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ON THE

CHIMPANZEES

AND THEIR

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BY

ARTHUR KEITH, M.D., F.Z.S.

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On the Chimpanzees and their Relationship to the Gorilla.

By Arthur Keith, M.D., F.Z.S.

(Plate XX.)

At the present time there is in the Menagerie of Messrs. Barnum and Bailey an adult female anthropoid ape, known by the name of "Johanna," regarded by its owners as a Gorilla, but which, there can be no doubt, is in reality a Chimpanzee. No difficulty has ever been experienced in distinguishing between the male Gorilla and the male Chimpanzee, nor between the females when an anatomical investigation has been possible; but on several occasions, as in the case of this Ape, living female Chimpanzees have been mistaken for Gorillas. There is the classical case of "Mafuka,"[1] of the Dresden Zoological Garden. "Johanna" shares all the features of "Mafuka"; she answers to the description given by Du Chaillu of the species he names "*Troglodytes kooloo-kamba*"[2]. The animal dissected and described by Gratiolet and Alix[3] under the name of *T. aubryi* was also of the same variety. "Johanna" is of interest because she represents a variety of Chimpanzee which approaches the Gorilla in so many points that it is evident the characters which separate the two African anthropoids are not so well marked as many suppose. The difficulty of distinguishing the one from the other, as shown by a recent communication by Mr. Duckworth[4] to this Society, is such that it has become necessary to sum up, from a much wider examination of material than has ever been at anyone's disposal before, the structural and physiological differences which separate the Gorilla from the Chimpanzee, and at the same time to sum up the evidence as to the existence of one or more species of Chimpanzee. Some five years ago, on working minutely over all the anthropoid material in the collections of the Natural History Museum at South Kensington and the Museum of the Royal College of Surgeons, which contain the skulls of 31 Gorillas, 44 Chimpanzees, 73 Orangs, and 56 Gibbons, I was struck by the fact that nearly all the characters which had been used to differentiate species were points which varied in structure and form with age, sex, and the individual, but I have never had any difficulty in distinguishing between the skulls, even of fœtal Gorillas and Chimpanzees.

1. *The Eruption of the Permanent Teeth in Chimpanzees.*

Mr. Duckworth has promised the Society a full description of "Johanna," but I learned certain facts from her keeper,

[1] Keith. 'Introduction to the Study of Anthropoid Apes,' pp. 8, 23. London, 1897.

[2] Du Chaillu. 'Explorations and Adventures,' 1861, p. 360.

[3] Gratiolet et Alix. "Recherches sur l'Anatomie du *Troglodytes aubryi*," Nouv. Archiv. du Mus. Hist. Nat. 1866, t. ii. pp. 1–263.

[4] W. L. H. Duckworth. P. Z. S. 1898, p. 989.

Mr. Mackay, whom I believe to be reliable, adding so considerably to our knowledge of the habits of the Chimpanzee that I wish to give them here.

She is, so far as I know, the first Chimpanzee that has ever lived long enough in captivity to complete its permanent dentition. All her permanent teeth have cut, with the doubtful exception of the third molar on one side, and it becomes important to determine her age so as to ascertain the period of life at which these animals attain a complete set of permanent teeth. Man attains his about the twenty-second year, but the Chimpanzee evidently much earlier. Johanna has been twelve years in captivity—six years in Messrs. Barnum and Bailey's Menagerie, six years in the Zoological Gardens at Lisbon; and we may infer, as it is the common age, that she was one or two years old when Portuguese traders brought her there from the West Coast of Africa, probably Loango. When she came into his care six years ago, Mr. Mackay is positive she had then cut all her permanent incisors. From the appearance of the third molars, I think the permanent dentition has been completed very recently, so that we may accept the 12th or 13th year as the terminal period of the Chimpanzee dentition. As is usual in the female Chimpanzee, the canine teeth cut before the last molars. There are only two other records of the period at which the Chimpanzee teeth erupt. One is the case of "Sally"[1]. She was probably ten years of age when she died; the permanent premolars had cut, but the canines and the second and third molars had not appeared. Ehlers[2] also records the case of a Chimpanzee in which the permanent dentition was being completed about the 11th or 12th year by the eruption of the canine and last molar when the animal died.

2. *Menstruation.*

Little is known concerning the menstruation of the Anthropoids. The only observation is that of Ehlers[2], of a Chimpanzee which began to menstruate about the tenth year, and continued, until it died two years later, to show a monthly discharge. Mr. Mackay's observation on "Johanna" verifies Ehler's statement; she began to show a monthly discharge when she was believed to be ten years old. The discharge appears every 28th day, and lasts for three days. It is sanguineous in colour, profuse, amounting to perhaps 4 or 6 oz., staining freely her skirt. She is then very irritable. For 6 to 8 days before the discharge appears she is in heat, the genital labia are turgid and swollen; the nipples are fuller and more erect. When the discharge appears, the state of turgescence in the pudendal organs passes away. She shows a friendly disposition to men rather than to women. She frequently plays with her nipples, but has

[1] Beddard, F. "Contributions to the Anatomy of the Anthropoid Apes," Trans. Zool. Soc. Lond. 1892, vol. xiii. pp. 177–218.

[2] Ehlers, P. "Beiträge zur Kenntniss des Gorilla und Chimpanse," Abh. phys. Cl. Ges. Wiss. Göttingen, 1881, Bd. xxviii. No. 1, 77 pp., 4 pls.

acquired no degenerate sexual habits. The sexual state, so far as Mr. Mackay has observed, does not change with the season of the year. Of menstruation in the Gorilla, nothing is known.

3. *The Relationship of the Chimpanzee to the Gorilla.*

An examination of all the structural systems of the African Anthropoids leads to the inference that the Gorilla is the more primitive of the two forms, and approaches the common parent anthropoid more nearly than the Chimpanzee. The teeth of the Gorilla, individually and collectively, form a complete dentition, a dentition at the very highest point of development; the teeth of thh Chimpanzee show marked signs of retrogression in development of size and structure. The muscular development and the consequent bony crests for muscular attachment of the Gorilla far surpass those of the Chimpanzee. The muscular development of the adult Chimpanzee represents the system of the adolescent Gorilla. Some of the bodily organs of the Gorilla belong to a simpler and earlier primate type than those of the Chimpanzee. But in one point the Chimpanzee evidently represents more nearly the parent form—its limbs and body are more adapted for arboreal locomotion; of the two, the Gorilla shows the nearer approach to the human manner of locomotion. On the whole, the evidence at our disposal at the present time points to the fact that the Chimpanzee is a Gorilline derivative, in which, with a progressive brain-development, there have been retrograde changes in most of the other parts of the body. The various forms of Chimpanzee differ according to the degree to which these changes have proceeded.

4. *The Brain-development in the Chimpanzees and Gorilla.*

The temperament of the Gorilla and Chimpanzee is absolutely different. All the Gorillas of which we have any knowledge agree in being sullen, untamable, and ferocious, even the youngest of them. They do not tolerate confinement: only one has lived over a year in captivity in Europe; one is said to have been in the possession of an African chief for six years. The Chimpanzee, on the other hand, at any rate in its younger stages, takes to confinement easily, is teachable and playful. The elaborate toilet and performance gone through daily by "Johanna," the skilful way in which she decants her glass of wine, removing and replacing the stopper, declares her to be a Chimpanzee more clearly than any other character she could show. Her education is probably the most elaborate ever possessed by any ape. She appears to be colour-blind.

Du Chaillu states that the Chimpanzee to which he gives the name of *T. kooloo-kamba* had a distinctive cry; from her physical features "Johanna" appears to belong to that species. When in a fit of passion, into which she is easily thrown, the hair of the scalp becomes erect, she beats the floor with her feet and hands,

and utters a cry beginning with a low *hoo, hoo*, gradually raising it in volume to a loud climax. I do not think her cry differs from that of the young *Anthropopithecus niger* in character; what is peculiar in her cry may be put down to her more advanced age. The Chimpanzee cry is very different from the howl of the Gorilla; "Johanna" does not beat her breast, as the Gorilla does, when in temper. She allows her keeper, only, to handle her; she is vicious towards others and takes her revenge on an offender by suddenly throwing handfuls of litter at him from the floor of her cage. She has never been given an opportunity of manifesting any nest-building habit, and the experiment seems well worth trying. On making her escape on one occasion she was found carrying away large pieces of wood on her shoulder.

She is fed mostly on fruit. A day's rations consists of :—

2 dozen bananas.
1 „ oranges.
1 „ raw eggs.
½ „ apples.
Lemons.
Carrots.
Coffee, tea, port wine.
Toast and sandwiches.

When given an opportunity, she caught, plucked, and ate a sparrow, but she rejects no pellets from the stomach, as was the case with "Sally."

She sleeps on her side and spends the day sitting on a broad box, with her legs spread out in front and her arms on her belly.

There is a very marked difference between the size of the brain of the Gorilla and Chimpanzee. The average cranial capacity of seven adult female Gorillas I found to be 450 c.c.; of ten similar Chimpanzees 364 c.c.; but although the average is greater in the Gorillas, the highest of Chimpanzees exceeded the lowest of the Gorillas, so that the size of brain is not a feature that can be used to discriminate the one from the other. The average cranial capacity of six adult male Gorillas is 530 c.c.; of sixteen male Chimpanzees 405 c.c. The smallest Gorilla skull had a greater capacity than the largest Chimpanzee. The largest Chimpanzee skull measured 460 c.c. The cranial capacity appears to be diagnostic for the males of those animals. An important distinction appears in the size of the brain as in the general appearance of those Anthropoids; the sexual difference is much more marked in the Gorilla than in the Chimpanzee.

The cranial capacity of those animals, stated in c.c., may be taken as representing the brain-weight, stated in grammes[1]; but in comparing the relative size of the brains of the Gorilla and Chimpanzee a greater deduction has to be made from the brain of the Gorilla than from that of the Chimpanzee, owing to the much

[1] Keith. Journ. Anat. & Physiol. 1895, n. s., vol. ix. pp. 282–303.

greater body-weight of the former[1]. The weight of "Johanna" is 140 lbs. The greater cranial capacity of the Gorilla is marked before the end of the milk-dentition.

Cranial capacity does not help us to distinguish between the various forms of Chimpanzee. The skull of a male "Kooloo-kamba" brought home by Du Chaillu measures 420 c.c., rather more than the average capacity of the male Chimpanzee; four skulls of males brought by Emin Pasha from Central Africa average 422 c.c.; two females measured 378 c.c., showing distinctly a high average, and confirm in some degree the supposition that the Central-African form is a distinct variety: a male of the variety known as *A. calvus* measured 420 c.c.; two females averaged 368 c.c. These figures, so far as they go, show that the Chimpanzee, although widely spread, has not broken up into forms separated widely by a divergence in brain size.

5. *The Palate and Dentition of Gorillas and Chimpanzees.*

The size and shape of the hard palate, counting as the palate the whole area lying with the outer margin of the dental arcade, seem to me of great importance. The size and shape of the palate express better than other features the brute development of the race. The larger the relative size of the brain, the smaller the relative development of the palate. Its size and shape depend on the degree of development of the teeth. In an animal like the Gorilla, in which the dentition is complete and robust, the palate is extremely large and its length is much greater than its breadth. In the Chimpanzee at birth the breadth of the palate, as in Man, is greater than its length, whereas in the Gorilla the length is, even at birth, greater than the breadth. The development of the facial parts of the skull and of its bony crests depends on the size and shape of the palate.

As in the case of the cranial capacity, the palatal differences of the male Gorilla and Chimpanzee are very marked. The average palatal area of seven adult male Gorillas was 7200 mm.: the breadth was 63 per cent. of the length: the corresponding figures in 15 adult male Chimpanzees were, palatal area 4580 mm. and the breadth was 77 per cent. of the length. The maximum measurements in the Chimpanzees were less than the minimum measurements of the Gorillas. But the difference between the females was less marked; the palates of some Chimpanzees exceeded those of some Gorillas. Here, again, the palate affords no certain index as to the animal. But, on an average, the palate of the female Gorilla is much the larger: for 7 adult female Gorillas it was found to measure 5600 mm., the breadth being 73 per cent. of the length; in 11 female Chimpanzees the average area was 4200 mm., and the breadth 77 per cent. of the length. The figures quite bear out my opening statement that the brute development of the Gorilla, even in the female, is much greater than in the Chimpanzee.

[1] Dubois, E. "Ueber die Abhängigkeit des Hirngewichtes von der Körpergrösse beim Menschen," Archiv für Anthrop. 1898, Bd. xxv. p. 423.

The palate of the Central-African Chimpanzee most resembles that of the Gorilla. The average area for 3 males amounted to 4350 c.c., rather less than the ordinary Chimpanzee; the breadth is only 71 per cent. of the length—a very low amount. The skulls of *Anthropopithecus calvus* and *A. kooloo-kamba* are too few to draw inferences from, but in both the breadth index is over 80 per cent.

The difference in form and size of the teeth of Gorillas and Chimpanzees is very emphatically marked. The cusps of the molars of the Gorilla are extremely prominent, almost prismatic, with the enamel deposited in a sharp crystalline manner, with only round the bases of the cusps evidence of the crenated folds of enamel which form a pronounced character in the teeth of Chimpanzees. The cusps of the Chimpanzee are bluntly conical and not nearly so prominent as in the Gorilla. The crenation of the enamel is perhaps the most diagnostic feature of the great Anthropoids. Cusps resembling those of the Gorilla occur in the teeth of the Siamang and some South-American monkeys (*Brachyteles* and *Lagothrix*), and represent the molar cusp at its most robust development. The cusps of the Central-African Chimpanzee most resemble those of the Gorilla, but never approach them in degree of development.

The molar teeth of the Gorilla, as may be seen from the accompanying measurements, are very much larger than those of the Chimpanzee:—

	$m.^1$	$m.^2$	$m.^3$	$\overline{m.^1}$	$\overline{m.^2}$	$\overline{m.^3}$
Length of molar teeth, stated in mm., an average of both sexes of Gorilla...	14·6 (×14)	15·2	14·1	15	16	17
Do. Chimpanzee	10 (×10·5)	10·2	8	11·5	12	11

One may say, almost with certainty, that any upper molar tooth over 12 mm. in length is that of a Gorilla, and under 12 is that of a Chimpanzee. The molar teeth of the female Gorilla are almost as large as those of the male: the molars of the female Chimpanzee are smaller than those of the male and show more marks of retrogression: while the third molar of the Gorilla, especially the lower, is as fully developed as the other two teeth, the corresponding tooth in the Chimpanzee, as in Man, and as in the Orang, shows distinct retrograde changes. The table on p. 302, the result of the examination of 22 Gorilla and 26 Chimpanzee skulls, shows the retrograde development of the cusps in the Chimpanzee, especially in the third molar tooth.

The observations show that in point of size, in development of cusps, and in arrangement of enamel the teeth of the Gorilla far exceed those of the Chimpanzee, and, unlike former points of difference, the distinction between the molars of the females is as well drawn as between the molars of the males.

In every point the teeth of the Central-African Chimpanzee make the nearest approach to the Gorilla; the molars of the Bald Chimpanzee have probably undergone the most retrograde change.

Number of Cusps on the upper Molar Teeth of Gorillas and Chimpanzees.

	$\underline{m.^1}$			$\underline{m.^2}$			$\underline{m.^3}$		
	4 cusps only.	Small 5th present.	Small 6th present.	4 only.	Small 5th.	Small 6th.	4 only.	Small 5th.	Small 6th.
Gorillas	100 p.c.	Freq. present.	.....	56 p.c.	43 p.c.	1 p.c.	20 p.c.	55 p.c.	25 p.c.
Chimpanzees	100 p.c.	.....	.....	85 p.c.	15 p.c.	.....	90 p.c.[4]	10 p.c.	

[4] 4th cusp was very much reduced in size in over 50 per cent.

Number of Cusps on the lower Molar Teeth of Gorillas and Chimpanzees.

	$\overline{m.^1}$			$\overline{m.^2}$			$\overline{m.^3}$		
	4 cusps only.	5th.	6th.	4 only.	5th.	6th.	4 only.	5th.	6th.
Gorillas	10 p.c.	90 p.c.	.....	.....	80 p.c.	20 p.c.	.....	70 p.c.	30 p.c.
Chimpanzees	.....	90 p.c.	10 p.c.	.....	80 p.c.	20 p.c.	25 p.c.	65 p.c.	10 p.c.

The differences between the premolar teeth of the Gorilla and Chimpanzees are even more marked than between the molars, and these teeth will probably afford the best clue to the indentification of different races of Chimpanzee. The premolars of the Gorilla are much larger than those of the Chimpanzee and show very little individual variation.

The average Length of the Premolars in Gorillas and Chimpanzees.

	$\underline{pm.^1}$	$\underline{pm.^2}$	$\overline{pm.^1}$	$\overline{pm.^2}$
Gorilla	10 mm.	10 mm.	16 mm. (male). 14 mm. (female).	11 mm. 11 mm.
Chimpanzee	7·5 mm.	7 mm.	10 mm. (male). 9 mm. (female).	8·5 mm. (male). 7·5 mm. (female).

The most characteristic feature of the Gorilla, male and female alike, is the great development of the first lower premolar tooth. To a certain extent this is dependent on the great development of their canines. The upper premolars of the Gorilla are of equal size; in the Chimpanzee the second premolar is, with occasional exceptions, less than the first and shows in the size of its cusps and the union of its fangs signs of a retrograde development. A feature of the Central-African Chimpanzee is the relative small size of its second premolars, both upper and lower; there is not

enough of material to make any statement as to their development in *Anthropopithecus calvus* and *A. kooloo-kamba*. The premolars of the Chimpanzee although differing in size, do not differ much in the number and arrangement of their cusps.

The canine teeth have attained their greatest development amongst the large Anthropoids in the Gorilla. Their large size expresses the ferocity of the animal. The sexual difference between the canines of the male and female is much greater in the Gorilla than in the Chimpanzee: the canines of the male Chimpanzee equal in their development those of the female Gorilla. The upper canines of the male Gorilla project 14–18 mm. above the other teeth; their antero-posterior diameter varies from 18–20 mm.; the lower project above the premolar teeth from 8–10 mm. The development of the upper canines of the male Chimpanzee is much less than those of the Gorilla: the upper projects 8–12 mm. with an antero-posterior diameter of 12–15 mm.; the lower reaches above the other teeth from 4–6 mm. In the female Gorilla the upper canines reach above the other teeth from 8–10 mm.; the corresponding measurement in the Chimpanzee is from 6–8 mm.: in the lower teeth, the canines of the Gorilla project 4–6 mm.; in the Chimpanzee seldom more than 3 mm. The size of the canine teeth helps in the diagnosis of the Chimpanzee.

The incisor teeth of the Gorilla are a fourth larger than those of the Chimpanzee, but the relative size of the individual incisors is almost the same. The upper lateral incisors, owing to the great size of the canines, are relatively small in the Gorilla. The arrangement of the cuspules of enamel on the teeth of the one is different from that of the other, but the small amount of material at my disposal precludes me from making any more definite statement.

In both the Chimpanzee and Gorilla the last permanent and canine teeth commonly cut together; but in the Chimpanzee the canine cuts more frequently before the last molar than in the Gorilla.

"Johanna" has the habit of yawning frequently, when a full view is got of her teeth, and there cannot be a doubt for an instant that in every point she possesses the dentition of a female Chimpanzee.

I know of four instances of supernumerary molars in the Gorilla. I know of only one in the Chimpanzee, and yet Chimpanzee skulls are three times more numerous than those of the Gorilla.

6. *The Myological and Osteological Differences in the Bodies and Limbs of the Gorilla and Chimpanzee.*

It is a very remarkable fact, and one that very forcibly proves the close relationship between the Gorilla and Chimpanzee, that there is scarcely a feature in any muscle or bone found in one animal which is not also found in the other. What is the exception in the one, frequently proves the rule in the other, and

it is only by dealing with a large number of the two races that their essential characteristics can be arrived at. The statements made here, concerning the arrangement of muscles, are founded on accounts more or less complete of the dissections of 13 Gorillas and 30 Chimpanzees. When the osteological and myological differences that separate the Chimpanzee and Gorilla are analyzed it is found that they all centre round the adaptation of the Chimpanzee for a life almost completely arboreal, while in the Gorilla they indicate an adaptation for spending a life in the open as well as on trees. In short, the body of the Gorilla is more adapted for the human manner of progression than that of the Chimpanzee.

The approach to plantigrade progression is seen in the development of the heel and calf-muscles of the Gorilla. The os calcis projects behind the astragalus, to serve as a lever for the soleus and gastrocnemius, twice as far in the Gorilla as in the Chimpanzee. The projection in the Chimpanzee is always less than 1·5 cm.; it is never less than 3·5 cm. in the adult Gorilla. The soleus, too, shows a much greater tendency in the Gorilla than in the Chimpanzee to assume the form found in Man. It had acquired an origin from the tibia in 3 out of 8 Gorillas and in only 2 out of 12 Chimpanzees, while in the Gorilla the soleus resembles to some extent the human arrangement by being more closely fused with the tendon of the gastrocnemius.

As a grasping-organ, made up of two limbs, a hallucial limb on the one side and a digital limb on the other, the foot of the Gorilla does not differ materially from that of the Chimpanzee. The proportional length of these limbs to each other and to the lower extremity, as seen in the skeleton, are alike in both. The muscles that act on them, except in minor details, are almost alike. The foot of the Gorilla is the more bulky, broader, and the two proximal phalanges of the toes lie within the plantar web.

The muscles that flex and adduct the great toe show the same arrangement and same variations in both, and in the extensor muscles of that digit only the tibialis anticus is different, making an approach to the human form in the Gorilla. Of 7 Gorillas, only the tendon was divided in 5; the division extended deeply into the muscle in 2: in the Chimpanzee, on the other hand, resembling the lower Primates, the muscle and tendon were divided in 16, the tendon only in 3. This, again, is a point in which the Gorilla shows an adaptation to plantigrade progression.

When the digital limb of the foot is examined, the Chimpanzee shows the greater number of primitive features. The contrahentes muscles, either as fibrous bands or as fibro-muscular slips, are always more evident in the Chimpanzee than in the Gorilla. The interosseous muscles in the foot of the Chimpanzee are arranged as in all the lower Primates, the third digit receiving the insertion of the 2nd and 3rd dorsal interossei muscles; but in 3 out of 7 Gorillas the second digit, as is the case in Man, received the insertion of the 1st and 2nd dorsal interossei muscles. In this feature also the Gorilla shows an approach to an adaptation for plantigrade

progression. In both, the muscles of the fifth toe show a marked tendency to become vestigial—a condition which occurs in Man, and which Mr. Herbert Spencer believes to be due to the wearing of boots; but the retrograde changes are most marked in the Gorilla. In 4 out of 11 Chimpanzees this digit received a tendon from the *extensor brevis digitorum*, a tendon found in only 1 Gorilla out of 8. The flexor brevis of this digit was absent in 3 Chimpanzees and fibrous in 11; it was absent in 3 Gorillas, fibrous in 6, and muscular in 3. The flexor accessorius is equally variable in both; it was found in the feet in 6 out of 10 Gorillas and in 6 out of 11 Chimpanzees. The origin of the flexor brevis digitorum shows much variation in both animals, but the tendency for a complete transference of the origin of this muscle from the tendon of the long flexor of the foot to the tuberosity of the heel is most marked in the Chimpanzee, a character in which it more resembles Man than its congener.

The better adaptation of the lower extremity of the Chimpanzee for a climbing-organ is seen in the extensive insertion of the semitendinosus, gracilis, sartorius, and biceps to the fascia of the leg, in the occasional slip from the *adductor magnus* to the inner head of the *gastrocnemius*, and in the separation of the *scansorius*. The scansorius is a segmention from the anterior border of the deepest gluteal sheet, for the more complete flexion of the hip-joint. It existed as a separate muscle in 6 out of 11 Chimpanzees and in only 2 out of 8 Gorillas. The lower extremity is nearly equal in length (sometimes longer) to the upper extremity; in the Gorilla it is always shorter; but the proportion of the anterior and posterior limbs varies considerably.

Some well-marked features, related to their methods of locomotion, distinguish the upper extremity of the Chimpanzee from the Gorilla. The arm of the Chimpanzee is that of the brachiators, anthropoids like the Orang and Gibbon, which use the arms as one of the main organs of locomotion. The arm of the Gorilla resembles more in its proportions that of the lower Apes. Both the Chimpanzee and Gorilla agree in showing many retrograde changes in the thumb. In neither is it a grasping-organ. The flexor longus pollicis is vestigial in both; in Gorillas it was represented by a tendinous thread springing from the deep flexor of the index digit in 2; in the remaining 10 it was completely absent or represented by a piece of tendon in the thumb only. In 25 Chimpanzees it was present as a thread in 15, and in the remaining 10 it was completely absent or merely the terminal part of the tendon was present. The retrograde change has made furthest progress in the Gorilla. The short muscles that flex the thumb have the same arrangement in both, except that the *opponens pollicis* is better marked in the Gorilla.

There are differences in the extensor muscles of the thumb. The tendon of the extensor ossis metacarpi is much more completely divided into a carpal and a metacarpal part in the Chimpanzee; and while this tendon sent a slip to the proximal phalanx of the thumb, as it always does in Man, in 4 out of 9 Gorillas,

such a slip occurred in only 1 out of over 20 Chimpanzees. On the other hand, the *extensor longus pollicis* of the Chimpanzee frequently sends a slip to the proximal phalanx, an occurrence not met with in Gorillas. The thumb in the Chimpanzee is on the whole the more robust, but in the arrangement of the extensor muscles the Gorilla approaches most nearly to Man. In proportion to the length of the upper limb, the thumb of the Chimpanzee is slightly the longer.

There are certain well-marked points of distinction between the palmar and digital parts of the hand of the African Anthropoids. The hand of the Chimpanzee is long and narrow, a hook to cling by; the hand of the Gorilla is shorter and broader. The metacarpal and phalangeal parts of the Chimpanzee hand make up over 25 per cent. of the length of the upper extremity; it seldom exceeds 22 per cent. of the Gorilla's arm and is frequently less. The hand of the Chimpanzee is adapted for brachiation, the hand of the Gorilla is not. The contrahentes muscles to the 4th and 5th digits are very seldom absent in the Chimpanzee; they are seldom present in the hand of the Gorilla. The tendon of the flexor profundus digitorum to the index digit commonly sends a slip to the tendon of the third, a rare occurrence in the Chimpanzee.

The arrangement of muscles on the back of the hand, as in the case of those of the flexor aspect and of the thumb, is most primitive in the Chimpanzee. In both apes the superficial extensor muscle to the fifth finger is small or absent; the extensor indicis, a muscle of the deep layer of extensors, was present in all the Chimpanzees examined, but only in 7 out of 8 Gorillas; the deep extensor of the 3rd digit was present in none of the Gorillas, but in 5 of 12 Chimpanzees; the corresponding tendon to the 4th digit was present in 1 of 8 Gorillas and in 4 of 12 Chimpanzees. The deep extensor of the fifth digit was present with equal frequency.

A curious transmigration in the origin of the forearm muscles, resembling the change that has occurred to a greater extent in Man, is seen at the elbow of the Chimpanzee. The *pronator radii teres* has in the Chimpanzee an origin from the coronoid process of the ulna in 9 animals out of 11, in only 3 out of 8 Gorillas; an origin of the *flexor corpi radialis* from the radius is more common amongst Chimpanzees; the flexor sublimis digitorum had a coronoid origin in 10 out of 12 Chimpanzees and in only 1 out of 8 in the larger ape.

A consideration of muscles which have become more or less vestigial in Anthropoids shows how closely the Chimpanzee and Gorilla are related to each other, and at the same time how they differ. The following list will show this at a glance:—

	Gorilla.		Chimpanzee.	
	Present.	Absent.	Present.	Absent.
Palmaris longus	4	7	9	3
Plantaris	0	12	25	17
Penoneus quinti digiti.	Equally small or absent in both.			
Pyramidalis	,,	,,	,,	
Psoas parvus	,,	,,	,, (absent 40 p.c.).	

The *latissimo-condyloideus*, a muscle which has been reduced to a mere fibrous vestige in Man, is much diminished in size in both Gorilla and Chimpanzee, but it is larger and more primitive in its attachments in the Chimpanzee than in the Gorilla. The humerus is proportionally long in the Gorilla (40 per cent. or more of the limb). The arm of the Chimpanzee, considering all its characters, approaches the conditions found in the brachiating Apes and shows features adapted for climbing not shown by that of the Gorilla.

A distinctive feature of the Gorilla, and one adaptative to plantigrade progression, is the great development of the anterior-superior part of the ilium. The breadth of the iliac fossa, measured from the posterior-superior to the anterior-superior iliac spine is never less than 17 cm in the adult Gorilla and never more than 13 cm. in the Chimpanzee. The result of this development is that the posterior part of the external oblique muscle of the abdomen is inserted to it; the tensor vagina femoris arises from it; the iliac crest acts as a fulcrum for these muscles to balance the body on its lateral aspects.

The bones and muscles of the Chimpanzee thorax resemble the arrangement found in lower Primates more closely than those of the Gorilla.

One of my pupils, Mr. Tredgold [1], has shown that the average costal development of the Chimpanzees is 13·20 ribs, for Gorillas 12·86; there are commonly 13 pairs in both, but 12 pairs occur in the Gorillas occasionally and 14 pairs not unfrequently in the Chimpanzees. The lower limbs of the Gorilla show a tendency to be fixed to a vertebra higher up than in the Chimpanzee [2]. The lumbar curve is more pronounced in the Gorilla [3]. Further, in the more extensive attachment of the pectoral muscles to the chest-wall, and in the absence of a hiatus between the clavicular and sternal parts of the pectoralis major, the Chimpanzee recalls the arrangement in the lower Primates more than is the case in the Gorilla. The secondary attachment of the pectoralis minor to the coracoid process, a constant insertion in Man, is the rule in Gorillas and the exception in Chimpanzees; it occurred in 8 out of 9 Gorillas and 7 out of 18 Chimpanzees. That point also indicates adaptation in the arm of the Chimpanzee to brachiation.

There is a very well-marked difference between the Gorilla and Chimpanzee in the attachment of the extensor muscles of the neck. The difference is seen in the Chimpanzee's more extensive cervical origin or insertion of the *trapezius*, *rhomboideus*, *splenius colli*, *levator anguli scapulæ*, and *omo-trachelien* muscles; they have also a more extensive attachment to the dorsal vertebræ below. The wide cervical attachment, which was the rule for these muscles in the Chimpanzee, was the exception in the Gorilla. These attachments are adaptive to the greater mobility of the head of the Chimpanzee, a feature in which it much more resembles Man than the Gorilla.

[1] Journ. of Anat. & Physiology, vol. xxi. p. 288.

[2] A. M. Paterson. Trans. Roy. Society, Dublin, 1893, ser. 2, vol. v. pt. iii.

[3] D. T. Cunningham. Cunningham Memoirs, Roy. Irish Acad. 1892, no. vii.

It will be thus seen that there is scarcely a feature in any muscle or any bone in the body of the Chimpanzee or Gorilla that can be said to be distinctive, and yet, when their characters are summed up, on an average, there are very striking differences between the body of the one and the body of the other.

7. *The External Ear of the Gorilla and Chimpanzee.*

The external ear of Man and the Anthropoid Apes, as well as that of some South-American monkeys, is in a retrograde phase of development. Retrogression has proceeded furthest in the ear of the Orang-utan, to a less degree in the ears of Man and the Gorilla, and least in that of the Chimpanzee. "Johanna" has what may be described as the typical Chimpanzee ear, a form not known to occur amongst Gorillas. It measures 85 mm. from the top of the helix to the lower border of the lobule, and 50 mm. from the base of the tragus to the posterior border of the helix. The height of the Gorilla ear seldom exceeds 60 mm. and its breadth is commonly about 40 mm. The ear of the Chimpanzee stands out from the side of the head at an angle, like the wind-sail from the port-hole of a steamer; the ear of the Gorilla is appressed to the side of the head. Du Chaillu describes the ear of *A. kooloo-kamba* as very large; the ear of *A. aubryi*, supposed to be of this species, was much smaller than that of "Johanna"; while the ear of "Mafuka" resembled in size that of the Gorilla. The small, Gorilla type of ear is seen occasionally in the Chimpanzee. The Chimpanzee type of ear is quite a common human form. The folding of the posterior border of the ear, which must be regarded as evidence of a retrograde development, has proceeded to a further extent in the Gorilla than the Chimpanzee.

The degree to which the posterior border of the Helix is folded in Gorillas and Chimpanzees.

	Number.	Not folded.	2 mm. fold or less.	4 mm. fold or less.	Average.
Gorillas	19	2	15	5	1·30
Chimpanzees . .	22	9	12	1	·60

The lobule of the ear is more developed in the Gorilla. "Johanna" possesses a very large lobule, measuring about 12 mm. in depth.

The development of a Lobule in Gorillas and Chimpanzees.

	Total number.	Lobule less than 10 mm. deep.	Less than 15 mm. deep.	More than 15 mm. deep.	Average.
Gorillas	25	4	16	5	10·4 mm.
Chimpanzees .	14	9	4	1	3·4 mm.

The average development of the lobule of the human ear is nearly 15 mm. Its meaning is unknown.

Darwin's point appears more frequently in the Gorilla than in the Chimpanzee. It appears in 9 per cent. Chimpanzees and 26 per cent. Gorillas, the last figure corresponding to its appearance in Man—taking an average of various races. The development of the antehelix in the Gorilla approaches that of Man more nearly than the Chimpanzee. The muscles of the ear are more rudimentary in the Gorilla than in the Chimpanzee. Almost in every point the ear of the Gorilla is the more human of the two. The external ear is certainly an aid in distinguishing between the Chimpanzee and the Gorilla.

8. *The Circulatory and Digestive Systems of the Gorilla and Chimpanzee.*

Our knowledge of these systems in the two African anthropoids is founded on a too limited amount of material to allow of any definite statement being made as to the points on which they differ. On the whole, they appear to resemble each other very closely. The only feature that appears to demarcate them is seen in the liver. The right lobe of the Gorilla liver shows always a deep fissure, separating off a right lateral lobe, a fissure which occurs vary rarely in the Chimpanzee and only occasionally in the Orang. The liver of the Gorilla, in its division, is the most primitive form found in the Anthropoids and most nearly resembles that of the lower Catarrhini. On the other hand, especially in its bulbous glans penis, the genital system of the Gorilla is the more human. Laryngeal sacs occur both in the Gorilla and Chimpanzee, and it is rather strange that "Johanna" has never been observed to manifest its presence.

9. *Hairs and Pigment as distinctive Features of the Gorilla and Chimpanzee.*

Neither the colour nor arrangement of hair, nor the degree to which the skin is pigmented assist much in the differentiation of the adult female Chimpanzee and Gorilla. In *Anthropopithecus niger* the pigment appears much later than in the other Chimpanzees, and circum-oral and supra-orbital parts of the face appear never to become deeply pigmented. The skin of the Gorilla, especially the face, ears, palms, soles, and dorsal aspects of the trunk and limbs, are deeply pigmented at birth. The adults of *A. calvus* and *A. kooloo-kamba* show an equally intense deposit of pigment; so does the Central-African variety, but it is unlikely they are so deeply pigmented at birth. The scalp of *A. kooloo-kamba*, taking Johanna as an example, seems almost as thinly supplied with hair as *A. calvus*. The arrangement of hair is the same in all.

10. *Features of the Face and Skull which are characteristic of the Chimpanzee.*

Next to the teeth, the most characteristic features of the Gorilla are to be found in the structure of its nose. The Gorilla retains

the long nasal bones of the lower Catarrhini; in all the other Anthropoids and in Man they have undergone marked retrogression, especially in the Orang. The nasal bones, as can be seen in the living Chimpanzee, extend downwards to the level of the lower border of the orbit and are never over 25 mm. long; in the Gorilla they extend much lower down and are never less than 40 mm. in length. The nasal bones of the Gorilla show a sharp median ridge, evident in the living animal. This ridge appears at adolescence and sometimes disappears in very old animals. A trace of this ridge is seen on the nasal bones of the Central-African Chimpanzee. The nasal bones unite before birth in the Gorilla, at or after birth in the Chimpanzee. At their upper end the nasal bones of the Gorilla always project within the interfrontal suture, sometimes to a slight degree, frequently to a very considerable extent, and at their lower ends unite into a spine in over 60 per cent. of skulls. On the other hand, the nasal bones of the Chimpanzee seldom project within the interfrontal suture and only to a slight extent, the examples occurring mostly in Central-African Chimpanzees, and show an inferior spine in only 15 per cent. of skulls, and these were mostly from Central Africa. The inter-orbital breadth and the shape of the bridge of the nose have frequently been used as characters of differentiation. They both depend on age, and to some extent on sex. All through the life of a Chimpanzee the bridge of the nose keeps changing in conformation, owing to the continual growth of the lachrymo-ethmoidal air-sinus; the convex bridge of the young adult becomes converted into the flat or depressed bridge of the old adult. The inter-orbital breadth is practically the same for Gorillas and Chimpanzees, being greater in males than females, but the bridge of the nose in the Gorilla never becomes flattened and depressed like that of the Chimpanzee.

In her wide, smooth, rounded alar nasal folds, Johanna, and all the Chimpanzees ascribed to the variety of which she is an example, shows a marked Gorilline feature. *A. niger* never possesses these folds so markedly, although they do increase in size with age; but in the Gorilla they extend almost to the margin of the lip, the middle part of which shows a widely grooved philtrum. In Johanna a distinct transverse groove marks the upper lip from the nose, and such a groove occurs always in Chimpanzees. The middle and inferior turbinate bones of the Chimpanzee are more convoluted than in the Gorilla, and the nasal duct less inflated.

In development, the palatine processes of the palate-bone of the Gorilla frequently fail to meet, giving rise to a form of cleft palate; they always, when they unite, leave an open angle between them: the corresponding processes in the Chimpanzee are always well developed and unite so as to leave the bony palate with a transverse posterior border. The nasal spines of the premaxilla are commonly present in the Gorilla (17 out of 28) and seldom in the Chimpanzee (5 out of 43). The nostrils are widest in the Gorilla. The anterior opening of the nasal cavity in the adult Chimpanzee

measures on an average 25 mm. high and 25 mm. broad; in the female Gorilla 29 mm. high and 31 mm. broad; 34 mm. high and 38 mm. broad in the adult male Gorilla. The orbits vary according to age, sex, and the individual, but they measure, almost without exception, most in the transverse diameter in the Chimpanzee, in the vertical in the Gorilla, a feature dependent on teeth development.

Certain features in the foramina for the exit of nerves in the facial part of the skull separate the Gorilla and Chimpanzee. The infra-orbital foramen in the Gorilla is divided into two or more compartments by a vertical bar, that in the Chimpanzee by a horizontal bar. This difference depends on the fact that the infra-orbital nerve in the Gorilla sinks down within the maxilla from the margin of the orbit; in the Chimpanzee it passes horizontally inwards from the maxillary-malar suture. The foramina for the nasal nerves are always to be seen in the nasal bones of the Gorilla, never in those of the Chimpanzee; in the Chimpanzee these foramina occur in, or at the side of, the upper part of the premaxilla. Malar foramina occur only occasionally in the Gorilla; they are always present in the Chimpanzee. The inferior palatine foramen of the Chimpanzee is divided by a process of bone—a division not seen in the Gorilla.

The supra-orbital ridges in Johanna project from the frontal bone to a depth of 22 mm., and are separated by a glabellar notch. This notch is very seldom seen in the female and never in the male Gorilla. It rarely occurs in the male Chimpanzee and is variable in the female, but does not appear to be confined to any particular race. The supra-orbital ridges keep on growing through life: in 5 young adult Chimpanzees their average depth was 14 mm., in 4 old adults 18 mm.; at corresponding periods of the same sex of the Gorilla they measure 20 and 25 mm. In this feature Johanna resembles the Gorilla. These ridges begin to form before the milk-dentition is completed, and the part they play in the animal economy is to strengthen the facial portion of the skull to give a firm dental support.

The skull of the Chimpanzee is the more brachycephalic. The average length of 10 skulls of Gorillas, excluding from the measurements the prominence due to the frontal air-sinuses and the external occipital protuberance, was 118 mm., the corresponding measurement in 10 skulls of Chimpanzees 103·6; the breadth of skull, from one parietal eminence to another, was in the first 94 mm., in the second 89 mm. The breadth of the skull in Gorillas is 80 per cent. of the length, in Chimpanzees 86 per cent. But the measurements overlap, and many of the measurements of the female Gorilla correspond to those of the female Chimpanzee.

The temporal ridges in Johanna are about 25 mm. apart on the crown of the head, a Chimpanzee character. In only 1 out of 5 adult female Gorillas had these ridges not fused into a median crest, and in that particular case the cranial capacity was uncommonly great. In it the temporal ridges were 20 mm. apart.

In 9 adult female Chimpanzees, on the other hand, in only one had the temporal ridges united to form a slight crest: the average distance between them is 22 mm. These ridges in the male Gorilla reach the sagittal suture as the canine teeth cut and fuse into a ridge, which continues to grow all through life. In the male Chimpanzee they only occasionally unite to form a ridge. The development of the temporal ridges, the height to which they reach on the roof of the skull, depends on the dentition. The condition in the adult female Chimpanzee corresponds to the stage of development found in a male Gorilla cutting its second molar tooth.

The lower jaw in the female Gorilla, almost without exception, exceeds in every dimension that of the female Chimpanzee.

11. *Summary.*

The Gorilla may be distinguished in life from the Chimpanzee by its sullen, untamable, ferocious nature; its long nasal bones descending far below the level of the infra-orbital margin; its great alar nasal folds running to the margin of the upper lip; its great peculiar molar, premolar, and canine teeth; its broad, short, thick webbed hands and feet; its long heel and the great length of its upper arm with the smaller development of the forearm.

EXPLANATION OF PLATE XX.

Anthropopithecus troglodytes kooloo-kamba. Taken from the specimen named "Johanna," living in the collection of Messrs. Barnum and Bailey.

J. Smit del. et lith.

Mintern Bros. imp.

ANTHROPOPITHECUS TROGLODYTES KOOLOO-KAMBA, ♀.

(JOHANNA)