), which has better banding homology than the gorilla homologue, is heterochromatic, but is a major site of hybridization with human satellite DNAs III and IV.

It is thus impossible to find a phylogenetic sequence that fits both G-band homology (see 1.3.6.1.3) and the euchromatization of the centromere region of the HSA 2q. Euchromatization does not in itself imply inactivation, since GGO 11 and PPY 9 have no constitutive heterochromatin at the centromere, but show normal centromeric activity.

Using *in situ* hybridization, researchers have found what may be the remains of the inactivated ancestral centromere at 2q21, consisting of extra-centromeric sequences of alphoid DNA²⁴. Alphoid DNA is found at the centromere of all human and great ape chromosomes, extra-centromeric locations being human-specific such as at 9q13. These extra-centromeric sequences may be due to the persistence of residual alphoid repeats after the pericentric inversion that HSA 9 underwent during divergence from the great apes²⁴.

1.3.2.2 Translocation and centric fusion

Translocation is a chromosomal rearrangement involving two chromosomes, where a portion of one chromosome is transferred to the other. This is usually a reciprocal process, with the two broken chromosomes exchanging segments.

A reciprocal translocation has been suggested in *Gorilla* between the homologues of HSA 5 and HSA 17. The short arm, centromere and small proximal part of the long arm of GGO 4 are homologous to HSA 17, while the part of GGO 19 homologous to HSA 5 includes the short arm, centromere and the proximal half of the long arm²⁸⁴.

Centric fusion, or Robertsonian translocation, involves two acrocentric chromosomes. In centric fusion, the breakage points are at, or very close to, the centromere, and the smaller product containing the short arm is usually lost. The larger product is either metacentric (centromere centrally-located) or submetacentric (centromere located between central and terminal points) and contains all the genetic material of the two acrocentrics. This translocation reduces the chromosome complement by one, but is genetically balanced.

It is reasonable to hypothesize that HSA 2 may have resulted from a centric fusion of the two acrocentric chromosomes of the common ancestor of *Pan-Homo*. This centric fusion might account for a reduction in the chromosome number from 48 in great apes to 46 in *Homo*⁴⁸.

A comparison of the karyotypes of *Homo* and the great apes shows that homologies exist between some of the metacentric gibbon chromosomes and some acrocentric chromosomes in *Homo* and the great apes²⁹³. This may indicate that some acrocentric chromosomes have arisen by fission of metacentric chromosomes.

	HSA	PTR	PPA	GGO	PPY
HSA	-	4	4	6	5
PTR	4	-	0	2	5
PPA	4	0	-	2	5
GGO	6	2	2	-	7
PPY	5	5	5	7	-

Table 1.1. Total number of chromosome rearrangements in the great apes and *Homo*. Adapted from ²⁶⁷.

The number of chromosome rearrangements between *Homo* and *Gorilla* (6) is higher than that between *Homo* and *Pongo* (5), despite clear evidence that *Pongo* was the first to diverge from the great ape clade, as estimated by immunological distances¹⁰⁷, in vitro DNA hybridization^{30, 135}, and DNA sequence data^{163, 203, 206}. That *Homo* and *Pongo* have retained symplesiomorphic characters such as the absence of telomeric C-band regions, apparently obscures the fact that *Homo* and *Gorilla* have diverged from a more recent common ancestor. One reason for this may be that the chromosomes of *Gorilla* have diverged more rapidly from the ancestral karyotype than did those of *Pongo*. *Pan troglodytes* and *Pongo* have fewer rearrangements than *Gorilla* and *Pongo*, and only two rearrangements have occurred between *Pan troglodytes* and *Gorilla*. This implies that *Pan* and *Gorilla* are more closely related to each other than either is to *Pongo*. It also implies that the rate of change in *Pan* relative to that in *Pongo* has been slower than in *Gorilla*.

If *Pan* has evolved less rapidly than *Gorilla*, therefore retaining more symplesiomorphic characters, then the smaller number of rearrangements between *Homo* and *Pan* may be obscuring the possibility that *Homo* and *Gorilla* could share

phylogenetically more informative synapomorphic characters, and be more closely related than *Homo* and *Pan*.

1.3.3 Molecular clock

Sarich and Wilson^{245, 246} used immunological data and the molecular clock hypothesis to estimate the date of divergence between *Pan*, *Gorilla* and *Homo*. The molecular clock hypothesis is that the accumulation of molecular differences between taxa occurs at a constant rate characteristic to that molecule, and has a linear relationship to the length of time since those species diverged. The molecular clock was based on the observation that the number of different amino acids in haemoglobin is greater in those species more distantly related to humans than those which are closely related. Sarich and Wilson^{245, 246} used evidence from *Galago*, *Homo*, *Macaca* and *Cebus*, and the relative rate test, to confirm that the rate of immunological change for the blood protein albumin appeared to be constant over time. If the rate of evolution is constant rather than occurring at a faster rate in one lineage, the immunological distance between *Galago*, *Macaca*, *Cebus* and *Homo* will be similar. Sarich and Wilson^{245, 246} estimated that the relative distance between *Galago* and *Homo* is 10.8, for *Macaca* and *Homo* is 9.0 and for *Cebus* and *Homo* is 11.3. These estimates appear relatively similar given the possibility of experimental error. Albumin is a large molecule consisting of 584 amino acids, with a molecular evolution rate of about 1% per three million years. Every amino acid substitution adds 500,000 years to the date of divergence, but substitution is a random process, and there may not be a single amino acid substitution for every 500,000 years. This results in inaccuracies in dating speciation events. This is particularly important for

Pan, *Gorilla* and *Homo* because the time between the divergences of these species is relatively small. However, not all proteins evolve in the same way.

The molecular clock is calibrated with reference to a known divergence time between two species. Sarich and Wilson^{245, 246} used the assumed divergence time of the Old World monkeys (OWM) at 30 million years ago (mya) to calibrate their estimate of the divergence of humans from the great apes at between 2 and 8 mya. Horai *et al.* estimated the gorilla divergence at 7.7 +/- 0.7 mya¹³³, which is similar to other estimates^{36, 105, 111, 160, 205, 273, 275}, and the human divergence at 4.7 +/- 0.5 mya¹³³, which is similar to estimates from Miyamoto *et al.*²⁰⁶, Gonzalez *et al.*¹⁰⁵ and Ueda *et al.*³⁰⁶.

Ruvolo *et al.* placed the human divergence time much earlier, at 6 mya, based on a presumably highly-conserved mitochondrial COII gene²⁴². Miyamoto *et al.* used the *jh*-globin gene to estimate an initial divergence time for human, chimpanzee and gorilla sometime between 5.3 and 8.0 mya²⁰⁶, while Bauer used comparative protein divergence to calculate the last common ancestor of *Homo* and *Pan* at 5.2 mya, *Homo-Gorilla* at 7.4 mya, *Homo-Pongo* at 19.2 mya, and *Homo-Hylobates lar* at 20.3 mya²⁶. More recently, Arnason *et al.* have used mtDNA to estimate the *Pan-Homo* split at 10-13 mya, and that between *Gorilla* and the *Pan-Homo* lineage around 17 mya¹¹.

The most mitochondrially-different humans are less different than the only two siamangs sequenced to date, or than the lowland gorillas of West Africa. This limited genetic diversity implies a relatively recent time for the mitochondrial ancestor of modern humans²⁴³. Using an established reference marker of the molecular/palaeontological separation between artiodactyls and cetaceans at 60 mya, according to a homogenous-

rate model of sequence evolution, the mitochondrial DNA divergence between correspondingly, Hylobatidae and hominoids dates to approximately 36 mya, the *Pongo*-African ape/*Homo* divergence is at approximately 24.5 mya, for *Gorilla-Pan/Homo* at 18 mya, and that for *Pan-Homo* approximate to 13.5 mya. The split between Sumatran and Bornean orangutans was dated at approximately 10.5 mya, and that between common and pygmy chimpanzees at approximately 7 mya. These divergence times are at least twice as ancient as previously applied, for example *Gorilla-Pan/Homo* at 8.0 mya and *Pan-Homo* 4.5 mya²⁹², implying a much slower evolution in hominoid DNA in comparison to mtDNA¹⁰.

Minghetti and Dugaiczuk suggest that evolutionary rates differ significantly even if determined for a similar types of DNA sequence, such as a non-functional pseudogene²⁰³. Others have indicated that the rate of nucleotide substitution is slower in humans than in OWM^{83, 177}, and that this 'hominoid slowdown' is a general phenomenon rather than limited to a particular region⁹⁶.

The existence of the molecular clock is still debated, but does not mean that the size of the molecular differences between taxa cannot be used to provide an approximate estimate of the date of divergence, providing the assumptions involved in the estimate have been tested.

It was assumed originally that there was little genetic variation within populations and that occasional abnormal 'mutants' were mostly disadvantageous, with occasional advantageous mutants being selected for and leading to evolution. Electrophoresis of proteins revealed much more variation than at the morphological level. One explanation is that the variation is maintained by subtle differences in habitat which favour selectively slightly different variants. Another explanation is that the variation

is selectively neutral and that the main cause of molecular evolution is random factors rather than natural selection. DNA sequencing has revealed even more variation at the DNA level. Many of these variations are likely to be due to random, non-selective, processes. However, for any given variation it is not always easy to determine whether the reason is due to random processes, or natural selection.

1.3.4 Protein variation

1.3.4.1 Immunological techniques

In 1904 a book by Nuttall²¹⁴ included a test on the extent of the immunological reaction between *Homo* and *Pan*, *Gorilla* and *Pongo*. However, it was not until the 1950s and 1960s that immunological techniques were applied to assess the relationships between the hominoids and *Homo*. Immunological techniques provide an estimate of the differences in proteins by means of the immunological response of the antibodies of one species to the tissue of a second species. A vigorous response indicates closely-related species, with the response between more distantly-related species less vigorous. The magnitude of the response is therefore an indirect estimate of the similarity of proteins between species.

The micro-complement fixation technique was used by Sarich and Wilson^{245, 246}. The amount of additional antibody, specific to a single protein, required to produce an immunological reaction between two species equal to the response between representatives of the same species was measured. The greater the amount of antibody required to produce a defined response, the greater the immunological distance between the two species. The results showed that *Pongo* is the most

distantly-related of the great apes to *Homo*, but the method was not sensitive enough to resolve the relationships between the African apes and *Homo*.

Becker used serum cholinesterase activities and inhibition profiles to show that *Pan* and *Gorilla* had values within the normal human range²⁸. This study also showed that *Pongo* is closer to *Hylobates* than to the African apes. *Pan troglodytes* shows more human allotypes for the Bm, Gm and Km immunoglobins than *Gorilla*, but is closer to *Gorilla* than to *Pongo*⁷⁷. *Hylobates* is shown to be the most distantly-related species, although both *Pongo* and *Hylobates* seem to be polymorphic for several allotypes.

Westhoff and Wylie investigated the human RhD and c antisera, showing that the Rh locus was more polymorphic in *Pan* and *Gorilla* than in *Homo*³¹³. RhD, which was present in *Pan* and *Gorilla*, is either not expressed in *Pongo*, or the conserved structure of the gene in African apes and *Homo* does not extend to *Pongo*.

	M (%)	MN (%)	N (%)
HSA	30	50	20
PTR	60	40	-
PPA	100	-	-
GGO	-	83	17
PPY	59	-	-
Gibbon	22	25	23

Table 1.2. Frequency of the serological expression of blood groups M and N in the Hominoidea.

Adapted from ²⁷⁹.

The majority of a sample of orangutans express only the M blood group with the remaining 41% of orangutans expressing no M or N antigens²⁷⁹.

Serological phenotypes in primates appear to be random, and do not always follow the zoological classification²²². The same study showed that the chimpanzee phenotype was similar to the human phenotype, but also that two antigens were shared exclusively by *Homo* and *Gorilla*.

Immunoreactivity of galanin in the basal forebrain of *Pan*, *Gorilla* and *Hylobates* has an indistinguishable pattern of expression to that seen in *Homo*³¹, and the gorilla carbonic anhydrase I protein shows levels of catalytic activity similar to *Homo* and *Pan*⁸⁴.

1.3.4.2 Protein electrophoresis

Electrophoresis detects differences between proteins caused by amino acid substitutions that affect their size and total charge. About a third of point mutations fall into this category¹⁵⁴.

A recent study by Breed and Jolly showed that in *Pan*, the electrophoretic mobility of esterase isozymes was very similar, although not identical, to those of the human control, whereas the gorilla esterases migrated faster than those of *Homo* and *Pan*³⁷. Unlike any human plasma, all chimpanzees showed a narrow strongly-staining prealbumin carboxylesterase band. A faint narrow prealbumin carboxylesterase band was visible in *Gorilla*, but this band was not detectable in *Pongo*. The main band in *Pongo* had a mobility similar to that in other hominoids, but with marked intensity variation. Orangutan individuals with strongly staining plasma had three faint bands corresponding to those of the human which were not visible in low staining plasmas. Only two regions of esterase activity were visible in gibbons. The anodal/cathodal ratio was shown to be species-specific: *Pan*, *Gorilla* and *Homo* are high ratio forms,

Pongo is a low ratio form, and *Hylobates* is indeterminate. For *Pongo* to be phyletically more closely related to *Homo* than *Pan* and *Gorilla* would require an additional parallel mutation.

Electrophoresis of the vitamin-D-binding protein in chimpanzees has shown that both common and pygmy chimpanzees differ from *Homo*, and are also distinctly different from each other⁵³.

1.3.4.3 Amino acid sequencing

Comparison of amino acid sequences provides data on the number and type of amino acid substitutions. King and Wilson have estimated that an average human and chimpanzee protein differs by only 7.2-8.2 amino acids per thousand¹⁵⁴. The African apes and humans share a derived character in having serine at position 23 of the myoglobin chain. The presence of cysteine at position 110 may define an African ape and human clade excluding *Pongo*⁵. The presence of cysteine at this position in gibbon myoglobin would thus be parallel evolution, and the presence of serine in the orangutan at this position would be the ancestral condition. Phylogenetic trees produced from the amino acid sequencing of α and β haemoglobin chains depict extremely close, equally parsimonious, phyletic relationships between African apes and *Homo*. The African ape-human clade diverges by two mutations from *Pongo* and by three to four mutations from the hylobatids¹⁰⁸. The α haemoglobin chain and the fetal globin A chain each have an amino acid unique to *Pan* and *Homo*. No other pair of hominoid species share any unique amino acid substitutions^{5, 109, 265}.

The fibrinopeptide A and B sequences show that African apes and humans are identical, in spite of the rapid change that these structures usually exhibit from group

to group. The African ape-*Homo* clade was separated from *Pongo* by two substitutions, and from the gibbons by three or four substitutions^{76, 320}. Six different mutations were needed to account for the fibrinopeptide sequences of all six species. Fibrinopeptide sequences from *Symphalangus* might clarify the relationship of *Symphalangus syndactylus* to the *Hylobates* line and the great ape lineage¹⁹⁰. In the carbonic anhydrase sequence, Tashian *et al.* show two derived substitutions linking *Pan* and *Homo* that are absent from *Pongo*²⁹⁶. Goodman *et al.* showed that for carbonic anhydrase I, *Homo* and *Pan* are separated from *Pongo* by three to four mutations, but vary from each other by only one mutation¹⁰⁸. Data on carbonic anhydrase from *Hylobates* may locate more clearly the early divergence of the Hominoidea¹⁹⁰. The deduced amino acid sequences of carbonic anhydrase I (CAI) from *Pan* and *Gorilla* are identical to the human sequence at the known active site of the molecule. *Gorilla* CAI differs from *Pan* and *Homo* at residues 69 and 121⁸⁴.

	HSA	PTR	GGO	PPY
HSA	-	2 (0.77)	5 (1.9)	7 (2.7)
PTR	6 (0.77)	-	6 (2.3)	7 (2.7)
GGO	11 (1.4)	8 (1.0)	-	7 (2.7)
PPY	na	na	na	-

Table 1.3. Comparison of amino acid and nucleotide sequences of the CAI gene. Above the diagonal: amino acid difference followed by percentage difference in brackets; below diagonal nucleotide difference followed by percentage difference for the CAI gene. Na = not available. Adapted from ⁸⁴.

The human sequence of the flanking region of CAI differs less from *Pan* than from *Gorilla* by about 1% at the amino acid level, and about 0.6% at the nucleotide level, although the *Pan-Homo* clade is not significantly favoured over the *Homo-Gorilla*

clade. For the nucleotide sequences of the flanking regions of the CA1 gene, the human sequence is closer to *Pan* than to *Gorilla* by 0.8%.

Human and chimpanzee cytochrome C are identical¹⁰⁸. Inferred amino acid sequences however do not significantly resolve the hominoid trichotomy. Of 227 amino acid residues in the cytochrome oxidase subunit II gene, there is 2.6% difference between *Homo* and *Pan*, versus 3.1% between *Homo* and *Gorilla* and *Pan* and *Gorilla*²⁴¹.

A composite tree of haemoglobin α -chain, haemoglobin β -chain, haemoglobin δ -chain, carbonic anhydrase B and fibrinopeptide data placed the divergence of the human ancestor from the African great apes relatively late in the evolution of the group. *Hylobates*, *Symphalangus* and probably *Pongo* diverged from the line to *Gorilla* and *Pan* well before the divergence of a human branch¹⁹⁰. These proteins show only 0.2% difference between *Homo* and *Pan* in comparison to 1.2% average difference between all non-human hominoids, and 1.0% between *Homo* and the other non-human hominoids.

A recent study has analysed the total amino acid content of milk from the African apes and *Homo*, in addition to other primates and mammals⁶⁷. The milks of the hominoids examined had significantly lower total amino acid concentrations than those of lower primates, although the milk of *Gorilla* had a total amino acid concentration most similar to those of the lower primates (*Homo* 8.5 g/L, *Pan* 9.2 g/L, *Gorilla* 11.5 g/L, baboon 11.5 g/L, Rhesus monkey 11.6 g/L). Human milk was shown to be higher in the amino acid cystine than the milks of the great apes.

Protein	Number of amino acid differences	Number of amino acid sites
Fibrinopeptides A and B	0	30
Cytochrome c	0	104
Lysozyme	~0	130
Haemoglobin α	0	141
Haemoglobin β	0	146
Haemoglobin A- χ	0	146
Haemoglobin G- χ	0	146
Haemoglobin δ	1	146
Myoglobin	1	146
Carbonic anhydrase	~3	264
Serum albumin	~6	580
Transferrin	~8	647
Total	~19	2633

Table 1.4. Number of amino acid differences between human and chimpanzee¹⁵⁴.

1.3.5 Chromosome number

Yeager *et al.* correctly estimated the diploid number in *Pan troglodytes* to be 48³²⁴.

The normal diploid number in *Homo* is 46⁹⁴. With the improvement of chromosome preparation techniques, the study of the other primate species has showed that the diploid numbers of *Pan paniscus*, *Gorilla* and *Pongo* are 48^{46,47, 120}.

The Hylobatidae have different chromosome numbers, depending on the species. The 44-chromosome gibbons include *Hylobates lar*, *H. klossi*, *H. moloch*, *H. muelleri* and *H. agilis*, while the siamang (*Symphalangus syndactylus*) has a diploid number of 50 and *H. (Nomascus) concolor* has a diploid number of 52⁴⁹. In addition, *H. (Bunopithecus) hoolock* has 38 chromosomes²²⁸.

1.3.6 Chromosome morphology

The following morphological comparison is taken from Boyce³⁶ except where stated otherwise, and is based on Giemsa banding techniques and standard chromosomal descriptions. The descriptive terminology for chromosome morphology is explained in 1.3.1.2, 1.3.2.1 and 1.3.2.2, while chromosome banding techniques are discussed in 1.3.6.1. The great ape homologues are given in parentheses following each human chromosome.

HSA 1 (PTR 1, PPA 1, GGO 1, PPY 1)

The chromosome homologous to HSA 1 is similar in the three apes. The banding pattern is the same as HSA 1, but the human subcentromeric constriction is not present in the apes.

HSA 2p+q (PTR 13+12, PPA 13 +12, GGO 11 + 12, PPY 11 + 12)

No single chromosome similar to HSA 2 is observed in the great apes. There are however two acrocentric chromosomes that are equivalent to HSA 2p and 2q. Egozcue *et al.* state that the chromosome equivalents are acrocentric and submetacentric⁸⁰, and Seuanetz states that PTR 12 and 13 are subtelocentric, while GGO 11 and 12 are subtelocentric and acrocentric²⁶⁸. In *Pongo* the homology between HSA 2 and PPY 11 and 12 is good, whereas in African apes the proximal part of the homologue for HSA 2q is apparently missing. Chiarelli⁴⁸ and Boyce³⁶ suggest a centromeric fusion of the two acrocentrics, but Dutrillaux has suggested a more complicated telomeric fusion with a secondary loss of function of one centromere⁷⁸. Baldini *et al.* have found what may be the remains of the inactivated

ancestral centromere at position 2q21²⁴, and recently, an HSA 2p specific probe has been found to hybridize to the short arm of great ape chromosome 12²⁴⁴.

HSA 3 (PTR 2, PPA 2, GGO 2, PPY 2)

Homo, *Pan* and *Gorilla* possess an apparently identical metacentric chromosome. *Pongo* differs by the presence of a similar-sized chromosome that is subtelocentric. This difference could be explained by a pericentric inversion.

HSA 4 (PTR 3, PPA 3, GGO 3, PPY 3)

Great apes possess an equivalent chromosome that is more metacentric than that of *Homo*. This difference could be explained by a pericentric inversion in the human lineage. An HSA 4-specific alphoid satellite sequence, however, hybridizes to PTR 11 and 13, and GGO 19 rather than PTR 3 or GGO 3⁶⁵.

HSA 5 (PTR 4, PPA 4, GGO 4, PPY 4)

This chromosome is similar in *Homo* and *Pongo*, while African apes possess a more metacentric chromosome similar to the ape chromosome 3. Egozcue *et al.* stated that GGO 4 was more metacentric than PTR 4 and that this was probably the result of a pericentric inversion⁸⁰. However, a human probe for the region of HSA 5, that is responsible for cri du chat syndrome, is conserved on PTR 4 and PPY 4, but has diverged onto GGO 19²⁹⁵.

HSA 6 (PTR 5, PPA 5, GGO, 5, PPY 5)

Similar and metacentric in all species.

HSA 7 (PTR 6, PPA 6, GGO 6, PPY 10)

This is similar in *Homo* and African apes. There is no obvious equivalent in *Pongo*²⁸¹, but the banding pattern of PPY 10 is similar, mainly in the distal part of the long arm, although the overall size is smaller than HSA 7. Egozcue *et al.* states that GGO 6 shows a pericentric inversion with respect to PTR 6⁸⁰.

HSA 8 (PTR 7, PPA 7, GGO 7, PPY 6)

Chromosome 8 is similar in *Homo* and *Pan*, and very little different in *Pongo*. The chromosome is metacentric in *Pan* and *Gorilla*, suggesting a pericentric inversion.

HSA 9 (PTR 11, PPA 11, GGO 13, PPY 13)

This chromosome is different in all four species. It is acrocentric in *Pongo*, metacentric (or acrocentric^{78, 268}) and small in *Gorilla* with a secondary constriction, metacentric (or submetacentric⁷⁸) in *Pan*, without a constriction and with a different banding pattern. The secondary constriction, as well as a light band on the short arm of GGO 13, are present on HSA 9, but neither is present on PTR 11⁸⁰. The chimpanzee chromosome differs from that of the human by an inversion and a deletion. Gene mapping placed three loci from HSA 9 on PTR 11, and two of these are on GGO 13²⁸¹. Verma and Luke have found a gene from HSA 9q on PTR 11p, GGO 13q and PPY 13q³⁰⁸.

HSA 10 (PTR 8, PPA 8, GGO 8, PPY 7)

Chromosome 10 is similar in *Homo* and *Pan*. It is metacentric in *Pan* and *Gorilla*, and acrocentric in *Pongo*. A pericentric inversion may have occurred in African apes.

HSA 11 (PTR 9, PPA 9, GGO 9, PPY 8)

Similar in all four species³⁶. Dutrillaux shows that HSA 11 has an unusual T-band within the proximal one-third of the long arm⁷⁸. This band is present in the African ape equivalents, but not in *Pongo*.

HSA 12 (PTR 10, PPA 10, GGO 10, PPY 9)

This chromosome is similar in *Homo* and *Pongo*. The African ape homologues are identical, but more metacentric than their equivalents in *Homo* and *Pongo*.

HSA 13 (PTR 14, PPA 14, GGO 14, PPY 14), 14 (PTR 15, PPA 15, GGO 18, PPY 15) and 15 (PTR 16, PPA 16, GGO 15, PPY 16)

These acrocentric chromosomes appear to be relatively stable in hominoid evolution, being similar in all species. Seuanetz states that GGO 18 is metacentric²⁶⁸.

HSA 16 (PTR 18, PPA 18, GGO 17, PPY 18)

In all species, chromosome 16 is approximately metacentric. In *Homo* and *Gorilla*, it carries a secondary constriction that is not present in *Pan* and *Pongo*, but GGO 17 is more telocentric than HSA 16. The Q and C banding patterns of the *Pan* and *Gorilla* chromosome homologues are the same according to Egozcue *et al.*⁸⁰. The short arm of HSA 16 appears to be conserved in all great apes and *Homo*²⁹⁴.

HSA 17 (PTR 19, PPA 19, GGO 19, PPY 19)

This chromosome is metacentric in apes, but not in *Homo*. The banding patterns of GGO 19 are completely different from those of PTR 19. Egozcue *et al.*⁸⁰ and Stanyon and Chiarelli²⁸¹ state that the homologues have not been agreed. Part of

GGO 19 appears to have been reciprocally translocated to the short arm of chromosome 5²⁸⁴. Morrison *et al.* have mapped genes from HSA 17 to the long arm of GGO 19 and PPY 19, providing further support for homology²¹⁰.

HSA 18 (PTR 17, PPA 17, GGO 16, PPY 17)

Chromosome 18 is similar and acrocentric in the great apes, but slightly more metacentric in *Homo*. The Q and C banding patterns of PTR 17 and GGO 16 are the same⁸⁰.

HSA 19 (PTR 20, PPA 20, GGO 20, PPY 20)

Similar and metacentric in all species. Egozcue *et al.* however states that GGO 20 has a pericentric inversion with respect to PTR 20⁸⁰.

HSA 20 (PTR 21, PPA 21, GGO 21, PPY 21)

Metacentric and similar in African apes and *Homo*, being more telocentric in *Pongo*. However, an alphoid DNA subset specific for HSA 20 maps comparatively to PTR 11 and GGO 19, rather than to PTR 21 or GGO 21²³.

HSA 21 (PTR 22, PPA 22, GGO 22, PPY 22)

Similar and acrocentric in all species.

HSA 22 (PTR 23, PPA 23, GGO 23, PPY 23)

Similar and acrocentric in all species, except PPA 23 which is metacentric.

HSA-X (PTR X, PPA X, GGO X, PPY X)

Similar in all species. Egozcue *et al.* detected a more marked light band on the short arm of GGO X than in PTR X⁸⁰.

HSA-Y (PTR Y, PPA Y, GGO Y, PPY Y)

The Y chromosome seems to be smaller in the common chimpanzee than in the other species, even the Y chromosome of *Pan paniscus* is longer than that of *Pan troglodytes*. The Y chromosome may have lost the distal part of its long arm in *Pan troglodytes*, being submetacentric rather than submetacentric as in *Gorilla*. *Homo* and *Gorilla* are linked by having a Y chromosome with a brilliant fluorescent telomeric region. However, if the fluorescent tail is excluded, the chimpanzee Y may be more similar to that of *Homo*²⁸¹. Schempp *et al.* have found an inverted satellited almost acrocentric Y chromosome specific to Sumatran orangutans, all Bornean orangutans examined possessing a submetacentric Y chromosome²⁵¹. The chromosomes of *Pan* are morphologically and dimensionally very similar or almost identical to the corresponding human chromosomes. The few minor differences are in the centromeric region or in the length of the arms. Some chromosomes however do not show any real correspondence with their human counterparts⁴⁸. The assignment of homologues is still a matter for debate, but as more specific genes are positively located this should become clearer. The numerous almost metacentric chromosomes of the Hylobatidae have considerable similarities in size and shape despite the difference in number. A marked chromosome pair with a broad secondary constriction as seen in the Cercopithecidae, is found in the *Hylobates* subgenus, where they are metacentric as in Colobinae. In *Symphalangus*, a similar satellited medium sized acrocentric pair occurs, whereas in *H.(Nomascus)concolor* neither marked chromosomes nor medium sized satellited acrocentrics are found, although *Nomascus* does have three pairs of small acrocentrics⁴⁹.

Hylobates and the Colobinae have similar marked chromosomes and share diploid chromosome numbers (44). However, the metacentric marked chromosome in *Hylobates* could have originated independently, and further comparisons of karyological similarities are necessary to resolve the situation⁶⁸.

No chromosome has remained unaltered between *S. syndactylus* and *H. moloch*, not even the X chromosome which is relatively stable throughout the Hominoidea. In addition, the siamang haploid set is twenty percent longer than the gibbon haploid set²⁸². This suggests that gene duplication has been an important mechanism of change during gibbon speciation. The existence of a viable hybrid between siamang and gibbon suggests a similarity in genetic content despite the karyological differences²²⁵.

1.3.6.1 Chromosome banding

1.3.6.1.1 Ag-NOR

This technique stains the secondary constriction regions of chromosomes that are associated with nucleoli. Because it reveals active sites, Ag-NOR is a relatively good source of information about the evolution of gene expression.

Symphalangus syndactylus has one pair of acrocentric chromosomes containing the nucleolar organizing site¹²⁸. *Hylobates (Nomascus) concolor* has three pairs of acrocentric chromosomes, but NOR regions have not yet been conclusively located²⁸². The single pair of metacentric, NOR-bearing, "marked chromosomes", in Hylobatidae and Cercopithecidae has been used to ally the lesser apes with the Old World monkeys. However *in situ* hybridization of human chromosome-specific DNA

probes shows that the so-called “marked chromosomes” evolved by convergence, and cannot be used to exclude gibbons from Hominoidea²⁸⁵.

HSA	PTR	GGO	PPY
1	1	1	1
2p	12	12	12
2q	13	11	11
9	11	13	13
13	14	14	14
14	15	18	15
15	16	15	16
18	17	16	17
21	22	22	22
22	23	23	23

Table 1.5. Chromosome distribution of Ag-NOR staining regions in the Hominoidea, indicated by bold type. Adapted from ²⁶⁷.

Pan and *Homo* share two homologous Ag-NOR staining regions. However, *Pan* also shares two homologous regions with *Gorilla*.

1.3.6.1.2 C-bands

This is a staining method that demonstrates regions of constitutive heterochromatin, usually located near the centromere. Heterochromatin stains differently, and more clearly, from the rest of the chromosome, and appears to be mostly genetically-inactive DNA repeat sequences. The African apes show terminal C-bands, whereas *Homo* and *Pongo* do not. These telomeric C-bands correspond to positive Q-bands which do not seem to contain homologous sequences to any of the four human satellite DNAs.

According to Marks, seeing either *Gorilla* or *Pan* as closer to *Homo* requires that the telomeric bands on certain chromosomes in *Pan* and *Gorilla* existed in a common ancestor and were lost from almost all the chromosome complement of *Homo*¹⁹⁴.

Marks believes that this explanation for the loss is not impossible, but a more parsimonious solution is a single evolutionary gain event in the common ancestry of *Pan* and *Gorilla*. Royle *et al.* appear to provide support for Marks' theory about the telomeric regions by showing that the sub-telomeric regions of African apes contain a satellite that is absent from *Homo* and *Pongo*, and that the organization of the sequences adjacent to the telomeres differs greatly between *Pan* and *Homo*²³⁷.

Telomeric C-bands have appeared elsewhere in the Hominoidea, apparently linking *Hylobates (Nomascus) concolor* and *Symphalangus syndactylus*, the bands being mainly terminally located, with a few interstitial bands on some chromosomes^{196, 225} and the centromeric heterochromatin being frequently so reduced as to be negligible.

In *Pan* the telomeric C bands do not exist at the expense of the centromeric heterochromatin¹⁹⁴. The 44-chromosome gibbons show only small amounts of C-heterochromatin in the centromeric region, and no terminally located C-bands^{282, 301}.

The difference in the amount of C-heterochromatin in the lesser apes has been associated with species-specific differences in genome size²²⁵. The implication is that these telomeric C-bands have evolved twice, once in the *H. concolor/Symphalangus* ancestor, and once in the *Gorilla/Pan* common ancestor. Loss in *Homo* or independent evolution in *Gorilla* and *Pan* is less parsimonious¹⁹⁶.

In addition HSA 1, 9 and 16 show a C-banded secondary constriction, as do the homologues GGO 17 and 18, while *Pan* and *Pongo* do not¹¹³. In human populations, chromosome 9 has a large C-band in 5-8.3%, and chromosome 16 has a large C-band

in 5-6.5%¹⁴¹. The size of the chimpanzee band often falls within the human distribution²⁸¹. Secondary constriction C-bands are negatively Q-banded and in both *Homo* and *Gorilla* they hybridize with at least one human satellite DNA. An interstitial C-band region is found in the long arm of PTR 6 and 14 and on PPA 6. Of the African apes, *Gorilla* shows the most variation in the total amount of constitutive heterochromatin²⁶⁸. C-bands appear to vary in size within species, but not in location. Telomeric C-bands may be biochemically different from non-telomeric heterochromatin as telomeric C-bands do not coincide with DNA satellite hybridization sites. Marks has suggested presumed homoplasies between *Homo* and *Gorilla*: the paracentromeric C-band on chromosome 16, that is shared by *Homo* and *Gorilla*, but does not appear on the same arm, and the C-band on the Y chromosome, which is less prominent in *Gorilla*¹⁹⁶. The presumed shared-derived features suggested by Marks are the interstitial C-band on 7q shared by the two species of *Pan*, and the telomeric C-bands shared by *Gorilla* and *Pan*¹⁹⁶. The latter could however be a symplesiomorphy lost in *Homo*, but "gain from many sites is more likely than loss from many sites". If this is a homoplasy, it would require the parallel evolution of these bands. Several non-centromeric C-bands are shared by *Homo*, *Pan* and *Gorilla*. It would appear that no derived C-band features are shared exclusively by *Homo* and *Pan*.

1.3.6.1.3 G-bands (Giemsa bands)

A variety of different staining techniques produce G-bands. The pattern is usually sufficiently specific that individual chromosomes can be distinguished from others of almost identical unstained morphology.

Within the Hylobatidae, not only does the diploid number differ, but the level of karyological difference is such that few secure chromosomal homologies can be found between any two species differing in diploid number. Within the 44 chromosome gibbons, the G-banding patterns are nearly, or absolutely, identical. Three variant forms of chromosome 8 are present, two submetacentric forms (8a, 8b) and a metacentric form (8c). In the species *Hylobates agilis*, *H. mullerii* and *H. moloch*, all three polymorphic forms are found. In *H. lar*, mainly 8b and 8c were found, with 8a present in some populations. Only 8b was found in *H. klossii* and *H. pileatus*, but this may be explained by the small sample size. Hybridization between 44- chromosome gibbons has been recorded in the wild²⁸³.

1.3.6.1.4 G-11 staining

This technique stains heterochromatic regions, and shows larger regions of heterochromatin in *Pan*, *Gorilla* and *Pongo*. Bobrow and Madan suggest that G-11 staining demonstrates satellite III DNA-rich regions³³.

1.3.6.1.5 Q-bands

Q-bands are a fluorescent staining pattern produced by quinacrine dyes. The intensity of the fluorescence can be described as brilliant, intense, medium, pale or negative. *Homo* and the African apes have the only known mammalian chromosomes which display brilliant fluorescence²²³, *Homo* and *Gorilla* being the only apes showing a brilliant fluorescent distal region on the long arm of the Y chromosome. In *Homo*, brilliant fluorescent regions may also be found on the short arm satellited region of the acrocentric chromosomes (13, 14, 15, 21, 22). and the centromeric region of chromosomes 3 and 4. In *Pan troglodytes*, brilliant fluorescence is limited to pairs

14, 15, 17, 22 and 23, while unlike *Homo* and *Gorilla*, the distal arm of the Y chromosome stains pale¹⁵².

HSA	PTR	PPA	GGO
2	12+13	12+13	11+12
3	2	2	2
4	3	3	3
9	11	11	13
13	14	14	14
14	15	15	18
15	16	16	15
18	17	17	16
20	21	21	21
21	22	22	22
22	23	23	23
Y	Y	Y	Y

Table 1.6. Chromosomes showing brilliant fluorescent Q-bands, shown in **bold**²²³.

In *Pan paniscus*, Khudr *et al.* reported brilliant fluorescence on pairs 13, 14, 15, 21 and 22, but no fluorescence on 17 or 23, unlike *Pan troglodytes*¹⁵². Chromosome 23 is acrocentric in *Pan troglodytes*, and a small metacentric in *Pan paniscus*.

Nevertheless both may show brilliant fluorescent regions. In the gorilla, brilliant fluorescent regions may be found in the Y chromosome and in chromosome pairs 3, 12, 13, 14, 15, 16, 22 and 23. The frequency of brilliant Q-band polymorphisms in *Pan* is 8.85 regions per individual, compared to 14.9 in *Gorilla*, whereas in *Homo* the number of polymorphisms is only 2.9-4.6²⁶⁸. Medium intensity bands can be seen at the telomeres of many chromosome arms in the two species of *Pan* and *Gorilla*.

These regions are also positively C-banded and are probably genetically inactive.

Medium intensity telomeric Q-bands are not in found in *Homo* or *Pongo*.

The chimpanzee has variable Q bands on the five acrocentric chromosomes, and on the short arms of chromosomes 20 to 23¹⁷⁹. In *Gorilla*, Q-band polymorphisms are present at the terminal ends of the acrocentric chromosomes, and on the proximal short arm regions of 22 and 23²⁰². The chimpanzee chromosome falls within the range of variation reported for *Homo*²⁸¹.

Homo and *Gorilla* have one homologous pair with brilliant fluorescence at the centromere, but within human populations this is highly variable. *Homo* and *Gorilla* also share a secondary constriction in one homologous pair, and a Y chromosome with a brilliant fluorescent tail. However, the chimpanzee Y may be generally more similar to that of *Homo*, and all sites exhibit a high degree of variability. The chimpanzee level of fluorescence not only falls within the human and gorilla range, but if *Pongo* has these sites, then *Pan* may have lost them uniquely, and parsimony would suggest that the loss took place after the divergence of *Pan* from the common ancestor.

1.3.6.1.6 R-bands (Reverse bands)

These are produced by a staining technique that produces a banding pattern more or less the reciprocal of Q-bands. The bands are usually positive at the telomeres, enabling precise measurement of chromosome length and centromere position relative to the telomere.

1.3.6.1.7 T-bands

T-bands are produced by heat denaturation, followed by decolouration and staining with the fluorescent dye acridine orange⁷⁸. T-bands represent a fraction of the R-bands. The regions located by this technique are situated at the telomeres, and some other bands, on human chromosomes 11, 19 and 22. In African apes, the distribution of T-bands is very similar to that in *Homo*, whereas in *Pongo* the distribution does not quite correspond⁷⁸.

1.3.6.1.8 Summary of chromosomal banding

The pattern shown by chromosome banding does not directly reveal anything about actual gene expression, but does allow the identification of interspecific homologies, many of which have since been confirmed by gene assignment. Not all loci have maintained stable conservative relationships among banding patterns, but on the whole, identical structural gene loci are contained in the chromosomes of different species with a similar morphology and banding pattern²⁶⁸. This does not apply to highly repetitive DNA in *Homo* and the homologous sequences in the great apes¹¹³. Chromosome bands are simply areas that are more or less resistant to extraction, in other words areas of more or less tightly bound protein and DNA complexes; heterochromatin represents the areas most resistant to denaturation²⁸¹.

Variations in the size, intensity and position of Q and C bands seem to be almost continuous, and the African apes may be as variable as *Homo*²⁸¹. Analysis of these bands assumes that despite their high degree of intra-specific variability, these processes will locate the same chromosome in all the members of a species⁷⁸.

The similarity between the banding patterns of the chromosomes of *Gorilla* and *Pan troglodytes* is quite high, and all differences can be explained by simple structural rearrangements, such as pericentric inversions. No less than eight chromosomal rearrangements have occurred⁸⁰.

When gibbons are compared with *Homo sapiens*, no more than 5-10% of the chromosome material is homologous by banding. The clearest homology is between the X chromosomes where no differences can be seen²⁸².

A limitation of using whole chromosome probes is that they do not allow the mapping of intrachromosomal arrangements. There is no guarantee that the chromosomal regions between the markers are actually homologous²⁸⁴.

A recent study of fragile chromosomal sites, that are especially prone to breakage under certain culture conditions, used the close homology of chromosome banding in *Homo* and the great apes to compare locations between species²⁷⁸. The orangutan showed the least number of aberrations compared to the other three species, but this was based on only one individual and may not be characteristic of the species. The gorilla had the highest breakage rate of the four species, and this value was the mean of three different individuals. Seventeen sites were common to all four species, and ten defined the African ape-*Homo* clade, being absent from *Pongo*. The African apes expressed three sites not found in *Homo* and *Pongo*. One site was found linking *Homo* and *Gorilla*, and one site linking *Pan* and *Pongo*. In addition there were several species-specific fragile sites. Many fragile sites correspond to evolutionarily significant chromosome breakpoints, and Smeets and van de Klundert concluded that fragile sites have probably directed chromosomal changes in some way²⁷⁸.

Of these, *Homo* and *Gorilla* share four sites exclusive of *Pan*, *Gorilla* and *Pan* share four sites exclusive of *Homo*, and *Homo* and *Pan* share only one site exclusive of *Gorilla*.

	GGO	PTR	PPY
HSA	12 (4)	8 (1)	3 (0)
GGO	-	10 (4)	3 (1)
PTR	-	-	1 (0)

Table 1.7. Total number of chromosomal sites at which an evolutionary change towards the human karyotype occurred and at which a fragile site was found, in pairs of species. Numbers in parentheses indicate the number of these sites which are shared exclusively by these species.

Adapted from ²⁷⁸.

Simple enumeration of chromosomal differences is not a reliable method of measuring phylogenetic difference^{193, 281}. This is because karyological changes are subject to varying evolutionary rates.

A cladistic analysis treating discrete chromosomal data as morphological character states supports a *Pan-Homo* clade³⁵.

1.3.7 DNA variation

1.3.7.1 Satellite DNA

Satellite DNA is the fraction of DNA with a sufficiently different buoyant density to enable it to be distinguished on a density gradient. It contains non-functional repetitious DNA sequences.

The centromeric region of human chromosomes contains arrays of tandemly-repeated DNA sequences, called alpha satellite DNA, or alphoid DNA. Within the Hominoidea, the highest reported similarity for these regions so far is 91%²², much

lower than would be expected for selectively neutral sequences, since no function has so far been suggested for satellite DNA. The low similarity between such closely-related species suggests that the alphoid DNA is rapidly changing²⁴³. If this is so, sequence comparisons are of limited value due to the obvious difficulties in identifying orthologous DNA segments²⁴.

Satellite DNAs evolve rapidly in comparison with DNA with transcriptional functions. Satellites I to III have been mapped by *in situ* hybridization.

The gorilla is the only species of great ape with homologous sequences to all of the 4 major human satellite DNAs¹¹³. These repetitive sequences are found on the centromeres of the acrocentric chromosomes, the secondary constriction regions of chromosomes 17 and 18, and on the long arm of the Y chromosome.

In humans, satellite DNA I is found on the fluorescent distal region of the human Y chromosome, and on the centromeric heterochromatin of the autosomes. Satellite DNA II is mainly on human chromosomes 1 and 16, with a lesser region on 9 and minor regions on chromosomes 13 to 21. Satellite DNA III is mostly found on human chromosome 9 and minor regions on chromosomes 13 to 21³⁶.

1.3.7.2 Single-copy DNA hybridization

This technique measures the temperature at which hybridized single copy DNA from two different species separates in comparison to DNA from the same species^{36, 274}.

The structure of DNA may be melted by heating in solution. A melting curve can be plotted by spectrophotometric methods that measure the relationship between the temperature increase, and the increase in the absorbance of light at 260nm. The temperature at the midpoint of the curve is T_m , the melting temperature.

Single strands of DNA can be reassociated with the DNA, or RNA, strands of other species, and the melting temperature of the hybrid established. If the base pair sequence of the strands is not identical, the T_m is decreased compared to the T_m of a single species pairing. The amount of temperature decrease therefore provides a method for comparing the overall changes in base sequence that have occurred during molecular evolution, individual nucleotide substitutions appearing the same whether they are homologous or homoplastic, with no way of distinguishing conclusively between them. Complexity and abundance of characters has been argued to justify DNA-DNA hybridization; while single base changes can be the result of homoplasy, the similarity of a large group of characters would not be easily reproduced²⁷³. Britten has criticized the use of limited data sets in DNA hybridization³⁸.

Hoyer *et al.* were unable to resolve the relationships between the hominoid species using their thermostability data¹³⁵. They suggested a closer relationship between *Homo* and *Pan*, and also that *Gorilla* DNA is closer to that of *Pongo*.

Stanyon *et al.* have used "chromosome painting" to demonstrate that HSA 17 is structurally intact in the *Pan* and *Pongo* homologues, but not in the *Gorilla* homologue²⁸⁴. Chromosome painting involves the use of a large portion of unique sequence DNA of a given chromosome as a probe to another species' chromosome. In *Gorilla*, a reciprocal translocation has placed part of the homologous GGO 19 onto the short arm of GGO 5.

Chromosome painting was used by Verma and Luke to isolate the ABL protooncogene on HSA 9q34³⁰⁸. Similar gene sequences are found on PTR 11p24 which may indicate that the evolution of HSA 9 is more complicated than previously

suggested, however in *Gorilla* and *Pongo* the equivalent sequences are apparently located as expected at GGO 13q34 and PPY 13q26, putative telomeric positions with no discernible differences.

1.3.7.3 DNA content

Genome size, the total DNA content of a nucleus, is a species-specific constant.

Pellicciari *et al.* measured nuclear DNA content in primates^{224, 225}. The table below shows the results of the two studies.

From these results it can be seen that the Hylobatidae have a lower DNA content than the great apes and *Homo*, and that the great apes have a higher DNA content than *Homo*²²⁴. The content sequence for these values is; *Homo* < *Gorilla* < *Pan* < *Pongo*. This sequence was also found by Manfredi-Romanini¹⁹².

In the more recent study²²⁵, the siamang was found to have an even larger genome size than the great apes, whereas the 44-chromosome gibbons had lower amounts of DNA than *Homo*. A hybrid of *S. syndactylus* and *H. muelleri* had a diploid number of 47, and an amount of DNA equal to the sum of the haploid contents of the parents. Genome size differences in the lesser apes were found to be almost entirely attributable to differences in the amount of C-heterochromatin. The size of the siamang genome is about 15% larger than that of *H. muelleri*, and the siamang has 16-18% C-heterochromatin, compared with 6-8% C-heterochromatin in *H. muelleri*. The situation in the great apes may be more complicated, since the genome size differs despite relatively similar banding patterns. *Pan* and *Gorilla* have additional terminal and interstitial C-bands on some chromosomes which may partially explain the higher genome size. However the orangutan has the highest genome size despite

lacking the additional C-bands²²⁴. Other genome fractions may have to be considered to fully explain the genome size differences among the Hominoidea.

	DNA pg	DNA % <i>Homo</i>
<i>Homo sapiens</i>	7.30	100
<i>Pan troglodytes</i>	8.03	110
	7.57	104
<i>Gorilla gorilla</i>	7.45	102
<i>Pongo pygmaeus</i>	8.56	117
	7.63	105
<i>Hylobates agilis</i>	5.78	79
	7.25	99
<i>Hylobates klossi</i>	6.81	93
<i>Hylobates lar</i>	6.79	93
<i>Hylobates moloch</i>	6.75	92
<i>Hylobates muelleri</i>	6.86	94
<i>Symphalangus syndactylus</i>	6.22	85
	7.87	108
Hybrid (<i>H.muelleri</i> x <i>S.syndactylus</i>)	7.29	100

Table 1.8. DNA content in hominoids. Numbers in **bold** are from²²⁵, except that for *Homo* which is identical in both studies^{224, 225}.

1.3.7.4 DNA restriction endonuclease mapping

This method estimates the frequency and position of defined DNA sequence motifs. Crovella *et al.* have confirmed that highly-repeated DNA sequences are conserved within species, and that restriction data are a valid technique for phylogenetic analysis, although more hominoid samples need to be analyzed⁶³.

1.3.7.5 DNA sequencing

DNA sequencing determines the composition and order of nucleotides in a defined region of DNA. In recent times it has become relatively easy to obtain large quantities of DNA sequence data. During the period where the classical fossil record indicates that extensive speciation occurred in the Primates it appears that DNA was added to the presumptive human genome at a much faster rate than during other periods for which data are available, and the rate of nucleotide sequence divergence was also much higher relative to other periods¹⁵⁹. The rate of mixing of genetic material to provide new genetic combinations should also be generation-time dependant.

DNA sequences can be categorized with regard to their structural and functional properties. Single copy sequences are complex sequences represented just once in each haploid genome, and many of them are genes that code for functional polypeptides. Moderately repeated sequences are simpler sequences of variable length of up to a few thousand repeats, generally non-coding and scattered widely through the chromosomes. Functional repeated sequences, or multigene families, are complex sequences that code for specific functions, and are represented by several hundred to a few thousand repeats. Highly repeated sequences are short, highly variable non-coding sequences, usually represented by several thousand to several million repeats per haploid genome. These sequences are mostly clustered into large heterochromatic blocks which are identified as Giemsa bands (see 1.3.6.1.3). In addition, centromeric and telomeric sequences can be identified¹⁸⁶.

1.3.7.5.1 Nuclear DNA sequencing

The DRB1*10 allelic lineage was thought to be human-specific, but Kupfermann *et al.* have found it in *Gorilla*¹⁶⁴ and Mayer *et al.* have found the lineage in *Pan*²⁰¹. The related DRBZ allele lineage is present in *Gorilla*¹⁶⁴ and *Pan*^{151, 201}, but is thought to be absent from *Homo*, while the DRB6 gene has been found in all great apes tested, but only 26% of tested humans⁵⁷. The PLA2L gene, mapped to chromosome 8, is conserved in African apes and *Homo* to the exclusion of *Pongo*¹⁶³.

The nucleotide sequences for the red and green opsin genes are encoded on the long arm of the X chromosome, which appears to be highly-conserved among primates. The red and green opsin genes are equally conserved among the great apes, although the pigment coding sequences of *Gorilla* and *Pongo* differ more from the human sequences than do those of *Pan*. The *Gorilla* and *Pongo* sequences are as different from each other as they are from the *Pan-Homo* clade. As the amino acid residues known to account for spectral differences between red and green pigments²¹³ are completely conserved among the great apes and humans, it is thought that the difference in absorption spectra would be less than 2 nanometres throughout the hominoids⁶⁹.

Homologues of the MN blood group antigens are encoded by the glycoporphin A gene family (GPA), and have been studied in African apes and *Homo*. *Gorilla* GPA and GPB/E genes were unique, but *Gorilla* GPA and GPB were more similar to those of *Pan* than *Homo*, although a transspecies allele was identified in *Gorilla* that gave rise to the Henshaw (He)-like antigen similar to that found in *Homo*³²³.

Chimpanzee homologues to human HLA-A, B and C alleles have revealed high similarity, but no allele is identical between the two species^{166, 200}. The gorilla also has homologues to HLA-A, B and C, thus the basic arrangement of the HLA alleles pre-dates the divergence of *Gorilla*, *Pan* and *Homo*. The chimpanzee HLA-A-like sequences have a range of nucleotide differences within the human range. This is true for some but not all of the gorilla A-like sequences¹⁶⁷.

In humans, HLA-A alleles can be divided into five families, which have evolved from two ancestral families, one leading to HLA-A3 and A9, and the other to HLA-A2, A10 and A19. In *Pan*, all the A-like alleles show a close relationship with HLA-A3, whereas in *Gorilla*, the A-like alleles are closely related to the HLA-A10 and A19 families. It is suggested that the *Gorilla* and *Pan* alleles evolved from two distinct lineages, both of which are represented in *Homo*. This suggests that new species can inherit multiple alleles from the common ancestor and that for this locus, *Homo* is more like similar to *Pan* and *Gorilla* than *Pan* and *Gorilla* are to each other. Results from the involucrin gene⁷⁴ appear to be an exception to the overall molecular trend for a *Pan-Homo* clade, judging by the presence of four repeat units and seven marker nucleotides uniquely shared by *Pan* and *Gorilla*, although Bailey *et al.* suggest that three of the seven marker nucleotides should not be included, and that a single deletion in the human lineage could account for the loss of the four repeat units²¹. Ruvolo *et al.* state that the involucrin gene has DNA repeats²⁴³. This is problematic because, firstly, involucrin repeats are hard to align; secondly, the repeats are subject to DNA insertion/deletion and thirdly, gorillas are polymorphic for the reported synapomorphies linking *Pan* and *Gorilla*. The purported synapomorphies for *Pan* and *Gorilla* are either true synapomorphies, homoplasies, or

due to a discrepancy between species and allele branching patterns. This situation could have arisen if a polymorphism persisted through the *Homo-Gorilla-Pan* line as is shown by the HLA-A locus¹⁶⁷, in the case of the involucrin gene leading to one allele in *Gorilla* and *Pan*, and the other in the human genome. Lineage sorting for ancestral polymorphisms may produce a gene tree which is not congruent with the true species tree²⁰⁷. Oetting *et al.* also show a higher similarity between *Homo* and *Gorilla* for the tyrosinase gene, and *Homo* and *Gorilla* share a tyrosine-related gene locus²¹⁵. The gorilla HLA-B homologues differ from their human counterparts by a few nucleotide substitutions, all of which produce amino acid substitutions and are almost certainly the result of selection for differences in antigen presentation¹⁶⁷.

There are sequence similarities between the HLA-B alleles of African apes and *Homo*. The human HLA-C alleles and the gorilla homologues each divide into two groups, a feature that cannot be assessed in *Pan* as only one chimpanzee C-like allele has been isolated¹⁶⁷.

In the middle of the major histocompatibility complex are the C4 and CYP21 genes that appear to be unrelated, but are linked so that the two genes are duplicated together. Lack of a functional C4 gene leads to a severe autoimmune disorder, while lack of a functional CYP21 gene leads to a fatal adrenal hyperplasia¹³⁴. Single C4-CYP21 haplotypes have been reported in humans, also haplotypes with two C4 and two CYP21 genes. The double haplotype is present in *Pan*¹⁴⁷ and *Gorilla*¹⁴⁶. Triple and quadruple haplotypes have been found in *Homo* and *Pongo*^{146, 327}.

The major human red blood cell membrane sialoglycoproteins A (GPA) and B (GPB) express blood group antigens, and have been demonstrated to be present in both species of *Pan* and in *Gorilla*²³⁰. An additional human sialoglycoprotein E (GPE)

gene, that has not been demonstrated to have a protein product, was also isolated in *Pan*¹⁸². Five nucleotide positions in the GPA gene and one position in the GPE gene support the *Pan-Homo* clade²³¹.

Molecular divergence rates calculated using DNA-DNA hybridization dates²⁷³ show that the GPE region is evolving more rapidly than the GPA and GPB regions, which suggests that the GPE gene is non- or marginally functional²³¹.

Sequencing of the Xba1 DNA repeat element of the α -fetoprotein gene showed that compared with the human sequence, *Pan* differed by four, *Gorilla* by two and *Pongo* by nine nucleotide positions from a total of 303 base pairs²⁰³. This pattern was not shown by the CD8B1 gene⁷⁰, where of 119 nucleotides, the chimpanzee sequence differed from the human sequence by two bases, *Gorilla* by three bases and *Pongo* by three bases. For the CD8B 2 gene, the sequences for African apes and *Homo* were identical. The CD8B 1 and 2 genes are found on HSA 2, and further work may help to determine whether these genes are found on the great ape equivalents.

Early studies on the α and β -globin gene regions revealed no differences in the location of 14 specific Alu elements between African apes and *Homo*^{160, 161, 249}. More recently the β -globin gene cluster has strengthened the evidence for the *Homo*-common chimpanzee clade²¹, to the exclusion of the pygmy chimpanzee.

In the α -globin gene, two sites support a conversion in the *Pan-Homo* common ancestor. At the one site that opposes a chimpanzee α -globin gene conversion, the chimpanzee α -1-globin gene retains the ancestral nucleotide (C), but the chimpanzee α -2-globin gene and both human α -globin genes have a G nucleotide. This suggests

that a C to G mutation occurred in the α -2-globin gene of the ancestral *Pan-Homo* lineage and that the α -2-globin sequence replaced the α -1-globin sequence at the α -1-globin locus in the gene within the human lineage²¹.

The monophyly of *Pan* and *Homo* is supported by the 28S ribosomal genes¹⁰⁵ and an immunoglobulin pseudogene³⁰⁶. In the α -galactosyltransferase gene, the *Pan-Homo* clade was supported to the exclusion of all other possibilities⁹⁸. In a study of the δ and β -globin genes, the *Pan-Homo* clade was favoured²²⁶, when combined with results from the another globin region, the *Pan-Homo* clade was supported at a significant level. The γ -globin gene region supports a *Pan-Homo* clade, the percent divergences being *Homo-Pan* 1.61, *Homo-Gorilla* 1.72, *Homo-Pongo* 3.39, *Pan-Gorilla* 1.84, *Pan-Pongo* 3.52 and *Gorilla-Pongo* 3.47²⁰⁶. No hominoid has a functional urate oxidase gene. Three mutations were shared by *Homo* and *Pan*, one of which was found in *Pongo* while none of the three mutations were present in the gibbon; instead a thirteen base pair deletion was identified. This suggests that the loss of urate oxidase has arisen by two independent events post-dating the divergence of the gibbon lineage³²². Yeldandi *et al.* found two nonsense mutations in the coding region of the same gene shared by all great apes to the exclusion of Old World and New World monkeys³²⁵, but gave no data for *Hylobates*. The insertion of a particular PV Alu repeat, consisting of 500 to 2000 members, in a particular orientation, and at a particular locus, is essentially a unique evolutionary event, as there is significantly less than one chance in many billions that such an insertion would independently be duplicated in two separate lineages¹⁷⁰. Of the two known gorilla PV Alu repeats, one is *Gorilla*-specific, and the other is the only known shared PV Alu repeat between the African ape-*Homo* clade. There is an additional

member of the PV subfamily specific to *Pan troglodytes*, whereas others are present in both species of chimpanzee¹⁶⁹, confirming the relatively recent and independent expansion of this subfamily in the chimpanzee lineage. The existence of lineage-specific Alu repeats is a major sequence difference between *Homo* and *Pan*.

Protamine P1 genes from African apes and *Homo* are very similar, with fewer amino acid and nucleotide differences between *Homo* and *Gorilla* than between *Homo* and *Pan*²³². This may be related to the fact that protamine P1 is expressed in germ line rather than in somatic cells.

Much previous work with extension sequences in the primate globin clusters has provided very strong evidence for an African ape-*Homo* clade²²⁶ and narrowly excludes *Gorilla* from a *Pan-Homo* clade^{110, 226}.

Retief and Dixon investigated pro-protamine P2 genes, and showed a slightly closer relationship between *Homo* and *Gorilla* than between *Homo* and *Pan*²³².

	HSA	PTR	PPA	GGO	PPY	HYL
HSA	-	24	15	19	33	33
PTR	3.32	-	14	17	26	30
PPA	2.07	1.9 4	-	10	32	32
GGO	2.99	2.6 7	1.57	-	32	31
PPY	4.74	3.7 4	4.60	5.25	-	35
HYL	4.58	4.2 7	4.56	5.04	5.04	-

Table 1.9. Above the diagonal, total number of nucleotide differences in the pro-protamine 2 gene; below the diagonal, differences per 100 base pairs. From ²³².

The Y chromosome of the great apes has a highly-conserved region including the pseudoautosomal region and the testis-determining region. The rest of the Y chromosome appears to have undergone several rearrangements in the different great

apes^{101, 102, 299}. A Y-chromosomal DNA fragment from the long arm (Yq11) of HSA Y is conserved in male *Pan*, but absent from male *Gorilla* and male *Pongo*²²⁹. The conservation of the human Yq sequences on great ape Y chromosomes however indicates a greater degree of stability in this region of the Y than has been previously described. This region of the Y does not undergo meiotic recombination and the sequences do not appear to encode genes for which positive selection might occur⁴.

HSA			PTR		GGO		PPY	
Y	X	X/A	Y	X/A	Y	X/A	Y	X/A
MIA	MIA		+	+	-	-	-	-
p69/6			+		+		-	+
49f		49f	+	-	+	+	+	-

Table 1.10. Conserved human Yq chromosome sequence differences in the hominoids. X/XA = X chromosome or autosome. Adapted from ⁴.

Recently, Ruvolo has used fourteen independent data sets of DNA sequence data showing phylogenetic resolution among hominoids to give the majority opinion (11/14) supporting a *Homo-Pan* clade, with two supporting a *Pan-Gorilla* clade and one supporting a *Pan-Gorilla* clade; on this basis, she rejected a trichotomous speciation event²⁴⁰. Maximum likelihood estimates for the time between successive divergences are in the range 0.3 to 2.8 million years, based on estimates of population size and generation time. She uses the multiple-locus test³²¹, which favours the *Homo-Pan* clade, to imply that no further DNA sequence data needs to be generated for hominoid phylogenetic resolution, particularly with the DNA-hybridization evidence of Caccone and Powell also supporting *Homo-Pan*³⁶: the problem of hominoid phylogeny can be considered solved in her opinion.

Mitochondrial DNA sequencing has indicated a relatively large genetic distance between *Pan troglodytes verus* and the other two chimpanzee subspecies²⁰⁹, implying that *Pan t. verus* should be given full species rank. Within *P. t. schweinfurthii*, mitochondrial genetic variation is lower than within *P. t. verus* and *P. paniscus*, higher than within *P. t. troglodytes*, and similar to levels observed in *Homo sapiens*, with genetic similarity decreasing with geographic distance. Diversity within *P. paniscus* and *P. t. verus* exceeds that within *Homo*, despite small sample sizes^{103, 104}.

The cytochrome B gene sequenced in the gibbons has supported monophyly of the *concolor* gibbons, suggested affinities between *H. lar* and *H. klossi*, and between *H. lar* and *H. agilis unko*¹⁰⁰, and has also been used to distinguish between the three species of *Hylobates (Nomascus)*¹⁰⁰.

Mitochondrial DNA sequences for the cytochrome oxidase subunit II gene show a relatively long time between divergence events in the hominoid trichotomy, similar to that seen with DNA hybridization results²⁴². *Homo* and *Pan* show 9.6% difference, compared to 13.1% for *Homo-Gorilla* and 12.1% for *Pan-Gorilla*. By a maximum likelihood method, the *Homo/Pan* grouping is significantly better than alternative trees.

The monophyly of *Pan* and *Homo* is supported by mitochondrial DNA^{126, 133, 242}, 28S ribosomal genes¹⁰⁵ and an immunoglobulin pseudogene³⁰⁶. A 4.8 kb mitochondrial fragment showed the *Pan-Homo* clade to be 26+/-0.4 times more parsimonious than a *Pan-Gorilla* clade¹³³. Similar conclusions have been drawn by others^{36, 105, 110, 143, 160, 161, 162, 273, 275, 306}. Mitochondrial variability is much higher than DNA variability, for example *Gorilla* and *Pongo* intra-species variability exceeds that between the different

species of chimpanzee, and establishment of additional *Gorilla* and *Pongo* species may even be warranted²⁰⁸. Sequencing of the mitochondrial D-loop found that differences between western lowland and eastern lowland or mountain gorillas (~20%) were greater than those between *Pan paniscus* and *Pan troglodytes* (~17%). The eastern lowland and mountain gorillas form distinct but related clades separated by about 6% difference. However, sites within this region appear to be evolving at unequal and unpredictable rates in higher primates^{158, 317}. Foran *et al.* described a conserved termination-associated site present in *Pan* and *Homo*⁹³, but partially deleted and possibly relocated in *Gorilla*⁹⁹.

1.3.7.5.3

Problems with DNA sequence data

The number of nucleotide differences between two species is an underestimate of the total number of substitution events that have occurred, and this results in an underestimation of the amount of difference between the two species. The reason for this is that a site can have more than one substitution. This is a particular problem because the nucleotide base substituted is not random. Generally, adenine is replaced by guanine, and thymine is replaced by cytosine, and *vice versa*. These substitutions are called transitions and account for over 90 percent of all substitutions. Other types of base substitution are called transversions (e.g. guanine to adenine) and are relatively rare, accounting for about 10 percent of all substitutions. The problem of multiple substitution increases with the length of time since divergence. Lineages with a long period of evolution will have a larger proportion of multiple substitutions at the same site than a lineage with a shorter period of independent evolution. It is therefore important to calibrate for back-mutation. It is unlikely that two transversions would occur at the same site, so the number of transversions is generally assumed to represent the number of substitution events. The proportion of transitions that are the result of multiple

substitution can be estimated by calculating the transversion: transition ratio between the species, and then correcting for the number of observed substitutions²²⁷.

Wise *et al.* have found that humans have substantially lower levels of mtDNA diversity than *Pan*, but substantially higher levels of heterozygosity in both protein-coding and short tandem repeat loci nuclear genome³¹⁹. It would appear that humans have an unusual mitochondrial/nuclear diversity, since the ratio in *Pan* is similar to lower catarrhines. This cannot be explained by differences in mutation rate, but may result from one or more factors, such as, a difference in the extent of sex-ratio disparity, greater effect of population subdivision on mitochondrial rather than nuclear genomes, difference in levels of migration between subpopulations and selection to increase nuclear genome variation with or without selection to reduce variation in the mitochondrial genome³¹⁹.

Sampling error is a major problem with DNA studies. Gagneux *et al.* identified sampling problems using plucked hair from individuals, resulting in gene amplification errors in 31% of cases, and also from contamination and labelling errors⁹⁷. Plucked hair from dead individuals gave more consistent results (error rate <0.01%), and the single hair errors could be reduced to below 0.05% by using three separate amplifications from a single hair, or by pooling hair samples from one individual.

Mitochondrial genomic region	Shared (kb)	(H,C)	(C,G)	(H,G)
12S rRNA ¹³²	0.9	5	5	5
0.9kb fragment ¹²⁶	0.9	10	10	4
4.8kb fragment ¹³³	4.8	57	33	28
Total	6.6	72	48	37
Nuclear genomic region	Shared (kb)	(H,C)	(C,G)	(H,G)
Immunoglobulin C ₃ pseudogene ³⁰⁶	2.4	3	0	1
Involutrin ^{72, 73, 74}	1.2	0	5	0
28S rRNA, ITS1 ¹⁰⁵	3.5	13	4	2
X,Y, pseudoboundary ⁸²	1.2	3	2	2
1,3GT ⁹⁸	0.4	2	0	0
Immunoglobulin C1 ¹⁴⁸	2.6	4	3	2
δ - β intergenic ²²⁶	3.9	6	2	2
β ²²⁶	1.3	1	1	1
ϵ ²⁰	1.7	1	1	0
Nonconverted χ ²¹	7.1	15	4	1
jh ²¹	10.1	10	3	3
CD8B1 exon 9 ⁷⁰	0.1	1	2	0
XbaI DNA element of α -fetoprotein ²⁰³	0.3	1	1	3
Total	35.8	60	28	17

Table 1.11. Numbers of putative synapomorphic nucleotide sequence positions supporting alternative *Homo-Pan-Gorilla* pairings. Adapted from¹¹².

1.3.8 Conflict between nuclear DNA and mtDNA?

The molecular data imply that the genetic distance between humans and chimps is 25 to 60 times greater than that between any two major human geographical subdivisions such as Europeans, Africans or Asians⁷⁹. Nevertheless the genetic distance is quite within the range found in sibling species.

There is more interspecific variation for mtDNA sequence data than for nuclear DNA sequence data, and the mtDNA sequence differences are fewer between *Homo* and *Pan* than between either *Homo* and *Gorilla*, or *Pan* and *Gorilla*. Maximum parsimony analysis of the mtDNA data favours a *Pan-Homo* clade 26+/-9.4 times more than a *Pan-Gorilla* clade. Goodman *et al.* state that the number of positions supporting *Pan-Homo*, is 1.5 times greater than the number supporting *Pan-Gorilla* and 1.9 times greater than the number of positions supporting *Gorilla-Homo*. With nuclear DNA, the number of positions supporting *Pan-Homo* is 2.3 times greater than the number supporting *Pan-Gorilla*, and 4.1 times greater than the number supporting *Gorilla-Homo*¹¹². The disparity between the nuclear and mitochondrial DNA may be due to a lower level of homoplasmy in nuclear DNA than in mtDNA. The probability of conflict between nuclear DNA and mtDNA is lower if hominoid females transfer between groups.

Inclusion of multiple individuals per species does not produce a result different from that based on single individuals for the cytochrome oxidase II gene^{242, 243}.

Molecular evolution creates both newly derived substitutions and false similarities (homoplasmy). However some types of DNA regions are preferentially subject to homoplasmy-inducing processes such as sporadically occurring concerted evolution and DNA insertion/deletion. This added level of homoplastic noise can make DNA regions with repeats less reliable in phylogenetic reconstruction than those without repeats²⁴⁰.

1.4 A REVIEW OF THE STUDY OF APE ANATOMY

In the past, the anatomical study of apes, and indeed of exotic animals in general, was almost entirely limited to morphological and metrical studies of hard tissue evidence. The difficulties of preserving soft tissue under field conditions for long

voyages meant that many of the ape specimens that arrived in Europe had been skeletalized either immediately after death, or en route. As a result, for much of the last three hundred years, the study of the anatomy of apes has been skewed towards skeletal measurements and morphology.

Scientific descriptions of live specimens of orangutan and chimpanzee first appeared in the mid-seventeenth century with Bontius³⁴ and Tulp³⁰², but confusion between orangutans and chimpanzees was rife until the early nineteenth century³²⁶. Scientific description of the gorilla was established in the mid-nineteenth century by Savage and Wyman²⁴⁸, arriving as live specimens in Europe in the decades which followed, although often misclassified as chimpanzees. The majority of these animals captured in the wild to be transported to Europe and America died in transit, or after very short periods in captivity³²⁶.

Since this time, with the advent of flight reducing the time wild-caught specimens spend in transit, and with the captive breeding programmes of zoological gardens and experimental colonies, there is now more ready access to the soft tissue anatomy of hominoids than ever before, although some species, such as *Pan*, are better represented than others. However, this vast reservoir of potential phylogenetically and functionally useful information remains sadly under investigated. Dry bones and teeth provide much less inconvenience to their investigator than "wet" anatomy.

In addition, individual authors tend to specialise in a particular system, region or feature, which although not in itself a problem, means that as yet no-one has compiled a comprehensive review of the known anatomy of apes: in essence, an anatomical atlas for the extant Hominoidea which could be read in conjunction with one of the many such books which exist for *Homo sapiens* (such as³¹⁰). Swindler

and Wood have produced an excellent comparative anatomical atlas²⁸⁸, but it deals only with humans and chimpanzees (and the baboon), and is limited in the soft tissue anatomy which it covers.

The following sections summarise the present literature specifically devoted to the comparative anatomy of the hominoids, with special reference to the inferred phylogenetic relationships between the members of this primate group.

1.4.1 Comparative anatomy

For any species of hominoid, some characters are likely to represent adaptations present in the common ancestor of the Hominoidea, and some of these characters in turn are likely to have been present in the common ancestor of all Old World primates. Distinguishing new characters from ancestral ones is the basis for refining classification.

Classical comparative anatomy involves a straightforward comparison of form. However, only those features that are subject to selection pressures are significant in adaptation. Among the numerous differences between an ancestral and a descendant species, some will certainly be unrelated, or indifferent, to the new functional requirements of the novel species. Many morphological features, although fundamentally important, may be developmental consequences of other features that are under direct genetic control, such as an increase or decrease in growth rate. In addition, it is difficult, if not impossible, to demonstrate that any given condition is, or is not, related in some way to the functional requirements of the animal in question.

Studies of comparative anatomy can be divided into two main groups; metrical data and description of morphology. Metrical data are often converted into indices.

Morphological studies suffer from the effect of intentional, or unintentional, subjectivity. For example, the lateral epicondyle of the humerus has been described by McHenry and Corruccini as "not prominent" in hominoids¹⁸⁷, but Senut finds the same structure to "project markedly" in both species of *Pan* and in *Pongo*²⁶⁶. Another major problem with all anatomical studies is that of intraspecific variation. For example, the presence of a supratrochlear foramen is variably given as between 4% and 35% in *Homo*, 26% to 33% in *Pan*, 35% to 64% in *Gorilla*, 74% to 84% in *Pongo* and 0% to 3% in hylobatids²⁵⁵.

1.4.1.1 Features defining Hominoidea

Hominoids are distinguished as a group by a number of features^{1, 8, 52, 58, 91, 118, 187, 247, 309}.

Dental: Broad spatulate central incisors; low-crowned premolars with less honing on P₃; relatively broad molars with rounded cusps.

Soft tissue: Presence of a vermiform appendix; interstitial placental implantation; sperm mitochondria with few gyres.

Skeletal: Increased potential for raising the arm above the head, for extending the forelimb at the elbow joint, and for rotation of the forelimb; greater flexibility of the wrist; opposable thumb; distal migration of the pisiform and absence of the pisostyloid articulation; more erect posture during feeding with broadening of thorax and loss of tail; craniocaudally short vertebral bodies and elongated and angled sacrum; and greater mobility at the hip and ankle joints.

1.4.1.2 Features defining great apes and *Homo*

Within the Hominoidea, the great apes and *Homo* can be distinguished from the hylobatids (*Hylobates* and *Symphalangus*) by a number of features^{8, 118, 174}:

Dental: Shortened, but robust canines; great increase in the size of incisors relative to molars; robust and enlarged premolars relative to molars; reduced upper premolar heteromorphy; reduced molar cingula.

Soft tissue: Reduced body hair; loss of ischial callosities.

Skeletal: Enlarged maxillary sinuses; orbits higher than broad; increased alveolar prognathism with elongated premaxilla; facial lengthening with elongation of the nasal bones and narrow incisive foramen; robust mandible with large inferior transverse sulcus; carpal reorganization; saddle-shaped first carpometacarpal joint; and distal humerus with deep sulci either side of lateral trochlear keel.

1.4.1.3 Features defining African apes and *Homo*

Morphological similarities between *Homo* and African apes to the exclusion of *Pongo* include^{6, 8, 15, 29, 64, 247, 291}:

Soft tissue: Subdivision of the prostate; abundant apocrine glands; large axillary organ; low proportion (3-21%) of type 1 aorta; large uterus.

Skeletal: Presence of a frontal sinus; prominent continuous bar-like supraorbital torus; developed postorbital sulcus; greater middle ear depth; elongated nasoalveolar clivus of the premaxilla with narrowing of the incisive foramen; increased klinorhynchyⁱ; presence of a mastoid process; straight humeral shaft;

ⁱ Klinorhynchy is a condition in which there is a deep foreshortened facial skeleton which bends downward with respect to the cranial base.

fusion of os centrale to scaphoid in the wrist; enlarged ulna head with dual semicircular articulations; palmarly directed pisiform; robust metatarsal shaft; large middle phalanges; development of a lumbar curvature.

1.4.1.3.1 Relationships between *Homo* and the African apes

As discussed in 1.3, the consensus of the molecular data favours a *Pan-Homo* clade above any other combination.

Traditionally, and in conflict with the bulk of the molecular evidence, morphologists have favoured a sister-group relationship between *Pan* and *Gorilla*, primarily on the basis of morphological adaptations for knuckle-walking in the forelimb^{6, 7, 9, 52, 59, 115, 136, 144, 149, 150, 165, 173, 188, 199, 219, 220, 247, 263, 287, 304, 305, 311, 312}, but also based on cranial variables such as occipital condyle position², reduced precondylar basicranial length¹⁷ and incus size²⁷⁷. In addition, the intermembral index cannot distinguish between the two genera of African apes²⁵⁵. However, recently it has been suggested that the pattern of knuckle-walking differs biomechanically between the two African apes¹⁴⁰. The knuckle-walking characters are strongly interdependent, and vary within the African apes in their degree of development, based on body size and biomechanics^{138, 139}.

Support for a *Homo-Pan* clade from morphology has recently been provided by Shoshani *et al.* on the basis of a variety of anatomical evidence²⁷². Other studies supporting this clade include studies of the biometry of the forelimb^{60, 61, 127, 256}, the transverse and mid-sagittal robusticity of the lumbar vertebral bodies²³⁶, percentage of true ribs³⁰⁰, position of the occipital condyles^{153, 257}, presence of a crista galli¹³,

breadth of the incisive fossa¹⁸⁴, paranasal sinus development⁴⁴, position of the nasal and orbital openings²⁵², and percentage occurrence of a premaxillary suture¹².

Many authors have been unable to resolve the relationships between the African apes and *Homo*^{59, 85, 117, 118, 119, 127, 145, 175, 180, 187, 218, 236, 256, 258, 277}, while other studies have observed a closer relationship between *Homo* and *Gorilla*, for example in some features of the forelimb^{86, 176, 247}, dorsal wedging of the penultimate lumbar vertebra²³⁶, increased occurrence of a supraorbital foramen or notch and small zygomatic foramen²¹¹ and most frequent type of mental foramen¹⁴.

1.4.1.4 Alternative phylogenies

Alternative phylogenies have been proposed on the basis of morphology, but these are not supported by the vast majority of the molecular evidence (see 1.3), and are less well-supported by the morphological evidence^{6, 8, 9, 51, 117, 119, 272}. If the consensus molecular tree is accurate, these alternative phylogenies must be the result of homoplasies.

Some authors have grouped all great apes to the exclusion of *Homo*^{1, 16, 81, 125, 127, 156, 197, 198, 217, 221, 228, 256, 298, 307}, while others have described anatomical features which appear to support a *Homo-Pongo* clade^{32, 42, 71, 149, 172, 216, 228, 259, 260, 261, 262}. Analysis of some cranial and lower limb variables results in a *Pan-Pongo* clade^{40, 234}, while other cognate evidence suggests a *Pongo-Gorilla* clade⁴¹.

As morphological difference exaggerates genetic distance^{45, 79}, it would be expected to find far more difference between the hominoid species in their anatomy than in their molecular biology. The genetic changes resulting in morphological difference

presumably occurred in the hominid lineage after divergence from the chimpanzee/human common ancestor.

Since soft tissue morphology has been largely ignored in favour of skeletal and dental data in the past, this thesis will examine whether soft tissue anatomy follows the "traditional" morphological reconstruction of phylogeny, or conforms with the majority of the molecular evidence, and the morphological study of Shoshani *et al.*²⁷².

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CHAPTER 2.

MATERIALS AND METHODS

2.1 DATA

An extensive literature search was conducted on the soft tissue anatomy of the extant Hominoidea. The data collected by this method was collated and distilled into a comparative anatomical format.

The taxa involved in this study are *Gorilla*, *Homo*, *Hylobates*, *Pan*, *Pongo* and *Symphalangus*.

2.1.1 Anatomy

Chapter 3 presents the results of this search. It is divided into a single subchapter for the integumentary system, and six regional subchapters: Head and neck; Thorax; Upper limb and shoulder girdle; Back; Abdomen and Pelvis; and Lower limb and pelvic girdle.

Within each subchapter, the anatomical data are assigned to sections corresponding to systems. The systems, where available, are presented the following order.

1. Muscles
2. Vessels
3. Nerves
4. Alimentary
5. Respiratory
6. Urogenital

7. Endocrine

8. Sensory

Nomina Anatomica has been used as a guide to the order of individual anatomical structures⁴. When this is not the case, it will be designated after the title of the structure by a superscript letter ^a.

Most of the structures are given in alphabetical order within each section. The exceptions to this rule, either for functional or traditional reasons, will be designated in the text by a superscript letter ^b. For example, the cranial nerves are traditionally presented in numerical order rather than alphabetically, so this is how they are shown in this thesis. Likewise, for vessels and nerves, the branches/tributaries are given in the human order of branching.

An attempt has been made to standardize the description procedure for each anatomical structure. The name of each structure is italicized and indented to form a title. After the title of the anatomical feature, if there is no information for a particular species, or set of species, this is stated. The information for each muscle is given in paragraphs, each of which corresponds to, in order: Origin, Description (if available), Insertion and Innervation. Vascular and neuronal data are given, where possible, in the order: Place of origin, Description and Branches. Within the section 'vessels', arteries are considered first, followed by veins and finally lymphatics.

For the remaining systems, the descriptive format is based on Gray's Anatomy⁷.

Where possible, information for a structure is given in the order, *Homo*, *Pan*, *Gorilla*, *Pongo* and *Hylobates*. *Pan paniscus* is mentioned as a separate species when information is available, and all hylobatids can be assumed to be *Hylobates* unless

stated otherwise. Data for *Symphalangus* are given separately if the anatomy differs, or together with *Hylobates* as hylobatids, if their anatomy is similar.

The phrase "both species of *Pan*" means that both *Pan troglodytes* and *Pan paniscus* share a particular character. As few authors provide information about soft tissues separately for the subspecies of *Gorilla* or *Pongo*, no attempt has been made to separate them in this thesis.

The text is worded so that the absence of a structure is referred to, and should not be inferred. Thus, as an example, the sentence "a structure is present in *Homo* and *Pan*, but absent from *Gorilla* and *Pongo*" carries no implication about the state of the structure in *Hylobates*. Likewise, "a structure is present in *Homo* and *Pan*" has no implications for the presence or absence of the structure in *Gorilla*, *Pongo* or *Hylobates*.

The phrase "all apes" involves both great apes and hylobatids, "Asian apes" refers to *Pongo* and *Hylobates* and "African apes" corresponds to *Pan* and *Gorilla*.

All proximal attachments are referred to as "origins", and all distal attachments as "insertions". Fingers and toes are referred to as digits, with the subsequent Arabic number indicating the digit under discussion. Similarly, upper case M preceding a roman numeral indicates either metatarsal or metacarpal number, depending on whether the structure in question relates to the foot or the hand. Upper case C, T, L, S or Co preceding an Arabic numeral indicates a vertebra; cervical, thoracic, lumbar, sacral or coccygeal, respectively. Numerals separated by a forward slash, for example 1/4, indicate number of specimens, in this case, one out of four specimens. Thus,

1½/4 indicates that a particular feature occurs in one and a half out of four specimens; the ½ indicates its appearance on one side only.

2.2 APPENDICES

Five appendices are presented at the end of the thesis.

Appendix 1 lists the character names and states for Dataset A, which is the soft tissue data set based on the evidence reviewed in this thesis.

Appendix 2 shows the data matrix for Dataset A.

Appendix 3 lists the character names and states for Dataset B, taken from information given in Shoshani *et al.*⁵

Appendix 4 shows the data matrix for Dataset B.

Appendix 5 contains a listing of all the anatomical structures that come under the remit of this thesis as they are referred to in *Nomina Anatomica*⁴. This excludes the brain and central nervous system, skeletal anatomy and the dentition. For each species, when information is available, an asterisk is present in the box corresponding to the structure and species. This signifies only that information is available for that species, not necessarily the presence or absence of that structure. The final column shows the section number in Chapter 3 where the information for each anatomical structure is located. This appendix provides an accessible summary of which parts/regions of the body are represented in this study.

2.3 REFERENCES

For all chapters except Chapter 3, references are numbered in superscript in the body of the text and listed as an alphabetical bibliography at the end of each chapter. For

Chapter 3, references are numbered in superscript in the body of the text and listed as an alphabetical bibliography at the end of each anatomical subchapter. Numbers for repeated references do not correspond between chapters or subchapters. This procedure was adopted to reduce what would have been an unmanageable repetition of references, and to restrict the length of the text.

2.4 ANALYSIS

2.4.1 Selection of characters

From the information reviewed in Chapter 3, characters for the cladistic analysis were assembled using the following criteria:

- I Data must be available for all five species. This removes the problem of 'missing' data in the final dataset.
- II At least two character states must be present. This excludes invariable characters.
- III One of these character states must be present in two, or more, species. This last criterion removes those characters which are special (autapomorphic) for a particular species.

Using these criteria, a 200 character data matrix was produced.

A list of the characters used for the analysis is given in Appendix 1, with the data matrix in Appendix 2.

For comparison, the same criteria were applied to the data set of Shoshani *et al.*⁵. This resulted in 130 characters. These are listed in Appendix 3. The corresponding data matrix is given in Appendix 4.

In addition, two regional subsets of Dataset A have been analyzed, "Upper limb" and "Lower limb", each containing 71 characters. The "Upper limb" subset is referred to as Subset A1, and the "Lower limb" subset as Subset A2.

Subset A1 contains characters 54 to 99, 159 to 175 and 180 to 187 from the parent Dataset A, while Subset A2 incorporates characters 1 to 53, 150 to 158 and 190 to 200 from Dataset A.

For the purposes of character analysis, *Hylobates* and *Symphalangus* have been amalgamated into the taxon "*Hylobates*", and the two species of *Pan* into the taxon "*Pan*".

No *a priori* judgements were made as to the primitive or derived condition of characters, and all characters were treated as unordered for the purposes of analysis.

Two phylogenetic programs were used in the character analysis. Phylogenetic Analysis Using Parsimony Version 3.0s⁷, normally abbreviated to PAUP, and MacClade Version 3³. PAUP is a phylogeny reconstruction program, while MacClade allows the effects of different cladistic hypotheses to be explored within a parsimony framework. In both programs, the parsimony of a cladogram is assessed in relation to the sum of the lengths of its branches. Minimum length cladograms correspond to traditional most parsimonious cladograms, as minimizing the total number of character state changes is equivalent to minimizing the number of "extra" steps needed to explain the evolution of the characters involved in the cladogram¹.

2.4.2 Hypotheses

Two questions are addressed in this thesis.

Firstly, can soft tissue anatomy be used to reconstruct the cladistic relationships between the extant hominoids? That is, does it confirm, or conflict with, the consensus molecular phylogenetic tree? Secondly, do different regions of the body differ in their ability to reconstruct these relationships? This has been tested by comparing the performance of the upper and lower limb regional subsets.

2.4.3 Testing of the hypotheses

The raw data from the anatomical database was additively coded, as shown in Appendices 1 and 2, and input into a data matrix in MacClade. Subsequently, the data matrices of both Dataset A and Dataset B were subjected to parsimony analysis using the Branch and Bound routine in PAUP, which is guaranteed to find the shortest length cladogram⁶. All characters were given equal weights and treated as unordered. Equal weighting means that the influence of each character on any tree topology is related fundamentally to the number of states. The greater the number of states, the greater influence of the character, for example a character with five states will always contribute at least four steps, while a character with two states may contribute only one step. Weighting is particularly relevant if continuous characters are broken into an arbitrary number of discrete states.

A 10000 replication branch and bound bootstrap analysis was then performed in PAUP, and a 50% majority rule consensus cladogram was derived. This cladogram was compared with the consensus molecular cladogram (Figure 4.1). A clade was

considered well-supported if it was supported by the consensus molecular cladogram and by 70% or more of the bootstrap replications².

A list of synapomorphies for each internal node of each consensus cladogram was generated using the 'List of Apomorphies Option' in the 'Describe Trees' menu of PAUP.

The data matrices were then transferred back to MacClade, and the most parsimonious cladogram for each matrix brought up in the Tree Window.

Uninformative characters with respect to the most parsimonious cladogram were excluded from the data matrix, and the tree length, consistency index (CI) and retention index (RI) were noted. See 1.2.4.2.2 and 1.2.4.2.3 for a description of CI and RI. An uninformative character is one which contributes exactly the same length to every possible tree topology, and is therefore uninformative for parsimony.

Unordered characters, which have been used in these analyses, are informative only if at least two character states occur in more than one taxon, otherwise the single states can always be explained as autapomorphic changes on terminal branches.

Branch-swapping was performed to test the effect of different cladistic arrangements on the tree length.

The second hypothesis was tested in the same fashion using Subset A1 (Upper limb) and Subset A2 (Lower limb), as defined in the previous section.

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CHAPTER 3.0

RESULTS

This chapter presents the results of the literature search, as set out in Chapter 2.0.

3.1 SKIN AND HAIR

3.1.1 Glands

Axillary organ

The axillary organ is absent from *Pongo* and *Hylobates*^{3, 8, 10, 14} but present in *Homo* and African apes^{2, 3, 5, 8, 10, 18, 26, 6}.

Sternal glands

Sternal glands are present in hylobatids and *Pongo* but absent from African apes and *Homo*^{1, 4, 5, 9, 10, 11, 12, 14, 15, 16, 19, 24, 27, 28}.

3.1.2 Hair

Baldness

No information for *Hylobates*.

Great apes undergo varying degrees of baldness with maturity, which seems to be the same phenomenon as human baldness¹⁰, although there may be no significant male bias in *Pan*¹⁷.

There is a complete absence of extensive balding in chimpanzees under 5 years, while in the 5 to 9 years age group, balding of the forehead is slightly more common than no balding at all, and there is occasional extensive balding. From 9 years

onwards, balding is more common than no balding at all or extensive balding. With regard to balding, sex differences are negligible¹⁷.

Age (months)	N	1	2	3
0-60	38	34	4	-
61-108	57	25	29	3
109+	26	5	16	5
Total	121	64	49	8

Table 3.1.1. Age differences in head hair distribution in *Pan troglodytes*. 1 = No baldness; 2 = Bald patch in centre of forehead; 3 = Baldness extending back to crown; extensive baldness. Adapted from ¹⁷.

Hair density

	Hairs/cm ²			Total no of hairs, divided by 1000		
	Scalp	Back	Chest	Scalp	Back	Chest
<i>Homo</i>	290.5	0	1.1	157.5	0	2.5
<i>Pan</i>	112	48	21	40.7	101.8	44.5
<i>Gorilla</i>	440	127	4.5	323	650.5	23.0
<i>Pongo</i>	158	176	107	71.8	476.0	289.0
<i>Hylobates</i>	2105	1622	534	237.8	854.3	837.3

Table 3.1.2. Average values for hairs/cm², and total number of hairs (divided by 1000). Adapted from ²⁰.

Relative density: The relative density of the chest hair is less than that on the back or scalp. On average the hair on the back is slightly less dense than on the head, and the hair on the chest is always very much less dense than either the back or the head.

Total number of hairs: The Old World and New World monkeys and apes have fairly similar averages for the total number of hairs, namely about 135 K on the scalp, 415 K on the back, and 110 K on the chest²⁰.

The extensive loss of hair in *Homo* is merely the most extreme manifestation of a general evolutionary trend to reduce the coat in higher primates²⁰. Regions of localized hair loss “are equally futile to explain as selective advantages”²².

The juvenile siamang possesses much less hair than gibbons of about the same size²⁰.

Haimoff *et al.* report “sparse” fur in *H.concolor*, *H.hoolock*, *H.klossi* and *Symphalangus*, and “dense” fur in *H.agilis*, *H.lar*, *H.moloch*, *H.mullerii* and *H.pileatus*, stating that “sparse” is the primitive state⁷. However, according to Schultz, decreasing hair density is an evolutionary trend in higher primates²⁰, whereas Schwartz and Rosenblum show a negative correlation between hair density and surface area, and this difference between hylobatids may simply represent differences in body size. Surface area, not phylogeny, is a better predictor of relative hair density, and this may represent a thermal adaptation^{9, 13, 23}.

A relative loss of hair has occurred not only in *Homo* but also in other higher primates. The density of scalp hair in *Homo* surpasses that of most apes and the total number of scalp hairs in *Homo* is considerably higher than in *Pan* or *Pongo*. The ranges of variations in number of chest hairs overlap in *Homo* and great apes, and as Schultz put it, “the difference between practically no hair on the human back and 100,000 hairs in *Pan* loses some significance alongside the 10 fold difference between *Pan* and for example, a guenon with over a million hairs on its back”²⁰.

3.1.3 Nail

No information for *Gorilla* or *Hylobates*.

The nail of *Pan* and *Pongo* has a similar composition but a more distinct stratifying of the plate in comparison with *Homo*. However, the proximal matrix, which is the generative area of the 'intermediate nail' in *Homo*, is subdivided in the apes²⁵.

3.1.4 Nipple

Nipple position index

Adult *Homo* has the lowest placed nipples of all hominoids. The vertical index of nipple level to pubic symphysis distance and trunk height, and the horizontal index shown by percentage relation between the distance from right to left nipple and chest breadth, is shown below:

Species	Vertical index	Horizontal index
<i>Homo</i>	76	71
<i>Pan</i>	86	52
<i>Gorilla</i>	82	46
<i>Pongo</i>	90	89
<i>Hylobates</i>	84	32(28)

Table 3.1.3. Nipple position index in hominoids. Number in parentheses applies to *Symphalangus*. Adapted from ²¹.

Nipple position is remarkably constant in many lower catarrhines, in contrast to the higher primates in which the nipples have shifted in widely different degrees and even opposite directions²¹.

3.1.5 Skin colour

There is complete absence of black facial pigmentation in chimpanzees under 5 years. The commonest facial colour for this age group is pale with pale muzzle¹⁷.

In the 5 to 9 years age group, pale facial pigmentation is rare, but pale muzzle is still quite common. Mid-brown is the commonest facial colour, all other shades being represented¹⁷.

From 9 years onwards, the trend towards darker facial pigmentation continues, with 7/26 black, 4/26 mid-brown, 1/26 pale and 7/26 pale muzzle¹⁷.

Age (months)	N	BI	DB	MB	P	R	PM
0-60	38		2	6	27	3	23
61-108	57	7	14	23	3	10	21
109+	26	7	11	4	1	3	7
Total	121	14	27	33	31	16	51

Table 3.1.4. Age differences in face colour in *Pan troglodytes*. BI = Black; DB = Dark brown; MB = Midbrown; P = Pale; R = Red; PM = Pale muzzle. Pale muzzle can be additional to any other face colour. Adapted from ¹⁷.

With regard to face colour, sex differences are significant ($p < 0.01$), while with regard to muzzle colour, sex differences are not significant ($p > 0.20$). No particular facial colour distribution is found in one sex exclusively, but black, dark brown and pale facial colour are less frequent in males than females, while medium brown and red facial colours are more frequent in males than females¹⁷.

Sex	N	BI	DB	MB	P	R	PM
M	57	4	10	22	10	11	21
F	64	10	17	11	21	5	30
Total	121	14	27	33	31	16	51

Table 3.1.5. Sex differences in face colour in *Pan troglodytes*. BI = Black' DB = Dark brown' MB = Midbrown' P = Pale' R = Red' PM = Pale muzzle. Pale muzzle can be additional to any other face colour. 26 of 121 specimens are adults. Adapted from ¹⁷.

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3.2 HEAD AND NECK

3.2.1 MUSCLES

3.2.1.1 Suboccipital

Obliquus capitis inferior

No information for *Hylobates*.

In all great apes and *Homo* it takes origin from the spinous process of C2^{120, 147, 169, 170, 194}

The muscle runs obliquely to insert onto the transverse process of the atlas^{120, 147, 169, 170, 194}

Innervation is via a branch of the dorsal ramus of the first cervical nerve in *Homo*, *Pan paniscus* and *Gorilla*^{120, 147, 194}

Obliquus capitis superior

No information for *Pongo* or *Hylobates*.

It originates from the transverse process of C1 in African apes and *Homo*^{120, 147, 169, 194}

The muscle passes obliquely posterosuperiorly to insert onto the occipital bone^{120, 147, 169, 194}

Innervated by a branch of the dorsal ramus of the first cervical nerve in *Homo*, *Pan paniscus* and *Gorilla*^{120, 147, 194}

Rectus capitis anterior - major and minor

No information for *Hylobates*.

In *Pan* and *Pongo* rectus capitis anterior has two parts: rectus capitis anterior minor, corresponding to rectus capitis anterior in *Homo*, and rectus capitis anterior major¹⁶⁹,¹⁷⁰, which has no homologue in *Homo*.

Rectus capitis anterior major in *Pan* takes origin from C3 to C6,¹⁶⁹ and in *Pongo* from C7 and T1 to T5 in common with longus colli¹⁷⁰. In *Pan* it receives a slip from scalenus anterior¹⁶⁹.

In both species the muscle inserts onto the basiocciput¹⁷⁰.

Rectus capitis anterior(minor) in all great apes and *Homo* originates from the anterosuperior surface of the lateral mass of C1^{31, 147, 170, 194}.

The muscle is more fan-shaped in *Pongo* than in *Pan*³¹.

This muscle inserts onto the basiocciput¹⁷⁰, anterior to the foramen magnum and occipital condyle in all great apes and *Homo*, posterolateral to the insertion of longus capitis^{31, 147, 194}.

Innervated by a branch of the first cervical nerve in *Homo* and *Gorilla*^{147, 194}.

Rectus capitis lateralis

No information for *Hylobates*.

The muscle originates in all great apes and *Homo* from the transverse process of C1^{30, 147, 194}.

It is absent from 1/2 *Pongo*¹⁷⁰.

In all great apes and *Homo* it inserts onto the jugular process of the occipital bone, posterior to the jugular foramen, and lateral to the occipital condyle^{30, 147, 194}.

Innervated by the ventral ramus of the first cervical nerve in *Homo* and *Gorilla*¹⁴⁷, and also from the second cervical nerve in *Homo*¹⁹⁴.

Rectus capitis posterior major

No information for *Hylobates*.

In all great apes and *Homo* it originates from the spinous process of C2^{120, 147, 169, 170, 194}.

The muscle variably overlaps the rectus capitis posterior minor, which is described with the latter muscle. In *Gorilla* it is separated from the other rectus capitis anterior major by a narrow fascial band¹⁴⁷. Described as larger than the rectus capitis posterior minor muscle in *Homo*¹⁹⁴ and both species of *Pan*^{120, 169}, rectus capitis posterior major is a smaller muscle than rectus capitis posterior minor in *Gorilla*¹⁴⁷.

In all great apes and *Homo* it inserts between the inferior nuchal line and the foramen magnum, lateral to the insertion of rectus capitis posterior minor^{120, 147, 169, 170, 194}.

Innervation is by branches of the dorsal ramus of the first cervical nerve in *Homo*, *Pan paniscus*, and *Gorilla*^{120, 147, 194}.

Rectus capitis posterior minor

No information for *Hylobates*.

In all great apes and *Homo* this muscle takes origin from the posterior tubercle of C1^{120, 147, 169, 170, 194}.

The muscle ascends in all great apes and *Homo* in a fan-shape, to insert into the medial region of the inferior nuchal line^{120, 147, 169, 170, 194}. The insertion is covered laterally by rectus capitis posterior major in *Homo*¹⁹⁴, almost completely covered in

both species of *Pan*^{120, 169}, less covered in *Pongo*¹⁷⁰, and separated by a variably marked thin ridge in *Gorilla*¹⁴⁷.

Innervated by a branch of the dorsal ramus of the first cervical nerve in *Homo*, *Pan paniscus* and *Gorilla*^{120, 147, 194}.

3.2.1.2 Facial

3.2.1.2.1 Scalp

Occipitofrontalis

No information for *Hylobates*.

Occipitalis

In all great apes and *Homo* the occipital origin is from the superior nuchal line^{120, 147, 153, 169, 170, 178, 194}, and in *Homo* and *Pan paniscus* also from the mastoid part of the temporal bone^{120, 194}.

In all great apes and *Homo* the belly ends in the galea aponeurotica covering the scalp^{120, 130, 147, 169, 170, 194, 198}. Fibres pass laterally to the posterior auricular muscle in great apes^{147, 152, 153, 178, 189}.

The occipital part is innervated by posterior auricular branches of the facial nerve in *Homo* and *Pan paniscus*^{120, 194}.

A nuchal part is present in *Gorilla* and *Pongo*, originating from the superior nuchal line^{153, 178}, passing medially to the nuchal ligament in *Gorilla*¹⁵³.

In *Pongo* an additional small muscle may be present: the *occipitalis profundus*. It originates from the middle of the superior nuchal line and ends in the deep layer of the fascia of the cranial vault¹⁷⁸.

Frontalis

The frontal part originates in all great apes and *Homo* from the skin and subcutaneous tissue of the supraorbital ridges and glabella, and is continuous with orbicularis oculi^{120, 147, 153, 169, 170, 194}.

It inserts into the galea aponeurotica^{120, 147, 153, 194}.

The frontal part is innervated by temporal branches of the facial nerve in *Homo* and *Pan paniscus*^{120, 194}.

Temporoparietalis

No information for *Gorilla*, *Pongo* or *Hylobates*.

In *Homo* and *Pan* the muscle takes origin from the galea aponeurotica over the cranial vault^{189, 194}.

It inserts into the auricular cartilage in *Homo* and *Pan*^{189, 194}. In *Pan* it also inserts into the fascia behind the ear¹⁸⁹.

3.2.1.2.2 Eyelids

Corrugator supercilii

No information for *Hylobates*.

The corrugator takes origin in *Homo* and *Pan paniscus* from the medial angle of the supraorbital ridge^{120, 194}, and in African apes from the side of the frontal process of the maxilla^{153, 189}, while in *Pongo*, when present, it originates from the lacrimal bone¹⁵². The angulation of the origin differs between *Homo* and *Pan*; in *Pan* the level of the origin is higher medially than laterally; the opposite state is true for *Homo*¹⁸⁹.

A small muscle in all, it is absent from 1/2 *Pongo*¹⁷⁸.

The muscle in all great apes and *Homo* inserts into the deep surface of the skin of the middle of the supra-orbital region^{120, 147, 152, 153, 189, 194}.

Innervated by temporal branches of the facial nerve in *Homo* and *Pan paniscus*^{120, 194}.

Depressor supercilii

No information for *Hylobates*.

This muscle slip originates from the medial palpebral ligament in African apes^{153, 178, 189}, and from the nasal process of the frontal bone in *Pongo*¹⁷⁸.

This slip has differentiated from orbicularis oculi in great apes to form a true depressor supercilii^{153, 178, 189}. In *Homo* it is represented by upper bundles of orbicularis oculi fanning out toward the eyebrows¹⁹⁴.

It runs superficially to blend with orbicularis oculi in *Pan*¹⁸⁹, ending in the supraorbital fascia in *Gorilla* and *Pongo*^{153, 178}.

Innervated by temporal and zygomatic branches of the facial nerve in *Homo*¹⁹⁴.

Orbicularis oculi

No information for *Hylobates*.

In all great apes and *Homo* the muscle takes origin from the medial palpebral ligament and the nasal processes of the frontal and maxillary bones above and below the ligament^{120, 147, 153, 169, 178, 189, 194}. An origin from the posterior lacrimal crest is present in *Homo* and *Pongo*^{170, 178, 194}.

The lateral extent of the muscle fibres is greatest in *Homo* and reduces in the order *Pan*, *Gorilla*, *Pongo*¹⁵³. The muscles of the opposing sides meet at the midline in *Pan troglodytes*^{169, 180}.

A well marked lateral palpebral raphe is absent from 1/2 *Gorilla*¹⁵³ and 1/2 *Pongo*¹⁷⁸, present in the remaining *Gorilla*¹⁴⁷ and *Pongo*¹⁷⁸ specimens, both species of *Pan*^{120, 169} and *Homo*¹⁹⁴. A few bundles of orbicularis oculi may end on the lateral palpebral ligament as a variant in *Homo*¹⁷⁸.

Bundles pass to the zygomatic muscle mass in *Pan*¹⁶⁹ and to the zygomatic fascia in *Gorilla*¹⁵³. In *Pongo*, the orbicularis oculi may be attached to the zygomatic bone via a tendon¹⁷⁸. *Gorilla* and *Pongo* share an insertion into the supraorbital fascia^{153, 178}. These fibres of insertion may represent the depressor supercilii sometimes differentiated in *Homo*¹⁹⁴.

Innervation of orbicularis oculi is via branches of the facial nerve in *Homo*, both species of *Pan* and *Gorilla*^{120, 147, 169, 194}.

3.2.1.2.3 Nose

Nasalis

No information for *Hylobates*.

It originates in all great apes and *Homo* from the maxilla above the lateral incisor^{147, 153, 178, 189, 194}. In all except *Pongo* this origin includes the maxilla above the medial incisor^{147, 153, 189, 194}, and in African apes the bone above the canine tooth^{147, 189}.

A flat triangular muscle, in all great apes and *Homo* it runs superomedially deep to levator labii superioris^{147, 178, 194}, and is continuous across the midline in *Homo* and *Gorilla*^{147, 194}.

The insertion is into the skin and fibrocartilage of the nostril and nasal wings in all African apes and *Homo*^{147, 153, 189, 194}, reaching the nasal dorsum in *Homo*, *Gorilla* and *Pongo*^{147, 178, 194}.

Innervated by a branch of the facial nerve in *Homo* and *Gorilla*^{147, 194}.

Procerus

No information for *Pongo* or *Hylobates*.

In all African apes and *Homo* it interdigitates at its origin with the frontalis^{120, 147, 153, 194}. In *Pan* it also blends with depressor supercillii and orbicularis oculi¹⁸⁹, and in *Gorilla* with corrugator supercillii¹⁵³. In *Homo*, *Pan paniscus* and *Gorilla* the origin also includes the skin and fascia over the glabella^{120, 147, 153, 194}.

The insertion in all African apes and *Homo* is into the nasal bone on either side of the midline^{120, 153, 189, 194}, extending into the skin of the nasal wings in *Gorilla*¹⁴⁷.

Innervated by buccal branches of the facial nerve in *Homo* and *Pan paniscus*^{120, 194}.

3.2.1.2.4 Mouth

Buccinator

No information for *Hylobates*.

In all great apes and *Homo* the muscle takes origin from the external surface of the mandible and maxilla in the region of the molar teeth, and from the pterygomandibular raphe^{120, 147, 153, 169, 178, 189, 194}. In *Gorilla* the origin extends

further anteriorly to the region of the first premolar (Pm3) on both the maxilla and mandible^{147, 153}, and likewise on the mandible in *Pan*¹⁸⁹.

Insertion in all great apes and *Homo* is into the angle of the mouth and the upper and lower lips, continuous with orbicularis oris^{120, 147, 148, 153, 169, 178, 189, 194}.

Innervation in *Homo*, *Pan paniscus* and *Gorilla* is from buccal branches of the facial nerve^{120, 147, 194}.

Depressor anguli oris

No information for *Hylobates*.

In *Homo*, *Pan paniscus* and *Pongo* the muscle takes origin from the lower margin of the mandible posteroinferior to the mental foramen^{120, 178, 194}. In African apes there is no bony attachment to the mandible, instead the muscle originates from fascia covering the mandibular margin^{147, 153, 189}, this fascial origin is also present in *Pongo*, in addition to the bony origin¹⁷⁸.

In all except *Pongo* the muscle is continuous with orbicularis oris^{120, 147, 153, 189, 194}, in all except *Pan paniscus* with levator anguli oris^{153, 178, 189, 194}, and in all except *Gorilla* interwoven with platysma^{120, 169, 178, 189, 194}. In *Homo* alone it is continuous with the risorius¹⁹⁴, and in *Pongo* continuous with zygomaticus minor¹⁷⁹.

In all great apes and *Homo* the insertion of depressor anguli oris is to the angle of the mouth^{120, 147, 153, 169, 178, 194}, extending into the lips and superiorly to the maxilla in *Gorilla*^{147, 153}. Some fibres in *Pongo* insert with those of depressor labii inferioris¹⁷⁸.

Innervation of depressor anguli oris is via mandibular branches of the facial nerve in *Homo*, *Pan paniscus* and *Gorilla*^{120, 147, 194}.

Depressor labii inferioris

No information for *Hylobates*.

In all great apes and *Homo* it takes origin from the outer surface of the mandibular body^{147, 153, 169, 170, 178, 194}. This origin is inferomedial to the mental foramen in *Homo*¹⁹⁴, while in *Pan paniscus* the origin is from the symphyseal region¹²⁰, and in *Pan troglodytes* from the posterior half, close to the base of the mandibular body¹⁶⁹.

The muscle is continuous with platysma at its origin in great apes and *Homo*^{147, 153, 169, 178, 194}, and with orbicularis oris in all except *Gorilla*^{120, 169, 178, 194}. The depressors of the opposite sides interlace in *Homo* and both species of *Pan*^{120, 169, 194}.

The insertion of the muscle in all great apes and *Homo* is into the skin of the lower lip^{120, 147, 178, 194}. Some fibres in *Pongo* insert with those of depressor anguli oris¹⁷⁸.

Innervation of depressor labii inferioris is via branches of the facial nerve in *Homo*, *Pan paniscus* and *Gorilla*^{120, 147, 194}.

Levator anguli oris

No information for *Hylobates*.

In all great apes and *Homo* it takes origin from the maxilla inferior to the infraorbital foramen^{108, 120, 147, 169, 178, 194}.

The muscle intermingles in all great apes and *Homo* with depressor anguli oris and orbicularis oris^{147, 153, 169, 170, 178, 180, 189, 194}, in *Gorilla* and *Pongo* with the buccinator muscle^{147, 178}, and in *Homo* with the zygomatic muscles¹⁹⁴.

The muscle inserts into the angle of the mouth and the skin of the lower lip in all except *Pan paniscus*^{120,147, 178, 189, 194}. An insertion into the skin of the upper lip is present in both species of *Pan* and *Pongo*^{120, 169, 170}.

Levator anguli oris is innervated by buccal branches of the facial nerve in *Homo*, *Pan paniscus* and *Gorilla*^{120, 147, 194}.

Levator labii superioris

No information for *Hylobates*.

In all great apes and *Homo* the muscle originates from the maxillary infraorbital margin above the infraorbital foramen and the zygomatic bone^{120, 147, 153, 169, 178, 189, 194}. In a single specimen of *Pan* the muscle originates partly from below the infraorbital foramen¹⁵³. In *Pan paniscus* and *Pongo* the medial extent of the origin may extend superiorly to the medial palpebral ligament^{120, 178}.

In all great apes and *Homo* the insertion is into the skin of the upper lip^{120, 147, 153, 169, 178, 189, 194}, extending superiorly to the nasal wing in all great apes except *Pan paniscus*^{147, 153, 169, 178, 189}. *Pongo* has a slip to the mucosa of the upper lip in the plane of the maxillary canine¹⁷⁸.

Innervated by buccal branches of the facial nerve in *Homo* and *Pan paniscus*^{120, 194}.

Levator labii superioris alaeque nasi

No information for *Hylobates*.

In *Homo* the muscle originates from the frontal process of the maxilla around the medial angle of the orbital opening¹⁹⁴, while in *Pan troglodytes* it takes origin from the midline of the nasal dorsum¹⁸⁹. In *Gorilla* and *Pongo* the muscle originates from

the frontal subcutaneous tissue above the supraorbital margin^{153, 178}, while some fibres in *Gorilla* originate from the medial palpebral ligament¹⁵³.

The insertion in all great apes and *Homo* is into the skin of the nasal wing, and to the upper lip in all except *Pan*^{153, 169, 178, 189, 194}.

Mentalis

No information for *Hylobates*.

The muscle originates in *Homo*, *Gorilla*, and *Pongo* from the mandible in the region of the alveolar bone of the medial incisor^{147, 153, 178, 194}, extending to the region of the lateral incisor in *Gorilla* and *Pongo*^{147, 153, 178}, and further, to the region of the canine, in *Gorilla*^{147, 153}.

It is described as well-developed in *Gorilla* and *Pongo*¹⁷⁸. In all great apes it interdigitates with platysma and with the mentalis of the other side^{147, 153, 178, 189}.

In great apes and *Homo* it inserts into the skin of the chin^{153, 178, 189, 194}, and in *Pongo* a few bundles pass from mentalis to end in the connective tissue deep to depressor labii inferioris¹⁷⁸.

Innervated by the facial nerve in *Homo* and *Gorilla*^{147, 194}.

Orbicularis oris

No information for *Hylobates*.

This is a circular sphincter-like muscle in all great apes and *Homo*^{120, 147, 153, 169, 180, 194}, although in *Pongo* there are few true circular fibres¹⁷⁸.

Fibres of all the muscles which reach the mouth form the origin of orbicularis oculi, including platysma and buccinator^{120, 147, 153, 169, 178, 180, 189, 194}, while slips are sent to the alveolar bone of the maxilla in all except *Pongo*^{153, 169, 194}.

Lightoller states that a differentiated *pars marginalis*, present in *Homo*^{19, 194} but not in *Pan*¹⁰⁶, may be a modification for speech¹⁰⁶.

Fibres reaching the nasal septum and alar cartilages, the *nasolabialis*, are present in *Homo* and *Pan paniscus*^{120, 194}, the interval between these interlacing upper fibres of orbicularis forming the depression inferior to the nasal septum in *Homo*⁶.

Nerve supply is via the buccal branches of the facial nerve in *Homo* and *Pan paniscus*, by unspecified branches of the facial nerve in *Gorilla*, and in addition by mandibular marginal branches of the facial nerve in *Homo*^{120, 147, 194}.

Risorius

No information for *Hylobates*.

In *Homo* risorius originates from the parotid (masseteric) fascia¹⁹⁴, whilst in African apes it is undifferentiated at its origin from platysma, and no fibres derive from the masseteric fascia^{147, 169}.

This muscle is not differentiated in *Pongo*¹⁷⁰, and incompletely so in African apes^{147, 169}. It may be absent in *Homo*¹⁹⁴.

In African apes and *Homo* risorius inserts at the angle of the mouth^{147, 169, 194}.

Innervated by branches of the facial nerve in *Homo* and *Gorilla*^{147, 194}.

Zygomaticus major and minor

No information for *Hylobates*.

The origin in great apes corresponds to that in *Homo*, that is, from an oblique line on the zygomatic bone, parallel to the zygomaticomaxillary suture^{25, 120, 147, 153, 169, 170, 178, 189, 194}. In *Pan* and *Pongo* this origin extends aponeurotically into the fascia in the temporal region^{25, 169, 178, 189}, and in African apes^{106, 153, 169}, and sometimes in *Homo*¹⁰⁶, it blends with orbicularis oculi.

Whereas in *Homo* these two zygomatic muscles are separate at their origin¹⁹⁴, in 2/3 *Pan*^{25, 189}, 1/2 *Gorilla*¹⁵³ and 5/6 *Pongo*^{27, 170, 178} the muscles form an inseparable zygomatic mass. The muscle mass decussates in great apes and *Homo* with orbicularis oris^{147, 170, 180, 189, 194}, with depressor anguli oris in *Homo*, *Gorilla* and *Pongo*^{147, 178, 194}, in *Homo*, *Pan* and *Pongo* with levator anguli oris^{170, 178, 189}, in *Pan* and *Pongo* with platysma^{170, 178, 189}, while in *Pan paniscus* and *Pongo* with levator labii superioris and levator labii alaeque nasi^{120, 170, 178}.

The muscle(s) insert into the upper lip medial to the angle of the mouth in all great apes and *Homo*^{147, 153, 169, 170, 178, 194}.

Nerve supply is via the buccal branches of the facial nerve in *Homo* and *Pan paniscus*^{120, 194}.

3.2.1.3 Masticatory

Lateral pterygoid

No information for *Pan troglodytes* or *Hylobates*.

The *upper head* takes origin in *Homo*, *Pan paniscus*, *Gorilla* and *Pongo* from the infratemporal surface of the greater wing of the sphenoid bone^{120, 147, 194, 200}. In 1/10 *Pongo* there is a small tuberosity at the origin of this head²⁰⁰. In *Gorilla* the origin

extends onto the frontal bone a few millimetres in front of the sphenoparietal suture¹⁴⁷.

The larger *lower head* in *Homo*, *Pan paniscus*, *Gorilla* and *Pongo* originates from the lateral surface of the lateral pterygoid plate^{120, 147, 194, 200}.

The two parts are separate in *Homo* and *Pongo*^{170, 194, 200}, although they are in contact at insertion in the majority of *Pongo*^{170, 200} and have a common insertion in *Pan paniscus*¹²⁰ and 1/7 *Pongo*²⁰⁰.

The insertion is to the capsule and articular disc of the temporomandibular joint and the anterior part of the condylar neck of the mandible in all the above apes and *Homo*^{120, 147, 170, 194, 200}.

Innervation is via a branch of the mandibular division of the trigeminal nerve in *Homo*, *Pan paniscus* and *Gorilla*^{120, 147, 194}.

Masseter

No information for *Hylobates*.

In all great apes and *Homo* the muscle is separated into these two parts, superficial and deep^{147, 169, 194, 200, 205}. In both species of *Pan* the two parts are separated by an aponeurotic sheet^{120, 169, 182} which is absent from other apes¹⁷⁰.

Superficial masseter in all great apes and *Homo* takes origin from a variable proportion of the lower border of the zygomatic arch^{147, 194}; from a third in 1/11 *Pongo*²⁰⁰, from approximately half in 4/11 *Pongo*²⁰⁰ and from two-thirds in *Homo*¹⁹⁴, all African apes^{120, 147, 169}, and 6/11 *Pongo*^{170, 200}.

The mean size ratio between the origin and insertion of superficial masseter is 0.99 in *Homo*, 0.78 in *Pongo* and 1.29 in *Hylobates lar*⁶².

The *deep* part of the origin is from the entire length of the deep surface of the zygomatic arch in all great apes and *Homo*^{147, 169, 170, 194, 200}, while in *Homo* and *Gorilla* it also arises from the posterior third of the inferior border of the zygomatic arch^{147, 194}, in *Pan paniscus* from the lateral half of the arch¹²⁰ and in *Gorilla* from the temporal fascia above the arch¹⁴⁷.

The insertion of both parts is onto the whole ramus, mandibular angle and coronoid process in all great apes and *Homo*^{120, 147, 169, 170, 194, 200, 205}. The deep masseter in *Pongo* may insert more extensively, attaching in addition to the region around the mandibular notch and on the condylar neck²⁰⁰. The part of masseter inserting on the anterior border of the coronoid process is inseparable from the insertion of temporalis in *Gorilla* and *Pongo*^{147, 200}.

Innervation is via a branch of the mandibular division of the trigeminal nerve in *Homo*, *Pan paniscus* and *Gorilla*^{120, 147, 194}.

Medial pterygoid

No information for *Pan troglodytes* or *Hylobates*.

In *Homo* and *Gorilla* the muscle takes origin from the lateral surface of the lateral pterygoid plate^{147, 194}, and in *Homo*, *Pan paniscus* and *Pongo* from the medial surface of the lateral pterygoid plate^{120, 194, 200}. Fibres from the maxillary tuberosity and the pyramidal process of the palatine bone are present in *Homo* and *Pongo*^{194, 200}.

In addition, a slip in 1/10 *Pongo* arises from the pterygomandibular raphe, swinging inferomedially to course with the rest of the muscle²⁰⁰.

In *Homo*, *Pan paniscus* and *Gorilla* it inserts into the medial surface of the mandibular angle and posterior ramus^{120, 147, 194}.

Innervation in *Homo* and *Pan paniscus* is via branches of the mandibular division of the trigeminal nerve^{120, 194}.

Temporalis

No information for *Hylobates*.

In all great apes and *Homo* the muscle takes origin from the whole of the temporal fossa^{120, 147, 169, 170, 194, 200}, and in all except *Pan paniscus* from the temporalis fascia^{147, 169, 170, 194, 200}.

The muscle passes beneath the zygomatic arch to insert onto the coronoid process of the mandible in all great apes and *Homo*^{14, 120, 169, 170, 194, 200}, extending down onto the anterior border of the mandibular ramus in *Homo*, *Pan paniscus* and *Gorilla*^{120, 147, 194}.

Innervated by branches of the mandibular branch of the trigeminal nerve in *Homo*, *Pan paniscus* and *Gorilla*^{120, 147, 194}.

Winkler provides absolute and relative dry muscle weights for the masticatory muscles in *Pongo*²⁰⁰.

3.2.1.4 Neck

3.2.1.4.1 Anterior and lateral vertebral

Longus capitis

No information for *Hylobates*.

Longus capitis takes origin in *Homo*, *Pan paniscus* and *Gorilla* from the anterior tubercles of the transverse processes of C4 to C6^{120, 147, 194}, extending superiorly to C3 in *Homo*¹⁹⁴, further to C2 in *Gorilla*¹⁴⁷, and inferiorly to C7 in *Pan paniscus*¹²⁰.

An elongated muscle in great apes and *Homo*^{31, 147}, in *Pan* and *Pongo* a groove is formed on the posterior wall of the pharynx at the junction of the two bellies of longus capitis^{31, 63}.

In all great apes and *Homo* longus capitis inserts onto the basiocciput^{31, 147, 194}, extending further anteriorly in great apes than in *Homo*³¹. The shape of the insertion is oval in great apes and *Homo*, but in great apes the maximum diameter lies in the sagittal plane³¹.

The muscle is innervated in *Homo*, *Pan paniscus* and *Gorilla* by branches of the ventral rami of the upper cervical nerves^{120, 147, 194}; specifically the first to fourth cervical nerves in *Homo*¹⁹⁴, and first to fifth in *Gorilla*¹⁴⁷.

Longus colli

No information for *Hylobates*.

This muscle may be described in terms of *superior oblique*, *vertical* and *inferior oblique* divisions^{169, 194}.

The *superior oblique* division originates from the anterior tubercles of the transverse processes of C3, C4 and C5 in all African apes and *Homo*^{120, 147, 169, 194}, extending superiorly to C2 or C1 in *Homo*, and inferiorly to C6 in *Pan paniscus* and *Gorilla*^{120, 147}. This division is absent from *Pongo*¹⁷⁰.

The *inferior oblique* and *vertical* divisions take origin in all great apes and *Homo* from the body of C6^{147, 169, 170, 194}. In all except *Gorilla*, the origin extends inferiorly to the body of T3 and superiorly to the body of C7^{120, 169, 170, 194}. The inferior extent of this origin reaches T4 in *Pan troglodytes*¹⁶⁹, and T5 in *Pongo*¹⁷⁰. The superior extent reaches to C5 in *Homo* and *Pan paniscus*^{120, 194}, and to C2 in *Gorilla* alone¹⁴⁷.

In all great apes and *Homo*, the insertion is onto the anterior tubercle of C1^{120, 147, 169, 170, 194} and in all except *Pongo* also to the transverse process of C6^{120, 147, 169, 194}. It also includes the transverse process of C5 and the bodies of the upper cervical vertebrae in *Homo* and both species of *Pan*^{120, 169, 194}. A slip in *Gorilla* from the anterior tubercle of C6 reaches the transverse processes of C2 and C1¹⁴⁷.

Innervated by branches of the ventral rami of the cervical nerves in *Homo*, *Pan paniscus* and *Gorilla*^{120, 147}; specifically second to sixth cervical nerves in *Homo*¹⁹⁴ and second to seventh in *Gorilla*¹⁴⁷.

Scalenus anterior

In all great apes and *Homo* the muscle originates from the anterior tubercles of the transverse processes of C5 and C6^{24, 120, 147, 169, 170, 194}, extending inferiorly to C7 in a single specimen of *Pan*²⁵, and superiorly to C4 in all except *Gorilla*^{25, 120, 169, 170, 194}.

A further cranially extended origin from C3 is present in *Homo*¹⁹⁴, *Pongo*¹⁷⁰, and variably so in *Pan*¹⁶⁹. The origin in *Hylobates* is described as from a variable number of vertebrae between C3 and C6¹⁷⁰. No further information for *Hylobates*.

The muscle runs inferiorly to insert onto the anterior scalene tubercle of the first rib in all great apes and *Homo*^{25, 120, 147, 169, 170, 194}.

Innervation of the muscle is from the lower cervical nerves in all African apes and *Homo*^{25, 120, 147, 194}; specifically the fourth to sixth cervical nerves in *Homo*¹⁹⁴, the eighth cervical nerve in *Pan troglodytes*²⁵, and the fifth to seventh cervical nerves in *Gorilla*¹⁴⁷.

Scalenus medius

No information for *Hylobates*.

In all great apes and *Homo* a posterior scalene tubercle is present on the transverse process of C4²², and on C3 in *Homo* and *Pongo*²², C5 in African apes and *Homo*²², and C6 in *Homo* and *Gorilla*^{22, 147}. However the muscle originates without the presence of a specific tubercle from the transverse processes as far superiorly as C3 in *Homo*¹⁹⁴, C2 in *Pan paniscus*¹²⁰, and as far inferiorly as C7 in African apes and *Homo*^{120, 147, 194}. The superior extent of the origin may include C1 in *Homo*¹⁹⁴. The combined medius-posterior muscle of *Pongo* originates from the posterior tubercles of C2 to C6¹⁷⁰.

Posteriorly, the muscle is partly fused with scalenus posterior in great apes^{120, 147, 170}, and as a variation in *Homo*¹⁹⁴.

In African apes and *Homo*, scalenus medius inserts onto the superior border of the first rib^{120, 147, 169, 194}, extending to the second rib in both species of *Pan*^{120, 169}. In *Pan* the combined medius-posterior insertion may extend as an aponeurotic sheet to the fifth rib¹⁶⁹.

Scalenus medius is innervated by branches of the lower cervical nerves in *Homo*, *Pan paniscus* and *Gorilla*^{120, 147}; specifically the third to eighth cervical nerves in *Homo*¹⁹⁴ and the seventh and eighth cervical and first thoracic nerves in *Gorilla*¹⁴⁷.

Scalenus posterior

No information for *Hylobates*.

The muscle originates from the posterior tubercles on the transverse processes of C4 to C6 in *Homo*¹⁹⁴, and from C2 to C4 in *Gorilla*¹⁴⁷. The combined medius-posterior muscle of *Pan paniscus* originates from the posterior tubercles of C2 to C7¹²⁰, while that of *Pongo* takes origin from those of C2 to C6¹⁷⁰.

Scalenus posterior is partly fused with scalenus medius in great apes^{120, 147, 169, 170} and as a variant in *Homo*¹⁹⁴, and in *Homo* may be considered as the part of scalenus medius passing to the second rib¹⁹⁴.

Insertion in all great apes is into the superior border of the first rib^{25, 147, 170}, and in African apes and *Homo* to the second rib^{112, 147, 194}. The combined medius/posterior insertion in *Pan* extends to the fifth rib¹⁶⁹.

Innervation in *Homo* and *Gorilla* is from the lower cervical nerves^{147, 194}, reaching superiorly to the sixth cervical nerve in *Homo*¹⁹⁴, and to the third cervical nerve in *Gorilla*¹⁴⁷.

3.2.1.4.2 Superficial and lateral cervical

Levator claviculae

No information for *Hylobates*.

This muscle occurs only as an anomaly in *Homo*^{26, 104, 133}, and may be absent or weak in both species of *Pan*^{120, 180}.

In all great apes, and *Homo* when present, this muscle originates from the transverse process of C1^{26, 27, 120, 130, 133, 147, 169}, in *Pongo* also from the occiput¹³⁰, and in *Homo* sometimes also from C2¹³³.

In *Gorilla* the muscle is fused with levator scapulae¹⁴⁷.

Insertion is onto the lateral end of the clavicle in all great apes and *Homo*^{27, 130, 133, 147}, with the exceptions of a single specimen of *Pan troglodytes* in which it inserted onto the superolateral aspect of the acromion¹⁶⁹, and *Pan paniscus*, in which it inserts into the middle third of the clavicle¹²⁰. In *Pan paniscus* and *Gorilla* the insertion is lateral to the attachment of trapezius^{120, 147}, and in *Gorilla* it inserts additionally into the tendon of subclavius¹⁴⁷.

Innervated by the second to fourth cervical nerves in *Homo* and *Gorilla*^{133, 147}, and by the third cervical nerve in *Pan paniscus*¹²⁰.

Platysma

No information for *Hylobates*.

In great apes and *Homo* it originates from the fascia over the pectoralis muscles^{120, 147, 169, 170, 178, 194}, and from the fascia over the deltoid and trapezius muscles in all except *Pan paniscus*^{25, 147, 169, 170, 178, 194}. In *Homo* and *Pongo* the muscle has fibres attaching to the acromion¹⁷⁸, and in *Homo* and *Gorilla* to the clavicle^{147, 194}, although Levet states that platysma has no bony attachments¹⁰⁵. The origin in *Pongo* extends to the fascia covering the upper arms and shoulders, reaching the mid-dorsal line of the neck^{170, 178}. The nuchal extent of the muscle in *Pan* and *Pongo* is as far as the ear, almost reaching the midline^{169, 178}, while in *Gorilla* this dorsal extent is less than in *Pan* or *Pongo*^{153, 170}.

Lightoller¹⁰⁷ refers to the part of platysma originating from the posterior surface of the shoulder and the fascia of the neck for a variable distance between the ligamentum nuchae and the acromion-ear line as the *notoplastysma*, present in great apes, and the part of platysma originating from the anterior surface of the shoulder and from a large area of the thoracic wall extending as far as the xiphisternum as the *tracheloplastysma*, present in *Homo* and *Pongo*¹⁰⁷, and possibly in *Gorilla*¹⁵³.

In all great apes and *Homo*, the platysma muscles of the opposing sides decussate beneath the mental symphysis^{25, 107, 120, 170, 178, 194}.

Muscular fibres insert onto the inferior border of the mandible in great apes and *Homo*, continuing to the angle of the mouth and the lips and also becoming continuous with the facial muscles^{25, 120, 147, 153, 169, 170, 178, 180, 189, 194}. In the cheek fibres end as far cranially as the zygomatic arch in African apes and sometimes in *Homo*^{25, 147, 194}, about level with the bottom of the auricle in *Pongo*¹⁷⁸, and just below the auricle in *Gorilla*^{147, 153}.

Platysma is innervated by the cervical branch of the facial nerve in *Homo* and *Pan paniscus*^{120, 194}.

Sternocleidomastoid

The origin in all apes and *Homo* is in two parts^{8, 170, 180, 194}, although three heads are present in *Pan paniscus*¹²⁰.

One point of origin is from the upper and anterior part of the manubrium sternae in all apes and *Homo*^{87, 147, 169, 170, 180, 190, 194}. In *Hylobates* this origin extends down to the level of the notch for the third rib⁸⁷. The sternal origin is in two parts in 1/4 *Pan*²⁵ and 1/2 *Pongo*¹⁹⁰.

The second, wider, part of the origin in all great apes and *Homo* is from the medial third of the upper clavicular surface^{25, 120, 147, 169, 170, 194}. In both species of *Pan* bundles are sent to the sternoclavicular joint^{120, 169}. In a single specimen of *Pongo*, the clavicular origin is displaced laterally to the acromion¹⁹⁰, and lateral displacement may occur as a variant in *Homo*. No further information for *Hylobates*.

Fusion of the heads of sternocleidomastoid occurs in *Homo* and 1/3 *Pongo* below the middle of the neck^{50, 51, 194}, while in all other great apes the parts remain separate^{8, 26, 147, 169, 170}. The separate heads consist of *sternomastoid* in all apes^{87, 120, 147, 169, 170}, *cleidomastoid* in African apes^{120, 147, 169}, *sterno-occipital* in both species of *Pan*^{120, 170}, and *cleido-occipital* in *Pongo* alone¹⁷⁰. In the human fetus, the muscle consists of the unfused *sterno-occipital* and *cleidomastoid* portions, developing from the same material as the trapezius muscle⁸⁷.

The insertion of the combined or uncombined muscle in all great apes and *Homo* is to the lateral surface of the mastoid process, and the lateral portion of the superior nuchal line^{30, 120, 147, 169, 170, 180, 194}. In a single *Pan* part of the insertion is onto the lateral mass of the atlas¹⁸⁰.

Innervation is from the accessory nerve and a branch from the ventral ramus of the second cervical nerve in *Homo* and *Pan paniscus*^{120, 194}, sometimes with an additional branch from the third cervical nerve in *Homo*¹⁹⁴.

3.2.1.4.3 **Suprahyoid**

Digastric

The posterior belly of digastric is present in all apes and *Homo*^{1, 8, 27, 30, 50, 51, 120, 130, 133, 147, 155, 169, 170, 194, 200}. It takes origin in all great apes and *Homo* from the temporal

bone on the medial side of the mastoid process, lateral to the origin of rectus capitis lateralis^{30, 120, 147, 170, 194}. This origin extends posteriorly in *Gorilla*¹⁴⁷, and is more extensive on the mastoid process in *Pongo*²⁰⁰.

This belly in all apes and *Homo*, including the single described *Pongo* specimen with both bellies¹³³, ends in an intermediate tendon on the anterior belly^{133, 169, 194}. The lone posterior belly in *Pongo* has a tendinous and fleshy insertion onto the posterior border of the angle of the mandible^{30, 130, 133, 170, 200}. In human variants where digastric lacks its intermediate tendon, the muscle attaches to the midpoint of the mandibular body¹⁹⁴. In all except *Pongo*¹⁷⁰ the intermediate tendon of digastric perforates the stylohyoid^{147, 169, 194}.

The posterior belly is innervated by a branch of the facial nerve in *Homo*, *Pan paniscus*, *Gorilla* and *Pongo*^{120, 147, 194, 200}.

The anterior belly of digastric is described as absent from all but a single specimen of *Pongo*^{1, 8, 27, 30, 50, 51, 130, 155, 170, 200}. It is present in all other apes and *Homo*^{30, 120, 133, 147, 169, 185, 194}. When present, it originates from the intermediate tendon in all apes and *Homo*^{30, 133, 169, 194}, and additionally from the hyoid bone itself in *Gorilla*¹⁴⁷, perforating the stylohyoid in *Homo* and *Pan*^{169, 194}.

The two anterior bellies were in contact in the midline in both species of *Pan*^{120, 133} and *Hylobates*¹³³, and when present, in *Pongo*¹³³, but were not in contact in *Homo*¹³³ or *Gorilla*^{123, 147}. The intermediate tendon is connected by an aponeurotic loop to the hyoid in *Homo*¹⁹⁴, *Pan paniscus*¹²⁰, *Gorilla*¹⁴⁷, and in some specimens of *Pan* and *Pongo*¹³³.

The absence of the anterior belly in *Pongo* may be explained by a human variation in which the anterior belly is fused with mylohyoid^{194, 200}. This suggests that the large size and weight of the mandible in *Pongo* may be sufficient to achieve mandibular depression without the anterior belly of digastric²¹, but the mandible of *Gorilla* is of equal size, yet retains the anterior belly¹⁷. Hyolaryngeal specializations, including the presence of laryngeal air sacs, may be responsible, but these are present in the other great apes¹⁹³.

The anterior belly inserts in great apes, including *Pongo*, when present¹³³, and *Homo* into the inner side of the lower border of the mandible close to the symphysis^{120, 133, 147, 169, 194}.

The anterior belly is innervated by the mylohyoid branch of the mandibular division of the inferior alveolar nerve in *Homo*¹⁹⁴ and of the trigeminal nerve in *Pan paniscus* and *Gorilla*^{120, 147}.

Geniohyoid

No information for *Pongo* or *Hylobates*.

In African apes and *Homo* the muscle takes origin from the inner side of the mandibular symphysis; at the inferior mental spine in *Homo*¹⁹⁴, or genial fossa in African apes^{120, 147, 169}.

In African apes and *Homo*, the muscle runs deep to mylohyoid, contacting the muscle of the opposite side in the midline^{120, 147, 169, 194}. In *Pan troglodytes* there is a bursa between the geniohyoid muscles and the hyoid bone anteriorly, and genioglossi posteriorly¹⁶⁹.

The insertion in African apes and *Homo* is onto the anterior surface of the hyoid body^{120, 147, 169, 194}, extending to part of the greater horn of the hyoid in *Pan*¹⁶⁹, and to the lesser horn in *Gorilla*¹⁴⁷.

Innervation of the geniohyoid is from the ventral ramus of the first cervical nerve via the hypoglossal nerve in *Homo*, *Pan paniscus* and *Gorilla*^{120, 147, 194}.

Mylohyoid

No information for *Hylobates*.

In African apes and *Homo* this muscle originates from the internal surface of the mandibular body^{120, 147, 169, 194}; in *Homo* and *Gorilla* from the mylohyoid line^{147, 194}.

In *Pan* it may have a less extensive origin with no lateral attachment to the mandible producing a free edge of the mylohyoid curving posteriorly from the symphysis¹⁸⁵.

In all African apes and *Homo*, mylohyoid lies under cover of the anterior belly of digastric^{120, 147, 169, 185, 194}.

The fibres of mylohyoid are longer and more parallel to the mandibular body in *Pan* than in *Homo*, due to the more anterosuperior positioning of the hyoid bone in *Pan*³⁹.

In all African apes and *Homo* mylohyoid inserts onto the superior border of the hyoid bone^{120, 147, 169, 185, 194}. The muscles of the opposing sides usually meet in a median fibrous raphe in *Homo* and *Pan paniscus*^{120, 194}, which is absent from all other great apes^{170, 182}. In great apes^{147, 170} and sometimes in *Homo*¹⁹⁴, the opposing muscles are continuous across the midline.

In *Homo*, *Pan paniscus* and *Gorilla* mylohyoid is innervated by a branch of the mandibular division of the trigeminal nerve^{120, 147, 194}; specifically the mylohyoid branch of the inferior alveolar nerve in *Homo* and *Gorilla*^{147, 194}.

Stylohyoid

No information for *Hylobates*.

In all great apes and *Homo* it originates from the styloid process^{30, 120, 147, 169, 170, 194, 197}, including the adjacent bone in African apes^{30, 169}.

A slender muscle, in all except *Pongo*¹⁷⁰ it is perforated by the intermediate tendon of the digastric muscle^{147, 169, 194}. Developmentally, stylohyoid is a slip of the posterior belly of digastric¹⁹⁴, and is inseparable from this muscle belly in 1/6 *Pan*¹⁷⁰.

The insertion in all great apes and *Homo* is onto the body of the hyoid bone at the junction of the greater cornua with the lesser cornua^{120, 147, 169, 170, 194}. In *Gorilla* the insertion extends onto the lesser cornua, and is united with the insertion of omohyoid¹⁴⁷.

In *Pongo* stylohyoid also inserts into the laryngeal air sac, forming a *stylolaryngeus*^{48,49, 170}.

Innervated in *Homo*, *Pan paniscus* and *Gorilla* by a branch of the facial nerve^{120, 147}.

3.2.1.4.4 Infrahyoid

Omohyoid

The inferior belly of omohyoid in African apes and *Homo*, and the single-bellied muscle of *Pongo*¹⁷⁰, originates from the superior border of the scapula near the

scapular notch^{64, 120, 147, 169, 194}. In the human fetus, the origin is from the lateral third of the clavicle, moving developmentally to the scapula⁶⁴.

In African apes and *Homo* the superior belly of omohyoid originates from the intermediate tendon^{120, 147, 169, 170, 194}. In a specimen of *Pan troglodytes* with a third belly, this belly originates with the sternothyroid muscle from the dorsal surface of the first costal cartilage, meeting the superior and inferior bellies at a Y-shaped junction, giving off a tendinous thread which runs to join with the sternohyoid muscle¹⁶⁹. Fusion with the sternohyoid is also present in *Pan paniscus*¹²⁰ and as a variation in *Homo*¹⁹⁴.

With the exception of *Pongo*¹²⁰, the omohyoid muscle has two bellies connected by an intermediate tendon, held to the clavicle by a fascial sling^{8, 26, 64, 120, 147, 169, 170, 194}.

In 1/3 *Pan* and in *Pongo* the muscle is undivided by a central tendon, consisting of a single belly¹⁷⁰. Additionally in *Pan* and *Gorilla*^{147, 169}, three bellies may be present. No further information for *Hylobates*. The muscle is entirely absent from a single specimen of *Pongo*⁸, and may be absent from *Homo* as a variation¹⁹⁴.

The inferior belly in African apes and *Homo* ends in the intermediate tendon^{64, 120, 147, 169, 194}.

The superior belly in all great apes and *Homo*, including the single-bellied muscle of *Pongo*¹⁷⁰, inserts into the lower border of the hyoid body, lateral to the midline^{120, 147, 169, 170, 194}.

Innervated by branches of the ansa hypoglossi in *Homo*, *Pan paniscus* and *Gorilla*^{120, 147, 194}.

Sternohyoid

No information for *Hylobates*.

The muscle originates in all great apes and *Homo* from the posterior aspect of the upper part of the manubrium sterni^{120, 147, 169, 170, 194}. In *Homo* and *Pongo* the origin also involves the medial extremity of the clavicle^{170, 194}, and in *Homo* and *Gorilla* includes the capsule of the sternoclavicular joint^{147, 194}.

A ribbon-like muscle in *Homo*, *Pan paniscus* and *Gorilla*^{120, 147, 194}, in all great apes and *Homo* the muscles of the opposing sides are separated in the midline inferiorly^{147, 169, 170, 194}, with the laryngeal sac projecting into this interval in both species of *Pan* and *Pongo*^{120, 170, 180}. Transverse tendinous intersections are present in *Pan*^{25, 112}, and are often found in *Homo*¹⁹⁴.

The insertion in all great apes and *Homo* is onto the inferior border of the body of the hyoid bone^{120, 147, 169, 170, 194}.

The sternohyoid muscle is innervated in *Homo*, *Pan paniscus* and *Gorilla* by a branch of the ansa hypoglossi^{120, 147, 194}.

Sternothyroid

No information for *Pongo* or *Hylobates*.

In African apes and *Homo* it takes origin from the posterior surface of the manubrium sterni^{120, 147, 169, 194}. In *Homo* and *Pan* it also originates from the edge of the cartilage of the first rib^{169, 194} and in *Homo* and *Gorilla* from the sternoclavicular joint^{147, 194}.

In African apes and *Homo* the muscle is continuous with thyrohyoid^{25, 147, 169, 194}.

Tendinous intersections are variably present in *Homo* and *Pan*^{112,194}.

In *Homo* and *Gorilla* sternothyroid inserts onto the oblique line of the thyroid lamina^{147, 194}, while in both species of *Pan* it inserts into the upper part of the thyroid lamina^{120, 169}.

Innervated in *Homo*, *Pan paniscus* and *Gorilla* by a branch of the ansa hypoglossi comprising fibres of the first three cervical nerves^{120, 147, 194}.

Thyrohyoid

No information for *Hylobates*.

In all great apes and *Homo* it originates from the thyroid lamina^{89, 120, 147, 169, 170, 194}, from the entire width of the lamina in African apes and *Homo*^{147, 169, 194}, and from the upper half of the lamina in *Pongo*¹⁷⁰.

Fan-shaped in *Pan paniscus*¹²⁰, it is quadrilateral in *Homo* and *Gorilla*^{147, 194}. In African apes and *Homo*, the muscle is a continuation of sternothyroid^{25, 147, 169, 194}, and in *Homo* and *Gorilla* it is crossed by the omohyoid¹⁴⁷.

In all great apes and *Homo* the muscle inserts onto the anterior surface of the hyoid body^{169, 170, 194}, specifically the inferior border in African apes and *Homo*^{120, 147, 169}, extending onto the greater cornu of the hyoid in *Homo* and *Pan*^{85, 169, 194}.

Innervated in *Homo* and all African apes by a branch of the hypoglossal nerve^{120, 147, 169, 194}.

3.2.2 VESSELS

3.2.2.1 Arteries

3.2.2.1.1 External carotid^b

External carotid artery

No information for *Hylobates*.

The external carotid artery in *Homo* and *Pongo* is encircled by the hypoglossal nerve^{170, 194}.

The artery gives off the ascending pharyngeal, occipital, maxillary and superficial temporal branches in *Homo*, *Pan* and *Pongo*^{169, 170, 194}.

In *Homo* and great apes the superior thyroid branch^{147, 169, 170, 194}, and in *Homo* and *Pongo* the posterior auricular branch, also arise from the external carotid artery^{170, 194}.

The lingual and facial arteries, as in 20% of *Homo*^{170, 194}, are given off as a linguofacial trunk in *Pan* and *Pongo*^{169, 170}, dividing into lingual and facial arteries and giving off no other branches.

A parotid branch is present exclusively in *Pongo*¹⁷⁰. An ascending palatine artery is present in *Gorilla*¹⁷⁰, and the transverse facial artery is a branch from the temporomaxillary artery in *Pan*, rather than from the superficial temporal artery as in *Homo*^{169, 194}. In *Gorilla*, just above the bifurcation of the left common carotid, the external carotid gives off a branch which descends and passes posteriorly over the hypoglossal nerve at the point where the nerve gives off its descending branch. It divides into a superficial and a deep branch, the first of which terminates in the region of the lambdoidal crest, and the deeper to the parotid gland¹⁴⁷. This may correspond to the lower sternocleidomastoid branch of the occipital artery of *Homo*¹⁹⁴.

Superior thyroid artery

No information for *Hylobates*.

This artery is given off by the external carotid in *Homo*, 1/3 *Pan*, *Gorilla* and *Pongo*^{147, 169, 170, 194}, and from the common carotid in 2/3 *Pan*^{169, 170}, and as a variation in *Homo*¹⁹⁴.

It gives branches to the thyroid gland and the hyoid musculature in *Homo* and great apes^{147, 169, 170, 194}, and to the fat and glands of the neck in *Pongo*¹⁷⁰.

A superior laryngeal branch is given off in *Homo*, 6/8 *Pan* and in *Gorilla*^{84, 147, 169, 194}. In 1/8 *Pan* the superior laryngeal artery sprang from the internal carotid artery, and in 1/8 *Pan* unilaterally from the sublingual artery⁸⁴.

The artery anastomoses with the inferior thyroid arteries in *Homo*¹⁹⁴, with the thyroidea ima in *Pan*¹⁶⁹ and with the middle thyroid arteries in *Pongo*¹⁷⁰.

Superior laryngeal artery

No information for *Hylobates*.

In *Homo* and *Pan* the superior laryngeal artery pierces the thyrohyoid membrane^{84, 169, 194}. In 7/8 *Pan* the artery gives off the cricothyroid artery⁸⁴, which in *Homo* and 1/8 *Pan* is a branch of the superior thyroid artery^{169, 194}, passing across the cricothyroid membrane^{26, 194}.

Ascending pharyngeal artery

No information for *Gorilla* or *Hylobates*.

Present in *Pongo*¹⁷⁰, in *Homo* and *Pan* it arises close to the origin of the external carotid artery, running cranially to supply the pharynx, muscles of the palate, prevertebral muscles, and the tonsils^{169, 194}.

The vessel enters the jugular foramen in *Homo* and *Pan*^{169, 194}.

Lingual artery

No information for *Gorilla* or *Hylobates*.

As in 20% of *Homo*^{170, 194}, a linguo-facial trunk is present in *Pan* and *Pongo*^{169, 170}.

After division, in *Homo* and *Pan* the lingual artery runs deep to hyoglossus. After emerging from beneath the anterior border of hyoglossus, it runs to the apex of tongue, lateral to the genioglossus^{169, 194}.

It gives off suprahyoid branches in *Homo*, *Pan* and *Pongo*^{169, 170, 194}, and also dorsal lingual and several lingual branches in *Homo* and *Pongo*^{170, 194}. A large branch to the submandibular gland is present in *Pan*¹⁶⁹.

Occipital artery

No information for *Gorilla* or *Hylobates*.

The occipital artery arises in *Pongo*, as in *Homo*, as a separate branch from the external carotid artery^{170, 194}, while in *Pan* an occipito-auricular trunk is present¹⁶⁹.

It lies medial to splenius capitis in *Homo*¹⁹⁴, but subjacent to this muscle in *Pan*¹⁶⁹.

A descending branch is given off to the muscles of the neck, and the artery supplies muscular branches to the suboccipital muscles in both *Homo* and *Pan*^{169, 194}. No meningeal branches are present in *Pan*, unlike *Homo*^{169, 194}.

In *Pan* the artery does not end in the scalp and it is not crossed in its terminal part by the suboccipital nerve, while both occur in *Homo*^{169, 194}.

Facial artery

No information for *Gorilla* or *Hylobates*.

The facial artery, as in 20% of *Homo*^{170, 194}, is given off as a linguo-facial trunk in *Pan* and *Pongo*^{169, 170}.

In *Homo* and *Pongo* the facial artery runs deep to the submandibular gland, while in *Pan* it runs superficial to this gland^{169, 170, 194}. In *Homo*, *Pan* and *Pongo* it crosses the mandible and enters the face at the anterior border of masseter, running obliquely superoanteriorly to the angle of the mouth^{169, 170, 194}, where in *Pan* it becomes more vertical, and reaches the levator anguli oris¹⁶⁹.

Other than inferior and superior labial branches, present in *Homo*, *Pan* and *Pongo*^{169, 170, 194}, submental branches are present in *Homo* and *Pan*^{169, 194}, a branch to levator anguli oris in *Pongo*¹⁷⁰ and masseteric and inferior coronary arteries in *Pan*¹⁶⁹. An ascending palatine artery is present in *Homo*¹⁹⁴, while in *Gorilla* this artery is a branch of the external carotid¹⁷⁰.

The submental artery sends vessels to the mylohyoid in *Homo* and *Pan*^{169, 194}.

The facial artery ends by supplying labial branches in *Pan* and *Pongo*^{169, 170}, while in *Homo* it continues to the medial palpebral commissure¹⁹⁴.

Posterior auricular artery

No information for *Gorilla* or *Hylobates*.

In *Pan*, the posterior auricular artery is given off from the occipito-auricular trunk under the cleidomastoid, supplying the parotid gland and back of the auricle¹⁶⁹. In *Homo* and *Pongo* the artery is a direct branch from the external carotid artery^{170, 194}.

Superficial temporal artery

No information for *Gorilla* or *Hylobates*.

A terminal branch of the external carotid artery, in *Homo*, *Pan* and *Pongo* it runs upwards^{169, 170, 194}, giving off parotid branches in *Pongo*¹⁷⁰.

A transverse facial branch is present in *Homo*, *Pan* and *Pongo*^{169, 170, 194}. It supplies the parotid gland and the masseter, being continued along the zygomatic arch, in *Homo* and *Pan*^{169, 194}

It ends by dividing into two branches which supply the anterior part of the auricle in *Pongo*¹⁷⁰ and the scalp in *Homo*, *Pan* and *Pongo*^{169, 170, 194}. A non-terminal anterior auricular branch is present in *Homo*¹⁹⁴.

Maxillary artery

No information for *Gorilla* or *Hylobates*.

In *Homo* and *Pongo* the maxillary artery passes behind the neck of the mandible^{170, 194}, in *Homo*, *Pan* and *Pongo* running superficially over the lower head of lateral pterygoid^{169, 170, 194}, and in *Homo* and *Pongo* passing through the pterygomaxillary fissure^{170, 194}.

Muscular branches of the maxillary artery supply the pterygoid muscles and buccinator in *Homo*, *Pan* and *Pongo*^{169, 170, 194}, and the masseter in *Homo* and *Pongo*^{170, 194}. Branches run to the buccal fat pad in *Homo*, *Pan* and *Pongo*^{169, 170, 194}.

Inferior alveolar artery

No information for *Gorilla* or *Hylobates*.

A branch of the maxillary artery in *Homo*, *Pan* and *Pongo*^{169, 170, 194}, in *Homo* and *Pan* the vessel runs with the inferior alveolar nerve^{169, 194}.

Middle meningeal artery

A branch of the maxillary artery in *Homo*, *Pan* and *Pongo*^{169, 170, 194}, in *Homo* and *Pan* the meningeal branch of the maxillary artery produces middle and accessory branches^{169, 194}.

Sphenoidal artery

No information for *Hylobates*.

In *Homo* the recurrent meningeal branch of the lacrimal artery anastomoses with a branch of the middle meningeal artery^{123, 194}, which Diamond refers to as the sphenoidal artery³⁵. An enlargement of this anastomosis explains the occasional origin of the lacrimal artery from the middle meningeal artery in *Homo*¹⁹⁴. In great apes, the meningeal lacrimal artery is distinct from the middle meningeal artery, entering the brain case through the supraorbital fissure or the cranio-orbital foramen^{170, 49}.

From the appearance of endocasts, meningeal arteries may enter the braincase in two ways, either through the orbit via the internal carotid artery, or through the base of the middle cranial fossa via the middle meningeal artery from the external carotid artery⁴⁸. *Pongo* is dependant on the orbital arteries^{35, 49}, *Gorilla* less so⁴⁹, while *Pan* is the great ape most dependant on the middle meningeal arteries⁴⁹, although the

internal carotid still has a significant role³⁵. *Homo* rarely has a significant contribution from the orbit to the middle cranial fossa⁴⁸. There appears to be a trend for increased cranial capacity to be associated with increased reliance on the internal carotid artery for supply of the mid braincase, but it is apparently not statistically significant⁴⁸.

Posterior superior alveolar artery

No information for *Gorilla* or *Hylobates*.

A branch of the maxillary artery in *Homo*, *Pan* and *Pongo*^{169, 170, 194}, it runs in *Homo* and *Pan* to the molar teeth, and in *Homo* also to the premolar teeth^{169, 194}.

Infraorbital artery

No information for *Gorilla* or *Hylobates*.

In *Homo* and *Pongo* the artery runs with the infraorbital nerve^{170, 194}, although the infraorbital groove is absent from *Pongo*¹⁷⁰.

In *Homo* and *Pan* this artery supplies the mandibular incisor and canine teeth, some of the facial muscles, and the upper lip^{169, 194}.

In *Pongo* the artery ends by supplying the skin of the cheek¹⁷⁰.

Descending palatine

No information for *Gorilla* or *Hylobates*.

The descending palatine artery in *Homo*, *Pan* and *Pongo* supplies the mucosa of the mouth, soft palate and alveolar bone^{169, 170, 194}.

Deep temporal arteries

No information for *Gorilla* or *Hylobates*.

The two deep temporal arteries are very different in size in *Pongo*, and equally sized in *Pan*¹⁷⁰. In *Homo*, *Pan* and *Pongo* they anastomose on the temporalis muscles^{169, 170, 194}.

Sphenopalatine artery

No information for *Gorilla* or *Hylobates*.

The continuation of the maxillary artery in *Homo*, *Pan* and *Pongo*, this vessel supplies the nasal cavity^{169, 170, 194}. In *Homo* and *Pan* it also supplies the ethmoidal and sphenoidal sinuses, in *Pan* and *Pongo* the pharynx^{169, 194}, and in *Pan* also the Eustachian tube¹⁶⁹. The Eustachian tube in *Homo* is supplied by the ascending pharyngeal branch of the external carotid artery, the middle meningeal artery and the artery of the pterygoid canal¹⁹⁴.

3.2.2.1.2 Internal carotid^b

Internal carotid artery

No information for *Gorilla*.

In *Homo*, *Pan* and Asian apes, the internal carotid artery divides near the anterior perforated substance of the brain by dividing into anterior and middle cerebral arteries^{194, 196}.

In one specimen of *Pongo* three distinct branches arise from the right internal carotid artery and are distributed to the territory of the middle cerebral artery, while from the left internal carotid two branches supply this region of the right hemisphere¹⁹⁶. In a specimen of *Pan*, a relatively large communicating branch lying under the posterior

part of the optic chiasm connects the internal carotid arteries. From this vessel arises a branch which runs anteriorly under the optic chiasma to anastomose with the anterior cerebral arteries, and a relatively large branch from the right internal carotid lies on the inferior surface of the right optic nerve¹⁹⁶; the latter may correspond with the ophthalmic artery of *Homo*¹⁹⁴.

Ophthalmic artery

No information for *Gorilla* or *Hylobates*.

The ophthalmic artery is present in *Homo*, *Pan* and *Pongo*^{169, 170, 194}.

In *Homo* and *Pongo*, the artery enters the orbit on the lateral side of the optic nerve, and crosses over its superior surface to its medial side^{170, 194}.

It gives off a ciliary artery in *Pongo* which divides into *posterior ciliary vessels*¹⁷⁰, running as in *Homo*¹⁹⁴. One of these ciliary vessels gives off the central artery of the retina in *Pongo*¹⁷⁰; in *Homo* the latter is a direct branch of the ophthalmic artery¹⁹⁴.

A large lacrimo-frontal artery is present on the left side of a specimen of *Pongo*¹⁷⁰, while the right artery gives off a *lacrimal artery* as in *Homo*¹⁹⁴. The lacrimo-frontal artery in this specimen of *Pongo* divides into lacrimal and frontal arteries which diverge at right angles¹⁷⁰.

The lacrimal artery in both *Homo* and *Pongo* supplies the lacrimal gland, the upper eyelid and the lateral and superior recti. A meningeal branch runs back to the middle cranial fossa, and will be discussed with the middle meningeal artery^{170, 194}.

The ophthalmic artery in *Homo* and *Pongo* continues as a *dorsal nasal artery* supplying the skin of the lateral surface of the nose, and the eyelids^{170, 194}.

Posterior communicating artery

No information for *Pan*, *Gorilla* or *Hylobates*.

A smaller vessel than the anterior and middle cerebral arteries, in both *Homo* and *Pongo* the posterior communicating artery forms a connection between the internal carotid and the posterior cerebral arteries^{194, 196}.

In *Pongo* there may be a connecting branch between the posterior communicating arteries¹⁹⁶.

Anterior cerebral

Because of the complexity of the branches of the anterior cerebral arteries, only differences from *Homo* in the course of the artery will be given. For further detailed information on the arterial supply of the brain, see ^{59, 66, 165, 171, 196} for *Pan*, ^{65, 151, 196} for *Gorilla*, ^{151, 164, 196} for *Pongo*, and ^{191, 196} for *Hylobates*.

A terminal branch of the internal carotid artery, in *Homo* the anterior cerebral artery begins at the medial end of the lateral cerebral sulcus. It passes forwards and medially above the optic nerve to the commencement of the longitudinal fissure. Here it comes into close relationship with the opposite artery and is joined to it by a short transverse trunk, sometimes duplicated, named the anterior communicating artery¹⁹⁴.

In *Pan* and *Hylobates*, the anterior cerebral arteries unite to form a median unpaired artery^{151, 165, 180, 196}, and thus there is strictly speaking no anterior communicating artery. In *Pan* the unpaired vessel extends for a distance of about 2.5 cm to the level of the genu of the corpus callosum, and then divides into two anterior cerebral arteries¹⁶⁵.

In a *Pongo* specimen the first part of the artery shows on the left side, where the artery lies ventral to the medial olfactory stria, a well marked perforation; the artery divides and joins up again. On the left side in addition there is a direct inosculation between the recurrent branch of the anterior cerebral artery and the branch of the middle cerebral artery which gives off the striate arteries to the site of the erased endorhinal fissure. On the right side the usual condition is seen in which the striate branches of the two arteries are separate from each other¹⁶⁴.

From the anterior communicating artery onward, which Sonntag refers to as the second part of the anterior cerebral artery¹⁶⁴, in *Homo* the two anterior cerebral arteries run side by side in the longitudinal cerebral fissure, curving round the genu of the corpus callosum, and after running backwards along the upper surface of this structure to its posterior extremity, they end by anastomosing with the posterior cerebral arteries. Occasionally the two arteries join to form a single vessel, as in *Pan* and *Hylobates*^{151, 165, 180, 196}. In its course the anterior cerebral artery gives off central and cortical branches¹⁹⁴.

In 1/4 *Pongo*, the left anterior cerebral artery divides to form a loop close to the mouth of the longitudinal fissure¹⁹⁶.

The callosal arteries are often absent uni- or bilaterally in *Pongo*¹⁹⁶.

Anterior communicating artery

No information for *Gorilla*.

In *Homo*, *Pongo* and when present in *Pan*^{56, 151, 164, 194, 196}, the anterior communicating artery connects the two anterior cerebral arteries at the entrance to the longitudinal fissure, having a length of 4 mm in *Homo* and 3-4 mm in *Pongo*¹⁹⁶.

The anterior communicating artery is reported as absent from majority of *Pan*^{151, 165, 196} and from Asian apes^{11, 196}.

3.2.2.1.3 Other

Vertebral artery

The vertebral artery, which is a branch of the subclavian artery in all great apes and *Homo*^{54, 147, 164, 194} enters the foramen transversarium of C6 in *Homo* and *Pan*, giving off no branches before this point^{54, 194}.

In both *Homo* and *Pongo*, the vertebral artery ascends ventral to the roots of the hypoglossal nerve^{164, 194}. In 5/8 *Pongo* the left vertebral artery was larger than the right, in 1/8 the right was larger than the left, and in 2/8 the vessels were equal in size¹⁶⁴. Inequality in size is also found in *Homo*¹⁶⁴.

It joins with the vessel of the opposite side to form the basilar artery in *Homo*, *Pan*, *Pongo* and *Hylobates*^{47, 164, 194}; at the lower border of the pons in *Homo*¹⁹⁴, at the upper border of the medulla in *Pongo*¹⁶⁴, and at the junction of the middle and caudal thirds of the pons in *Hylobates*⁴⁷.

Anterior spinal artery

No information for *Pan*, *Gorilla* or *Hylobates*.

In *Pongo*, the anterior spinal arteries originate symmetrically from each vertebral artery in 4/8 cases, and after a series of transverse anastomoses, as in *Homo*¹⁹³, the anterior median artery is formed¹⁶⁴. In 1/8 *Pongo*, the left contribution does not appear to join the median trunk, the left branch being absent. In the other specimens the distribution was not given¹⁶⁴.

Branches of the anterior spinal arteries, and of the trunk formed by their union run to the medulla oblongata in both *Homo* and *Pongo*^{164, 194}.

Posterior inferior cerebellar artery

No information for *Pan*, *Gorilla* or *Hylobates*.

The posterior inferior cerebellar artery arises from the vertebral artery on both sides, turning around the lower end of the olive (*Homo*) or pyramid (*Pongo*) of the medulla oblongata, passing superolaterally through the roots of the hypoglossal nerve (*Pongo*), and posterior (*Homo*) or anterior to (*Pongo*) those of the glossopharyngeal and vagus nerves to the lower border of the pons. At this point it turns downwards once more, posterior to the vagus and glossopharyngeal rootlets^{164, 194}.

This vessel may be absent from *Homo* and from 1/8 *Pongo*^{164, 194}. In the specimen of *Pongo* in which it is absent, its cerebellar supply is taken over by the anterior inferior cerebellar artery¹⁶⁴.

The posterior inferior cerebellar artery gives off the posterior spinal artery in both *Homo* and *Pongo* before being distributed to the cerebellum^{164, 194}.

Basilar artery

No information for *Gorilla*.

The vertebral arteries join to form the single basilar artery in *Homo*, *Pan*, *Pongo* and *Hylobates*^{47, 164, 194}; at the lower border of the pons in *Homo*¹⁹⁴, at the upper border of the medulla oblongata in *Pongo*¹⁶⁴, and at the junction of the middle and caudal thirds of the pons in *Hylobates*⁴⁷.

Branches of the basilar artery include pontine, anterior inferior cerebellar, labyrinthine, superior cerebellar, and posterior cerebral arteries in both *Homo* and *Pongo*^{164, 194}, although the labyrinthine artery more often arises from the anterior inferior cerebellar artery in *Homo*^{175, 176, 194}.

In both *Homo* and *Pongo* the basilar artery terminates at the upper border of the pons^{164, 194}.

Pontine arteries

No information for *Pan*, *Gorilla* or *Hylobates*.

In *Pongo* the ventral pontine branches arise throughout the extent of the basilar artery, and are more numerous cranially and caudally¹⁶⁴, as in *Homo*^{175, 176}. The transverse pontine branches in *Pongo* pass outwards on the surface of the pons¹⁶⁴, giving branches to it as in *Homo*¹⁹⁴, and ending by supplying the cerebellum. They do not communicate with the ventral branches¹⁶⁴.

Anterior inferior cerebellar artery

No information for *Pan*, *Gorilla* or *Hylobates*

The anterior inferior cerebellar artery lies ventral to the abducent nerve in *Homo* and *Pongo*^{164, 194}, although Stopford has recorded cases in *Homo* in which the anterior inferior cerebellar artery lies dorsal to the abducent nerve^{175, 176}.

Superior cerebellar artery

No information for *Pan*, *Gorilla* or *Hylobates*.

The superior cerebellar arteries arose from the posterior cerebral artery in *Pongo*¹⁶⁴, rather than from the basilar artery itself, as is the case in *Homo*¹⁹⁴.

There are two or three superior cerebellar arteries on each side in *Pongo*¹⁶⁴, passing to the surface of the cerebellum in both *Homo* and *Pongo*^{164, 194}.

Posterior cerebral artery

No information for *Gorilla*.

The posterior cerebral arteries are formed by the division of the basilar artery in *Homo*, *Pan*, *Pongo* and *Hylobates*^{164,165, 194, 196}.

In *Homo*, *Pan* and *Pongo* and *Hylobates* the posterior cerebral artery receives the posterior communicating artery^{164, 196, 194}.

A parieto-occipital branch, present in *Homo*¹⁹⁴, is absent from *Pongo*, with its area of distribution taken over by the anterior cerebral artery¹⁶⁴.

In both *Homo* and *Pongo* the posterior cerebral arteries supply the anterior and posterior thalamus and the superior colliculus, the inferior temporal gyrus, and the visual area of the cerebral cortex^{164, 194}. This includes Brodmann cortical areas 19, 20 and 37 (inferior temporal, occipito-temporal and pre-occipital areas) in *Pongo*¹⁶⁴, and calcarine branches to the striate cortex in *Homo* and *Pongo*^{164, 194}, although the extreme edge of the striate cortex bordering the lunate sulcus is supplied by the anterior and middle cerebral arteries in *Pongo*¹⁶⁴.

The posterior cerebral artery curves sharply around the oculomotor nerve in *Pongo*^{164, 196}, then winds round the cerebral peduncle to terminate within the calcarine fissure in both *Homo* and *Pongo*^{164, 194, 196}.

3.2.2.2 Veins

3.2.2.2.1 External jugular^b

External jugular vein

No information for *Gorilla* or *Hylobates*.

The external jugular vein is formed by the union of the posterior division of the retromandibular (temporo-maxillary) vein with the posterior auricular vein in *Homo*¹⁹⁴, while in *Pongo*, the posterior division of the retromandibular vein forms a loop with one of the tributaries of the external jugular vein¹⁷⁰. It receives tributaries from the glands and fat in the clavicular and deltopectoral regions in *Pongo*¹⁷⁰. In *Pan* and *Pongo*, and sometimes in *Homo*, it communicates with the internal jugular vein in the neck^{170, 194}.

In *Homo* and *Pongo*, the external jugular vein crosses sterno(cleido)mastoid obliquely, while in *Pan* it runs deep to this muscle^{169, 170, 194}. It is described as very small in *Pongo*¹⁷⁰, and very large in *Pan*^{26, 170}.

The vessel terminates in the subclavian vein in *Homo*¹⁹⁴ and in the internal jugular vein in *Pongo*¹⁷⁰.

Anterior jugular vein

No information for *Pan*, *Gorilla* or *Hylobates*.

The anterior jugular vein, which in *Homo* starts near the hyoid bone by the confluence of several superficial veins from the submandibular region and ends in the external jugular vein or the subclavian¹⁹⁴, is absent from *Pongo*¹⁷⁰.

3.2.2.2.2 Internal jugular^b

Internal jugular vein

No information for *Hylobates*.

In African apes and *Homo*, the internal jugular vein is the main outlet of blood from the cranium¹⁵. Its upper bulb represents either a direct continuation of either the sigmoid and transverse sinuses, or the occipital/marginal sinus complex^{29, 115}.

This vessel receives the inferior petrosal sinus and facial vein in *Homo*, *Pan* and *Pongo*^{170, 194}. It collects blood from the pterygoid plexus, the lingual and pharyngeal regions and the thyroid veins in *Homo* and *Pongo*^{170, 194}. In *Pan* and *Pongo*, and sometimes in *Homo*, it communicates with the external jugular vein in the neck^{170, 194}. It receives the deep cervical and vertebral veins in *Pongo*¹⁷⁰, while in *Homo* the deep cervical vein ends in the vertebral vein, and the vertebral vein ends in the upper and posterior part of the brachiocephalic vein¹⁹⁴.

The internal jugular veins may be absent from *Pan*¹⁶⁹. In *Gorilla*, the distance between the medial borders of the right and left internal jugulars at the level of their junction with veins at the base of the neck is 5 cm. The length of the unconnected trunk of the left internal jugular is 11 cm. An extensive venous network surrounds the upper part of the common carotid artery and the beginning of the internal and external carotids, and most of these veins eventually join to form the internal jugular¹⁴⁷.

In *Homo* and *Pongo* the internal jugular vein unites with the subclavian vein to form the brachio-cephalic trunk^{170, 194}.

3.2.2.2.3 Sinuses

Cavernosus (cranio-orbital)

No information for *Gorilla*.

Diamond's description of the cranio-orbital sinus, including its communication with the superior ophthalmic vein³⁵ leads to the conclusion that it is the same structure as the cavernous sinus¹⁹⁴. The cranio-orbital foramen may correspond to the superior orbital fissure, although this is less certain.

The cranio-orbital foramen³⁵ admits the anterior division of the ramus superior of the stapedial artery into the orbit. The cranio-orbital foramen is situated in the vicinity of the junction of the frontal, alisphenoid and orbitosphenoid bones. This foramen is exclusively arterial in the majority of *Homo*, and in *Pan* and *Symphalangus*³⁵. In *Pongo*, in which a vein was observed passing through the foramen, the relatively small foramen was dominated by the artery³⁵.

Petrosquamous

No information for *Gorilla* or *Hylobates*.

The petrosquamous sinus extends along the petrosquamous suture from the transverse/sigmoid sinus junction to the postglenoid foramen. It is present in some *Homo*, *Pan*, *Pongo* and *Symphalangus*^{37, 194}. In *Homo*, the sinus may be feeble or absent or may drain entirely into the retromandibular vein^{37, 194}. Segmental sulci arising from the petrosquamous sulcus are present as an uncommon variation in extant primates, including *Homo*⁵⁸.

Sphenoparietal

In *Homo* the sphenoparietal sinuses are inferior to the lesser wings of the sphenoid, next to the periosteum and near their posterior edges. Each receives small veins from the adjacent part of the dura mater and sometimes the frontal trunk of the middle

meningeal vein; it opens medially into the anterior part of the cavernous sinus, at the point where the ophthalmic veins join the cavernous sinus¹⁹⁴.

The skulls of *Hylobates*, except *H.klossi*, lack a sphenoparietal sulcus that would carry the sphenoparietal sinus and/or the sphenoidal artery³⁴, while the sphenoparietal sulcus is present in 78% of *Homo* and *Pongo*³⁵. The sphenoparietal sulcus is poorly developed and relatively uncommon in African apes, occurring in less than 20% of *Gorilla* hemicrania (n=77) and only 6% of *Pan* hemicrania (n=190)³⁵. The cranio-orbital sulcus seldom communicates with the orbit (20% for *Pan* and *Gorilla*), and when it does, it almost always involves only the cranio-orbital foramen³⁵.

Sinus communicans (possibly part of the transverse sinus)

This sinus, as described by Diamond³⁶, "extends from the postglenoid foramen to an aperture in the cranial base, and connects the petrosquamous sinus to the pterygoid plexus of veins in the infratemporal fossa. It runs in the angle between the petrosal bone and the side wall of the cranial cavity, along the petrosquamous and petrosphenoid sutures. It is accompanied by the inferior ramus of the stapediaal artery"³⁶.

The emissary vein of the sinus passes through the floor of the middle cranial fossa and joins the pterygoid venous plexus. In *Homo* this vein is homologous with the terminal (inferior) part of the middle meningeal vein³⁶. Communication between the middle meningeal vein and the pterygoid plexus is well known in *Homo*^{36, 194}.

Passage of the emissary vein is frequently through the foramen spinosum in *Homo* and African apes, and otherwise through the petrosphenoid fissure in most other

primates³⁷. Passage of the emissary vein through the foramen ovale has also been noted in *Homo*^{132, 202}.

3.2.2.2.4 Other

Facial vein

No information for *Gorilla* or *Hylobates*.

In *Homo* and *Pongo* the facial vein begins at the medial canthus of the eye^{170, 194}, in *Pongo* formed by the frontal vein¹⁷⁰, and in *Homo* from the confluence of the supratrochlear and supraorbital veins¹⁹⁴.

In *Homo* and *Pongo* the facial vein receives the inferior and superior palpebral veins, parotid veins, the deep facial vein from the pterygoid plexus, and the submandibular veins^{170, 194}. In *Pongo* below the parotid gland it receives a large vein from the tissues overlying the hyoid vein¹⁷⁰, which may correspond to the submental vein of *Homo*¹⁹⁴.

In *Homo*, the facial vein is also joined by superior and inferior labial, buccinator, masseteric, tonsillar, and external palatine veins. It may be joined by the vena comitans of the hypoglossal nerve, and often the pharyngeal and superior thyroid veins¹⁹⁴. The superior thyroid vein enters the facial vein in *Pan*¹⁷⁰.

The facial vein in *Homo* and *Pongo* terminates by uniting with the anterior division of the retromandibular (temporo-maxillary) vein^{170, 194} to form the external jugular vein in *Pongo*¹⁷⁰, while in *Homo* it terminates in the internal jugular vein¹⁹⁴.

Pterygoid plexus

No information for *Gorilla*, *Pongo* or *Hylobates*.

In *Pan* the veins of the pterygoid plexus do not form a large diffuse plexus, but consist of tributaries accompanying the large arteries and as in *Homo*¹⁹⁴, opening into a maxillary vein¹⁶⁹. In *Homo* and *Pan* the maxillary vein divides into two veins which unite with the superficial temporal vein and communicate with the anterior facial vein and with deep veins in the neck^{169, 194}.

3.2.2.3 Lymphatics

Deep cervical nodes

No information for *Hylobates*.

In *Homo* and *Pongo*^{170,194}, two groups of deep cervical nodes are present, whilst in *Pan* and *Gorilla* a single group is present^{147, 170}. In *Gorilla* they are described as lying 4 cm above the clavicle beneath the medial border of levator claviculae¹⁴⁷.

Occipital nodes

No information for *Gorilla* or *Hylobates*

These nodes are present in *Homo* and *Pan*^{170, 194}, but absent from *Pongo*¹⁷⁰.

Parotid nodes

No information for *Hylobates*.

Parotid nodes are present in *Homo*, *Pan* and *Pongo*^{170, 194}. A node in contact with the deep portion of the parotid gland is described in *Gorilla*¹⁴⁷.

Prelaryngeal nodes

These nodes, present in *Homo*¹⁹⁴, are absent from *Pan* and *Pongo*¹⁷⁰.

Pretracheal nodes

No information for *Pan*, *Pongo* or *Hylobates*.

Present in *Homo*¹⁹⁴. In *Gorilla* there are 3 large lymph nodes in the fork of the trachea between the bronchi¹⁴⁷.

Retropharyngeal nodes

No information for *Gorilla* or *Hylobates*.

These nodes, present in *Homo*¹⁹⁴, are absent from *Pan* and *Pongo*¹⁷⁰.

Submental nodes

No information for *Gorilla* or *Hylobates*.

Submental lymph glands are present on the surface of the mylohyoid in *Homo*¹⁹⁴, while no such glands are present in *Pan* or *Pongo*¹⁷⁰.

Superficial cervical nodes

No information for *Gorilla* or *Hylobates*.

These nodes, present in *Homo*¹⁹⁴, are absent from *Pan* and *Pongo*¹⁷⁰.

3.2.3 NERVES

3.2.3.1 Cranial^b

Optic (II)

No information for *Gorilla* or *Hylobates*.

In *Pongo*, the optic nerve is described as long and thick¹⁷⁰. Sonntag gives an intraorbital length of 27 mm in *Pongo*¹⁷⁰, compared with 25 mm in *Homo*¹⁹⁴.

In both *Homo* and *Pongo* the central artery of the retina enters the nerve on the medial side^{170, 194}. It was not detected in *Pan*¹⁶⁹.

Oculomotor (III)

No information for *Gorilla* or *Hylobates*.

The motor root of the ciliary ganglion originates directly from the inferior division of the oculomotor nerve in *Pongo*¹⁷⁰, while in *Homo* it originates from the nerve to the inferior oblique muscle¹⁹⁴.

In *Pan*¹⁶⁹, but not in *Homo* or *Pongo*^{170, 194}, a twig runs from the superior division of the oculomotor nerve to the ciliary ganglion.

In *Pan*, the inferior ramus of the oculomotor nerve enters the ocular surface of the inferior oblique muscle^{80, 169}, while in *Homo*, it goes to the orbital surface or posterior border of the muscle^{80, 194}.

The oculomotor nerve supplies levator palpebrae superioris in *Homo* and *Pan*^{169, 194}.

Ciliary ganglion

The ciliary ganglion is absent from 1/2 *Pan*⁸⁰, while in *Homo* and *Pongo* it lies close to the apex of the orbit in the interval between the optic nerve and the lateral rectus muscle^{170, 194}. In *Homo* the ganglion is described as small and flattened¹⁹⁴, and in *Pongo* as small and spherical¹⁷⁰.

Several fine short ciliary nerves supply the adipose tissue of the orbit in *Homo* and *Pan*^{80, 169, 194}.

Trochlear (IV)

No information for *Gorilla*, *Pongo* or *Hylobates*.

In *Pan* the trochlear nerve divides into two or three¹⁶⁹ rami near the lateral margin of the oblique muscle and each ramus goes respectively into the orbital and ocular surfaces⁸⁰. In *Homo* the nerve ends in the orbital surface of the muscle⁸⁰.

Trigeminal (V)

Trigeminal (semilunar) ganglion

No information for *Pan*, *Gorilla* or *Hylobates*.

In *Homo* and *Pongo* the ganglion is large and placed on the petrous part of the temporal bone where it forms part of the back wall of the middle cranial fossa^{170, 194}.

In *Pongo* it reaches close to the floor of the fossa and is thus lower down than in *Homo*¹⁷⁰.

Ophthalmic nerve (V1)

No information for *Pan*, *Gorilla* or *Hylobates*.

The ophthalmic division in *Homo*, *Pan* and *Pongo* divides into lacrimal, frontal and nasociliary branches^{169, 170, 194}.

Maxillary nerve (V2)

No information for *Gorilla* or *Hylobates*.

In *Pongo* the maxillary division is described as long and thick¹⁷⁰. In both *Homo* and *Pongo* it passes through the infraorbital canal or fissure^{170, 194}, ending in *Homo*, *Pan* and *Pongo* as an infraorbital plexus^{169, 170, 194}.

In *Homo* and *Pan*, the infraorbital nerve, which is the continuation of the maxillary nerve, runs under cover of levator labii superioris, and anastomoses with branches of the facial nerve to supply skin and mucous membrane^{169, 194}.

The pterygopalatine ganglion is connected to the maxillary nerve by ganglionic branches in *Homo*¹⁹⁴, while in *Pongo* it may be present as a separate body, or fused with the maxillary nerve¹⁷⁰.

Mandibular (V3)

No information for *Gorilla* or *Hylobates*.

The mandibular division has the same course and divisions in *Homo*, *Pan* and *Pongo*^{26, 170}.

Lingual nerve

The communication between the lingual nerve and the hypoglossal nerve in *Homo*¹⁹⁴ is absent from *Pongo*¹⁷⁰.

The chorda tympani joins the lingual nerve in the pterygoid region in *Homo* and *Pongo*^{170, 194}. In *Pan*, the chorda tympani is positioned like that in *Homo*⁷⁵.

In *Pan*, the lingual branch of the trigeminal nerve is described as vanishing "under cover of the geniohyoid muscle"¹⁶⁹, which does not seem to be the case in *Homo*, and is then present subjacent to the genioglossi in *Homo* and *Pan*^{169, 194}.

Abducent (VI)

No information for *Gorilla*, *Pongo* or *Hylobates*.

In *Homo* and *Pan* this nerve sinks into the ocular surface of the lateral rectus^{169, 194}.

Facial (VII)

No information for *Gorilla* or *Hylobates*.

Having emerged from the stylomastoid foramen in *Homo*, *Pan* and *Pongo*^{169, 170, 194}, it has a longer course before branching in *Pongo*¹⁷⁰ than it does in *Homo*¹⁹⁴.

Cervical, zygomatic and mandibular nerves are given off in *Homo*, *Pan* and *Pongo*^{169, 170, 194}, and auricular branches in *Homo* and *Pongo*^{170, 194}. *Homo* and *Pan* display temporal and buccal branches^{169, 194}.

No temporal branches are given off in *Pongo*, but an infra-orbital branch is present¹⁷⁰. The infra-orbital branch supplies orbicularis oculi and the muscles of the upper lip, and also gives off the buccinator nerve¹⁷⁰. It may be homologous with the buccal branch of the facial nerve in *Homo*¹⁹⁴.

The branches of the facial nerve intermingle with branches of the trigeminal nerve in the face in *Homo*, *Pan* and *Pongo*^{169, 170, 194}.

Glossopharyngeal (IX)

No information for *Gorilla*, *Pongo* or *Hylobates*.

The glossopharyngeal nerve supplies stylopharyngeus in *Homo* and *Pan*^{169, 194}.

In two specimens of *Pan*, the glossopharyngeal nerve sent off a branch which pierced the sheath of the hypoglossal nerve immediately after it hooked round the occipital artery, then leaving the nerve, joined the descendens hypoglossi to form part of the ansa hypoglossi¹⁸⁰.

Vagus (X)

No information for *Hylobates*.

Within the jugular foramen in *Homo* and *Pongo* the vagus nerve is closely applied to the glossopharyngeal and accessory nerves, and it is strongly fused with the

hypoglossal nerve below the base of the skull^{170, 194}. Branches in the cervical region include communicating branches to the glossopharyngeal and accessory nerves, and pharyngeal, superior laryngeal, cardiac, recurrent laryngeal nerves in *Homo*, *Pan* and *Pongo*^{169, 170, 194}.

Within the thorax each vagus breaks up into a posterior pulmonary plexus in *Homo*, *Pan* and *Pongo*^{169, 170, 194}. The left vagus in *Pongo* is not reformed as a distinct branch after this point, some of its filaments running through the oesophageal opening in the diaphragm as in *Homo* and *Pan*^{169, 194}, and others winding around the oesophagus to join the right vagus nerve¹⁷⁰. In *Homo* two branches descend from the left posterior pulmonary plexus to form, with a twig from the right vagus, the anterior oesophageal plexus¹⁹⁴. The left vagus in *Pan* passes through the diaphragm and divides into two branches, one of which ramifies as an oesophageal plexus and anastomoses with the right vagus¹⁶⁹.

In *Gorilla* the sympathetic innervation of the lungs differs on the two sides. On the right the sympathetic branch from the first thoracic ganglion joins the right vagus and accompanies it to the lung. On the left side the sympathetic branch arises from the third thoracic ganglion and runs anteriorly above the root of the lung, then curves to enter the lung separate from the vagus¹⁹⁵.

In *Homo* and *Pongo* two cords emerge from the right posterior pulmonary plexus^{170, 194}. In *Pongo* a thick cord receives filaments from the left vagus nerve, and a thin cord joins the thick cord in the abdomen¹⁷⁰. In *Homo* both branches join with the left vagus to form the posterior oesophageal plexus, from which a trunk is formed which enters the abdomen through the oesophageal opening in the diaphragm¹⁹⁴. The right

vagus in *Pan* passes through the posterior part of the oesophageal opening in the diaphragm, ending in the left semilunar ganglion¹⁶⁹.

In *Homo* and *Pongo* the anterior surface of the stomach is supplied mainly by the left vagus^{170, 194}, with *Pongo* having fibres running to the pylorus¹⁷⁰, absent from *Homo* and *Pan*^{169, 194}. The posterior surface is supplied mainly by the right vagus in *Homo* and *Pongo*, in *Homo*, *Pan* and *Pongo* involving both sides of the lesser curvature^{169, 170, 194}. The main mass of the right vagus in *Pongo* passes behind the coronary and splenic arteries to the side of origin of the superior mesenteric artery¹⁷⁰, where in *Homo*, *Pan* and *Pongo* it communicates with the coeliac and superior mesenteric plexuses^{169, 170, 194}, and in *Homo* and *Pan* with the coronary, hepatic, and splenic plexuses^{169, 194}.

In *Homo* and *Pongo* branches run to the caecum^{170, 194}, supplying the large intestine as far as the left colic flexure in *Pongo*¹⁷⁰, rather than terminating along the transverse colon as in *Homo*¹⁹⁴.

Superior laryngeal nerve

No information for *Gorilla*, *Pongo* or *Hylobates*.

In *Homo* and *Pan*, internal and external branches of the superior laryngeal nerve are present^{84, 194}.

The external branch supplies the cricothyroid muscle in *Homo* and *Pan*^{84, 194}.

The internal branch passes through the thyrohyoid membrane in *Homo* and *Pan*^{84, 194}.

Inferior laryngeal nerve (ascending branch of the recurrent laryngeal nerve)

In *Pan* the inferior laryngeal nerve arises from the recurrent laryngeal nerve, similarly to *Homo*^{84, 194}.

Communication of the superior with the inferior laryngeal nerve was observed in *Homo* and 4/6 *Pan*^{84, 194}.

Accessory nerve (XI)

No information for *Pongo* or *Hylobates*.

The spinal branch derives from the third and fourth cervical segments in *Pan*¹⁷⁷, while in *Homo* it originates from nuclei in the first five or six cervical segments¹⁹⁴.

The spinal accessory nerve separates the two portions of the sternocleidomastoid muscle in *Pan*^{26, 169}, while in *Homo* it pierces the deep surface of the upper part of sternocleidomastoid¹⁹⁴. The two parts of sternocleidomastoid in *Gorilla* are supplied by an anastomosis of the accessory nerve and the third cervical nerve¹⁴⁷.

In both *Homo* and *Pan* the spinal accessory nerve joins the vagus nerve to be distributed by branches of the latter^{26, 194}. In a specimen of *Pan* the spinal accessory nerve sends a branch direct to the larynx which has no connection with the vagus¹⁸⁰.

Hypoglossal (XII)

No information for *Hylobates*.

The nerve encircles the external carotid artery in *Pan* and *Pongo*^{26, 170}, while in *Homo* and *Gorilla* it crosses the artery^{147, 194}. In *Homo* and *Gorilla* the hypoglossal nerve crosses under the submandibular duct, thereafter passing parallel to it in

Gorilla^{74, 194}. In *Homo*, *Pan* and *Pongo*, the nerve passes superficial to the hyoglossus muscle^{169, 170, 194}.

In *Pongo*, there are fewer branches on the surface of the hyoglossus muscle than in *Homo*¹⁷⁰, and unlike *Homo*¹⁹⁴, there is no communication between the hypoglossal nerve and the lingual nerve on the anterior border of hyoglossus¹⁷⁰. The descending branch of the hypoglossal nerve is given off on the anterior surface of the external carotid artery in *Pongo*, and at the level of the occipital artery in *Homo*^{170, 194}.

Branches are given to the geniohyoid, stylohyoid and genioglossal muscles in *Homo* and *Pan*^{169, 194}, and the ansa hypoglossi sends branches to the omohyoid, sternohyoid and sternothyroid muscles in *Homo* and *Gorilla*^{147, 194}.

3.2.3.2 Cervical

Great auricular nerve

No information for *Pan*, *Pongo* or *Hylobates*.

This nerve arises from the second and third cervical nerves in *Homo* and *Gorilla*^{147, 194}. In *Gorilla* on the left side it is joined by a branch from the accessory nerve, while on the right side this contribution is lacking and the great auricular nerve is associated with the supraclavicular nerves¹⁴⁷.

In *Gorilla* the great auricular nerve passes up deep to the sterno(cleido)mastoid muscle¹⁴⁷, then deep to the platysma as in *Homo*^{147, 194}. In *Homo* the nerve encircles the posterior border of the sternocleidomastoid muscle¹⁹⁴.

Branches of the great auricular nerve in *Homo* and *Gorilla* supply the skin of the face over the parotid gland and mandibular angle, and the skin over the mastoid process^{147, 194}. This latter distribution reaches halfway between the auricle and the

sagittal crest in *Gorilla*¹⁴⁷. They also supply the back of the auricle. No preauricular branch is present in *Gorilla*¹⁴⁷, while in *Homo* a filament pierces the auricle to reach its lateral surface and be distributed to the lobule and concha¹⁹⁴.

The auricular branches of the great auricular nerve communicate with the posterior auricular branch of the facial nerve in *Homo* and *Gorilla*^{147, 194}.

Lesser occipital nerve

No information for *Pongo* or *Hylobates*.

This nerve arises from the second cervical nerve in *Homo* and *Pan*^{169, 194}, and from the third cervical nerve in *Pan* and *Gorilla*^{147, 169}. Additional origin from the third cervical nerve may be present in *Homo*¹⁹⁴.

In *Homo* and *Gorilla* the nerve emerges from the deep fascia^{147, 194}, in *Gorilla* about half way between the ear and the shoulder, and in both supplies the skin of the back of the neck and occiput¹⁴⁷.

It sends a branch to join the posterior supraclavicular nerve in *Gorilla*¹⁴⁷.

Transverse cutaneous nerve of the neck

No information for *Pongo* or *Hylobates*.

This nerve arises from the second and third cervical nerves in *Homo* and *Pan*^{169, 194}.

In *Gorilla* in the lower part of the neck, a descending branch emerges 9 cm lateral to the midline. It ramifies as it descends toward the nipple and is accompanied by a vein¹⁴⁷. In *Homo* the descending branches are distributed to the skin of the lateral and anterior regions of the neck, as low as the sternum¹⁹⁴.

3.2.3.3 Sympathetic

Internal carotid plexus

No information for *Gorilla*, *Pongo* or *Hylobates*.

A large nerve plexus lies in the carotid canal around the internal carotid artery in *Homo* and *Pan*^{75, 194}.

Superior cervical ganglion

Each ganglionic neuron is limited as to the volume of effector tissue, such as a blood vessel, that it innervates. Since the effector tissue increases in volume and surface area as a function of body size, the number of ganglionic neurons should increase as a function of the "quantity" of effector tissue innervated⁴⁴.

	Ganglionic neurons	Preganglionic axons	Myelinated preganglionic fibres	% myelinated	Ganglionic neurons/ Preganglionic axons
Left <i>Pan</i> A	828240	8764	4372	49.9	95:1
Right <i>Pan</i> A	634800	5154	3409	66.1	123:1
Right <i>Pan</i> B	795547	9151	3019	33.0	87:1
Left <i>Homo</i> A	1003384	11816	2369	20.0	85:1
Right <i>Homo</i> A	760370	12008	2792	23.3	63:1
Left <i>Homo</i> B	941980	8031	1614	20.1	117:1
Right <i>Homo</i> B	1041652	5305	5028	94.8	196:1
Left <i>Homo</i> C	947300	7072	3147	44.5	134:1
Right <i>Homo</i> C	773076	5594	3416	61.1	138:1

Table 3.2.1. Estimate of the neuron population in superior cervical sympathetic ganglia and the preganglionic fibre population in the cervical sympathetic trunk caudal to the ganglia in *Homo* and *Pan*. Adapted from ⁴⁴. Data on *Homo* A and B from ⁴³, on *Homo* C from ⁴⁴.

Ganglion	BW (kg)	Length of ganglion (mm)	Volume of ganglion (mm ³)	Mean cell density (cells/mm ³)	Mean cell territory (mm ³)
Left <i>Pan</i> A	50.0	39.6	102	8129	0.0001230
Right <i>Pan</i> A	50.0	12.0	78	8192	0.0001221
Right <i>Pan</i> B	25.0	11.3	54	14654	0.0000682
Left <i>Homo</i> C	53.2	27.3	133	7101	0.0001408
Right <i>Homo</i> C	53.2	32.0	174	4455	0.0002245

Table 3.2.2. Neurometric data of superior cervical sympathetic ganglia and the body weights of *Homo* and *Pan*. Adapted from ⁴⁵.

There is a general biological rule that the larger a species, the larger is the territory of each neuron, so that, the space occupied by each neuron, including its surrounding glia, is a function of body size. In general, neuronal packing density decreases in larger species. Increase in body size correlates with increase in volume of the ganglia, number of ganglionic neurons, average cell territory and the resulting ratio of ganglionic to preganglionic neurons. The increase in size of the ganglia is the result of an increase in the number of neurons as well as an increase in the average space occupied by each neuron⁴⁵.

Middle cervical ganglion

No information for *Gorilla*, *Pongo* or *Hylobates*.

In *Pan*, the middle cervical ganglion is fused with the cervicothoracic ganglion²⁵, while in *Homo* it may be absent or fused with the superior cervical ganglion¹⁹⁴.

Cervicothoracic ganglion

No information for *Gorilla*, *Pongo* or *Hylobates*.

In *Homo* and *Pan* this ganglion lies at the root of the neck in an angle enclosed by the subclavian and vertebral arteries^{25,194}. In both species it sent twigs with the vertebral

artery into the vertebral canal in C7, one to join the eighth cervical nerve, and another to join the vagus nerve^{25, 194}.

3.2.4 ALIMENTARY SYSTEM

3.2.4.1 Oral cavity

Buccal fat pad

No information for *Pongo* or *Hylobates*.

In newborn *Gorilla* the buccal fat pad has been observed^{99, 154, 65}. Rumbaugh describes "muscular" bulging of the cheek¹⁵⁴, which is almost certainly adipose in origin. In a newborn *Gorilla* examined by Hofer⁷⁰, the back and forth movements of the adipose pad could easily be seen during suckling. The consistency of the fat pad was soft and elastic on palpation⁷⁰. Raven¹⁴⁷ describes in an older *Gorilla* a fat pad resembling that seen in human infants, 20 by 30 mm with its long axis in a transverse direction, situated immediately below the zygomatic process of the maxilla and anterior to the masseter as in *Pan*⁷⁰, anterior to the insertion of temporalis, and lateral to the posterior superior part of the buccinator muscle. The parotid duct curved around the anterior aspect of the pad¹⁴⁷.

In a 12 year old male *Pan*, the buccal fat pad did not cause an externally visible bulge since it was covered partly by the lateral wings of the nose, and partly by skin folds.

With the mouth closed, almost the entire fat body was situated in front of the masseter⁷⁰, as in *Gorilla*¹⁴⁷. The body of the fat pad lay immediately on the lateral surface of the dorsal part of the anterior buccinator muscle and its rostral pole was found immediately caudal of the part of the maxilla containing the root of the canine tooth. In an open mouth position the topographical relations may be different⁷⁰. The

fat pad is covered by a thin layer of fascia which is part of the parotid-masseteric fascia. The adipose tissue is not lobulated, as is characteristic for the fat pad in *Homo*. The fat pad was approximately 40 mm long and approximately 25 mm high. Two processes originated from the corpus adiposum buccae, one running dorsally, the other caudally. The dorsal process is situated immediately under the zygomatic process of the maxilla and probably approaches the orbit. The caudal process is situated in the buccinator muscle, running towards the infratemporal fossa. The shape of the pad in this specimen of *Pan* is similar to that in *Homo*⁷⁰.

Philtrum

No information for *Hylobates*.

The upper lip area ventral of the nasal septum is where the philtrum, or nasolabial sulcus, regularly occurs in *Homo*. The philtrum, unique to *Homo*, originates embryologically from the medial nasal process of the fetal nose, which becomes a part of the upper lip. In this respect it is anatomically different from the lateral parts of the upper lip⁷¹.

Other sagittal sulci of the upper lip are not characteristic for *Homo*, although many sagittal wrinkles and small furrows may appear in the upper lip of some ageing individuals, caused by the decrease of turgor⁷¹. Sagittal sulci are often present in the upper lip of *Gorilla* and *Pongo*^{17, 71, 72}, described in detail below.

In *Gorilla*, the sagittal sulci of the upper lip vary greatly in number. These sagittal furrows do not encroach onto the smooth skin of the nares. In the skin of the upper lip two very distinct medial sagittal furrows originate lateral to the basal part of the nasal septum, vanishing a short distance above the margin of the upper lip. In

addition two more lateral sagittal furrows were found without any relation to the nasal septum. In some specimens of *Gorilla* more lateral sagittal sulci of the upper lip run into the region of the cheeks, as in *Pan*^{71, 72}.

In *Pongo*, the basal part of the nasal septum intrudes into the skin of the upper lip, where it disappears. From this point, a median sagittal sulcus runs down to the free margin of the upper lip. This single sulcus originates from two very short sulci bounding the anterior part of the nasal septum, joining each other a short distance superior to the anterior margin of the septum. Lateral to this median sulcus, which is not very deep, two other sagittal sulci are found, a little more distinct than the latter¹⁷.

71.

3.2.4.1.1 Soft palate

Levator veli palatini

No information for *Hylobates*.

The muscle originates from the apex of the basilar surface of the petrous temporal in all great apes and *Homo*^{31, 169, 194}. In a single specimen of *Pan*, the muscle shares a common origin with the tensor veli palatini¹⁶⁹. In African apes and *Homo* it also takes origin from the cartilaginous part of the Eustachian tube^{31, 169, 194}.

The muscle passes into the pharynx over the superior border of the superior pharyngeal constrictor^{31, 63}, running more horizontally in *Pan* and *Pongo* than in *Homo*^{169, 170}.

In great apes and *Homo* the muscle ends by spreading out in the superior aspect of the soft palate, meeting the muscle of the other side in the midline^{31, 194}.

Musculi uvulae

No information for *Gorilla* or *Hylobates*.

The uvula contains muscular fibres in *Homo*, *Pan*, and some specimens of *Pongo*^{27, 86, 194}. The muscle may not enter the uvula in *Pongo*^{86, 170}.

In *Homo* and *Pan* the muscles take origin from the tendinous aponeurosis of the soft palate^{57, 169, 194}, and in *Homo* also from the posterior nasal spine of the palate¹⁹⁴.

Palatoglossus

No information for *Gorilla*, *Pongo* and *Hylobates*.

The muscle is small in both *Homo* and *Pan*^{169, 194}.

It inserts into the posterior part of the tongue in *Homo* and *Pan*^{39, 194}, extending into the lateral part of the tongue in *Homo*¹⁹⁴.

Soft palate

Glandular orifices are numerous in the mucosa of great apes and *Homo*^{74, 169, 170, 194}.

In a specimen of *Symphalangus*, a piece of cartilage about 7 mm long was found in the middle of the soft palate. This piece of cartilage also displayed a number of elastic fibres and was surrounded by a longitudinally arranged bundle of skeletal muscles running anteroposteriorly in the soft palate¹⁰¹.

The uvula has been stated to be absent from *Pongo*^{130, 170}, but Chapman²⁷ describes it as pointing directly backwards in a straight line from the posterior palatine spine, rather than hanging down as in *Homo*^{27, 194}. It is present in African apes and *Homo*^{9,}

74, 86

The dimensions of the uvula in *Gorilla* are given as 13 mm in height and breadth at its base⁷⁴. The tip of the uvula in *Gorilla* has a deep median notch, giving it a bifid form⁷⁴.

Tensor veli palatini

No information for *Hylobates*.

It originates from the scaphoid fossa at the base of medial pterygoid plate, and the anterior aspect of the cartilaginous Eustachian tube in *Homo* and *Pan*^{169, 194}. In *Gorilla* the scaphoid origin may be partly from the scaphoid spine¹⁹⁷. It has a common origin with tensor veli palatini in *Pan*¹⁶⁹.

The muscle is more horizontal in *Pan* and *Pongo* than in *Homo*^{169, 170}.

In *Homo* and *Pan* the tendon passes around the pterygoid hamulus and passes horizontally to end in the palatine aponeurosis of the soft palate^{169, 194}.

3.2.4.2 Salivary glands

Anterior lingual gland

This gland is present in *Homo*^{129, 150, 159, 168, 170, 69, 150, 168, 194}, 2/3 *Pan*^{69, 150}, 1/2 *Gorilla*¹⁵⁰, and in *Pongo*^{129, 150, 159, 168, 170}, and is absent from 1/3 *Pan*¹⁶⁸, 1/2 *Gorilla*¹⁶⁸ and *Hylobates*¹⁶⁸.

Parotid gland

No information for *Gorilla*, *Pongo* or *Hylobates*.

The gland is pyramidal in shape in *Homo* and *Pan* with the base superiorly. It is positioned inferior to the concha auris^{169, 194}. Described as large in *Pan*²⁶, a capsule is present in both *Homo* and *Pan*^{169, 194}.

The apex of the gland touches the submandibular gland in *Pan*¹⁶⁹, while in *Homo* the stylomandibular ligament intervenes between the two¹⁹⁴. In *Pan* the upper part is described as having small lobules, the lower part being coarse¹⁶⁹.

The parotid duct crosses the masseter muscle in *Homo* and *Pan*^{26, 194}.

Sublingual gland

The sublingual gland opens onto the sublingual fold in all apes and *Homo*, with the exception of *Symphalangus*^{168, 194}. In *Symphalangus*, the ducts open onto carunculae sublinguales¹⁶⁸.

The fold itself is triangular in African apes and *Hylobates*^{53, 168, 169}, but not in *Homo* or *Pongo*¹⁶⁸, and may be bifid in *Pan* and *Hylobates*^{53, 168}.

Submandibular gland

No information for *Hylobates*.

The gland is divisible into superficial and deep parts in *Homo* and *Pan*^{169, 194}.

Irregular in shape in *Homo*¹⁹⁴, in *Pan* it is described as flat and triangular¹⁶⁹. About the size of a walnut in *Homo*, it is described as large in *Gorilla* and *Pongo*^{27, 74}.

Dimensions have been given as 38 mm in diameter in *Pan*¹⁶⁹, while in a specimen of *Gorilla* the gland is 42 mm long, 23 mm wide and weighs 17.5 g⁷⁴.

The submandibular gland is positioned in African apes as in *Homo*^{74, 169, 194}.

The duct of the submandibular gland arises from the deep surface of the gland in *Homo* and *Pan*^{169, 194}, opening onto a sublingual papilla in *Homo* and *Pan*^{169, 194}, while in *Gorilla* it opens onto the middle of the ventral surface of the tongue⁷⁴. The

hypoglossal nerve crosses under the proximal part of the submandibular duct in *Homo* and *Gorilla*^{74, 194}.

3.2.4.3 Tongue

Foramen caecum linguae

No information for *Pongo*.

This foramen was absent from African apes and hylobatids^{73, 74, 168}, but present in *Homo*¹⁹⁴.

In *Pan* a small circular depression appears in the midline close to the central circumvallate papilla, which could be the remnant of the foramen caecum⁷³.

Tongue

The tongue has a rounded apex in *Homo*, *Pongo* and hylobatids^{168, 194}, while in African apes the tongue has a blunt or square apex¹⁶⁸. A mesial apical notch is absent from all apes and *Homo*^{74, 168, 194}, with the exception of *Hylobates muelleri*¹⁶⁸.

Sonntag considers that *Pongo* has the most human-like proportions of length to width¹⁶⁸, while the tongue is described as elongated in hylobatids and *Pan*^{53, 168}, and broad in *Gorilla*^{9, 168}. A frenulum linguae is present in all apes and *Homo*^{32, 46, 169, 170, 171}, with the possible exception of 1/4 *Gorilla*⁹, while the plica fimbriata is absent only from hylobatids^{74, 114, 150, 169, 171, 194}.

Pigment of the tongue occurs in *Gorilla*¹¹⁴ and *Hylobates*¹⁷⁰, and on the inferior surface alone in *Homo*¹⁹⁴.

3.2.4.3.1 Muscles

Genioglossus

No information for *Gorilla*, *Pongo* or *Hylobates*.

In *Homo* the muscle originates from the superior mental spine on the inner surface of the mandibular symphysis¹⁹⁴, and in *Pan* the muscle from the bottom of the genial fossa¹⁶⁹.

Triangular in *Homo*¹⁹⁴, it is a thick, narrow muscle in *Pan*¹⁶⁹. The muscles of the two sides are separated by a septum in *Pan*¹⁶⁹, but are in contact in *Homo*¹⁹⁴.

In both *Homo* and *Pan* fibres insert into the upper part of the hyoid bone, the remainder inserting into the tongue^{39, 169, 194}.

Hyoglossus

No information for *Hylobates* or *Gorilla*.

In *Homo* and *Pan* the muscle takes origin from the lateral body and the whole of the greater cornua of the hyoid bone^{169, 194}.

The anterior fibres run more horizontally in *Pongo* than in *Pan*¹⁷⁰.

In *Homo* and *Pan* the muscle inserts into the side of the tongue, beneath styloglossus^{169, 194}.

Styloglossus

No information for *Hylobates*.

In all except *Gorilla* the muscle takes origin from the outer surface of the styloid process^{30, 169, 194}. In *Pan* and *Gorilla* it originates from the temporal bone adjacent to the process³⁰.

In *Homo* and *Pan*, the longitudinal fibres of the muscle insert into the side of the tongue, almost to the apex, while the oblique fibres overlap hyoglossus and decussate with its fibres^{169, 194}.

3.2.4.3.2 Papillae

Filiform

The filiform papillae are present on the anterior two-thirds of the tongue in all apes and *Homo*^{53, 74, 168, 194}. In African apes and hylobatids, they are also present on the posterior third of the tongue^{53, 168}. Both conical and cylindrical papillae are present in all apes and *Homo*, with the conical form predominating in Asian apes¹⁶⁸.

In *Homo* the papillae are arranged in rows parallel to the vallate papillae, except at the apex of the tongue where the rows run transversely¹⁹⁴. Rows or ridges are also present in Asian apes (no information for African apes), which also show clusters, and in *Pongo* oblique chains¹⁶⁸. The points of the papillae are directed posteriorly in all apes, while in hylobatids the points may also be directed posteromedially or posterolaterally¹⁶⁸. The size of the papillae increases from anterior to posterior and from lateral to medial in *Pan* and Asian apes^{53, 168}.

The filiform papillae have secondary dermal papillae in all except *Pongo*^{168, 194}, and partly overlap the fungiform papillae in *Pan*, *Pongo* and *Hylobates*, but not in *Gorilla* or *Symphalangus*¹⁶⁸.

Fungiform

The fungiform papillae are present in all apes and *Homo* on the dorsum, sides and apex of the tongue^{168, 194}. In all apes they are also present on the inferior surface of the tongue¹⁶⁸. There are very few fungiform papillae on the lateral borders of the tongue in *Hylobates*, and *Symphalangus* lacks these papillae in the midline¹⁶⁸. A double row of fungiform papillae is present around the frenulum in *Pongo* and *Hylobates*¹⁶⁸.

Scattered irregularly in *Homo* and 1/2 *Gorilla*^{74, 194}, in all apes the papillae are arranged in clusters and transverse rows¹⁶⁸, and in African apes in oblique chains¹⁶⁸. The papillae are larger in African apes than in Asian apes, and *Pan* has larger papillae than *Gorilla*¹⁶⁸. No information for *Homo*.

The fungiform papillae are partly concealed by the filiform papillae in *Pan*, *Pongo* and *Hylobates*, but not in *Gorilla* or *Symphalangus*¹⁶⁸. Pedunculated papillae, which are intermediate between fungiform and filiform papillae, are present in African apes and *Hylobates*, but absent from *Pongo*^{74, 168}.

Vallate

The vallate papillae are situated on the dorsum of the tongue immediately in front of the sulcus terminalis. They are large in all apes and *Homo* with the exception of *Hylobates*⁵³. The number of papillae varies from eight to twelve in *Homo*^{114, 194}, from three to fifteen in *Pan*^{42, 77, 168, 204}, five to eight in *Gorilla*^{9, 32, 41, 46, 74, 114, 168}, six to twelve in *Pongo*^{13, 50, 51, 53, 124, 155, 168}, and three to five in hylobatids¹⁶⁸.

The papillae are arranged in a row, which is V-shaped in *Homo*¹⁹⁴, 4/14 *Pan*^{26, 27, 46}, 6/7 *Gorilla*^{9, 32, 41, 46, 74}, 6/7 *Pongo*^{13, 27, 50, 51, 53, 124, 155, 168} and 1/5 hylobatids⁵³.

Alternatively, the row is Y-shaped in 3/14 *Pan*^{9, 57, 124}, 1/7 *Gorilla*¹⁶⁸ and 3/5 hylobatids¹⁶⁸. A T-shaped row is present in 5/14 *Pan*^{42, 53, 78, 79, 183}; and 1/7 *Pongo*¹⁸⁶. The remaining two specimens of *Pan* have vallate rows described as "cruciate"¹¹⁶ and "linear"⁷⁷, and in 1/5 hylobatids the row is described as "triangular"¹⁶⁸.

In all apes and *Homo*, each papilla is encircled by a sulcus with a surrounding vallum, and the papillae are shaped like truncated cones with the small end attached to the tongue^{114, 168, 194}.

The outermost vallate papilla is level with the central rows and sulci of the foliate papillae in *Homo*, *Pan* and hylobatids, while in *Gorilla* and *Pongo* this papilla is level with the posterior extremity of the foliate papillae¹⁶⁸.

Foliate

Four or five vertical folds are present on the lateral side of the tongue just in front of the palatoglossal arch in *Homo*¹⁹⁴, while seven to fifteen are present in *Pan*^{13, 42, 168}, eleven to twenty in *Gorilla*^{74, 114, 168}, twelve to fourteen in *Pongo*^{13, 168}, and four to twelve in hylobatids^{53, 168}.

3.2.4.4 Pharynx

3.2.4.4.1 Muscles

Inferior constrictor

No information for *Gorilla*, *Pongo* or *Hylobates*.

The muscle originates in *Homo* and *Pan* from the side of the cricoid cartilage and the oblique line on the thyroid cartilage^{169, 194}. *Pan* sometimes has an additional origin from the first tracheal ring¹⁶⁹.

In both species the horizontal fibres overlap the oesophagus, and the vertical fibres ascend and overlap the middle constrictor^{169, 194}.

The muscles of opposite sides in both species meet in a fibrous raphe in the posterior median line^{169, 194}.

Middle constrictor

No information for *Gorilla*, *Pongo* or *Hylobates*.

In both *Homo* and *Pan* the muscle takes origin from the superior border of the hyoid bone along the greater cornu to the angle between the greater and lesser cornua^{169, 194}, and in *Homo* alone from the stylohyoid ligament¹⁹⁴.

In both species the lower fibres of the middle constrictor are overlapped by those of the inferior constrictor^{169, 194}.

The insertion of the muscle in *Homo* and *Pan* is into the posterior median fibrous raphe^{169, 194}.

Stylopharyngeus

No information for *Hylobates* or *Gorilla*.

In *Homo*, *Pan* and *Pongo* it takes origin from the base of the styloid process^{30, 57, 194}, in *Pan* extending to the adjacent temporal bone and also taking origin from the tendon of styloglossus^{30, 169}.

Insertion in *Homo* and *Pan* is into the side of the pharynx between the superior and middle pharyngeal constrictors, with fibres ending in the constrictors themselves^{169, 170, 194}. No fibres pass into the constrictors in *Pongo*¹⁷⁰.

Innervation of stylopharyngeus in *Homo* and *Pan* is via a branch of the glossopharyngeal nerve^{169, 194}.

Superior constrictor

No information for *Hylobates*.

In all great apes and *Homo* the muscle takes origin from the anterior region of the basiocciput between the two bellies of longus capitis, continuing to a point medial (posteromedial in *Pongo*³¹) to the origin of levator veli palatini on the petrous apex, the pharyngeal tubercle^{31, 169, 194}. In all except *Gorilla* the muscle takes origin from the lower margin of the medial pterygoid plate^{31, 169, 194}. An origin from the pterygomandibular ligament, the mandibular alveolar region above the posterior extremity of the mylohyoid line, and the tongue, is present in *Homo* and *Pan*^{169, 194}. *Pan* and *Gorilla* display origins from the mucous membrane of the mouth and pharynx respectively^{31, 169}. *Homo* alone possesses an origin from the reflected tendon of tensor veli palatini and a portion of the bony palate¹⁹⁴.

The space between the superior constrictor and the basicranium is filled by levator and tensor veli palatini in *Pongo*⁶³, while it is a real space in *Pan*¹⁶⁹.

In all great apes and *Homo* the insertion of the muscles of the opposing sides is to the median raphe, prolonged onto the basilar process of the occipital bone^{31, 194}.

3.2.4.4.2 Pharyngeal cavity

Palatine tonsil

No information for *Pongo* or *Hylobates*.

The palatine tonsils are present in *Homo*, *Pan* and *Gorilla*^{74, 169, 194}. In *Gorilla* the palatine tonsil measured about 20 mm in length and 10 mm in breadth⁷⁴.

In *Homo* and *Pan* the tonsils were supplied by the ascending pharyngeal artery^{169, 194}, although the main supply in *Homo* is via the tonsillar branch of the facial artery¹⁹⁴.

Pharyngeal tonsil

No information for *Gorilla* or *Pongo*.

A pharyngeal tonsil is present in the roof of the nasopharynx in *Homo*, *Pan* and *Symphalangus*^{101, 169, 194}, extending onto the posterior wall of the nasopharynx in *Homo*¹⁹⁴.

The tubal tonsil, which is the lateral prolongation of the pharyngeal tonsil behind the pharyngeal opening of the auditory tube, is present in *Homo*¹⁹⁴ and absent from *Symphalangus*¹⁰².

Pharyngobasilar fascia

No information for *Pan*, *Gorilla* or *Hylobates*.

The pharyngobasilar fascia lies between the superior pharyngeal constrictor and the basicranium in *Homo*¹⁹⁴. Hill found it to be absent in *Pongo*⁶³, while Dean found it present³¹.

3.2.4.5 Oesophagus

Pars cervicalis

No information for *Gorilla* or *Hylobates*.

The oesophagus is entirely behind the trachea in the neck in *Homo*, *Pan* and *Pongo*^{169, 170, 194}.

3.2.5 RESPIRATORY SYSTEM

3.2.5.1 Nose

Both serous and mucous glands are present in the entire respiratory region of

*Hylobates*¹¹⁰, a condition similar to that in *Homo*^{19, 149, 156}.

3.2.5.1.1 Cartilages

Alar

The major alar cartilages in great apes are small, and have their facial surfaces directed anteriorly³⁸. As in *Homo*, these surfaces are slightly convex and oval in outline, although unlike *Homo*, in great apes their long axes are vertical^{38, 194}.

In great apes the facial parts of the cartilages occupy small narrow vertical areas³⁸, as in *Homo* immediately above and lateral to the point of the nose^{38, 194}. The medial crus of each cartilage is small and irregular in shape, but quite distinct³⁸.

In *Gorilla* the edge of the ala is not approximately horizontal as in *Homo*, but is continued, as a rounded thick fold, downwards and laterally and then downwards and medially into the upper lip³⁸. This rim-like fold is the most striking characteristic of the nose in *Gorilla*, and its outer edge which is convex laterally is sharply defined³⁸.

Accessory nasal cartilages are absent from great apes³⁸.

In front the major alar cartilages are separated by a notch which can be felt at the apex of the nose in *Homo* and *Gorilla*^{38, 71, 194}. In *Pan* and *Pongo* the medial sulcus is very faint³⁸.

Lateral

In great apes the lateral cartilages of the nose are small and have their facial surfaces directed forwards, the region of the nose in which they lie being flat from side to side³⁸.

Septal

The nasal septum is short in *Hylobates*, and long in *Symphalangus*²⁰¹. In a specimen of *Hylobates*, at 60% of the distance from the anterior end of the nose, the height of the nasal septum was 32 mm, and the maximum nasal cavity width was 28 mm, giving an approximate height/width ratio of 1:0.9¹⁰⁹.

In great apes the septal cartilage does not come far forwards and its anterior part ends in a nearly vertical border which is convex forwards. This anterior edge is far from the point of the nose and lies a considerable distance from the posterior end of the medial crus of the alar cartilage³⁸.

The anterior attachment of the nasal septum in *Pongo* is located within or anterior to the plane formed by the lateral margins of the nasal aperture¹¹³. In *Pan* and *Gorilla* the septal attachment is positioned more anteriorly than in *Pongo*¹¹³. The anterior attachment of the cartilage in great apes creates a substantial horizontal distance between the septal and anterior vomeral attachments¹¹³.

In *Hylobates* the nasal septum was attached to the hard palate only¹⁰⁹.

Alteration of anterior facial growth rates is not a consequence of total submucosal resection of the cartilaginous nasal septum in *Pan*¹⁶⁶, therefore it can be tentatively concluded that the septal cartilage plays no significant role in anterior facial growth in *Homo*¹⁶⁶.

3.2.5.2 Larynx

Quadrangular membrane

No information for *Gorilla*, *Pongo* or *Hylobates*.

Present in *Homo* and *Pan*^{84, 89, 194}.

Vestibular ligament

No information for *Hylobates*.

The vestibular fold is fixed anteriorly to the angle of the thyroid cartilage immediately below the attachment of the epiglottis in *Homo*¹⁹⁴, while in *Pan* it does not extend to the thyroid cartilage, only to the epiglottis near its junction with the thyroid cartilage^{85, 89}.

In *Pan*, when the cuneiform cartilage forms an eminence, the vestibular fold attaches onto the lower segment of the cuneiform cartilage, strictly connected with the arytenoid cartilage⁸⁵. When in *Pan* the cuneiform cartilage does not extend into the fold, it inserts as in *Homo* onto the arytenoid cartilage, forming a small process^{85, 194}.

Small cartilaginous fragments are present in the vestibular fold in *Pan* and *Pongo*^{16, 84, 85}, usually absent from *Homo*⁸⁴. These fragments are remnants of an originally uniform cartilaginous connection between the epiglottis and the cuneiform⁵⁵.

Muscle fibres, consisting of upper bundles of thyroarytenoid are present in the fold in *Homo* and African apes⁴⁰, although Jordan did not find such fibres in *Pan*⁸⁵.

Vocal ligament

No information for *Gorilla*.

The upper edge of the lateral part of the cricothyroid ligament is free and thickened slightly to form the vocal ligament, which is thick in *Pan*⁸⁵ and thin in *Pongo*¹⁷⁰.

The vocal folds stretch from the middle of the angle of the thyroid cartilage in *Homo* and *Pan*^{85, 89} to the vocal processes of the arytenoid cartilages in *Homo*, *Pan* and *Pongo*^{85, 89, 170}. In *Pan* they extend to the arytenoid cartilage beyond the process⁸⁵.

The position of the *plica vocalis* in *Hylobates* resembles that in *Homo*, that is, the level of the lower third of the thyroid cartilage⁴⁰. The double vocal ligament in *Hylobates* permits complete closure of the glottis¹²⁷.

An accumulation of elastic fibres in the form of a glomus in the anterior segment of the vocal ligament is present in *Pan*, and may also be observed in *Homo*⁸⁵.

In its middle part, in fixed specimens of *Pan*, the free edge of the vocal fold is thinner and directed upward. In fresh specimens, the upward "extension" of the fold is less distinct and its shape resembles the vocal fold in *Homo*⁸⁵. According to Kelemen, the membranous structure of the free edge and upward extensions are characteristic of the vocal fold of *Pan*, and make possible inspiratory voice^{89, 90}.

The length of the vocal fold is 13-14 mm in juvenile *Pan* and 18-20 mm in adult *Pan*, which is equal to the length of the intermembranous part of the rima glottidis.

The length of the vocal folds in male *Homo* is 18-25 mm and in females 12-17 mm¹²⁵. The intercartilaginous segment of the rima measures 4-6 mm. Hence in *Pan*, the vocal fold constitutes about three-quarters of the length of the rima glottidis⁸⁵, compared with three-quarters to three-fifths in *Homo*^{85, 194}. The length of the vocal ligament in *Pan* is nearly half of the length of the rima glottidis, similarly to *Homo*⁸⁵.

The cartilaginous part of the glottis is lower than the vocal folds in *Pan*⁸⁹, as a result of which they are able to emit simultaneous double tones⁸⁵.

Between the vocal and vestibular ligaments lie the openings of the laryngeal ventricles in *Pongo*¹⁷⁰ which corresponds to the sinus of the larynx in *Homo*¹⁹⁴. In *Pongo* these lead upward to the laryngeal air sacs¹⁷⁰, and in *Homo* to the sacculus of the larynx¹⁹⁴.

3.2.5.2.1 Muscles

Aryepiglotticus

No information for *Gorilla*, *Pongo* or *Hylobates*.

This muscle is absent from 10/11 *Pan*^{3, 84}.

Arytenoideus

No information for *Hylobates*.

The muscle extends from one arytenoid cartilage to the other on the internal surface, including the muscular processes in *Homo*, *Pan* and *Pongo*^{84, 170, 194}.

In all great apes and *Homo* the arytenoid muscle has a transverse plane of fibres^{84, 89, 169, 170, 194}. Oblique planes are present in *Homo*¹⁹⁴, *Gorilla*¹⁷² and 2/6 *Pan*^{3, 169}, and absent from *Pongo*¹⁷⁰ and 4/6 *Pan*^{84, 89, 97, 122}. These oblique fibres are blended with thyroarytenoid in *Homo* and also when present in *Pan*^{84, 194}.

The magnitude of the angle formed in sagittal section by a line corresponding to the plane of the thyroid lamina, and the long axis of cross-section of the arytenoid muscle, is quoted by Kleinschmidt as 25° in *Homo*, mean 27° (range 15°-47°) in *Pan*, 82° in *Gorilla* and 46° in *Pongo*^{84, 91, 92}.

Cricoarytenoideus lateralis

No information for *Gorilla* or *Hylobates*.

In *Homo* and *Pongo* the muscle originates from the superior border of the side of the cricoid cartilage^{170, 194}.

The muscle passes obliquely cranioposteriorly to insert in *Homo*, *Pan* and *Pongo* onto the muscular process of the arytenoid cartilage^{84, 89, 170, 194}. In *Pan* and *Pongo* fibres insert in addition onto the external surface of the thyroid cartilage^{16, 84}, or onto the internal surface in 1/2 *Pongo*⁹⁷.

Cricoarytenoideus posterior

No information for *Gorilla* or *Hylobates*.

In *Homo* and *Pongo* the muscle takes origin from each lateral half of the posterior surface of the cricoid cartilage^{126, 170, 194}, and in *Pan* from a tubercle on the upper border⁸⁴.

The muscles of the opposite sides are separated by an interval in *Homo*¹⁹⁴, either fused or separated in *Pan*^{84, 89}, and fused inferiorly in *Pongo*¹⁷⁰.

Insertion in *Homo*, *Pan* and *Pongo* is onto the muscular process of the arytenoid cartilage^{84, 89, 170, 194}.

Cricothyroid

This muscle originates from the cricoid cartilage in *Homo* and *Pongo*^{84, 194}.

The muscles of the two sides form into two layers in *Homo* and *Pan*^{57, 84, 194}, separated in the midline by the cricothyroid membrane.

In all apes and *Homo* the muscle inserts onto the inferior border and internal surface of the thyroid cartilage, as far as the inferior cornua^{3, 40, 84, 89, 97, 194}. In *Pan* and *Hylobates* a further insertion is present to the external surface of the thyroid cartilage on the posterior lamina⁸⁴, occupying one-third of the laminar surface in *Pan*⁸⁴. The internal insertion occupies one-third of the deep surface of the thyroid lamina in *Pan*⁸⁴, and is described in *Hylobates* as more extensive than in *Homo*⁴⁰.

Thyroarytenoid

No information for *Gorilla* or *Hylobates*.

In *Homo*, *Pan* and *Pongo* it takes origin from the inner surface of the thyroid lamina near the midline^{40, 84, 89, 170, 194}; from the lower half in *Homo*¹⁹⁴, and from a third to two-thirds in *Pan*⁸⁴.

A broad flat muscle, it is in two parts in *Homo* and *Pan*^{89, 194}, but forms a single sheet in *Pongo*¹⁷⁰. It is adherent to the true vocal cord in *Pan* and *Pongo*^{84, 89, 170}, and does so occasionally in *Homo*¹⁹⁴.

It inserts in *Homo*, *Pan* and *Pongo* onto the lateral border and muscular process of the arytenoid cartilage^{84, 89, 170, 194}, including the vocal process in *Pan*⁸⁹. In *Pan* the thyroarytenoid muscle may insert with the cricoarytenoid muscle onto the upper part of the cricoid cartilage^{84, 97, 172}.

Thyroepiglotticus

No information for *Gorilla*, *Pongo* or *Hylobates*.

In *Homo* and *Pan*, it originates from the internal surface of the thyroid cartilage^{169, 194}, in *Homo* lateral to the origin of the thyroarytenoid¹⁹⁴.

It is absent from 1/3 *Pan*⁸⁴, and may be given off by the thyroarytenoid muscle¹⁹⁴.

In *Homo* it merges into the aryepiglottic fold¹⁹⁴, inserting in *Pan* onto the stem¹⁶⁹, and in *Homo* onto the margin¹⁹⁴, of the epiglottis.

Vocalis

No information for *Gorilla*, *Pongo* and *Hylobates*.

In *Homo* and *Pan* the lower and deeper fibres of the thyroarytenoid muscle form a band, the vocalis, which is attached to the vocal process and to the inferior impression on the anterolateral surface of the arytenoid cartilage^{84, 194}.

In both *Homo* and *Pan* many of its deeper fibres take origin from the vocal ligament, and so do not extend so far forwards as the thyroid cartilage^{84, 184, 194}.

3.2.5.2.2 Cartilages

Arytenoid

No information for *Gorilla* or *Hylobates*.

Each is pyramidal in *Homo*, *Pan* and *Pongo*^{84, 170, 194}.

The arcuate crest is more horizontal, and is not arched upward in *Pan*, unlike *Homo*^{84, 89, 169}. The oblong fovea is therefore more pronounced, and there is no triangular fovea connected with the arcuate crest⁸⁴.

Its lateral angle or muscular process, rounded and prominent, projects backward and laterally, giving attachment to the thyroarytenoid, posterior cricoarytenoid, lateral cricoarytenoid and arytenoideus in *Homo*, *Pan* and *Pongo*^{84, 89, 170, 194}.

The anterior angle or vocal process is pointed in *Homo* and *Pan*^{89, 194}, and globular in *Pongo*¹⁷⁰. The vocalis inserts onto the vocal process in *Homo* and *Pan*^{84, 194}, and the thyroarytenoid inserts onto the vocal process in *Pan*⁸⁹.

The apex curves backwards and medially in *Homo* and *Pan*^{84, 194} and articulates with the corniculate cartilage in *Homo* and *Pongo*^{170, 194}.

The interrelated arytenoid, corniculate and cuneiform cartilages may form a single aryteno-corniculate-cuneiform complex in *Pan*⁸⁴, with the arytenoid and corniculate cartilages having a common perichondrium⁸⁹.

Corniculate

No information for *Gorilla* or *Hylobates*.

The corniculate cartilages are fused with the arytenoid cartilages in *Pan*^{3, 84, 89} and *Pongo*¹⁷⁰, and as a variation in *Homo*¹⁹⁴.

The interrelated arytenoid, corniculate and cuneiform cartilages may form a single aryteno-corniculate-cuneiform complex in *Pan*^{84, 89}. It is composed of a number of small cartilaginous fragments of irregular shape surrounded by a common perichondrium. Loose connective tissue, adipose tissue and glands are quite numerous among the segments⁸⁴.

Nodular in form in *Homo*¹⁹⁴, the corniculate element in *Pan* is formed by a thin lamina bent posteromedially under the arytenoid muscle⁸⁴. The ends of the bilateral cartilages almost always converge, and may be fused⁸⁴.

Cricoid

No information for *Gorilla* or *Hylobates*.

Seen from above, in *Pan* the cartilage is either oval, or is round as in *Homo*⁸⁴.

Compared with *Homo*, *Pan* has a more funnel-shaped cricoid¹⁹⁹.

The lamina is rectangular in *Pan*, with superior and inferior borders of approximately equal length, while in *Homo* the inferior part of the lamina is wider⁸⁴. The posterior surface is marked by a median vertical ridge in *Homo* and *Pongo*^{170, 194}, weakly so in *Pan*^{84, 89}. The angle of inclination of the dorsal line of the lamina in relation to the inferior border of the arch ranges from 90° to 100° in *Homo*⁹³, and between 95°-115° in *Pan*^{84, 93}. This angle measured 120° in *Gorilla* and 110° in *Pongo*⁹³.

The external surface affords attachment to the cricothyroid in *Homo*¹⁹⁴, while in *Pan* the cricothyroid articular surface is at the transition of the lamina to the arch, at which point there may be a spike⁸⁴. A cricotracheal ligament is present in *Homo*, *Pan* and *Pongo*^{84, 170, 194}.

In *Pan* the inferior border of the lamina possesses a notch, usually shallow, which is absent from *Homo*⁸⁴.

The superior border slants runs obliquely in *Homo* and *Pan*^{89, 194}, but reaches almost as high as the upper border of the hyoid cartilage in *Pan*, a marked difference from *Homo*⁸⁹.

Cricothyroid membranelligament

No information for *Gorilla* or *Hylobates*.

This membrane separates the cricothyroid muscles of the opposing sides.

In *Homo*, *Pan* and *Pongo* it has a well developed conus elasticus, and is thicker anteriorly, and thinner laterally^{84, 89, 170, 194}. In all taxa, the upper border of the membrane forms the vocal ligament^{84, 89, 170, 194}.

The thick anterior part in *Pan* forms a ligament, higher than in *Homo* due to the presence of an inferior notch in the thyroid cartilage⁸⁴.

Cuneiform

Cylindrical in *Homo* and *Pan*, the cartilages extend down to the vestibular fold^{84, 194}.

These cartilages are absent from 1/5 *Pan*⁴², *Gorilla*⁴⁰ and 1/2 *Pongo*¹⁷⁰, and present in *Homo*¹⁹⁴ and *Hylobates*⁴⁰.

A aryteno-corniculate-cuneiform complex may be present in *Pan*^{84, 89}. The cuneiform and corniculate cartilages constitute a whole ellipsoidal or spherical lamina connected with the upper part of the arytenoid cartilage⁸⁴. As an alternative to this "complex", the cuneiform in *Pan* may be separate from the fused corniculate and arytenoid cartilages⁸⁴.

Epiglottis

A thin, spade, or leaf-like, lamella in *Homo* and *Pan*^{85, 89, 194}, the epiglottis projects obliquely upwards behind the tongue and the body of the hyoid, and in front of the entrance to the larynx. The free extremity is directed upwards in *Homo*, while in *Pan* and *Pongo* the epiglottis is curved posteriorly^{84, 85, 170}. The lateral borders in *Pan* are also curved downward, owing to the oblique position of the epiglottis. As a result, the epiglottis limits the *aditus laryngis* to a greater degree than in *Homo*⁸⁵.

The upper border of the epiglottis may display a median notch in *Pan*⁸⁴. While the upper part of the epiglottis is a solid lamina, its lower part is divided into several

cartilaginous segments of various size and shape, each separately covered by perichondrium. Connective and adipose tissue and glands lie among these fragments⁸¹.

The stalk of the epiglottis is connected by the thyroepiglottic ligaments to the thyroid cartilage in *Homo* and *Pongo*¹⁷⁰. The sides of the epiglottis are attached to the arytenoid cartilages by the aryepiglottic folds of mucous membrane in *Homo* and great apes^{42, 74, 84, 89, 194}, although in *Pan* these folds are short^{42, 89} and may contain a large cuneiform tubercle produced by the cuneiform cartilage⁸⁴.

In *Homo*, the epiglottis is separated from the soft palate by a long interval. In adult *Pan* the epiglottis is separated from the palate by 4-5 mm^{7, 85}, while direct contact with the palate is present in juveniles^{85, 89}.

Hyoepiglottic membrane

No information for *Gorilla*, *Pongo* or *Hylobates*.

In *Homo* and *Pan* this membrane originates from the anterior surface of the epiglottis near the apex, and inserts onto the posterior surface of the hyoid body^{84, 89, 194}.

Thyroid

A subcutaneous laryngeal prominence is present in *Homo* and *Pan*^{84, 194}, forming an angle of 90° in male *Homo*, 120° in female *Homo*¹⁹⁴, and about 75° (range 70°-84°) in *Pan*⁸⁴, although Dwight and Kelemen state that the prominence is slight in *Pan*^{42, 89}.

Immediately above the prominence the laminae are separated by the superior thyroid notch in *Homo*, *Pan* and *Pongo*^{3, 42, 84, 89, 170, 194}. An inferior thyroid notch is present in *Pan* and *Pongo*^{3, 40, 84, 89, 169, 170}, but absent from *Homo*^{84, 170, 194}.

Unlike *Homo*, in *Pan* the upper margin of the lamina is nearly horizontal, forming a slight upward convexity only in its middle part⁸⁴.

The superior cornu is connected to the hyoid bone by a cricothyroid ligament in *Homo* and *Pongo*^{170, 194}, in which there is a small triticeal cartilage in *Pan* and *Pongo*^{40, 84, 170}. The superior cornua in *Pan* form an angle of 45°-60° with the vertical line, and their ends are curved inward, while they are more vertical in *Homo*⁸⁴. They may be straight in *Pan*, or a slight curvature in their middle may form a small tubercle on the posterior margin and a depression on the anterior one⁸⁴.

The superior cornua pass into the upper margin of the lamina gently in *Pan*, whereas in *Homo* a distinct incisure is produced⁸⁴.

The inferior cornu is connected to the cricoid lamina by a ligament in *Homo* and *Pongo*^{170, 194}. Shorter than the superior cornua in *Homo* and *Pan*^{84, 93, 194}, in both these species the transition from the inferior cornu to the inferior margin of the lamina is marked by a distinct incisure^{84, 194}.

In *Homo* the angle formed by the oblique line with the midline of the thyroid cartilage is 43°-49°⁹³, compared with a more vertical 18°-32° in *Pan*^{84, 93}, 17° in *Gorilla*⁹³, 30° in *Pongo*⁹³ and 36° in *Hylobates*⁹³.

A thyroid foramen was present either bilaterally or unilaterally in 2/7 *Pan*, marking the developmental boundary between the fourth and fifth branchial arches⁸⁴.

Thyrohyoid ligaments

No information for *Gorilla* or *Hylobates*.

These ligaments are absent from 8/10 *Pan*⁸⁴, replaced by a cartilaginous connection represented in 50% of *Homo*, *Pongo* and 8/10 *Pan* by small cartilaginous or bony nodules, the triticeal cartilages, within that ligament^{84, 89, 170, 194}.

The ligaments originate from the superior cornua of the thyroid cartilage, inserting into the extremity of the greater cornua of the hyoid bone in *Homo* and *Pongo*^{170, 194}.

Thyrohyoid membrane

No information for *Gorilla*.

In *Homo*, *Pan* and *Pongo* the thyrohyoid membrane is thickened in the midline^{170, 194}. Laterally in *Pan*, *Pongo* and *Hylobates* it is pierced by the laryngeal air sacs^{77, 84, 89, 170}.

3.2.5.2.3 Laryngeal air sacs

Laryngeal air sacs

In *Pan*^{3, 7, 26, 33, 46, 57, 77, 85, 89, 93, 118, 119, 125, 130, 131, 169, 190, 192}, *Gorilla*^{27, 82, 119, 147, 173}, *Pongo*^{16, 18, 50, 51, 52, 119, 130} and *Symphalangus*¹¹⁹, a paired laryngeal sac arises from the laryngeal ventricle, projecting through the thyrohyoid membrane. The sac is confined to the submental region in *Symphalangus*¹¹⁹. In great apes the laryngeal sacs form a number of recesses among the muscles of the neck, thorax and axilla⁸⁵.

In size, the sacs are best developed in *Pongo*, reducing in size in the order *Gorilla*, *Pan* and *Symphalangus*¹¹⁹. The sacs are larger in adults, and are also larger in males than in females^{27, 32, 85, 119, 190}. Asymmetrical development is usually found, but with no obvious species preference as to which side is best developed^{33, 85, 119}.

These sacs are absent from *Homo* and *Hylobates*¹¹⁹, although in *Homo*, enlarged laryngeal ventricles can be produced by pathological conditions⁸⁵. Small true laryngeal pouches have been found as a rare variant in *Homo*^{119, 160, 161, 162}.

Reasons which have been given for the existence of these sacs include the presence of tumours in the larynx¹¹⁸, resonating chambers for the voice^{33, 50, 51}, a cushion to protect the neck from the heavy jaw³³ and structures for rebreathing air¹⁸.

Species	Sac	Dimension
<i>Gorilla</i> *	Submaxillary	40 x 40
	Hyoid	20 x 20
	Episternal	70 x 70
	Infraclavicular	120 x 50
	Pectoral	70 x 40
	Axillary	100 x 50
<i>Gorilla</i> **	Submaxillary	5 x 5
	Hyoid	7 x 7
	Infracoracoid	10 x 10
<i>Pan</i>	Subhyoid	left 24 x 9 right 26 x 14
	Hyoid	18 x 13 x 10
	Ventral thyroid	23 x 11 x 14

Table 3.2.3. Dimensions (mm) of the laryngeal sacs in *an adult male *Gorilla*¹¹⁹, **an infant female *Gorilla*¹¹⁹ and an adult male *Pan*⁹³.

3.2.6 ENDOCRINE

3.2.6.1 Parathyroid

No information for *Pongo* or *Hylobates*.

There are four parathyroid glands in *Homo* and 1/2 *Gorilla*, two on each side^{74, 194}.

Three parathyroid glands, two on the left, one on the right, have been found in 1/2

*Gorilla*¹⁸⁸, and this may also occur in *Homo*^{67, 187, 194}. Two parathyroid glands have been found in *Pan*¹⁶⁹.

In *Gorilla* the superior parathyroid glands are reported to be oval, and larger than the inferior, spherical, parathyroid glands⁷⁴. The glands average 6 x 3-4 x 1-2 mm in *Homo*¹⁹⁴, and 8-14 x 5-10 x 2.5-3 mm in *Gorilla*⁷⁴. The weight of each gland averages 50 mg in *Homo*¹⁹⁴, and 200-400 mg in *Gorilla*⁷⁴.

Histologically, in both *Homo* and *Gorilla* principal and oxyphilic cells are identifiable^{74, 194}.

3.2.6.2 Pineal

	Length	Breadth	Height
<i>Homo</i>	12	8	4
<i>Pan</i>	2	3	-
<i>Pongo</i>	1.7*	-	1.1*
	4.59	3.3	1.35
<i>Hylobates</i>	2.1	2.4	1.4

Table 3.2.4. Dimensions (mm) of the pineal gland. Data for *Homo* from⁹⁶, for *Pan* and *Hylobates* from⁴, and for *Pongo* from^{142*} and¹⁸¹.

In *Homo*, *Pan*, *Pongo* and *Hylobates* the bulk of the pineal lies closely related to the third ventricle^{4, 96, 141, 142}. In *Pongo* the pineal has a more extensive exposure on the third ventricle and between the habenular and posterior commissures than in *Pan*^{98, 142}.

While the ependymal covering of the pineal in the pineal recess is smooth in *Pongo*, that covering the pineal dorsally and separating it from the lumen of the suprapineal recess is irregular and extensively perforated by complexly branching channels which run for 100-200 μm within the pineal body¹⁴².

The inferior lamina contains the posterior commissure and the superior lamina the habenular commissure in *Homo*¹⁹⁴. In *Pongo* the main mass of the habenular commissure is embedded in the pineal, with only a part of its anterodorsal margin free of pineal tissue, and the pineal is in extensive contact with the posterior commissure posteroventrally¹⁴².

Aberrant commissural fibres may loop into the substance of the body through its stalk in both *Homo* and *Pongo*^{142, 194}, but they do not terminate in relation to parenchymal cells in *Pongo*¹⁴².

A partially lobulated appearance of the pineal in *Homo* and *Pongo* is shown by stromal cords and incomplete partitions, and in *Pongo* by a dorsal medial furrow⁷⁶,

141, 142, 181

In *Homo* nerve fibres enter the dorsal or dorsolateral aspects of the body from the region of the tentorium cerebelli where they form a single or paired *nervus conarii*¹⁹⁴. The *nervus conarii* was not found in *Pongo*, possibly due to the staining technique¹⁴². The absence of distinct pineal ganglion or nerve cell bodies separate from those of the habenular commissure and the neuronoid parenchyma cells relates the *Pongo* pineal more closely to that of *Homo* than to monkeys¹⁴². The ganglion cells are also absent from *Pan*¹³⁴. It is possible that the pineals of great apes and *Homo* are distinguished from those of monkeys by the paucity of such ganglion cells¹⁴².

Histologically, both pinealocytes and neuroglial cells are distinguishable in *Homo* and *Pongo*^{142, 194}. Three structural types of pinealocytes have been distinguished in *Pongo*: Large cells with abundant and finely granular cytoplasm; smaller cells with

relatively less cytoplasm and larger, more irregular cytoplasmic granules, and cells with highly vacuolated cytoplasm¹⁴².

	N	Body weight (kg)	Pineal body
<i>Homo</i>	1	65000 -	142* 46.12**
<i>Pan</i>	1	46000 -	38.0* 20.5**
<i>Gorilla</i>	1	105000 -	7.96* 3.28**
<i>Pongo</i>	1	-	20.5
<i>Hylobates</i>	-	-	4.66**

Table 3.2.5. Volume of the pineal body (mm³). Values marked * from ¹⁷⁴, values marked ** from ¹⁰³. Value for *Pongo* calculated from ¹⁸¹.

3.2.6.3 Pituitary

The weight of the gland in adult male *Gorilla* has been given as 1398 mg¹⁴⁶ and 1357 mg⁹⁴, which is about 2.5 times the average for adult male *Homo*¹⁴⁶ of 500-570 mg^{146, 194}, although Hosokawa and Kamiya⁷⁴ found the gland to weigh only 300 mg in a captive male *Gorilla*. Oboussier has concluded that domestication in mammals adversely influences the size and activity of the glandular lobe, especially in animals born in captivity¹²⁸. Maximum weight of the gland for male *Homo* is 855 mg, and for non-pregnant female *Homo*, around 1000 mg. A male *Gorilla* had 0.0055 gm of hypophysis per kg body weight¹⁴⁶, while a 267 kg male had 0.0051 gm of hypophysis per kg body weight⁹⁴. *Homo* has on average 0.088 gm per kg body weight¹⁴⁶.

The dimensions of the gland have been given as 7 x 12 x 5 mm⁷¹ and 9 x 15 x 16 in adult male *Gorilla*¹⁴⁶, compared with 12 x 8 mm in *Homo*¹⁹⁴. In *Pongo* the dimensions have been given for each lobe, the anterior lobe measuring 8 x 5 x 4 mm,

the posterior lobe 6 x 4 x 8 mm¹³⁵, while in *Hylobates* the hypophysis measured 6 x 3 x 1.7 mm¹³⁵.

The gland was rounder in *Gorilla* than is typical for *Homo*¹⁴⁶.

The anterior lobe weighed 1137 mg in a male *Gorilla*, which as a proportion of the total was well above the male human average, but within the human range¹⁴⁶. It constitutes about four-fifths of the hypophysis, a larger portion than in the average male *Homo*, but about the same proportion as in adult female *Homo*. However in men the anterior lobe may represent as little as 56% of the entire gland or as much as 90%¹⁴⁶. In two specimens of *Pan*, the anterior lobe represented 74% and 82% of the hypophysis¹²⁸.

The posterior lobe weighed in *Gorilla* about half the average in male *Homo*, very close to the adult human minimum. However in relation to brain weight, the neural lobe was very large, the brain weighing only 605 gm¹⁴⁶.

In *Gorilla* the *pars intermedia* at 7 mg was distinctly smaller than average for male *Homo*^{60, 61, 94}, but well within the adult human range of 0.5 to 20 mg^{143, 144}. It had the same proportional size as the female *Homo* average, at around 0.5% of total pituitary weight¹⁴⁶. The *pars intermedia* is also small, with a similar relative size, in *Pan*, *Pongo* and *Hylobates*^{128 135}. Hanström considers that the reduced size of the *pars intermedia* in *Homo* and apes distinguishes them from monkeys^{60, 61}.

Histologically, the intermediate region in *Homo* and *Gorilla* is polymorphic^{94, 135, 144, 146}. Simple tubules with a prominent lumen, composed mostly of indifferent staining cells extend some distance into the neurohypophysis, mostly in its lateral and inferior regions where they end blindly. These ducts generally contain no

stainable material. Such 'glands' are encountered frequently in *Homo*¹⁴⁵, and some have been found in *Pan*⁹⁴.

The *processus infundibuli* represents about 10% of the total hypophysis in *Gorilla*, compared with an average of over 20% in *Homo*, although as small as 7% has been observed in human adults¹⁴⁶. The absolute weight of the infundibulum of 134mg in *Gorilla* is not far above the male *Homo* average of 120mg¹⁴⁶.

There are great many small cells of all types in the anterior lobe in *Gorilla*, none reaching the size often seen in *Homo*¹⁴⁶. Köhne mentions thick nests of basophils in the anterior lobe in *Gorilla*⁹⁴, and the acidophils are most concentrated in the posterior portion of the lateral thirds¹⁴⁶. This is also a characteristic of *Homo* and tends to be the general primate pattern⁶⁰.

The proportions of the 3 types of cells in *Gorilla* is within the limits of *Homo*¹⁴⁶.

In *Gorilla* in a small area near the centre of the gland some apparently anterior lobe cells abutting the residual lumen have differentiated into ciliated columnar epithelium and mucous-secreting or goblet cells^{94, 146}. Ciliated cells, frequently accompanied by mucous cells, have been noted in the walls of the residual lumen or cysts in other parts of the gland in 19 of 100 *Homo*¹⁶³.

The blood supply of the pituitary is similar in *Homo* and *Gorilla*¹⁴⁶.

3.2.6.4 Thyroid

No information for *Hylobates*.

The thyroid gland consists of two lobes connected across the midline in *Homo*¹⁹⁴, 2/3 *Pan*^{169, 170} and *Gorilla*⁷⁴, the lobes being unconnected in 1/3 *Pan* and *Pongo*¹⁷⁰.

Each lobe is conical in *Homo*, *Gorilla* and *Pongo*¹⁷⁰, but not in *Pan*¹⁶⁹, while the base of the lobe is superior in *Pongo*¹⁷⁰, and inferior in *Homo*¹⁹⁴.

Each lobe averages 50 x 30 x 20 mm in *Homo*¹⁹⁴, and measures 65 x 20-25 x 10 mm in *Gorilla*⁷⁴. The isthmus averages 12.5 x 12.5 mm in *Homo*¹⁹⁴, and measures 35 x 10 mm in *Gorilla*⁷⁴.

The total weight of the thyroid gland averages about 25 gm in *Homo*¹⁹⁴, compared with 21 gm in a *Gorilla* with a body weight of 130 kg⁷⁴.

The superior end of the lobe lies at the level of the oblique line of the thyroid cartilage in *Homo* and *Pan*^{169, 194}, and at the inferior end of the larynx in *Pongo*¹⁷⁰.

The inferior end of the lobe lies level with the fourth or fifth tracheal ring in *Homo*¹⁹⁴, and with the seventh tracheal ring in *Pongo*¹⁷⁰.

Histologically, the structure of the gland differs between *Homo* and *Gorilla*. In *Gorilla*, the parenchyma is very rich in perifollicular tissue, with thyroid follicles scattered here and there^{56, 74}, unlike *Homo*, where the thyroid follicles are more abundant¹⁹⁴.

3.2.7 SENSORY ORGANS

3.2.7.1 Ear

3.2.7.1.1 Middle ear

Tympanic membrane

No information for *Gorilla*, *Pongo* or *Hylobates*.

As in *Homo*, in *Pan* the vertical diameter is longest, measuring 8.5 mm in a specimen of *Pan*⁷⁵, and 9 to 10 mm in *Homo*¹⁹⁴. The transverse diameter in *Homo* is 8 to 9 mm¹⁹⁴, and 9.0 mm in *Pan*⁷⁵.

As in *Homo*, in *Pan* the membrane shows a distinct depression at the umbo where the tip of the manubrium of the malleus shows clearly⁷⁵.

In *Pan* the membrane forms a more acute angle, around 30°, with the floor of the external canal⁷⁵, compared with about 55° in *Homo*¹⁹⁴.

3.2.7.1.2 External ear

The human auricle is about the same size as that of *Gorilla*, but much smaller than that of *Pan* and relatively larger than that of *Pongo*^{136, 157}.

A male *Pan* has a substantial asymmetry in the dimensions of the auricles, the right auricle being 80 mm long by 60 mm wide, while the left auricle is 87 mm long by 50 mm wide⁴². A further specimen of *Pan* has an auricle measuring 90 mm by 55 mm⁵⁷, and a female *Pan* has an auricle measuring 76 mm by 53 mm⁵.

In *Homo*, *Pan* and *Pongo* the auricle grows in relation to head size throughout fetal growth¹⁵⁸. After birth this increase continues steadily in *Pan*, resulting in a large ear, whereas in *Homo* and *Pongo* it reverses its trend to a postnatal relative decrease which is not quite as great in *Homo*¹⁵⁸.

The lobule is absent from 1/3 *Pan*⁵ but present in a rudimentary form in 2/3 *Pan*^{42, 57}.

	<i>H.concolor</i>	<i>H.leucogenys</i>	<i>H.lar</i>	<i>H.hoolock</i>
Sample size	4 M, 5 F	5 M, 2 F	1 M, 3 F	4 M, 1 F
Auricle length(mm)	36(28-40)	33(28-41)	31(30-32)	29(21-33)

Table 3.2.6. Average auricle length (in mm, range in parentheses) in species of *Hylobates*¹¹¹. All specimens are adult. M = Male, F = Female.

3.2.7.1.2.1 Muscles

Anterior auricular

No information for *Hylobates*.

In *Homo* and African apes the muscle originates from the epicranial aponeurosis^{153, 169, 189, 194}. In *Pan paniscus* and *Gorilla* the combined origin with the superior auricular muscle also includes the temporal fascia^{120, 147, 153} in *Gorilla* additionally involving the fascia of the orbital margin and zygomatic arch^{147, 153}.

This muscle is absent from 1/5 *Pan*¹⁸⁰ and *Pongo*^{170, 178}. The bundles of the anterior auricular muscle in *Gorilla* are frequently interrupted by fascia¹⁵³.

The fibres of the anterior auricular muscle insert in *Homo* and African apes onto the anterosuperior part of the helix^{120, 147, 153, 194}, in *Pan* deeper than the superior auricular muscle¹⁸⁹.

Innervated by temporal branches of the facial nerve in *Homo* and *Pan paniscus*^{120, 194}.

Posterior auricular

No information for *Hylobates*.

In *Homo* and *Pan paniscus* the muscle takes origin from the mastoid part of the temporal bone¹²⁰, while in *Pan* and *Gorilla* it originates from the occipital bone^{147, 153, 169, 189}.

It is fused with occipitalis in *Pan paniscus* and *Pongo*^{120, 178}, and is absent from 1/5 *Pan*¹⁸⁰. In *Pan* it may be combined with the superior auricular muscle^{169, 198}.

In *Homo* and African apes this small muscle inserts into the posterior part of the auricular cartilage^{120, 147, 152, 153, 189, 194}.

Innervated in *Homo* and *Pan paniscus* by the posterior auricular branch of the facial nerve^{120, 194}.

Superior auricular

No information for *Hylobates*.

In all African apes and *Homo* this muscle originates from the galea aponeurotica^{120, 153, 169, 189, 194}, and in *Gorilla* and *Pongo* from the temporal fascia^{147, 153, 178}, including in *Gorilla* the orbitozygomatic fascia¹⁵³.

A small thin muscle, in *Pongo* it is fused with occipitalis¹⁷⁸, while in *Pan* it is combined with the posterior auricular^{169, 198}, and in *Gorilla* with the anterior auricular¹⁵³. It is absent from 1/5 *Pan*¹⁸⁰.

Insertion in all great apes and *Homo* is into the concha^{120, 152, 178, 194}, specifically to the anterior and superior part of the root in *Homo* and African apes^{147, 169, 194}.

Innervation in *Homo* and *Pan paniscus* is via temporal branches of the facial nerve^{120, 194}, and in *Gorilla* via unspecified branches of the facial nerve¹⁴⁷.

Tragicus

No information for *Gorilla* or *Hylobates*.

Present as a short, flattened vertical band on the lateral surface of the tragus in *Homo* and *Pan*^{152, 169}, the muscle is absent from *Pongo*¹⁷⁰.

3.2.7.2 Eye

3.2.7.2.1 Bulbus oculi

Choroid

No information for *Gorilla*, *Pongo* or *Hylobates*.

The choroid is pigmented and highly vascular in *Homo* and *Pan*^{28, 194}.

Cornea

No information for *Pongo* or *Hylobates*.

Homo and African apes have a pericorneal pigmented ring^{28, 117}.

Structurally, the cornea consists of five layers from anterior to posterior: the corneal epithelium, the anterior limiting membrane of Bowman, the substantia propria, the posterior limiting membrane of Descemet and the endothelium of the anterior chamber¹⁹⁴.

Homo, *Pan* and *Gorilla* are characterized by the existence of a high total corneal and epithelial thickness, and by the presence of thick endothelia and Bowman's membrane, *Pan* being closer than *Gorilla* in corneal morphology to *Homo*¹¹⁷.

	ccen	cper	epic	epip	des	end	bow
<i>Homo</i>	770	1144	35	47	4.5	5.5	5.0
<i>Pan</i>	829	1017	25	38	3.6	5.5	4.1
<i>Gorilla</i>	857	994	39	46	1.8	4.5	4.1

Table 3.2.7. Corneal morphology in *Homo* and African apes. Central corneal thickness (ccen), peripheral corneal thickness (cper), central epithelial thickness (epic), peripheral epithelial thickness (epip), Descemet thickness (des), endothelial thickness (end) and Bowman thickness (bow), in microns¹¹⁷.

Fovea

No information for *Pongo* or *Hylobates*.

In *Homo* and *Gorilla* the small fovea and macula lutea are readily seen, located about 4 mm toward the nasal side of the entrance of the optic nerve. The macula is well demarcated from the surrounding retina¹⁶⁷.

The foveal cone population was less in *Pan* than in *Homo*¹³⁷, while the parafoveal region in *Pan* has the greatest number of ganglion cells in the entire retina²⁸.

Lunula cornulae

No information for *Gorilla* or *Hylobates*.

A milk-white crescent appears on the temporal corneal border in *Homo* and primates at birth and in early infancy⁸¹. In monkeys it does not disappear during development, while in *Homo* it gradually disappears with age. Corneal reduction may have occurred on the temporal side leading to the disappearance of the lunula on the same side⁸¹. The rudimentary lunula of *Homo* always appears in newborn babies, but decreases to 15.7% presence at 23 years of age⁸¹. The lunula is absent from *Pan*^{80, 81}, while a fine lunula is present in *Pongo*^{80, 81}.

Optic disc

No information for *Hylobates*.

The optic disc has clear fibres around it in great apes¹⁷⁰, but this is not normal for *Homo*^{83, 170}.

Retina

No information for *Gorilla*, *Pongo* or *Hylobates*.

The retina of *Pan* is very similar to *Homo*^{28, 100, 203, 95, 137,138,139,140}

3.2.7.2.2 Accessory organs

3.2.7.2.2.1 Muscles

Inferior oblique

No information for *Gorilla* or *Hylobates*.

The inferior oblique has a tendinous insertion in *Homo* and *Pan*^{170, 194}, whilst it is fleshy throughout in *Pongo*¹⁷⁰. In *Homo*, *Pan* and *Pongo* it inserts into the posterior aspect of the sclerotic coat¹⁷⁰.

Innervated in *Homo* and *Pan* by the oculomotor nerve^{80, 194}.

Inferior rectus

No information for *Pan*, *Gorilla*, or *Hylobates*.

This muscle is cylindrical in *Pongo*, with a more intimate attachment to the globe of the eye than the other muscles¹⁷⁰.

Lateral rectus

No information for *Gorilla*, or *Hylobates*.

In *Homo*, *Pan* and *Pongo* the muscle has two heads of origin¹⁷⁰. No structures pass between the two heads in *Pan* or *Pongo*, unlike *Homo*^{169, 170, 194}.

Levator palpebrae superioris

No information for *Gorilla* or *Hylobates*.

A triangular muscle in *Homo* and *Pongo*, it spreads out to a wide aponeurotic insertion^{170, 194}.

In *Homo*, *Pan* and *Pongo*, some fibres pass through orbicularis oculi to the skin of the upper eyelid, while others are attached to the anterior surface of the superior tarsus^{169, 170, 194}. In addition, in *Homo* and *Pongo* the aponeurosis splits the lacrimal gland and attaches to the zygomatic bone^{170, 194}. In *Pongo* other fibres attach to the superior conjunctival fornix, and insert into the lacrimal bone¹⁷⁰.

Innervated in *Homo*, *Pan* and *Pongo* by the oculomotor nerve^{169, 170, 194}.

Superior oblique

No information for *Gorilla* or *Hylobates*.

A fusiform muscle in *Homo*¹⁹⁴, it is cylindrical in *Pongo*¹⁷⁰, and more closely apposed to the inner wall of the orbit than in *Homo*¹⁷⁰.

In *Homo*, *Pan* and *Pongo* the tendon of the superior oblique passes through a fibrocartilaginous trochlea^{169, 170}, although the tendon does not twist at the trochlea in *Pan*⁷⁷, unlike *Homo*^{80, 194}.

Innervated in *Homo* and *Pan* by the trochlear nerve^{80, 169, 194}.

Superior rectus

No information for *Pan*, *Gorilla*, or *Hylobates*.

In *Homo* and *Pongo* this muscle is fused at its origin with levator palpebrae superioris^{170, 194}.

Innervated in *Homo* and *Pongo* by the oculomotor nerve^{170, 194}.

3.2.7.2.2 Palpebrae

Conjunctiva

No information for *Gorilla* or *Hylobates*.

The palpebral conjunctive is unpigmented in *Homo* and *Pongo*^{80, 121, 170, 194}. In *Pan* the pigment level varies from light-brown to markedly pigmented^{28, 80, 169}.

The plica semilunaris, a semilunar fold of conjunctiva, contains some non-striated muscle in *Homo* and may represent the nictitating membrane¹⁹⁴. A small plica semilunaris is present in *Pongo*¹⁷⁰, while the plica is described as a well-developed third eyelid in *Pan*^{80, 169}.

Tarsal glands

No information for *Gorilla* or *Pongo*.

The ridges formed by the tarsal glands in *Homo*¹⁹⁴ are not visible in *Pan* or *Pongo*^{169, 170}.

3.2.7.2.3 Lacrimal apparatus

Lacrimal gland

No information for *Gorilla* or *Hylobates*.

The lacrimal gland consists of a larger orbital part and a smaller palpebral part in *Homo*, *Pan* and *Pongo*^{77, 169, 170, 194}, which in *Homo* and *Pongo* are separated by levator palpebrae superioris^{170, 194}.

The composition of tear fluid in *Pan* does not differ significantly from that in *Homo*¹⁰.

Lacrimal sac

No information for *Pan*, *Gorilla* or *Hylobates*.

In *Pongo* the lacrimal sac is embraced by fibres of the levator palpebrae, and is compressed by fibres from orbicularis oculi¹⁷⁰, while in *Homo* the soft tissue related closely to the lacrimal sac is described as lacrimal fascia¹⁹⁴.

Nasolacrimal duct

In all apes and *Homo* the nasolacrimal duct ends in the inferior meatus of the nose²³,
24, 75, 109, 169

The opening into the inferior meatus in *Homo* is somewhat expanded¹⁹⁴, while in *Gorilla* the nasolacrimal duct has a dilated lower portion, the bulla nasolacrimalis¹²,
24, 88. Keith also stated that it was present in *Pan*⁸⁸. Bolk has described the successive stages of the bullous transformation of the nasolacrimal duct in *Gorilla*, indicating in old animals, its attainment of the orbital floor, leading to the lacrimal sac opening directly into it¹². Aichel² however, correlated variations in size of the nasolacrimal bulla in *Gorilla* with subspecies rather than with age².

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3.3 THORAX

3.3.1 MUSCLES

3.3.1.1 Extrinsic

Levatores costarum

No information for *Pongo* or *Hylobates*.

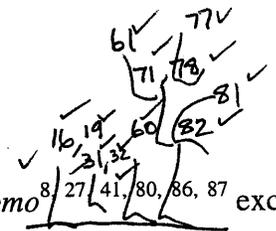
In *Homo*, *Pan paniscus* and *Gorilla* the levatores costarum originate from the transverse processes of C7 and T1 to T11^{65, 74, 87}, extending to T12 in *Gorilla*⁷⁴ and *Pan paniscus*⁶⁵.

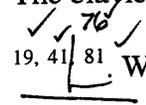
They are described as poorly developed and ligamentous in *Gorilla*⁷⁴, with the slip originating from C7 best developed⁷⁴.

The insertion of the muscles in African apes and *Homo* is by short fibres to the costal angle of the next rib^{65, 74, 87}, with the long fibres attaching to the second rib below present only in *Homo*⁸⁷.

Innervation in *Homo* is from the dorsal rami of the spinal nerves⁸⁷ and in *P.paniscus* from branches of the intercostal nerves⁶⁵.

Pectoralis major

Pectoralis major consists of two parts in all apes and *Homo*  except in 4/13 *Pan*^{31, 32, 61, 71, 77} and 6/9 *Pongo*^{19, 71, 78, 81} where three divisions are present, while in 4/13 *Pan* no divisions can be found^{16, 27, 60, 82}. The sternocostal part may be divided as a variation in *Homo*⁸⁷.

The clavicular head of pectoralis major is absent from 2/13 *Pan*^{5, 76} and 6/9 *Pongo*^{8, 9}
. When present, in all apes and *Homo* it originates from the medial third of the

anterior surface of the clavicle^{16, 65, 74, 77, 78, 87}, in all except *Gorilla*⁷⁴ and *Pongo*⁷⁸ extending to half the clavicle, reaching two-thirds in 1/4 *Pan*⁶¹ and *Hylobates*^{50, 80}. In *Gorilla* and Asian apes the clavicular origin extends further medially to the manubrium^{41, 74, 78, 80}.

The sternocostal part of the muscle in all apes and *Homo* takes origin from the anterior surface of the sternum^{8, 16, 19, 61, 65, 74, 77, 78, 81, 87}. In all except *Hylobates*

further fibres take origin from the costal cartilages of the third to seventh ribs^{8, 18, 19, 61, 65, 74, 77, 78, 81, 87}. The costal origin extends superiorly to the second rib in *Homo* and *Gorilla*^{16, 74, 87}, and to the first rib in both species of *Pan* and *Pongo*^{16, 61, 65, 74, 87}.

The origin may extend inferiorly to the eighth rib in *Pan troglodytes*¹⁶ and *Gorilla*⁷⁴.

An abdominal origin for pectoralis major consisting of fibres originating from the aponeurosis of the external abdominal oblique is present in great apes and *Homo*, united with the lower portion of the costal origin^{41, 61, 65, 77, 78, 81, 87}.

In all apes and *Homo* the muscle inserts onto the outer lip of the intertubercular groove on the humerus, inferior to the greater tubercle of the humerus^{8, 18, 41, 61, 65, 74, 77, 78, 80, 81, 87}. The intertubercular groove is absent in *Gorilla*⁴¹, the muscle inserting from the humeral neck running inferiorly to the insertion of the deltoid muscle. The insertion in *Hylobates* is partly fused with the short head of biceps brachii⁸⁰.

A separate *pectoralis abdominalis* or chondro-epitrochlearis, is present in 2/3 *Gorilla*, inserting onto the coracoid process of the scapula, partly fused with the tendon of biceps brachii^{25, 74}. It may be separate in *Pan* as a thin strap-like tendon inserting onto the humerus^{25, 61, 65}. A right side pectoralis abdominalis was found in an adult male *Symphalangus*, originating from the inferiormost bundle of pectoralis

major and the rectus sheath, proceeding diagonally upwards to insert partially into the coracobrachialis fascia, continuing to insert deep the humeral head¹², and Keith states that this muscle is best developed in *Hylobates*⁵⁰. The pectoralis abdominalis has been described in *Homo* as a slip or slips originating from the fascia beneath pectoralis major and inserting into the bicipital groove^{5, 55, 57, 61, 90}

Innervated in *Homo* and both species of *Pan* by nerves including elements from all factors of the brachial plexus^{16, 65, 87}, or from the seventh cervical and the combined trunk of the eighth cervical and first thoracic nerves³⁴.

Pectoralis minor

In all apes and *Homo* pectoralis minor originates from the upper margin and external surface of a variable number of the third to fifth ribs near the costal cartilage^{8, 16, 35, 41, 65, 74, 77, 78, 81, 82, 87, 93}. The origin may extend inferiorly to the sixth rib in *Gorilla* and *Pongo*⁸, and to the seventh rib in *Gorilla*⁴¹. The superior extent of the origin may be to the second rib in both species of *Pan*, in *Pongo* and in *Homo* as a variant^{16, 35, 41, 61, 65, 77, 78, 87, 93}, and to the first rib in *Pan troglodytes* and as a rare variation in *Homo*^{6, 61, 87}.

In *Pan troglodytes* a band runs to the sternum from the coracoid process of the scapula, partially fused with the subclavian sheath¹⁶.

The muscle is divided into two parts in great apes^{8, 26, 27, 61, 78}.

It inserts in all apes and *Homo* onto the coracoid process^{8, 9, 27, 31, 32, 35, 41, 65, 73, 74, 78, 81, 89}, in *Homo* with a flat tendon⁸⁷, whilst great apes have a rounded tendon of insertion^{16, 41, 61, 74, 81, 82}. In *Pan troglodytes* the main insertion is into the capsule of the shoulder joint^{16, 35, 41, 61, 77, 82, 89, 93}, extending over the coracoid process to the

greater tuberosity of the humerus^{44, 93}. As a variation in *Homo* part of the tendon of pectoralis minor may pass over the coracoid process to blend with the coracohumeral ligament⁸⁷.

In *Hylobates* there is an additional insertion into the anterior surface of the clavicle⁴¹, and in both *Gorilla* and *Hylobates* pectoralis minor inserts into the common tendon of origin of the short head of biceps^{27, 41}.

Innervated in both species of *Pan* by the anterior thoracic nerve^{16, 65}, including components from the entire brachial plexus¹⁶, or from the seventh cervical and combined trunk of the eighth cervical and first thoracic nerve³⁴. In *Homo*, pectoralis minor is innervated by the sixth, seventh and eighth cervical nerves⁸⁷.

Serratus anterior

⁷⁴
Serratus anterior ⁷⁴ takes origin by fleshy digitations in all apes and *Homo* from the first to ninth ribs ^{2, 6, 65, 77, 89} _{8, 56, 81, 87} extending inferiorly to the tenth rib in *Pan paniscus*⁶⁵ and *Homo* as a variation⁸⁷, to the eleventh rib in all other apes ^{2, 77, 81, 89}, and to the last rib in great apes, either twelfth or thirteenth ^{8, 69, 74}.

A continuous sheet in most apes^{41, 81}, in 1/2 *Gorilla* it has two parts⁷⁴, and in *Homo*⁸⁷ and 1/5 *Pan*¹⁶ the muscle is in three parts; no further information for *Hylobates*. The digitation from the first rib is small in *Pan*⁷⁷, but larger in *Homo*, *Gorilla* and *Pongo*^{74, 81, 87}.

In *Homo* and *Pongo* serratus anterior is overlain by the pectoral muscles^{81, 87} and also by subscapularis in *Homo*⁸⁷. The last four digitations in *Gorilla* are covered by latissimus dorsi⁷⁴. In *Pan*, *Pongo* and in *Homo* as a variation, the lower seven slips interdigitate with the external abdominal oblique^{77, 81, 87, 89}.

Insertion in great apes and *Homo* is onto the medial scapular margin on the anterior surface^{8, 16, 41, 65, 77, 81, 87}. In all apes and *Homo*, with the exception of *Gorilla*⁷⁴ and 1/5 *Pan*¹⁶, this insertion is continuous, from the superior angle to the inferior angle of the scapula^{41, 87}.

Innervated in *Homo* and *Pan paniscus* by the long thoracic nerve^{64, 65, 87}.

Sternalis

No information for *Gorilla* or *Hylobates*.

Sternalis is absent from *Pan* and *Pongo*^{8, 78}, but present in a male *Symphalangus*¹².

When present in *Homo*, it is a narrow band of muscle in front of pectoralis major, in line with sternomastoid and rectus abdominis. It appears in 4% of Europeans, and 12.8% of Japanese subjects¹².

Subclavius

In great apes and *Homo*, but not in *Hylobates*⁴¹, subclavius takes origin from the bone/cartilage junction of the first rib^{41, 61, 65, 74, 77, 81, 87}. In Asian apes there is a slip of origin from the second rib⁴¹, and in *Hylobates* also from the third rib⁴¹.

It is poorly developed in *Homo*⁸⁷ and *Pongo*⁷³, but well developed in *Pan*¹⁸.

The insertion in all apes and *Homo* is onto the middle third of the inferior surface of the clavicle^{41, 61, 65, 74, 77, 81, 87}, extending further medially in *Pan troglodytes*⁸ and further laterally in *Pan troglodytes*⁶¹ and *Hylobates*⁴¹.

Innervated in *Homo*, both species of *Pan*, *Gorilla* and *Hylobates* from the sixth cervical nerve^{41, 65, 87} and in all these except *Hylobates*⁵³ from the fifth cervical nerve^{41, 65, 87}.

3.3.1.2 Intrinsic

External intercostals

No information for *Pongo* or *Hylobates*.

In African apes and *Homo* the external intercostals are attached to the adjacent margins of each pair of ribs, from the tubercles of the lower border of the rib posteriorly, to the commencement of the cartilage of the upper border of the rib in front^{65, 74, 77, 87}. In all the fibres are directed inferomedially^{65, 74, 77, 87}.

They are membranous to the sternum in *Homo* and *Pan paniscus*^{65, 87}, while in *Pan troglodytes* they are replaced by membrane in all but the first three and last two intercostal spaces⁷⁷. The external intercostal muscles do not reach the costal cartilage until the sixth rib in *Gorilla*⁷⁴.

Innervated by the intercostal nerves in *Homo*, *Pan paniscus* and *Gorilla*^{65, 74, 87} specifically the first thoracic to eleventh thoracic in *Homo*⁸⁷ and the second thoracic to thirteenth thoracic in *Gorilla*⁷⁴.

Transversus thoracis

No information for *Pongo* or *Hylobates*.

Originates in African apes and *Homo* from the internal surface of the xiphoid process and the body of the sternum^{65, 74, 77, 83, 87}. The sternal origin reaches as far superiorly as the fourth intercostal space in *Homo*⁸⁷, the first or second space in *Pan*⁸³ and the third space in *Gorilla*⁷⁴.

The muscle is separated from transversus abdominis by slips of the diaphragm in *Gorilla*⁷⁴, which occurs in *Homo* when the costal origin of the diaphragm from the seventh rib is well developed⁸⁷.

Insertion in African apes and *Homo* is into the inferior border of the costal cartilage of the second to sixth ribs^{65, 74, 77, 83, 87}. In *Gorilla* the insertion extends superiorly to the first rib⁷⁴, in *Pan paniscus* and *Gorilla* inferiorly to the seventh rib^{65, 74}, and in *Gorilla* alone to the eighth rib⁷⁴. The number of slips is variable in *Homo*⁸⁷.

Innervated in *Homo*, *Pan paniscus* and *Gorilla* by the intercostal nerves^{65, 74, 87}; specifically the second thoracic to sixth thoracic nerves in *Gorilla*⁷⁴.

3.3.1.3 Diaphragm

No information for *Pongo*.

The weak points of the diaphragm are the same in *Homo* and *Pan*¹⁶.

The diaphragm is innervated by the phrenic nerve in *Homo*, *Pan paniscus* and *Gorilla*^{65, 74, 87}.

Aortic hiatus

In *Homo*, *Pan* and *Symphalangus* the position of the aortic aperture is higher than in lower catarrhines⁴⁷. It is shorter by two-thirds of a vertebra in *Homo* than in *Pan* and *Symphalangus*⁴⁷.

In *Pan* and *Symphalangus* the hiatus extended inferiorly on average to the level of the upper part of L3, and superiorly to T11 or T12, higher than in *Homo*, in which the aperture extends from L1 to L3⁴⁷, although it may reach the level of the inferior border of T12 in *Homo*⁸⁷.

Central tendon

The division of the central tendon into folia⁸⁷ is less distinct in *Homo* and *Pan* than in *Symphalangus*⁴⁸. In 1/3 *Pan* the central tendon was not divided into leaflets, being kidney-shaped⁴⁸, and has been described in *Gorilla* as "C-shaped", with its concavity directed posteriorly⁷⁴. In *Homo*, 2/3 *Pan* and *Symphalangus* the overall shape of the central tendon was similar, with lateral and anterior leaflets of approximately the same size⁴⁸.

The central point of decussation is present in *Homo* and *Pan*^{11, 87}.

Muscle fibres were found only in the anterior leaflet in 2/10 *Homo* and 1/3 *Pan*⁴⁸, while in 1/2 *Symphalangus* muscle fibres were observed running obliquely through the anterior leaflet, and also at the base and centre of the right folia⁴⁸.

Oesophageal hiatus

The oesophageal hiatus is situated in the muscular part of diaphragm at the level of T10 in *Homo*⁸⁷, although Juraniec places it in the space from the middle of T11 to L1 in *Homo*⁴⁷ and at the level of T11, and the middle of T10, in *Pan*⁴⁷. The position is higher in *Symphalangus*, being at the level of T9 to T11⁴⁷.

It is elliptical in shape in *Homo* and *Symphalangus*^{47, 87} and is formed by the splitting of the medial fibres of the right crus in *Homo*, both species of *Pan* and *Symphalangus*^{47, 54, 59, 65, 87}. In 3/12 *Homo* the hiatus was bounded on the right side by a strand of fibres from the left crus, and on the left side by a similar strand of the right crus⁴⁷.

The hiatus was much shorter in *Pan* than in *Symphalangus*⁴⁷.

It is usually stated as being situated above and a little to the left of the aortic opening in *Homo*^{40, 87}, although Juraniec found it to be present above and a little to the right of the aortic hiatus in 8/12 *Homo*, similarly to *Pan* and *Symphalangus*⁴⁷. In 3/12 specimens of *Homo* the oesophageal hiatus was directly above the aortic hiatus, and in only 1/12 was it shifted to the left⁴⁷. The opposing ends of the oesophageal and aortic hiatuses are separated by half a vertebra in *Homo*, *Pan*, and *Symphalangus*⁴⁷.

	I					III
	1	3	4	5	6	2
<i>Homo</i>	4	1	2	2	3	-
<i>Pan troglodytes</i>	-	-	1	-	-	3
<i>Symphalangus</i>	1	-	-	-	-	1

Table 3.3.1. Types of crossing of the fibres of both diaphragmatic crura in front of the oesophageal hiatus in *Homo*, *Pan* and *Symphalangus*. Adapted from ⁴⁷.

Juraniec distinguished four types of fibre crossing at the oesophageal hiatus in primates⁴⁷. Only those present in hominoids are given here. In type I, only muscular crossing was present, with 6 subtypes distinguished.

- In I1, the muscle fibres of the right crus crossed the fibres of the left crus, mingling with them.
- Subtype I3 was characterized by parallel course of the fibres on the abdominal side and crossed fibres on the thoracic side.
- I4, I5 and I6 represent various types of crossing of the fibres of the crura to the opposite side in bundles. These account for half the cases of *Homo* and 1/4 *Pan*.

In type III, not found in *Homo*, a tendinous strand at the site of the crossing of the fibres was present on both the thoracic and the abdominal side, present in *Pan* and *Symphalangus* on the right side only (subtype III2)⁴⁷.

Pars costalis

The costal part of the diaphragm originates from the anterior portion of the lower six ribs on each side in *Homo*⁸⁷, while in both species of *Pan* and in *Gorilla* it originates from the lower seven ribs^{65, 74, 77}.

It interdigitates with transversus abdominis in *Homo* and both species of *Pan*^{65, 77, 87}.

Pars lumbalis

The lumbar part of the diaphragm originates from the lumbar vertebrae by two crura in *Homo*, both species of *Pan* and *Gorilla*^{65, 74, 77, 87}. Additional slips arise from the transverse process of L2 and from the side of the body of L1 in *Pan*⁷⁷.

It also originates from two medial and lateral arcuate ligaments in *Homo* and both species of *Pan*^{65, 77, 87}.

In *Gorilla*, the pars lumbalis is not divided into lateral and medial arcuate ligaments and a crus, but into a broad lateral arcuate ligament and a pointed division corresponding to the crus of *Homo*⁷⁴.

The *right crus* is broader and longer than the left in *Homo* and *Gorilla*^{54, 74, 87}, arising from the bodies and intervertebral discs of L1 to L3 in *Homo*⁸⁷, and as far inferiorly as L2 in both species of *Pan*^{65, 77}.

The *left crus* arises from L1 and L2 in *Homo* and *Pan paniscus*^{65, 87}, and from L1 in *Pan*⁷⁷.

The *lateral arcuate ligament* is a thickened band in the quadratus lumborum fascia which attaches to the transverse process of L1 in *Homo* and *Pan paniscus*^{65, 87}. It also

attaches to the inferior margin of the twelfth rib in *Homo*, and to the last two ribs (ribs thirteen and fourteen) in *Pan paniscus*⁶⁵.

The lateral arcuate ligament as described by Raven takes origin from the tendinous fibres of the upper portion of psoas and the centrum of L1 in *Gorilla*⁷⁴, and may be more more homologous with the human medial arcuate ligament on the basis of its attachments. Raven describes a tendinous raphe between the last rib and the transverse process and centrum of L1 which may correspond to the human lateral arcuate ligament⁷⁴.

The *medial arcuate ligament* is a tendinous arch in the psoas major fascia in *Homo* and *Pan paniscus*^{65, 87}. It attaches to the side of the body of L1 in *Homo* and *Pan paniscus*^{65, 87}, or L2 in *Homo*⁸⁷, being laterally fixed to front of the transverse process of L1 in both *Homo* and *Pan paniscus*^{65, 87}.

Pars sternalis

The sternal part of the diaphragm originates by two slips from the inner surface of the xiphoid process in *Homo*, *Pan paniscus* and *Gorilla*^{65, 74, 87}, while in *Pan* it takes origin by two slips from the inner surface of the sternum⁷⁷. The xiphoid slip is sometimes absent from *Homo*⁸⁷.

3.3.2 VESSELS

3.3.2.1 Heart

The heart lies obliquely in the chest, with the greater part to the left of the midline in *Homo* and *Gorilla*^{4, 87, 88}.

The heart is more pointed in great apes than in *Homo*^{58, 88}. Steiner did not find this in the heart of an adult male *Gorilla*, but this may have been abnormal⁷⁹. The heart is less pointed in *Hylobates* than in *Macaca*⁷².

The axis of the heart in great apes and *Homo* is much more oblique than in monkeys^{75, 88}.

The apex lies in the fifth intercostal space in *Homo* and *Pan*^{77, 87} and behind the medial end of the fifth costal cartilage in *Pongo*⁷⁸. The superior border is level with the second costal cartilage in *Homo* and *Pan*^{77, 87}.

Species	Sex	Body weight	Heart weight
<i>Homo</i>	Male ⁴³	-	280-340
	Female ⁴³	-	230-280
<i>Gorilla</i>	Male ⁷⁹	227	805
	Male ³	209	738
	Male ³⁸	134	730
	Male ⁴²	130	760
	Female ⁴²	68	365

Table 3.3.2. Body weight (kg) and heart weight (gm) in *Homo* and *Gorilla*. Data for *Homo* are adult ranges.

The heart of a fetal gorilla was larger in proportion to body size than in fetal *Homo*²⁴.

Species	Sex	Base to apex	Transverse	AP
<i>Homo</i>	- ⁸⁷	12	8-9	6
<i>Pan</i>	Male ²⁸	11.5	8	-
	Female* ⁷	8	6	4
<i>Gorilla</i>	Male ⁴²	14	14	8
	Female ⁴²	14	9	7
<i>Hylobates</i>	- ⁷²	-	4	4

Table 3.3.3. Dimensions (cm) of the heart in *Homo*, *Pan*, *Gorilla* and *Hylobates*. Data for *Homo* are adult averages. The transverse diameter is at the broadest point, AP = anteroposterior diameter. All specimens are adult except that marked *, which is subadult.

The pulse of a young male *Pan* was 150 beats per minute, with heart sounds similar to in *Homo*⁷⁷.

A newborn female *Pongo* had ectopia cordis⁸⁷, which is when much of the ventricular part of the heart herniates to the left through an opening in the pericardium²².

3.3.2.1.1 Pericardium

The pericardium adheres very closely to the diaphragm in *Homo*, *Pan*, *Pongo* and *Hylobates*^{72, 77, 78, 83, 87}, more extensively so in *Hylobates* than in *Homo* and *Pan*^{72, 87}.

A transverse sinus is present in *Homo* and *Gorilla*^{30, 87, 88}. The right inferior pulmonary vein is more medial in *Gorilla* than in *Homo*, thus altering the form of the oblique pericardial sinus⁸⁸.

3.3.2.1.2 Atria^a

The right atrium is larger than the left in *Homo* and *Pan*^{83, 87}.

3.3.2.1.2.1 Left atrium

No information for *Gorilla* or *Hylobates*.

Auricle

The left auricle is longer, narrower and more curved than the right auricle in *Homo*⁸⁷, while the left auricle is smaller than the right auricle in *Pan* and *Pongo*^{28, 78}. Both auricles are described as large in *Pan*⁸³.

It possesses muscoli pectinati in *Homo*, *Pan* and *Pongo*^{28, 78, 87}.

3.3.2.1.2.2 Right atrium

No information for *Gorilla* or *Hylobates*.

Atrium

Musculi pectinati are present in the anterior wall of the atrium in *Homo*, *Pan* and *Pongo*^{28, 78, 87}. In *Pan* and *Pongo* they end in the crista terminalis^{28, 78, 87}, while in *Homo* they also reach the lateral wall of the right atrium⁸⁷.

The orifice of the inferior vena cava is guarded by a rudimentary valve in *Homo* and *Pongo*^{78, 87}, that appears to be absent from *Pan*²⁸.

The valve protecting the orifice of the coronary sinus is described as incompetent in *Pongo*⁷⁸, while in *Homo* it prevents the regurgitation of blood into the sinus during atrial contraction⁸⁷.

Auricle

The right auricle overlaps the ascending aorta and possesses musculi pectinati in *Homo* and *Pongo*^{78, 87}.

Fossa ovalis

The foramen ovale was completely closed, indicated by a well marked fossa ovalis in *Homo*, *Pan* and *Pongo*^{28, 77, 78, 87}.

In a newborn female *Pongo* with ectopia cordis, the foramen ovale is represented by a narrow slit 4 mm long²², while in a young female with a patent ductus arteriosus, the foramen ovale is closed⁷⁷.

3.3.2.1.3 Ventricles^a

3.3.2.1.3.1 Left ventricle

No information for *Gorilla* or *Hylobates*.

The walls of the left ventricle are thicker than those of the right ventricle in *Homo*, *Pan* and *Pongo*^{22, 28, 83, 87}.

The trabeculae carneae are highly interlaced at the apex in *Homo* and *Pan*^{28, 87}.

An adipose cell infiltration was present in an adult male *Gorilla* into the left ventricular myocardium, which would be regarded as abnormal in *Homo*⁷⁹.

Left atrioventricular valve (mitral valve)

The two cusps of the mitral valve possess chordae tendineae in *Homo*, *Pan* and *Pongo*^{22, 78, 83, 87}.

In *Homo* and *Pongo*, the anterior cusp of the valve is larger than the posterior cusp^{22, 87}.

A newborn female *Pongo* with ectopia cordis displays a slender accessory cusp with four chordae tendinae attached, lying medially between the anterior and posterior cusps²².

3.3.2.1.3.2 Right ventricle

No information for *Gorilla* or *Hylobates*.

Conus arteriosus

The conus arteriosus has smooth walls in *Homo*⁸⁷, while in *Pan* although mostly smooth, trabeculae carneae are present⁷⁸, and in *Pongo* papillary muscles cross the communication between the body of the ventricle and the conus arteriosus⁷⁸.

A supraventricular crest partially separates the conus from the ventricular body in *Homo* and *Pan*^{83, 87}, but not in *Pongo*⁷⁸.

Pulmonary valve

The semilunar valves surrounding the pulmonary orifice are the right, left, and anterior cusps in *Homo* and *Pan*^{83, 87}.

Right atrioventricular valve (tricuspid valve)

Three cusps are present in *Homo*, *Pan* and *Pongo*^{28, 78, 87}.

In *Homo*, *Pan* and *Pongo* the papillary muscles give rise to chordae tendineae for the cusps of the tricuspid valve, and some chordae tendineae arise from the interventricular septum^{78, 83, 87}.

Septomarginal band

This ridge is present in the right ventricle of *Homo* and *Pan*^{28, 87}. It is about 3 mm in diameter in *Pan*²⁸.

3.3.2.2 Arteries

3.3.2.2.1 Aorta^{a, b}

The overall structure of the *thoracic aorta* will be dealt with in this section, with subsequent sections describing the branches of each portion of the thoracic aorta: ascending, aortic arch and descending. For the *abdominal aorta*, see 3.6.2.1.1.

The aorta is relatively wider in *Pongo* than in *Pan*⁷⁸. Dimensions of the various parts of the aorta in *Gorilla* have been given by Steiner⁷⁹ and Kleinschmidt⁵². The thoracic:abdominal length ratio is 100:88 in *Gorilla*, but more similar in *Homo*⁵².

The arch of the aorta gives way to the descending aorta at the inferior border of T4 in *Homo*⁸⁷, and at T6 in *Pan*⁷⁷.

The thoracic aorta passes through the diaphragm at the aortic hiatus to become the abdominal aorta in all apes and *Homo* (see 3.3.1.3).

3.3.2.2.1.1 Ascending

Left coronary artery

No information for *Hylobates*.

The left coronary artery arises from the left posterior aortic sinus in *Homo* and *Gorilla*^{38, 87}.

After a short course in *Homo* and African apes^{38, 83, 87}, in great apes and *Homo* the trunk divides into its two main branches^{38, 78, 83, 87}. A third division is present in *Gorilla* between the two primary branches, running over the sternocostal surface of the left ventricle towards its left border³⁸.

The *circumflex* branch runs in the atrioventricular groove, supplying atrial and ventricular branches in *Homo* and great apes^{38, 78, 83, 87}.

The *anterior interventricular* artery runs in the atrioventricular groove to the cardiac apex in great apes and *Homo*^{38, 78, 83}. This anastomoses with the interventricular branch of the right coronary artery in *Homo* and *Pongo*^{78, 87}.

The left coronary artery may give off the *sinuatrial nodal* artery in *Homo*⁴³.

Right coronary artery

No information for *Hylobates*.

Arising from the anterior aortic sinus, the right coronary artery is smaller than the left coronary artery in *Homo* and African apes^{20, 83, 87}.

It gives off branches to the atrium and the ventricle as it passes vertically downwards in great apes and *Homo*^{20, 38, 78, 83, 87}. Other branches include the *conus* artery in *Homo* and *Gorilla*^{20, 87}, although this branch may arise directly from the aorta in *Gorilla*²⁰.

The *right marginal* branch is present in great apes and *Homo*^{20, 38, 78, 83, 87}. This branch may be reduced to two slender twigs in *Gorilla*²⁰, and has been described as "minute" in *Pongo*⁷⁸.

A *posterior interventricular* branch is present in great apes and *Homo*^{20, 38, 78, 83, 87}. In *Homo* and *Pongo* it anastomoses with the anterior interventricular branch of the left coronary artery^{78, 87}.

Sinuatrial and *atrioventricular nodal* arteries may be present in *Homo*^{43, 46}.

3.3.2.2.1.2 Arch

The aortic arch usually gives off three branches in *Homo*; the *brachiocephalic trunk*, the *left common carotid* and the *left subclavian* arteries^{83, 87}. This is also the case in 23/32 *Pan*^{18, 49, 78, 82, 86}, and 12/13 *Gorilla*^{19, 24, 79, 88}.

In 1/32 *Pan*⁷⁷ and 2/3 *Pongo*^{19, 78} the arch gives rise only to the brachiocephalic trunk and left subclavian arteries.

A common trunk for the brachiocephalic and left common carotid has been found as a frequent variation in *Homo*⁹¹ and in 4/32 *Pan*³⁴, 1/13 *Gorilla*²⁵ and 2/3 *Pongo*^{19, 71}.

In a female *Pan*, two brachiocephalic trunks were present, a long and a short one. The short trunk divided into the left carotid and subclavian arteries¹⁸. In a further three specimens of *Pan*, the left carotid and the left subclavian arise by a short communal trunk^{28, 34}, which may well be designated a left brachiocephalic trunk, as is occasionally found in *Homo*⁸⁷.

A fourth branch, the *thyroidea ima*, occurs rarely in *Homo*^{1, 21, 83, 87}, but far more frequently in *Pan*^{28, 34, 49, 82, 83}. In *Homo* it arises from the aortic arch, or the right common carotid, subclavian or internal thoracic arteries⁸⁷, while in African apes it arises either from the aortic arch or from the base of the left common carotid artery^{34, 49, 82, 83}. A *thyroidea ima* arises from the left common carotid artery in 4/20 *Hylobates*⁴⁹.

A *bronchial* artery arising from the aortic arch has been found as a variant in *Homo* and *Pan*^{77, 81}.

Brachiocephalic trunk

No information for *Hylobates*.

The brachiocephalic artery is 4-5 cm in length in *Homo*⁸⁷, and has been found to be 5 cm in length in *Gorilla*⁷⁴. It crosses the trachea in *Homo* and *Gorilla*^{87, 88}.

The brachiocephalic trunk divides into the right common carotid and right subclavian arteries in *Homo* and African apes^{17, 18, 77, 86}.

In *Pongo* the brachiocephalic trunk gives off the left common carotid, then divides into the right common carotid and right subclavian^{19, 71}.

The *right common carotid* divides to form the external carotid and the internal carotid arteries just above the superior border of the thyroid cartilage in *Homo* and *Gorilla*^{74, 87}.

Left common carotid artery

The left common carotid may give off a thyroidea ima in *Pan*^{34, 77, 82, 83}, 1/9 *Gorilla*⁴⁹, and 4/20 *Hylobates*⁴⁹ but does not do so in *Homo*⁸⁷ or *Pongo*⁷⁸.

Left subclavian artery

No information for *Pongo* or *Hylobates*.

Branches of the left subclavian artery in *Homo* and *Pan* include the vertebral and internal thoracic arteries and the thyrocervical and costocervical trunks^{34, 87}.

In *Homo* and *Gorilla* a *dorsal scapular* branch is present^{74, 87}, and in *Pan*, an unnamed vessel is given off to the prevertebral muscles³⁴.

The left subclavian artery is relatively larger and less vertical in *Pan* than in *Homo*⁷⁷.

Internal thoracic artery

No information for *Pongo* or *Hylobates*.

The internal thoracic artery arises from the subclavian artery near the thyrocervical trunk in *Homo* and African apes^{74, 83, 87}.

It is separated from the pleura by the transversus thoracis muscle for more of its thoracic course in *Pan* than in *Homo*⁸³.

Branches include the *anterior intercostal* arteries in *Homo* and *Pan*, which are distributed to the superior five or six intercostal spaces, while the *musculophrenic* artery supplies the more inferior intercostal spaces^{83, 87}.

3.3.2.2.1.3 Descending thoracic

Bronchial arteries

No information for *Gorilla* or *Hylobates*.

Right and left bronchial arteries are present in *Homo* and *Pan*^{34, 77, 87}, but only a left bronchial artery has been found in *Pongo*⁷⁸.

Oesophageal arteries

No information for *Gorilla* or *Hylobates*.

These branches anastomose with ascending oesophageal branches of the left phrenic and left gastric arteries in *Homo*⁸⁷, and with those of the coelic trunk in *Pan* and *Pongo*^{77, 78}.

Posterior intercostal arteries

No information for *Hylobates*.

Nine pairs of posterior intercostal arteries are derived from the thoracic aorta in *Homo* and 1/2 *Pan*^{34, 87}. Twelve pairs are present in *Gorilla*⁵² and eleven pairs in *Pongo*⁷⁸, while ten pairs of arteries may be given off by the thoracic aorta in *Pan*⁷⁷.

The first posterior intercostal artery in *Pan* is large, supplying the fourth and fifth spaces on the right, and the third to fifth spaces on the left. The remaining intercostal arteries form eight symmetrical pairs³⁴.

The first and second intercostal spaces are supplied by the superior intercostal artery from the costocervical trunk in *Homo* and *Pan*^{34, 83, 87}, and also the third intercostal space unilaterally in *Pan*³⁴.

A large intercostal artery to the first intercostal space is present in *Gorilla*³⁰, but not in *Pongo*⁷⁸.

Subcostal arteries

No information for *Gorilla* or *Hylobates*.

A single pair of subcostal arteries is present in *Homo* and *Pan*^{34, 87}.

3.3.2.2.2 Pulmonary^a

Left pulmonary artery

No information for *Gorilla*.

It runs horizontally in front of the descending aorta and left bronchus in *Homo*⁸⁷, but on the posterolateral side of the left bronchus in *Pongo*⁶⁹ and on the posterior surface in *Hylobates*⁷⁰.

Above it is connected to the concavity of the aortic arch by the ligamentum arteriosum in *Homo*⁸⁷. The left pulmonary artery is united to the aortic arch by a wide open ductus arteriosus in a young female *Pan*⁷⁷.

The left pulmonary artery runs across the posterior side of the left middle lobe bronchiole in *Pan* and Asian apes^{68, 69, 70}. In *Hylobates* it then runs between the dorsal and lateral bronchiole systems⁷⁰.

Right pulmonary artery

No information for *Gorilla*.

The right pulmonary artery runs in front of the right bronchus in *Homo*⁸⁷, but runs along the posterolateral side of the right bronchus in *Pan* and Asian apes^{68, 69, 70}. In

Pongo in its distal portion the right pulmonary artery crosses obliquely over the posterior side of the right bronchus to course on its medial side⁶⁹.

At the root of the right lung it divides into two branches in *Homo*⁸⁷, but may divide into three branches in *Pongo*⁷⁸ and gives branches to each lobe in *Pan*, *Pongo* and *Hylobates*^{68, 69, 70}.

3.3.2.2.3 Axillary

Lateral thoracic artery

This artery is an independent branch of the axillary artery in African apes and *Homo*^{34, 62, 87}, while in Asian apes and as a variation in *Pan*^{66, 67}, it is a branch of the thoracoacromial artery⁶².

Thoracoacromial artery

This artery is present in all apes and *Homo*^{34, 62, 66, 67, 87}.

It has clavicular, acromial and deltoid branches in all except *Pongo*^{34, 62, 87}, while in *Homo*⁸⁷, variably in *Pan*³⁴, and in *Pongo* a pectoral branch is present⁶², absent from *Gorilla* and *Hylobates*^{62, 87}.

A lateral thoracic branch is present in Asian apes⁶² and as a variant in *Pan*^{66, 67}.

Superior thoracic artery

This artery is present in African apes and *Homo*^{62, 87}, but absent from Asian apes⁶².

66, 67, 87

3.3.2.3 Veins

3.3.2.3.1 Pulmonary

Right pulmonary veins

No information for *Gorilla*.

In the hilus of the right lung, the superior right pulmonary vein is formed by the union of veins from the upper lobe and the middle lobe vein in *Homo*, *Pan* and Asian apes^{68, 69, 70, 87}.

The inferior right pulmonary vein is formed in the hilus by the union of veins from the lower lobe in *Homo*, *Pan* and Asian apes^{68, 69, 70, 87}.

In *Hylobates*, a right accessory lobe vein enters the inferior right pulmonary vein⁷⁰.

Left pulmonary veins

No information for *Gorilla*.

In the hilus of the lung in *Homo*, a superior left pulmonary vein drains the upper lobe⁸⁷.

The inferior left pulmonary vein drains the lower lobe in *Homo*, *Pan* and Asian apes^{68, 69, 70, 87}.

A left middle pulmonary vein is present in *Pan* and Asian apes^{68, 69, 70}, entering the left atrium directly in *Pan* and *Hylobates*^{68, 70} and entering the inferior left pulmonary vein in *Pongo*⁶⁹.

Consequently, in *Pan*, four pulmonary veins enter the left atrium: the superior right lobe vein, the inferior right lobe vein, the middle left lobe vein and the inferior left lobe vein⁶⁸.

3.3.2.3.2 Cardiac

Anterior cardiac veins

No information for *Pan*, *Pongo* or *Hylobates*.

The anterior cardiac veins empty directly into the right atrium in *Homo*⁸⁷, and into the right auricle in *Gorilla*³⁸.

Coronary sinus

No information for *Pan*, *Pongo* or *Hylobates*.

The coronary sinus in *Homo* and *Gorilla* lies in the posterior part of the atrioventricular groove and opens into the right atrium posteroinferior to the opening of the inferior cava^{38, 87}.

The valve of the coronary sinus is not clearly marked in *Gorilla*³⁸.

Great cardiac vein

No information for *Pan*, *Pongo* or *Hylobates*.

The great cardiac vein receives tributaries from both ventricles in *Homo* and *Gorilla*^{38, 87}, and from the left atrium in *Homo* alone⁸⁷.

It courses around the base of the left auricle and empties into the superior end of the coronary sinus, where it is joined by the posterior vein of the left ventricle in both *Homo* and *Gorilla*^{38, 87}.

Middle cardiac vein (posterior interventricular vein)

No information for *Pan*, *Pongo* or *Hylobates*.

In *Homo* and *Gorilla* the middle cardiac vein is formed at the apex of the heart, running towards the right in, or near, the posterior interventricular groove. On

reaching the atrioventricular sulcus it turns to the left and empties into the inferior end of the coronary sinus^{38, 87}.

Posterior vein of the left ventricle

No information for *Pan*, *Pongo* or *Hylobates*.

In *Homo* this vein usually opens into the coronary sinus⁸⁷, as in *Gorilla*³⁸, but may end in the great cardiac vein⁸⁷.

Two smaller but sizeable veins were found draining the posterior surface of the left ventricle directly into the coronary sinus in *Gorilla*³⁸.

Small cardiac vein

No information for *Pan*, *Pongo* or *Hylobates*.

This vein, which in *Homo* runs in the coronary sulcus between the right atrium and ventricle posteriorly, opening into the termination of the coronary sinus⁸⁷, was not found in *Gorilla*³⁸.

3.3.2.3.3 Superior vena cava

No information for *Gorilla* or *Hylobates*.

The superior vena cava is formed by the union of the right and left brachiocephalic veins and receives the azygos vein in *Homo*, *Pan* and *Pongo*^{77, 78, 83, 87}.

In *Pongo*, the superior vena cava receives the right vertebral vein directly⁷⁸, which in *Homo* enters the brachiocephalic vein⁸⁷.

3.3.2.3.4 Inferior vena cava

No information for *Hylobates*.

In *Homo* and *Pan*, the inferior vena cava is formed by the union of the common iliac veins, deep to the right common iliac artery^{77, 87}. In *Homo* and *Pan* it ascends on the right side of the abdominal aorta^{77, 87}, while in *Pongo* it ascends on the left side of the aorta⁷⁸.

The inferior vena cava in African apes was completely surrounded by liver tissue, as is occasionally the case in *Homo*^{15, 77, 87}. In *Homo*, the right ovarian artery overlaps the inferior vena cava⁸⁷, while in *Pan* the artery passes posterior to the inferior vena cava⁷⁷.

The inferior vena cava receives the right ovarian vein, the right suprarenal vein and the hepatic veins in *Homo* and *Pan*^{77, 87}, and both renal veins in *Homo*, *Pan* and *Pongo*^{77, 78, 87}. In *Homo* four pairs of lumbar veins enter the inferior vena cava⁸⁷, while in *Pan* four single lumbar veins⁷⁷, and in *Pongo* two lumbar veins enter this vessel⁷⁸. A gastric vein enters the inferior vena cava in *Pan*, serving as a link between the systemic and portal circulations⁷⁷, while in *Homo* the gastric veins end directly or indirectly in the portal vein⁸⁷.

3.3.2.3.5 Azygos

Accessory hemiazygos vein

No information for *Pongo* or *Hylobates*.

The accessory hemiazygos vein is present in *Homo*, 1/2 *Pan* and *Gorilla*^{30, 36, 37, 87}, draining the upper left intercostal spaces^{30, 87}.

In *Homo* it opens into the azygos or hemiazygos veins⁸⁷, while in *Gorilla* it joins the superior vena cava³⁰.

Azygos vein

The azygos vein has been found in all apes and *Homo*^{37, 74, 77, 84, 87}.

It collects from the posterior intercostal veins of the inferior nine intercostal spaces in *Pan*⁷⁷, and from all the intercostal spaces except the first in *Homo* and *Symphalangus*^{84, 87}.

Its tributaries are subject to a great deal of variation in *Homo*³³.

The vessel ends in the superior vena cava in *Homo*, *Pan* and *Symphalangus*^{37, 77, 87}.

Hemiazygos vein

A hemiazygos vein is present in *Homo* and great apes^{30, 37, 84, 87}, but not in *Symphalangus*⁸⁴.

It drains the inferior three intercostal spaces in *Homo*⁸⁷, the inferior four intercostal spaces in African apes^{30, 84}, and the inferior five intercostal spaces in *Pongo*⁸⁴.

3.3.2.4 Lymphatics

Bronchopulmonary nodes

No information for *Pan*, *Pongo* or *Hylobates*.

These nodes are present in *Homo* and *Gorilla*^{45, 87}.

Thoracic duct

No information for *Pongo* or *Hylobates*.

The thoracic duct enters the thorax through the aortic hiatus and lies between the aorta and the vertebral centra in the midline in *Homo* and *Gorilla*^{74, 87}.

In *Pan*, the two thoracic ducts unite at the level of T6 to form a single trunk⁷⁷.

It ascends, passing to the right in *Gorilla* so that opposite the twelfth to tenth ribs it lies nearer the right side⁷⁴ while in *Homo* it ascends leftwards throughout its course⁸⁷. Unlike *Homo*, in which the duct lies between the aorta on the left and the azygos vein on the right⁸⁷, the duct at this point is wedged between the aorta anteriorly and the azygos vein posteriorly in *Gorilla*⁷⁴. From the ninth to the fifth ribs the duct lies on the right side of the aorta in *Gorilla*, as in *Homo*^{74, 87}.

The duct ascends posterior to the oesophagus in African apes^{74, 77}, and on the left side of the oesophagus in *Homo*⁸⁷, eventually curving around the left side of the oesophagus in African apes^{74, 77}. It lies medial to the left subclavian artery in *Gorilla*⁷⁴, but posterior to the artery in *Homo*⁸⁷.

The length of the thoracic duct in *Gorilla* from the aortic hiatus to its termination on the superior aspect of the subclavian vein just lateral to its junction with the internal jugular has been noted as 31 cm, and from the cisterna chyli to the aortic hiatus as 10 cm, giving a total length of 41 cm in *Gorilla*⁷⁴, within the human range of 38 to 45 cm⁸⁷.

3.3.3 NERVES

3.3.3.1 Intercostal/subcostal

Intercostal

No information for *Pongo* or *Hylobates*.

The first intercostal nerve ends as a cutaneous nerve of the chest and axilla in *Homo*⁸⁷, while in *Pan* a branch of the first intercostal nerve reaches the axillary

glands⁷⁷. In *Gorilla*, branches of the first intercostal nerve are distributed to the medial and posterior surface of the arm as far as the olecranon process⁷⁴. This may correspond to variations in *Homo* where the first intercostal nerve communicates with the intercostobrachial nerve, or with the medial cutaneous nerve of the arm^{14, 87}.

Subcostal

No information for *Pongo* or *Hylobates*.

Homo has twelve thoracic nerves, the twelfth thoracic nerve being beneath the last rib, and is therefore called "subcostal"⁸⁷, while *Pan* has thirteen thoracic nerves in total, so the subcostal nerve is thus the thirteenth thoracic nerve⁸³. The subcostal nerve may be the twelfth or thirteenth thoracic nerve in *Gorilla*⁷⁴.

3.3.3.2 Cervical

Phrenic

No information for *Hylobates*.

The phrenic nerve arises from the third, fourth and fifth cervical nerves in *Homo* and great apes^{16, 18, 41, 74, 77, 78, 87}. Fine fibres from the second cervical nerve may also be present in *Pan*⁷⁷.

It passes across the anterior surface of scalenus anterior in *Homo* and African apes^{18, 41, 74, 77, 87}, and in *Homo* and *Pan* the nerve runs between the subclavian artery and vein^{77, 87}.

Close to the diaphragm, the phrenic nerve divides into three branches in *Homo*⁸⁷, five branches in *Pan*⁷⁷ and two branches in *Pongo*⁷⁸.

The phrenic nerve supplies the diaphragm, pleura and pericardium in *Homo*, *Pan* and *Pongo*^{77, 78, 87}, and communicates with phrenic sympathetic branches in *Homo*⁸⁷, 3/4 *Pan*⁷⁷, *Gorilla*^{30, 26} and 2/3 *Pongo*^{30, 26}, but this communication was not found in 1/4 *Pan*¹⁶ or 1/3 *Pongo*⁷⁸.

Supraclavicular

No information for *Pongo* or *Hylobates*.

The supraclavicular nerves arise from the third and fourth cervical nerves in *Homo* and African apes^{74, 77, 87}.

3.3.3.3 Vagus See 3.2.3.1

3.3.3.4 Brachial plexus See 3.4.3.1

3.3.4 ALIMENTARY SYSTEM

3.3.4.1 Oesophagus

No information for *Hylobates*.

Two layers of muscles, an outer longitudinal and an inner circular layer are present in *Homo* and *Pongo*^{78, 87}. An additional longitudinal muscular layer may be present in *Pan*⁷⁸.

The mucous membrane of the thoracic part of the oesophagus was totally devoid of rugae in *Pongo*⁷⁸, while in *Homo* and *Pan* longitudinal folds are present^{77, 87}. The mucous membrane of the oesophagus was oedematous in an adult male *Gorilla* who died of bronchopneumonia⁴⁵.

The muscular layer has been shown to extend more than three-quarters of the distance to the cardiac opening of the stomach in *Gorilla*⁶. Washburn states that the muscular layer of the oesophagus is restricted to the upper quarter of the oesophagus in *Homo*⁸⁸, but this is not supported by Warwick and Williams, in which the muscularis mucosae is said to be absent or scattered at the commencement of the oesophagus⁸⁷.

In the contracted state the oesophageal wall in an adult *Gorilla* was about 50% thicker, and the diameter of the oesophagus about 25% greater than in *Homo*⁷⁹. The oesophageal walls are thinner and more dilated inferiorly than superiorly in *Pan*⁷⁷.

With regard to position, in *Homo* and *Gorilla* the thoracic oesophagus is situated to the left of the trachea at first^{87, 88}, more so in *Gorilla* than in *Homo*⁸⁸. The curvature of the oesophagus as it travels through the mediastinum is more pronounced in *Gorilla* than in *Homo*^{87, 88}. In *Homo* the trachea is visible between the brachiocephalic artery and the left common carotid artery, while in *Gorilla* the oesophagus is in this position^{87, 88}.

3.3.5 RESPIRATORY SYSTEM

3.3.5.1 Trachea

No information for *Pan*, *Pongo* or *Hylobates*.

The trachea is composed of about twenty rings in *Homo*⁷ and sixteen to eighteen rings in *Gorilla*^{10, 24, 29, 39, 88}.

The lumen in *Homo* may be rounded, lunate or flattened in transverse section¹³, and is almost round in *Gorilla*⁷⁹.

The bifurcation of the trachea is at the level of T5 in *Homo*⁸⁷, and at the level of T4 in *Gorilla*⁸⁸.

3.3.5.2 Bronchi^b

No information for *Pan*, *Pongo* or *Hylobates*.

In both *Homo* and *Gorilla*, the right bronchus is wider and more vertical than the left^{42, 87, 88}.

3.3.5.3 Left lung

The lungs in *Pongo* are not divided into externally into lobes^{19, 70, 71, 78}, but internally two lobes can be distinguished⁷⁰.

As in *Homo*⁸⁷, two lobes were present in the left lung of *Pan*^{18, 35, 70, 77, 83, 85, 86}, and *Gorilla*^{42, 70, 79, 88}, with the fissure being shallower in male *Gorilla* than in female *Gorilla*^{42, 88}. The left lung also has two lobes in *Hylobates*⁷⁰.

Three lobes have been observed in the left lung of *Pan*⁶³.

	Length	Breadth	Thickness	BW	Weight
Male	27	15.5	10.5	130	1500 (1.15%)
Male*	-	-	-	68	850 (0.38%)
Female	18	14	-	227	760 (1.117%)

Table 3.3.4. Dimensions (cm) and weights (gm) of the left lung in two male and one female *Gorilla*. Body weights (BW) in kg. Numbers in parentheses are lung weight in percentage of body weight. Data from ⁴², except * from ⁷⁹.

3.3.5.4 Right lung

The lungs in *Pongo* are not divided externally into lobes^{19, 70, 71, 78}, but three lobes can be distinguished internally in the right lung⁷⁰.

In *Pan*, three lobes are present in the right lung^{18, 35, 70, 77, 83, 85, 86}, as in *Homo*⁸⁷, although two lobes have been observed⁶³.

In *Gorilla*, three⁴² or four^{70, 79, 88} lobes are present. The azygos lobe was defined on both sides of the lung in an adult female *Gorilla*, while in an adult male, the azygos lobe has separated only anteriorly⁸⁸.

Four lobes are present in the right lung of *Hylobates*⁷⁰.

	Length	Breadth	Depth	BW	Weight
Male	26	19.5	11.5	130 kg	1800 (1.38%)
Male*	-	-	-	68 kg	1100 (0.49%)
Female	23	12	-	227 kg	830 (1.22%)

Table 3.3.5. Dimensions (cm) and weights (gm) of the right lung in two male and one female *Gorilla*. Body weights (BW) in kg. Numbers in parentheses are lung weight in percentage of body weight (BW). Data from ⁴², except * from ⁷⁹.

3.3.5.5 Pleurae

No information for *Pan*, *Pongo* or *Hylobates*.

In *Gorilla* the anterior pleural reflection from the mediastinal surface to the ribs was far out on the rib cage so that the anteromedial margins of the pleural spaces and the lungs were rounded⁷⁹. The pleural spaces were not immediately exposed when the sternum and adjacent costal cartilages were removed, unlike *Homo*⁸⁷, because of this wide reflection of the pleura⁷⁹.

The interpleural space appeared relatively shorter from base to apex, and broader and thicker in *Gorilla* than in *Homo*⁷⁹.

Microscopically, a section of visceral pleura showed a group of fat cells in *Gorilla*, which is not normally seen in *Homo*⁷⁹, and in three adult *Gorilla* the parietal pleura and pulmonary pleura had fibrous adhesions^{79, 45}, especially at the pulmonary apex⁷⁹, while in an adult female, the pleura was smooth⁴⁵, as in *Homo*⁸⁷.

3.3.6 ENDOCRINE

3.3.6.1 Thymus

The size of the thymus varies in *Homo* with age, increasing in size until puberty, after which it gradually shrinks, undergoing progressive atrophy and replacement by fat, so that after mid-adult life it may weigh a third to a quarter of the weight at puberty, although it may remain large^{51, 87, 92}. This also appears to occur in African apes^{45, 74, 79, 83, 88}, although possibly at a slower rate in *Pan* than in *Homo*⁸³. In three adult *Gorilla*, only fat and fascia were found where the thymus should be^{45, 88}, the inferior and superior portions contained fat in a *Gorilla* examined by Raven⁷⁴, while in an adult male *Gorilla* about three-quarters of the gland had been replaced by fat⁷⁹.

The thymus extends as far inferiorly as the fourth costal cartilage in *Homo*⁸⁷, the fourth or fifth costal interspace⁸³ or the second or third costal cartilage in *Pan*⁷⁷, and the fifth costal cartilage in *Pongo*⁷⁸. The inferior extent of the thymus reaches the level of the apex of the heart in *Gorilla*^{74, 79}.

Its upper tapering parts extend into the neck, and may reach the inferior border of the thyroid in *Homo* and great apes^{74, 78, 79, 83, 87}. A portion of the left lobe in *Gorilla* extends posteroinferiorly between the pericardium and the left mediastinal pleura, reaching the root of the left lung⁷⁴.

Anteriorly it is covered by the sternum in *Homo* and African apes^{74, 83, 87} and by the sternothyroids in *Homo* and *Gorilla*^{74, 87}.

Posteriorly it covers the pericardium in *Homo* and great apes^{74, 77, 78, 79, 83, 87}, and also the great vessels in *Homo* and *Pan*^{83, 87}.

The gland is finely lobulated, consisting of two unequally sized pyramidal lobes connected by areolar tissue in *Homo* and great apes^{78, 79, 83, 87}. Deniker noted a three-lobed thymus in a fetal gorilla²⁴. The left lobe is larger than the right in *Pan*, 2/3 *Gorilla* and *Pongo*^{74, 77, 78}, the right larger in 1/3 *Gorilla*⁷⁹.

The thymus is innervated by the vagus nerve in *Homo* and *Pan*⁸³, and additionally by sympathetic nerves in *Homo*⁸⁷.

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