Journal of Anatomy and Physiology.

THE COMPARATIVE ANATOMY OF THE MUSCLES AND NERVES OF THE SUPERIOR AND INFERIOR EXTREMITIES OF THE ANTHROPOID APES.[1] By DAVID HEPBURN, M.D., F.R.S.E., *Senior Demonstrator of Anatomy, University of Edinburgh.* PART I. (PLATE III.)

SOME time ago, through the kindness of Sir William Turner, of the University of Edinburgh, and of Professor D. J. Cunningham, of Trinity College, Dublin, I found myself in the unique position of having the upper and lower limbs of each of the great Anthropoid Apes in my possession at the same time. From the former I received a young male Gorilla, and from the latter the upper and lower extremities of a Chimpanzee, an Orang-utan, and a Gibbon. Accordingly, I determined to make fresh dissections of the limbs of these animals, and, while not ignoring what had previously been contributed to the literature of the subject, I wrote entirely independent descriptions of the various muscles and nerves as they presented themselves in my own dissections. They were described with the same attention to detail as the corresponding parts of human anatomy, and that quite irrespective of their frequent close resemblance to their representatives in Man. When the detailed descriptions were completed, I went carefully over them a second time, instituting a series of comparisons which were set forth in a separate chapter of the thesis, and which constitutes the bulk of the following pages.

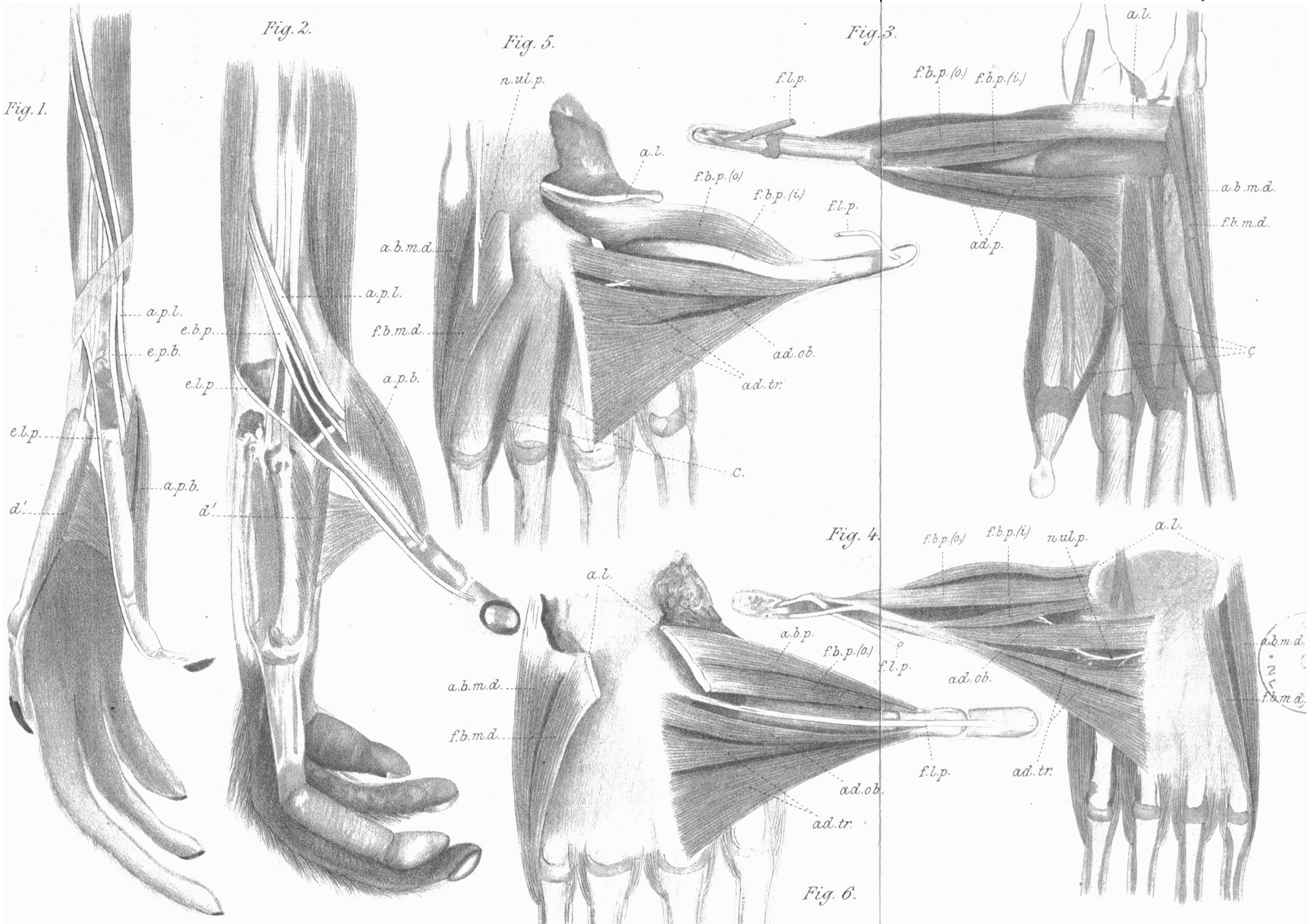
As a result, it will be found that many of the seeming

[1] This paper consists mainly of extracts from my Thesis presented to the Medical Faculty of the University of Edinburgh, for which a Gold Medal and the degree of Doctor of Medicine were awarded, Aug. 1, 1891.

anomalies in the anatomy of the limbs of Man have found intelligent explanation, and the general facts of the comparative anatomy of the limbs of mammalia have been frequently corroborated.

With regard to the question of the nerve-supply of muscles affording a key to muscle homologies, I am of opinion that my dissections will show that there are exceptions to this rule; and, therefore, I cannot agree with Gegenbaur and Ruge in regarding nerve-supply as an infallible guide to muscle homology. As illustrating the possibility of variation, I would specially direct attention to that part of the comparative statement which deals with the flexor brevis pollicis muscle, and also to the remarkable variation in the nerve-supply of the pronator quadratus muscle of the Gibbon. There can be no doubt that it is the pronator quadratus muscle which is situated transversely between radius and ulna on the anterior aspect of the forearm immediately above the wrist-joint, and yet in this case it undoubtedly received its nerve-supply from the *posterior interosseous nerve,* which required to perforate the delicate interosseous membrane before it could enter the deep surface of the muscle in question. This instance alone would be sufficient to show that nerve-supply is not an absolute guide in determining muscle homologies.

Among other interesting points, these dissections throw light on the composition of the human coraco-brachialis muscle; on the development of the extensores ossis metacarpi pollicis et primi internodii pollicis; on the line of cleavage of the flexor profundus digitorum, in order to account for its double nerve-supply in Man; on the composite nature of the adductor magnus muscle, as indicated by its double nerve-supply; on the presence of the obturator nerve in relation to the posterior aspect of the knee-joint; on the double nerve-supply of the pectineus muscle as described in Man; on the probability of the peroneus brevis being the outer segment of a fibular extensor, the remainder of which, as suggested by Ruge, has moved downwards to the dorsum of the foot, where it remains as the extensor brevis digitorum; on the development of the long flexor tendons in the sole of the foot; on the arrangement of the dorsal interosseous muscles of the foot in relation to a



D. Hepburn del. F. Huth, Lith. Edin.

HAND OF ANTHROPOID APES.

median line which tends to move from the medius to the index digit, in virtue of a changing mode of pedal progression.

This enumeration merely includes the principal features of the results obtained, and it will be seen that the dissection of these Anthropoid Apes has enabled me to formulate a remarkable series of deductions.

In the following pages each muscle will be referred to under its own name, but the details of its description will either be omitted or subordinated to its comparative aspects. Here I may be permitted to state that, in the case of the Gorilla, my manuscript was completed before the monograph of Eisler on "Das Gefäss- und Periphere-Nervensystem des Gorilla" came into my hands.

Myology of the Superior Extremity.

Muscles of the Shoulder Girdle.

Trapezius.—In all the four Apes this muscle formed a continuous sheet, and although the origin was incomplete in two of them (Chimpanzee and Gibbon), still there was evidence that the general origin in all of them was fairly similar.[1] In the Gorilla the occipital origin was slightly more extensive than in Man, while in the Orang it was considerably more extensive, and ran outwards to the mastoid process of the temporal bone, where it came in contact with the posterior border of the sterno-mastoid muscle, and formed an accurate apex for the posterior triangle of the neck.

As regards the insertion, in all of them it was practically alike and similar to the arrangement found in Man, but in the Orang fibres were inserted into the upper surface as well as into the posterior border of the acromial end of the clavicle.

Latissimus Dorsi.—In general appearance this muscle corresponded to that found in Man, but there were variations in the character and extent of its origin. In the Gorilla and Orang it arose from the spinous processes and supra-spinous

[1] The animals lent by Professor Cunningham had been divided mesially, and in consequence the origins of muscles arising from the mesial line were fragmentary or absent.

ligaments of the three lower dorsal vertebrae. (In the Chimpanzee and Gibbon this part of the origin was mutilated.) The origin from the iliac crest varied in its amount: in the Chimpanzee it arose by fleshy fibres from the anterior half of the outer lip of the crest, while in the Orang it reached to within half an inch of the anterior superior spine. There were no digitations from ribs in the case of the Orang, but in the three other apes these were present—the Chimpanzee having three, the Gibbon five, and the Gorilla six.

In no case was there any additional origin from the inferior angle of the scapula over which the muscle ran to its insertion, narrowing down into a flattened tendon as it proceeded outwards. In each case the insertion was into the bottom of the bicipital groove of the humerus in front of the insertion of teres major. In the Chimpanzee and Orang a few muscular fibres from the latissimus dorsi were inserted into the posterior aspect of the tendon of the teres major, while in the Gibbon these two tendons were inseparably blended at their insertions.

Rhomboideus (Major et Minor).—In the Gibbon this muscle was entirely destroyed owing to the line of section, and for the same reason it was incomplete in the Orang and Chimpanzee, but wherever it could be examined it showed a muscle indivisible into component parts. There was no occipital origin in the Gorilla; but, on the other hand, its origin from the spinous processes of the dorsal vertebræ extended as low down as the 6th dorsal vertebra. The occipital origin was found in the Orang.

As regards the insertion of this undivided muscle, it was attached to the vertebral border of the scapula: in the Orang and Chimpanzee, from the inferior angle upwards to a point about an inch above the base of the scapular spine; in the Gorilla, from the inferior angle to a point opposite the base of the scapular spine.

Levator Anguli Scapulæ.—(This muscle could not be examined in the Gibbon.) In the Orang, Chimpanzee, and Gorilla this muscle was present in a well-developed state, but in the Orang the individual fasciculi, of which the muscle is composed, remained separate from each other until near their common insertion, when they amalgamated to form the usual mass. In the three animals named, the insertion occupied the remainder of the vertebral border of the scapula not already taken up by the rhomboideus. In the Chimpanzee there were *three* slips of origin from the transverse processes of a corresponding number of the upper cervical vertebræ; in the Gorilla, *four* slips of origin of a similar kind; and in the Orang, *five* slips of origin—four of them from the transverse processes of the upper four cervical vertebræ, and the remaining one from the outer surface of the mastoid process under cover of the sternomastoid muscle. This mastoid origin in the Orang was quite distinct, and separated by a considerable interval from the occipital origin of the rhomboideus in the same animal, but their muscular fibres blended intimately close to the scapula.

Pectoralis Major.—The arrangement of the pectoral muscles closely resembled the condition which prevails in Man. They were arranged in two strata—the pectoralis major and pectoralis minor. In all the four animals the pectoralis major consisted of two distinct portions—an upper or clavicular and a lower or sternal—both of which were well marked in the Gorilla, and separated from each other by an intermuscular interval half an inch in width at its sternal end; but, in the Chimpanzee, there was no cellular or intermuscular interval between these two origins. On the other hand, in the Orang the upper portion of the muscle, although separated from the remainder of the muscle by a very distinct cellular interval, received no fibres whatever from the clavicle, but arose from the manubrium sterni and the cartilage of the 1st rib. In the Gibbon, again, the cellular interval between the clavicular and sternal origins did not extend through the entire thickness of the muscle. In none of the apes was there any distinction of the lower fibres, viz., those arising from the aponeurosis of the external oblique muscle of the abdomen—into a pectoralis quartus. In each animal there was a marked crossing of the fibres from the two main sources of origin as they approached their line of insertion, which was into the outer lip of the bicipital groove of the humerus, or external to the long tendon of the biceps when the groove was deficient or shallow, as it was in the Gorilla, in which the insertion extended from the surgical neck of the humerus almost as low down as the insertion of the deltoid muscle.

Pectoralis Minor.—In every instance this muscle was quite distinct from the pectoralis major. While it had the same general direction and attachments as the corresponding muscle in Man, yet it showed considerable variety both in regard to its origin and insertion in the different Apes. Thus, for example, the origin in the Gorilla was by a series of slips arising from the 3rd to the 7th ribs, both inclusive, close to the junction of rib with costal cartilage; in the Chimpanzee, from the 2nd, 3rd, and 4th ribs in a similar position; in the Orang, from the 3rd and 4th ribs opposite the junction of rib with costal cartilage; in the Gibbon, from the 3rd, 4th, and 5th ribs. In all the four animals the tendon of insertion passed obliquely upwards and outwards superficial to the axillary artery, but there was a different method of insertion in each case. Thus, in the Gorilla, the rounded tendon was inserted into the inner border of the coracoid process near to its tip; in the Orang, the rounded tendon was inserted into the upper surface of the coracoid process near its base. In the Gibbon, there were three points of insertion—(*a*) into the under surface of the shaft of the clavicle, just external to its middle; (*b*) into the inner border of the coracoid process; (*c*) into the common tendon of origin of the coraco-brachialis and biceps (short head), a short distance below the tip of the coracoid process.

In the interval between insertion (*a*) and insertion (*b*) one of the nerves for the pectoralis major passed through, and since it is customary to find this nerve *perforating* the pectoralis minor of Man, we are fairly entitled to consider this clavicular insertion as a part of pectoralis minor, and not a displaced portion of the subclavius. Besides, as we shall afterwards see, the subclavius muscle of the Gibbon had an origin from the 3rd rib subjacent to, and perfectly distinct from, the clavicular insertion of pectoralis minor just referred to.

In the Chimpanzee, the rounded tendon of insertion passed above the coracoid process, and was continued outwards beneath the coraco-acromial ligament to be inserted into the capsule of the shoulder-joint, partly directly, and partly with the tendon of the supraspinatus.

The manner of insertion of the pectoralis minor in the Chimpanzee corresponded to what is found in some of the lower mammalia, and even as low down as the marsupials, as has been pointed out by Professor Cunningham[1] in the *Challenger Reports.*

Subclavius.—In the Gorilla and Chimpanzee, this muscle did not present any noteworthy difference from the condition in which it is found in Man. On the other hand, it had an additional slip of origin from the 2nd rib in the case of the Orang, and in the case of the Gibbon it had no origin from the 1st rib, but derived slips from the 2nd and 3rd ribs—the latter slip being quite distinct from one which arose from the same rib and belonged to pectoralis minor. With the exception of the Gibbon, the insertion of this muscle agreed with its insertion in Man. In the Gibbon the insertion included the inferior and posterior surfaces of the outer half of the shaft of the clavicle.

Deltoid.—In all the animals examined this muscle had practically the same disposition as the corresponding muscle in Man, and in one animal it was essentially the same as in another. In the Gibbon the area of its insertion into the shaft of the humerus was more elongated than in the others, but in no instance did it extend beyond the middle of the outer surface of the humeral shaft. As in Man so in the Apes; the three origins from clavicle, acromion, and spine of scapula were fused together to produce a single muscle. It is worthy of note that in the Chimpanzee the clavicular part of the muscle was intimately connected with the clavicular part of the pectoralis major near their insertions.

Supraspinatus.—In all the dissections this muscle was smaller than the infraspinatus, and each one closely resembled its prototype in Man. The only exception was found in the Chimpanzee, in which a considerable part of the tendon of the pectoralis minor joined the tendon of this muscle.

Infraspinatus.—This muscle also closely resembled the corresponding muscle in Man, and there were no striking differences to be observed in comparing one muscle with the other. In the Chimpanzee the great obliquity of the scapular spine reduced the proportion in size between infraspinatus and supraspinatus.

[1] *Challenger Reports,* part xvi., "Report on Marsupials," p. 8.

Teres Minor.—This was a distinct muscle in all the dissections, and, with the exception of the Gibbon, it was more or less visible while the deltoid was yet in position. In the Gibbon no part of the muscle was visible until the deltoid was reflected. In all it arose from the axillary border of the scapula on its dorsal aspect. In the Gibbon it occupied an inch of the border close to the glenoid cavity; in the Orang, one-half of the border; in the Chimpanzee, the upper two-thirds; and in the Gorilla, the middle third.

From these observations it will be seen that the Chimpanzee most nearly presented the condition of the muscle as found in Man, and herein my dissection differs from that of Champneys,[1] who found the muscle attached to the middle third of the ventral border of the scapula. In each case the insertion was as in Man.

Teres Major.—In each animal this muscle arose from the dorsal surface of the inferior angle of the scapula, and from a varying amount of the axillary border, being greatest in the Gibbon, and to the smallest extent in the cases of the Gorilla and Orang, where it only occupied the lower third of the border. In all it was inserted into the inner lip of the bicipital groove of the humerus, more or less intimately blended with the insertion of the latissimus dorsi. In the Gorilla it extended lower down than the latissimus dorsi, and in the Gibbon the latissimus dorsi folded itself round the lower margin of the tendon of the teres major.

Subscapularis.—In all, this muscle was well marked, and in its arrangement and attachments it presented no points of noteworthy difference from the condition which prevails in Man.

Serratus Magnus.—In every instance this muscle formed a continuous sheet, arising from a varying number of ribs. In the Orang it arose from the upper ten ribs; in the Chimpanzee and Gibbon, from the upper eleven ribs; in the Gorilla, from all—thirteen ribs. In none of them was there any cervical part, although Champneys[2] found such a portion in his Chimpanzee. The insertions occupied the usual amount of the vertebral border of the scapula on its ventral aspect, as seen in Man.

[1] *Jour. Anat. and Phys.*, vol. vi., 1872. [2] *Loc. cit.*

(In the Gibbon the insertion had been removed in the plane of section.)

Muscles of the Upper Arm.

Coraço-Brachialis.—No statement regarding the comparative anatomy of this muscle would be complete without reference to the paper on "Muscular Variations" by Professor John Wood,[1] in which he teaches the threefold constitution of this muscle—coraco-brachialis brevis, coraco-brachialis medius, and coraco-brachialis longus. In the Gibbon this was a single muscle; moreover, it was not pierced by the musculo-cutaneous nerve which travelled along its inner surface and crossed outwards and downwards at its lower border. In the Chimpanzee and Orang the muscle was distinctly double, and the musculo-cutaneous nerve passed outwards and downwards between the two parts. In the Gorilla the condition of this muscle presented variations on the two sides of the body. On the right side the coraco-brachialis arose from the tip of the coracoid process of the scapula by a tendon common to, inseparably blended with, and under cover of the origin of the short head of the biceps. From this origin the muscle passed downwards and backwards to be inserted into the middle third of the inner surface of the shaft of the humerus. From the lower border of the muscle a few fibrous strands passed downwards superficial to the musculo-cutaneous nerve and became attached to the internal intermuscular septum, and probably these represent coraco-brachialis longus. In addition to the parts above described, the left side showed that a few muscular fibres—sufficient to make a bundle considerably less than a lumbrical muscle—left the under surface of coraco-brachialis to be inserted into the inner side of the neck of the humerus above the level of the teres major tendon, and doubtless these fibres represent the coraco-brachialis brevis. In this animal we have, therefore, representatives of the three primary components of the coraco-brachialis muscle, and of these, two are extremely rudimentary, while the coraco-brachialis medius persists. These observations agree with the experience of Champneys[2] and Vrolik[3] in the Chimpanzee, with Church[4] in

[1] *Jour. Anat. and Phys.*, vol. i.
[2] *Loc. cit.* [3] *Recherches d'Anat. sur le Chimpansé*, 1841.
[4] Church, *Nat. Hist. Review*, Jan. 1862.

the Orang, with Kohlbrügge[1] in the Gibbon; but they differ from Duvernoy[2] in the Gorilla.

According to Wood, the coraco-brachialis brevis is inserted into the humerus above the tendon of the teres major, the coraco-brachialis medius into the humerus about its middle, and the coraco-brachialis longus into the lower part of the shaft of the humerus on its inner aspect in the region of the supra-condyloid ridge.

In none of my specimens, except in the left arm of the Gorilla, could the coraco-brachialis brevis be said to exist, for in all the others the highest part of the muscle did not come superior to the insertion of the teres major, whereas in the Gibbon, where the muscle was single, it extended well down below the lower border of teres major. On the other hand, in the Chimpanzee and Orang, where the muscle was double, the lower portion ran down to the upper part of the internal supra-condyloid ridge.

The conclusion is, therefore, forced upon us that the coraco-brachialis medius is the representative of this group of three muscles in the Gibbon and Gorilla, while in the Chimpanzee and Orang the coraco-brachialis medius and coraco-brachialis longus are both present. As the coraco-brachialis longus becomes shorter, it rises higher on the shaft of the humerus, until it fuses with the medius, and the condition found in Man is the result, in whom an apparently single muscle is perforated by the musculo-cutaneous nerve.

Biceps Flexor Cubiti.—In the Gorilla, Chimpanzee, and Orang, this muscle possessed the usual well-known features which characterise the corresponding muscle in Man; but in the Gibbon the short head of the muscle has become detached from the coracoid process, and was found arising from the margins of the upper part of the bicipital groove of the humerus covering the rounded tendon of the long head, which arose from the apex of the glenoid fossa of the scapula inside the capsule of the shoulder-joint. In the same animal the muscles round the elbow-joint were considerably fused together, and the

[1] Kohlbrügge, *Anatomie des Genus Hylobates*, 1890 (Dr Max Weber, Amsterdam).

[2] Duvernoy, *Archives du Museum d'Hist. Nat.*, viii.

biceps received fibres of origin from the whole length of the anterior surface of the internal intermuscular septum, thereby forming a complete muscular covering for the brachial nerves and vessels which were not visible from the inner aspect of the upper arm.

Brachialis Anticus.—In all essential details this muscle corresponded to the same muscle in Man, and even in the Gibbon the points of difference were very small. In it we may note the fact that the highest limit of the muscle did not reach the coraco-brachialis, and neither did it embrace the insertion of the deltoid where it was found anterior to, but not behind, the insertion of the deltoid muscle.

Triceps Extensor Cubiti.—In all the animals under consideration this muscle was strongly developed, and presented the characteristic arrangement from which it derives its name. The long or scapular head had a more extended origin than is usually found in Man. In each case there was a series of more or less fleshy fibres arising from the upper third or half of the axillary border of the scapula, and situated between the origins of teres minor and teres major. These fibres were in direct continuity with the long head, and were not separable into a distinct origin apart from the long head. The outer and inner heads of the muscle and the insertion of the whole had the usual arrangement found in Man.

Anconeus.—In all the specimens this small muscle was distinctly developed, and had its customary attachments, but in the Orang and Gibbon the upper margin of the muscle was ill defined, being in reality a continuation of the triceps, while in the latter ape its fibres blended with those of the extensor carpi ulnaris.

Latissimo-Condyloideus (Dorsi-epitrochlear).—This muscle was found in each animal. It arose from the tendon of latissimus dorsi, about 1 inch from its insertion, but in no case did it reach the internal condyle, and its insertion was into the internal intermuscular septum between the coraco-brachialis and internal condyle. It always had a distinct branch from the musculo-spiral nerve, and it is therefore to be regarded as a separate muscle, since the latissimus dorsi is supplied by the long subscapular nerve.

Muscles of the Forearm.

Pronator Radii Teres.—In all, this muscle was well developed, but in the Gorilla and Gibbon no coronoid head was found. In the Chimpanzee and Orang the coronoid head was well represented, and the median nerve passed between the humeral and coronoid origins. In the two latter animals the insertion was somewhat lower down than in Man, the lowest part of the insertion being fleshy. In the Gibbon the insertion was into the anterior surface as well as the outer border of the radius.

Flexor Carpi Radialis.—This was also a well-marked muscle throughout the series, its general origin, course, and insertion being similar in each animal, and agreeing with the conditions found in Man. In the Gorilla, Orang, and Gibbon there was an additional source of origin from a fibrous septum attached to the oblique line of the radius immediately internal to the insertion of pronator radii teres. In the Gorilla this additional origin extended some distance lower down than the insertion of the pronator teres. This origin was not present in the Chimpanzee. All of them agreed in their double insertion into the palmar aspects of the bases of the second and third metacarpal bones.

Palmaris Longus.—This muscle was present in all except the Gorilla, and it had its usual origin, course, and insertion after the manner of its disposition in Man.

Flexor Sublimis Digitorum.—The points wherein differences could be noted in this muscle throughout the series of animals, and in the corresponding muscle of Man, were very few. In all, the origin presented condylar, coronoid, and radial parts; but, in addition to these, in the Gibbon it showed an additional origin from rather more than the middle two-fourths of the anterior surface of the shaft of the ulna, between flexor carpi ulnaris and flexor profundus digitorum. In each animal the muscle provided four tendons for the four inner digits. In the Gibbon, it may be noted that the 2nd and 3rd digits received their tendons from the radial segment or aspect of the muscle, while the ulnar side of the muscle supplied tendons to the 4th and 5th digits. This is not the case in the Orang and Chimpanzee, in which the tendons for the 3rd and 4th digits arose from that part of the muscle situated radiad, while the tendons for the 2nd and 5th digits spring from that part of the muscle placed ulnad, and hence it follows that the tendon for the 2nd or index digit crossed obliquely outwards beneath those for the 3rd and 4th digits. The same remarks apply to the arrangement of the tendons in the case of the Gorilla. In the palm of the hand the tendons were bound more firmly in position by means of deep and powerful prolongations of the palmar fascia than is the case in Man, so that each tendon was practically enclosed in a sheath from the point of its emergence from under the anterior annular ligament, but after entering the flexor sheaths on the palmar aspects of the fingers, their disposition and insertions were similar to those of Man.

Flexor Carpi Ulnaris.—In each of the animals this muscle had a similar disposition, and throughout it closely resembled the corresponding muscle in Man. In each it had a condylar and an olecranon head of origin, as well as an attachment to the shaft of the ulna by means of an aponeurosis. In the Orang the origin from the olecranon was aponeurotic and not muscular. In all, the ulnar nerve entered the forearm between the condylar and olecranon heads. In every instance the tendon of the muscle was inserted into the pisiform bone.

Flexor Longus Pollicis; Flexor Profundus Digitorum.—We now come to the consideration of a stratum of muscle placed beneath the superficial group of flexors. In many of the lower animals this mass is intimately associated with the flexor sublimis digitorum, and in the Gibbon we still find a remnant of this arrangement, for in it the stratum under discussion possessed a source of origin from the internal condyle of the humerus. We therefore see that this deep stratum represents the radial and ulnar segments of the muscular mass, which in the lower animals is divisible into condylar, radial, and ulnar segments. In the Gorilla, Orang, Chimpanzee, and Man the condylar segment has become completely differentiated as flexor sublimis digitorum; but in the Gibbon a portion of this segment is still found extending from the internal condyle to the deep stratum. In Man this condition is occasionally found as a muscular variation. The radial and ulnar segments are responsible for the production of five tendons—one for each digit. Of these, the tendon for the pollex becomes the flexor longus pollicis, while those for the remaining digits constitute the tendons of the flexor profundus digitorum. In the Gibbon this stratum of muscle did not present the same distinct line of segmentation into radial and ulnar portions which it did in the other three apes; but those parts arising from the radius and humeral condyle, *i.e.*, the humero-radial segment, gave origin to three muscular bellies, ending in rounded tendons, distributed to the thumb, index, and middle fingers, and supplied by the median nerve. The ulnar segment of the stratum gave origin to two muscular bellies, sending tendons to the ring and little fingers, and supplied by the ulnar nerve.

In the Orang, Chimpanzee, and Gorilla the natural line of segmentation was such that, of the *five* tendons, my series of dissections showed that *three*, viz., those for the 3rd, 4th, and 5th digits, were provided by the ulnar segment; while *two*, viz., those for the pollex and index, were provided by the radial segment; but still the median nerve supplied three of the muscular bellies and the ulnar nerve supplied two. Concentrating our attention on the radial segment, the Gibbon shows that it produces a distinct rounded tendon (associated with a small fleshy belly) for the thumb,—this constitutes a true flexor longus pollicis,—and, in addition, separate tendons for the index and middle fingers—their deep flexors. In the Chimpanzee the radial segment provided one powerful tendon, the bulk of which went to the index finger, and only a small offshoot reached the thumb, where it occupied the position of the long flexor tendon. In the Orang the same arrangement was found as in the case of the Chimpanzee, only the offshoot for the thumb had almost lost its attachment to the tendon for the index finger, and therefore its action as a deep flexor for the thumb must be of the feeblest kind. In the Gorilla, on the other hand, the radial segment only provided one tendon, viz., that for the index finger; but an examination of the flexor aspect of the thumb revealed a tendinous band, occupying the position of the long flexor, and attached by one end to the carpus, and by the other to the palmar aspect of the base of the terminal phalanx of the thumb (fig. 6). Clearly this fibrous band was of no value as a flexor, and therefore we may consider that the Gorilla has lost its flexor longus pollicis. It is certainly somewhat remarkable that the tendon of the flexor longus pollicis should present a different disposition in each of the Apes, although the muscular mass from which it might be expected to arise is well developed.

We can now understand how this radial segment differentiates more and more, so as to provide deep flexors for the thumb and index finger as the specialisation of function advances. Gradually that portion associated with the thumb increases, and dissociates itself from the part belonging to the index finger until the pollical portion grows large enough to assume the position and importance of the flexor longus pollicis as we see it in Man. By this time that part belonging to the index finger has been moved towards the ulnar segment, with which it ultimately fuses, and forms part of the flexor profundus digitorum as it is found in Man. The tendency seems to be for the line of vertical cleavage into radial and ulnar segments to move towards the radial side; for, whereas, in the Gibbon three tendons lie to the radial side of this line of cleavage, in the Orang, Chimpanzee, and Gorilla only two tendons lie to the radial side, and, finally, in Man the number is reduced to one, viz., flexor longus pollicis, by reason of the line of cleavage having again moved still more towards the radial side.

Further, we are in a position to explain the double nerve-supply of the flexor profundus digitorum of Man by an examination of the nerve-supply of the radial and ulnar segments previously referred to. The radial segment is supplied directly from the median nerve, while the radial aspect of the ulnar segment derives its nerve-supply from the anterior interosseous branch of the same nerve, *i.e.*, in each Ape the same amount of the stratum is supplied by the median nerve. Hence, it follows that muscular substance to correspond with three of the five deep tendons derives its nerve-supply from the median nerve, and the remaining muscular substance for the two innermost tendons is supplied from the ulnar nerve—that is to say, the flexor profundus digitorum, as we understand it in Man, has its ulnar half supplied by the ulnar nerve, and its radial half supplied by the median nerve; and as we know the same plan of nerve-supply persists all through this muscle, affecting even the lumbricales associated with these deep tendons in the palm, and thereby the two outer lumbrical muscles are provided with branches from the median nerve, and the two inner lumbricals with branches from the ulnar nerve.

Lumbricales.—In each of the Apes examined these muscles were present, and *four* in number. They had a tendency to decrease in size from the first to the fourth. As regards their origins they were subject to variety. The first always arose from a single tendon; in the Chimpanzee and Gibbon the second also arose merely from the radial side of the deep tendon for the middle digit; in all, the third had a double head of origin. In the Chimpanzee the fourth arose only from the ulnar side of the deep tendon for the ring finger, and in the Orang the fourth arose from the radial side of the deep tendon to the 5th digit. Their insertions were similar to those found in Man.

Pronator Quadratus.—In all the series this muscle was present, but was most feeble in the Orang, in which there was scarcely enough of muscular fibre to make a continuous layer. It had its usual position at the lower end of the forearm, but the direction of its fibres was, as a rule, more oblique than in Man. This was especially the case in the Gibbon and Orang, in which it distinctly lay from above downwards and outwards.

Turning now to the muscles on the extensor aspect of the forearm, we find that just as in Man, so in all the animals under consideration they arrange themselves in a superficial and a deep group.

Supinator Radii Longus.—In all the series of dissections this was a distinct muscle, and in each instance it took origin from more or less of the external supracondyloid ridge and septum higher up than the other muscles arising from the same ridge. In the Chimpanzee it extended as high as the insertion of the deltoid, and in the Gibbon it was intimately blended with the outer surface of the brachialis anticus. In every case its course lay along the radial border of the forearm to its point of insertion, which varied in the different animals. In the Gorilla the insertion was the same as in Man; in the Chimpanzee the tendon was attached to the radius for ½ inch above the styloid process; in the Orang this attachment had increased to 1 inch in length; while in the Gibbon, not only was it attached to the anterior surface and outer border of the radius for $2\frac{1}{2}$ inches, but it failed to reach the styloid process by a distance of $2\frac{1}{2}$ inches.

Extensor Carpi Radialis Longior.—In its general arrangement this muscle was similar to its fellows throughout the series as well as to the corresponding muscle in Man. It arose from the lower part of the external supracondyloid ridge and septum: in the lower part of the forearm it was crossed superficially by special extensors of the thumb, and it was inserted into the radial aspect of the base of the metacarpal bone of the index finger on its dorsal surface. In the Gibbon its muscular belly was little more than 3 inches in length, while its tendon measured 10 inches, and in addition to the usual insertion it sent a prolongation to the base of the 1st metacarpal bone on its ulnar side.

Extensor Carpi Radialis Brevior.—Although in intimate relationship to the preceding muscle, it was in no way amalgamated therewith, and it possessed the same general features throughout the series, and closely resembled the corresponding muscle in Man. In the Orang and Chimpanzee it derived fibres of origin from the external lateral ligament of the elbow-joint. In all four animals its insertion resembled that found in Man.

Extensor Communis Digitorum.—In all its features this muscle throughout the series harmonised closely with the corresponding muscle in Man. In the Gibbon the tendon to the annularis sent a small slip to the minimus. The arrangement of the tendons on the dorsum of each digit was the same as is commonly found in Man.

Extensor Minimi Digiti.—This muscle had the familiar origin seen in Man in the case of the Orang and Chimpanzee, but in the Gorilla and Gibbon its origin was from a septum placed between the extensor communis digitorum and the extensor carpi ulnaris rather than from the external condyle of the humerus. Its course and insertion were similar to those in Man in all except the Orang, in which it divided into two tendons on the dorsum of the carpus. These were distributed to the 4th and 5th digits, where they joined the tendons from the common extensor. This arrangement affords evidence of its being the same muscle as the extensor digitorum secundus of the marsupials to which Professor Cunningham has directed attention in his memoir.[1]

Extensor Carpi Ulnaris.—In each of the animals examined the arrangement of this muscle corresponded with that which prevails in Man, and in all, the insertion was a single one into the ulnar side of the base of the 5th metacarpal bone.

Extensor Indicis vel *Extensor Profundus Digitorum.*—With the exception of the Gorilla, in which this was a slender muscle, in the other animals it showed a considerably greater development than in Man. As far as the origin was concerned, it closely resembled the condition present in Man, but in regard to the insertion there were great differences. In the Gorilla, it resembled that of Man; in the Chimpanzee, it supplied tendons to the index and annularis; in the Orang, it supplied tendons to the index and medius; in the Gibbon, it supplied tendons to the index, medius, and annularis. In addition, these tendons in the case of the Orang sent slips, which were inserted into the dorsal surface of the bases of the 1st phalanges, and in the Gibbon they were entirely inserted into the dorsal surfaces of the bases of the 1st phalanges, and did not become blended with the common extensor expansion.

Supinator Brevis.—In all the animals this muscle was well marked, and practically it was identical throughout the series. Moreover, it corresponded closely with the same muscle in Man in regard to all essential details.

There are three special muscles for the pollex taking origin from this, the extensor aspect of the forearm. Undoubtedly these represent the three special extensors of the thumb of Man, but, on account of their insertions being considerably modified in two instances, it is necessary to make a change in the nomenclature to suit these special requirements. The following tabular statement gives the terms which are synonymous:—

I. Extensor Ossis Metacarpi Pollicis *vel* Abductor Pollicis Longus.

II. Extensor Primi Internodii Pollicis *vel* Extensor Pollicis Brevis.

[1] *Challenger Reports*, part xvi., "Report on Marsupials," p. 15.

III. Extensor Secundi Internodii Pollicis *vel* Extensor Pollicis Longus.

In the course of our examination we shall find that III. is a constant muscle throughout the series, but that I. and II. are more or less amalgamated at their origins; that the two tendons arising therefrom always occupy the positions characteristic of them; but that in three of the animals—viz., Chimpanzee, Orang, and Gibbon—the tendons have failed to reach the insertions peculiar to these extensors as found in Man, and that the modified or synonymous terms are thereby rendered necessary.

Commencing with the *Extensor Ossis Metacarpi Pollicis* vel *Abductor Pollicis Longus,* we find that, in the Gorilla, this muscle occupied its ordinary position, and had its usual insertion into the base of the 1st metacarpal bone (fig. 2). The origin of this muscle was, however, inseparably amalgamated with that of the extensor primi internodii pollicis.

In the Chimpanzee, Orang, and Gibbon this muscle was always the highest of the three special muscles under consideration, and its special insertion in these animals necessitates the alternative terms. In all of them it was inserted in relation to the outer side of the carpus, viz., in the Gibbon, into a sesamoid bone (prepollex) (fig. 1); in the Chimpanzee, into a sesamoid bone and the trapezium; in the Orang, into a sesamoid bone and the base of metacarpal I. From these data it must be quite evident that it is one and the same muscle which runs through this series of variations.

Extensor Primi Internodii Pollicis vel *Extensor Pollicis Brevis.*—Dealing now with this muscle, there was no difficulty in recognising from its line of origin,—which was always more especially the posterior surface of the radius lower down than the preceding muscle, with which it was closely amalgamated in the Gorilla and Chimpanzee,—that it was the extensor primi internodii pollicis. But when we come to examine its insertion, then this name will not always apply. In the Gibbon, Orang and Chimpanzee, it was inserted into the base of metacarpal I. (fig. 1). In the Gorilla it was inserted into the base of *metacarpal I. and the base of the* 1*st phalanx of the thumb* (fig. 2). Considered in this way, as well as from its general relationships, it seems to me that the above synonymous terms are fully warranted. Certainly, in three of the animals examined, this muscle had no insertion into the 1st phalanx of the pollex, but I do not think it is necessary to say that extensor primi internodii pollicis *vel* extensor pollicis brevis is on that account absent.[1] It is better to look upon the muscle as imperfectly developed, for, in the Gorilla, we see how very easily it might move forward to its true position.

Extensor Secundi Internodii Pollicis vel *Extensor Pollicis Longus*.—There was no difficulty whatever in determining this muscle. Its position, origin, course, and point of insertion, all indicated that it was the homologue of the corresponding muscle in man. There were, however, some points of great interest in connection with its insertion. We have seen that in the Gibbon, Orang, and Chimpanzee, the true extensor of the first phalanx of the pollex failed to reach this bone. Now, *in each of these cases*, a prolongation from the tendon of extensor secundi internodii pollicis supplied the deficiency, and it was inserted into the base of phalanx I. In the Gorilla, on the other hand, where the true extensor of the 1st phalanx was present, there was no additional slip from the extensor of the 2nd phalanx. Another extremely interesting feature of the tendon was found in the Gorilla, in which this muscle sent a tendon to the index as well as the special one to the pollex. The importance of this additional slip is seen when we remember that in lower forms, *e.g.*, marsupials, we may find as many as three tendons from this muscle.[2]

The Posterior Annular Ligament.—Throughout the series of dissections this strong ligament had the same number of synovial compartments and transmitted the same groups of tendons as in Man, and it presented no features requiring special mention.

Intrinsic Muscles of the Hand.—This term includes those muscles which are left after the flexors, extensors, and lumbricales are removed. They consist of groups of muscles which fulfil the functions of adductors, abductors, and short flexors of the various digits.

[1] Champneys, *loc. cit.*

[2] Cunningham, *loc. cit.*

Abductor Pollicis (Brevis).—In its general arrangement this muscle was similar throughout the series. In the Gorilla and Orang the muscle had no direct attachment to the carpal bones, its origin being from the radial aspect of the upper part of the palmar surface of the anterior annular ligament, but in the Gibbon and Chimpanzee it received in addition fibres of origin from the scaphoid and the sesamoid bone (prepollex). As regards its insertion, in all it was attached to the radial side of the base of the 1st phalanx of the pollex. In addition, in the Chimpanzee it gave a prolongation to the base of the terminal phalanx, and in the Gibbon it was attached to the head of the 1st metacarpal bone.

Opponens Pollicis.—In the Gibbon this muscle differed somewhat from the others by reason of its projecting towards the palm between the heads of the flexor brevis pollicis. In the other animals its position was the usual one, under cover of the abductor pollicis to a greater or less extent. The insertion closely corresponded with the condition found in Man, except in the Gibbon, where, in addition to the metacarpal insertion, slips were sent forward to the radial side of the bases of the 1st and 2nd phalanges.

Adductor Pollicis Transversus.—In every instance this muscle was intimately associated with a fibrous aponeurosis and septum, which ran distally from the base of the middle metacarpal bone. In all of the dissections there was a decided tendency for the muscle to become fasciculated, and in consequence each muscle in the series presented proximal and distal segments easily separable from each other. In the Gorilla the distal portion of the muscle had fibres of origin from the palmar surface of the distal third of the shaft of the 2nd metacarpal bone, while the proximal portion arose from the palmar aspect of the proximal half of the 3rd metacarpal bone. From such a wide origin there was naturally considerable convergence of the fibres as they passed outwards to their insertion. In the Gorilla, Chimpanzee, and Orang, the insertion was into the ulnar side of the base of the 1st phalanx of the pollex. So it was in the Gibbon, but in this animal there was no definite line of demarcation between this muscle and adductor pollicis obliquus, and so in addition it was inserted into the distal two-thirds of the ulnar border of the 1st metacarpal bone. Reference will again be made to this additional insertion when discussing the homologies of the muscles of the foot.

Adductor Pollicis Obliquus.—Until recently, in descriptive human anatomy, this muscle was regarded as the inner or ulnar head of the flexor brevis pollicis, but the condition in which it is presented in the hands of the Apes greatly facilitates a proper conception of its nature. In the Gibbon, as we have already seen, there was no definite line of demarcation between the oblique and transverse segments of the adductor muscle, nevertheless the oblique portion arose from the palmar aspect of the base of the 2nd metacarpal bone and from the tendon of insertion of the flexor carpi radialis muscle, in close proximity to the carpus. The muscle is here presented in its simplest condition. In the Gorilla, Chimpanzee, and Orang, the adductor pollicis obliquus was distinctly separated from adductor pollicis transversus, but whereas in the Orang it did not extend any nearer to the carpus than the corresponding part of the adductor muscle of the Gibbon, in the Gorilla it arose from the front of the carpus in the region of the os magnum, and in the Chimpanzee from the aponeurosis covering the base of the 3rd metacarpal bone, from the radial side of the os magnum, and from the sheath of the tendon of the flexor carpi radialis. In all this we see its close similarity to the corresponding muscle in Man, and moreover we may trace its tendency to move proximalwards and radiad, so that ultimately it assumes a position which led to its being mistaken for the inner head of the flexor brevis pollicis, an error which occurred all the more readily as, in presence of this actively developing muscle, the true inner head of the short flexor of the thumb was liable to be diminished in size or crowded out of existence.

The insertion of this muscle was fairly constant in all the Apes, being in association with the oblique adductor.

The writings of Cunningham,[1] Bischoff,[2] and Halford[3] have taught us to regard the adductor pollicis (oblique and transverse)

[1] Cunningham, *Jour. Anat. and Phys.*, 1878.

[2] *Beiträge zur Anatomie des Hylobates leuciscus*, München, 1870; *Beiträge zur Anatomie des Gorilla*, München, 1879.

[3] *Lines of Demarcation between Man, Gorilla, and Macaque*, Melbourne, 1864.

as one of a special group of adductors, to which Professor Halford applied the name of "contrahentes digitorum," a name which has been generally adopted. Considering the muscle just described as one member of this series, there remain others, which are also adductors, towards the median line of the hand. In the Gorilla and Orang no other contrahentes were seen (figs. 4 and 6), although in the latter animal the palmar interossei —which are also adductors—received fibres of origin from the deep aspect of the aponeurosis, with which the adductor pollicis was associated. In the Chimpanzee, on the other hand, there were two small muscles belonging to this group (fig. 5). These arose from the ulnar aspect of the median septum and aponeurosis, and were inserted so as to act as adductors of the annularis and minimus. In the Gibbon, the number of contrahentes was four, and they acted as adductors of the pollex, index, annularis, and minimus respectively (fig. 3).

Flexor Brevis Pollicis.—A mere glance is sufficient to satisfy us that in each of the Apes, as in Man, this muscle in its primitive form possessed two heads—an outer or radial, an inner or ulnar. Moreover, in the Orang the nerve-supply of these two heads agreed with what is found in Man, but was different in the case of the Gibbon. That is to say, in the Orang the radial head received the median nerve, while the ulnar head was supplied by the deep branch of the ulnar nerve; but the Gibbon presented an exception to this rule, for in it both heads of the muscle were supplied by branches from the median nerve. Bearing in mind therefore the strong support that nerve-supply affords as a key to muscle homologies—a proof, however, which I am by no means disposed to regard as absolute—we are bound to make a closer scrutiny of the so-called inner head of the flexor brevis pollicis, and it is certainly somewhat remarkable that an examination of the four animals under consideration should throw so much light on this point.

In the Gibbon the inner or ulnar head arose deeply in the palm from the ligamentous structures in the vicinity of the trapezium and from the bases of the 1st and 2nd metacarpal bones. The muscle lay in close contact with the shaft of the metacarpal bone of the thumb and was inserted in conjunction with the adductor pollicis.

In the Orang a slender muscular slip, which at one time would have been described as a middle head to the flexor brevis pollicis, was found. This was a perfectly distinct but slender piece of muscle placed in relation to the ulnar border of the shaft of the 1st metacarpal bone, from which it arose—an interosseous primus volaris of Henle, or inner head of flexor brevis pollicis. The insertion of this slip was in conjunction with the adductor muscles.

In the Chimpanzee, instead of a muscular slip, there was a fibrous band in the position of the inner head, while in the Gorilla even this fibrous band had disappeared.

Reducing these facts to a tabular form, they at once become quite clear.

	Gorilla.	Chimp.	Orang.	Gibbon.
Flexor brevis pollicis—(outer head), -	x	x	x	x
Flexor brevis pollicis—(inner head)—(*Interosseous primi volaris*), - -	o	*rudimentary.*	x	x
Adductor pollicis obliquus, - - -	x	x	x	o
Adductor pollicis transversus, - -	x	x	x	x

Such a table shows us that in the Gibbon we find the original condition of parts. In it the flexor brevis pollicis possesses a true inner head, *i.e.*, interosseous primus volaris, and the adductor pollicis has not yet segmented sufficiently to produce an adductor obliquus pollicis or spurious inner head for the short flexor. But the tendency is for the proximal part of the adductor pollicis to separate itself from the rest of the muscle, and move radiad as the spurious inner head of the short flexor, in reality, adductor obliquus pollicis. This condition is well seen in the Orang, and as a consequence of the increase of this spurious inner head, the true inner head has become reduced in size and pressed into a deeper position. A further stage of the same process may be seen in the Chimpanzee, in which the spurious inner head has still further reduced the true head until it is merely represented by fibrous tissue. Finally, in the Gorilla we have the completed process, and the result is that the true inner head has entirely disappeared, unable to resist the developmental activity of the spurious inner head.

Turning now to the question of nerve-supply, the Gibbon again gives us the original condition, viz., the supply of both heads of the flexor brevis pollicis by the median nerve, and the supply of the adductor pollicis (obliquus et transversus) by the deep branch of the ulnar nerve. In the Orang, however, we find that the true inner head of flexor brevis pollicis—interosseous primus volaris—is also supplied by the ulnar nerve, and this must be explained. Brooks[1] has dealt with this subject in a special paper, and I agree with him in considering that as the true inner head becomes reduced in size by the advancing spurious head (adductor obliquus pollicis), so in like manner the median nerve is displaced by the greater activity of the ulnar nerve. Not only so, but in Man we occasionally find the ulnar nerve in the substance of the outer head of the flexor brevis pollicis. This was the case in a subject dissected for demonstration purposes in the University Anatomy Department during the past winter session. A probable explanation of such a condition is, that the true inner head of the flexor brevis pollicis is not only a meeting-point for the median and ulnar nerves, from which the median nerve is ultimately displaced; but it may also act as a bridge across which the ulnar nerve may travel to reach the outer head of the short flexor of the pollex.

Abductor Minimi Digiti.—In all the animals this muscle was present in a well-developed state, and it possessed the same attachments as are characteristic of the corresponding muscle in Man. Commencing at the pisiform bone, it lay along the ulnar border of the palm, and was inserted into the ulnar aspect of the base of the 1st phalanx of the little finger, closely blended with the insertion of flexor brevis minimi digiti.

Flexor Brevis Minimi Digiti.—As in Man, this muscle possessed only a single head of origin, which was attached to the anterior annular ligament and the hook of the unciform bone. This arrangement was constant throughout the series. The muscle was inserted in common with the abductor minimi

[1] Brooks, *Jour. Anat. and Phys.*, vol. xx., 1882.

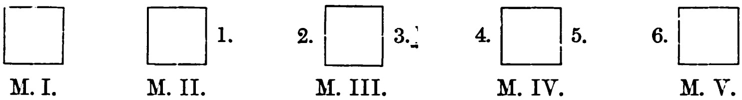
digiti, but in addition the Gibbon showed a tendinous prolongation, which was sent forwards to be inserted into the fibrous structures at the distal extremity of the 1st phalanx.

Opponens Minimi Digiti.—In each of the animals the origin of this muscle was similar, viz., from the unciform process of the unciform bone and from the anterior annular ligament. Crossing obliquely inwards, it was inserted into the ulnar border of the shaft of the 5th metacarpal bone. In each case its origin was closely blended with that of the flexor brevis minimi digiti, and together they lay superficial to the deep ulnar nerve and vessels.

Interossei.—This important group of muscles fulfils the functions of adductors and abductors of the digits. In each of the animals the line of adduction and abduction was the same as in Man, viz., the middle digit. Throughout the series the main features of the arrangement which prevails in Man held good here. The mesial plane of the hand was the same; the muscles divided themselves into two groups—an abductor or dorsal group, an adductor or palmar group. Each muscle of the former set arose by two heads of origin; each muscle of the latter set had a single head of origin. Thus, in all of the animals, there were four dorsal interosseous muscles and three palmar ones. In addition to these features, which were common throughout the series, the Chimpanzee presented some points of peculiarity. Viewed from the dorsum of the hand, its dorsal interossei were the same as in the other animals, but looked at from the palm, there were not only the usual three palmar interosseous muscles performing the function of adductors, but in addition there were other three muscles, distinct from the dorsal interossei, performing the function of abductors. Champneys[1] has described these as palmar interossei, thus bringing up the number to six in the Chimpanzee. In my detailed description of these muscles[2] I have also included them in this group for descriptive purposes, and because they appear entirely on the palmar aspect, but I doubt whether they should be so regarded. The six palmar interosseous muscles are arranged in pairs—one pair in each of the three inner

[1] *Loc. cit.* [2] *Thesis,* in Library of University of Edinburgh.

interosseous or inter-metacarpal spaces. Applying to each a numerical name, we may schematically arrange them thus :—



In this way we see quite clearly that 1, 4, and 6 are the usual palmar interossei; while 2, 3, and 5 are the additional muscular slips. Each of these additional muscles has fibres of origin from both of the metacarpal bones between which it is placed. Thus No. 2 arises from the radial side of the metacarpal III. and slightly from the ulnar side of metacarpal II.; No. 3 arises from the ulnar side of metacarpal III. and slightly from the radial side of metacarpal IV.; No. 5 arises from the ulnar side of metacarpal IV. and slightly from the radial side of metacarpal V.

But not only do they resemble dorsal interossei in their two-headed origin; their insertions also place them in harmony with the dorsal muscles; for No. 2 is inserted with dorsal interosseous II.; No. 3 is inserted with dorsal interosseous III.; and No. 5 is inserted with dorsal interosseous IV. I think that additional confirmation of this view may be obtained from Professor Cunningham's[1] description of the dorsal interosseous muscles of *Thylacinus cynocephalus*. After describing the dorsal interossei as seen from the dorsal aspect, he says :—

"If we examine them upon their palmar surfaces after the removal of the palmar and intermediate muscles, we find an accessory slip in connection with each of the three ulnar muscles . . . . Two arise from the base of the middle metacarpal bone —one on each side of it—and they are inserted one into each side of the base of the 1st phalanx of the same finger. The third slip arises from the base of the metacarpal of the ring finger, and is inserted into the ulnar side of the base of the corresponding phalanx."

These three accessory slips which Cunningham found in Thylacine, and which he regards as undoubtedly belonging to the dorsal interossei, seem to me identical with the three

[1] Cunningham, *loc. cit.*

additional muscles which appear in the palm of the Chimpanzee. I am therefore of opinion that instead of describing them as the 2nd, the 3rd, and the 5th palmar interossei, it would be more accurate to regard them as accessory slips to the 2nd, 3rd, and 4th dorsal interossei, for not only does their function place them in this group, but the double-headed nature of their origins and their arrangement in Thylacine also point to the dorsal group as their true position.

On the other hand, we may regard the typical manus as presenting three layers of intrinsic muscles, viz., an adductor stratum (contrahentes); an abductor stratum (dorsal interossei); and an intermediate stratum, consisting of short flexors of the digits, each of which possesses two heads. In the hand of Man and of the Apes, the abductor stratum presents the same general features, but, with the exception of the Gibbon and Chimpanzee, the adductor stratum is so modified that only the adductor muscles of the pollex remain. With regard to the intermediate stratum —the short flexors—various modifications have resulted in the disappearance of certain of these muscles and in the persistence of others which, in Man and the Apes, are described as the palmar interossei. Now, the three additional interossei, seen in the palm of the Chimpanzee, occupy positions which entitle them to be ranked among the short flexors of their respective digits in a typical hand.

Palmaris Brevis.—Notwithstanding that in every case the dissections were conducted with the utmost care, no trace of this muscle could be found in any of the animals examined.

The *Palmar Fascia* had the same general arrangement as in Man. Its central triangular portion was always a well-marked feature, and from the deep surface of this portion, very strong septa sank into the palm, so that the long flexor tendons very soon became confined in tunnel-like grooves. On the flexor aspects of the digits the usual flexor sheath was present and lined by a synovial membrane. Similarly the tendons passing from the forearm into the palm beneath the anterior annular ligament were surrounded by the loose folds of a synovial membrane. The anterior annular ligament was a strong fibrous arch, having the usual attachments to the outer and inner ends of the series of carpal bones.

The Nerves of the Superior Extremity.

For the reasons previously noted, I was not able to examine the brachial plexus of the Gibbon, but in all the other Apes this plexus was formed by the anterior primary divisions of the lower four cervical nerves and by the anterior primary division of the 1st dorsal nerve. In all there was a loop of communication from the anterior primary division of the 4th cervical nerve. The formation of the plexus was in every case closely akin to that of Man, resulting in the production of three principal cords. That of the Orang (fig. 3) most nearly resembled the human plexus, while that of the Chimpanzee (fig. 2) was somewhat simpler, and that of the Gorilla (fig. 1) rather more broken up, especially as regards the roots of the outer cord. My dissection closely corresponded with the figure given by Eisler[1] in his description of the vessels and nerves of the Gorilla.

The branches from the brachial plexus, both supra-clavicular and infra-clavicular, were nearly identical with those of Man. The individual nerves were wonderfully similar to those of Man in regard to the details of their distribution.

The nerve for the rhomboid muscle was given off by the 4th cervical nerve in the cases of the Gorilla and Chimpanzee,[2] but in the Orang it arose from the posterior aspect of the 5th cervical nerve.

Unfortunately the nerve to the subclavius muscle was not found in the Orang, but in the Gorilla and Chimpanzee it arose from the junction of the anterior branches of the 5th and 6th cervical nerves. Kohlbrügge[3] found this nerve arising from the 6th cervical nerve in the Gibbon.

The phrenic nerve received a small root from the 5th cervical nerve in the Gorilla and Chimpanzee. In the Gorilla this branch passed downwards and inwards to reach the anterior aspect of the scalenus anticus muscle, where it united with the phrenic nerve close behind the subclavian vein.

The *Posterior Thoracic Nerve*—nerve to serratus magnus

[1] Eisler. Das Gefäss und Periphere-Nervensystem des Gorilla. 1890.
[2] *Loc. cit.* Champneys. [3] *Loc. cit.*

muscle—had the same direction and distribution as in Man, and arose in the Gorilla from C. V. and VI.; in the Orang from C. V. and VI.; in the Chimpanzee from C. IV. V. and VI.

The *Suprascapular Nerve* in the Gorilla differed in its origin from that of the Chimpanzee and Orang. In the Gorilla it sprang from C. IV. and V. before the junction of the latter nerve with C. VI., and so it was also found by Eisler.[1] In the Chimpanzee and Orang it arose from C. V. and VI. In the Gibbon, Kohlbrügge[2] states its origin from C. V. As regards its distribution it corresponded throughout the series and with the same nerve in Man. It supplied muscular branches to the supra- and infra-spinatus muscles and an articular branch to the shoulder joint. Only in the Gorilla was a suprascapular ligament found, and underneath this band the nerve travelled to enter the supra-spinous fossa.

Anterior Thoracic Nerves—external and internal.—In the Gibbon, Chimpanzee, and Orang, these nerves arose from a common trunk which descended behind the clavicle to break up for the supply of the two pectoral muscles. In the Gorilla, on the other hand, the two nerves were always distinct; the upper or external arising from C. VI. and VII., the lower or internal from C. VII. and the inner root of the median nerve. In the Gorilla and Gibbon it was clearly seen that the one which pierced the pectoralis minor ended in the sternal origin of the pectoralis major, whereas the upper of the two nerves (which did not pierce the pectoralis minor) was entirely distributed to the upper or clavicular origin of the pectoralis major.

The *Subscapular Nerves* varied in number from three to five. They all arose from the posterior cord of the brachial plexus, and they supplied the usual muscular branches. It is of interest to note that the nerve for the teres major—which is a subscapular nerve—arose in the Gorilla from the circumflex nerve, which gave off two branches, one entirely distributed to the subscapularis muscle, and the other partly to this muscle but chiefly to the teres major as just mentioned. A somewhat similar arrangement is occasionally found in the human subject.[3]

[1] *Loc. cit.* [2] *Loc. cit.*

[3] W. Turner in *Natural History Review*, 1864, and *Journal of Anat. and Phys.*, vol. vi. p. 104, 1872.

Circumflex Nerve.—This nerve had the same general course and distribution as in Man, and it was similar throughout the series of animals. It gave off its branches to the same parts as in Man, but no ganglionic swelling could be distinguished on the branch to the teres minor. In the Gibbon its external cutaneous branch ran downwards through the substance of the deltoid muscle and appeared at the lower part of the insertion of this muscle to be distributed cutaneously as low as the external condyle of the humerus. A branch with a somewhat similar distribution was found in the Chimpanzee, only it pierced the external head of the triceps instead of the deltoid.

Musculo-spiral Nerve.—In all the animals this was a large nerve, the origin, course, and distribution of which closely corresponded throughout the series and with the same nerve in Man, that is, it supplied branches to the triceps anconeus, supinator longus, and extensor carpi radialis longior muscles, besides cutaneous and articular branches. Wherever the latissimo-condyloideus muscle was present, it derived its nerve-supply from this trunk, showing that the latissimo-condyloideus must be considered as a portion of the triceps, although it takes origin from the tendon of the latissimus dorsi.

Only in the Gorilla were slender filaments of this nerve found entering the external aspect of the brachialis anticus muscle.

In every instance this nerve ended by dividing into radial and posterior interosseous nerves.

The radial was always a cutaneous nerve on the outer aspect of the forearm, and extended to the digits on their dorsal aspect. The amount of digital supply which the radial nerve provided depended on the point of termination of the posterior interosseous nerve. In the Gorilla the radial nerve and the dorsal branches of the ulnar nerve shared the cutaneous supply of the digits equally—two and a half digits each. In the Chimpanzee the radial nerve supplied both sides of the pollex and the radial side of the index, while the posterior interosseous nerve supplied contiguous sides of the index and medius, and thus between them they overtook the supply of two and a half digits. In the Gibbon, the radial nerve supplied both sides of the pollex and the radial side of the index, while the posterior interosseous nerve supplied contiguous sides of the index and

Fig. 3.

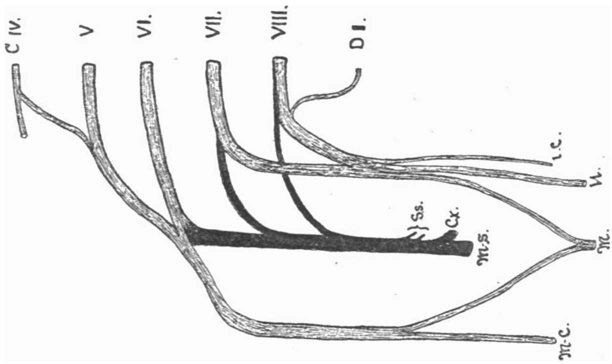


Fig. 2.

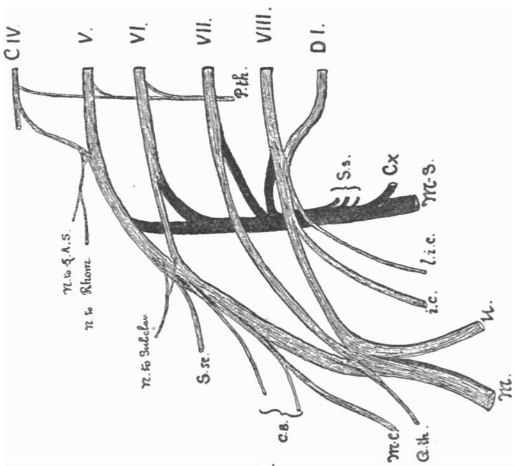
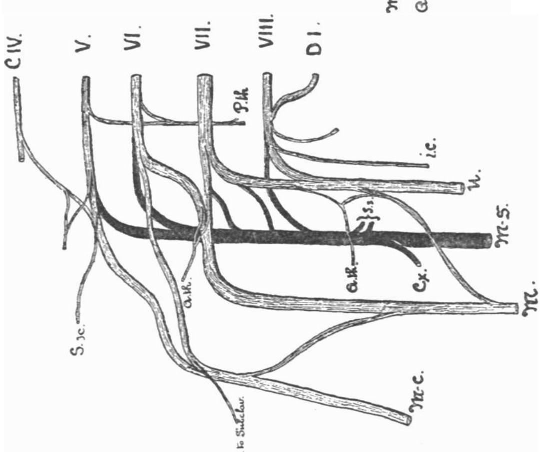


Fig. 1.



medius and contiguous sides of the medius and annularis. Thus between them they supplied three and a half digits.

Although the source of the nerve-supply of skin is never of so much importance as the source of the nerve-supply of muscles, it is interesting to see that the radial and posterior interosseous nerves can take up between them the same amount of cutaneous nerve-supply as may be associated with the radial alone in the case of Man, especially when we remember that both of these nerves are derivatives of the same nerve trunk, viz., musculo-spiral. We may therefore conclude that although at first the posterior interosseous nerve is a mixture of motor and sensory fibres, yet the tendency is for this nerve to become more fully specialised as development advances and greater co-ordination of the muscles of the hand and forearm are required, and consequently the cutaneous nerve fibres become more confined to the radial nerve.

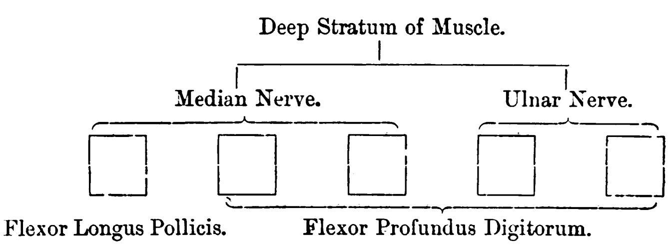
The posterior interosseous nerve supplied the same series of muscles as in Man, except in the Gibbon, where a slender filament quite distinctly passed forwards and pierced the interosseous membrane, to end in the deep surface of the pronator quadratus. In my dissection there was no other source of nerve-supply for this muscle, and of the identity of the muscle there could be no doubt. It is possible that this source of nerve-supply was abnormal even in the Gibbon, but it shows that absolute dependence is not to be placed on nerve-supply as an infallible guide to muscle homology. There was one point in connection with the posterior interosseous nerve of the Chimpanzee which deserves special mention, because it afforded some explanation of the position of this nerve as we find it in Man, embedded in the substance of the supinator brevis muscle. As the nerve passed from the anterior to the posterior aspect of the forearm it was never altogether hidden from view, being merely covered by a very thin aponeurotic fascia on the surface of the supinator brevis, and it can readily be understood how an increase in the size of the muscle and in the number of its fibres taking origin from this investing fascia would cause a submergence of the nerve and produce the characteristic appearance of the nerve piercing the muscle.

Musculo-cutaneous Nerve.—As its name indicates, this was a mixed nerve, since it provided motor branches to certain muscles and terminated cutaneously. The muscles which it supplied were those usually seen in Man. It is interesting to note that the branches for the coracobrachialis medius and longus arose separately in the Chimpanzee, and moreover the branch for the lower muscle arose first. In the Gibbon, the musculo-cutaneous nerve was not so distinctly isolated as in the other animals. After supplying a twig to the coracobrachialis it then gave filaments to the biceps and continued its course on the brachialis anticus. While lying on that muscle it sent twigs of communication to the ulnar nerve and terminated in a long slender continuation as its cutaneous termination. In all the animals these cutaneous branches were distributed on the outer aspect of the forearm, extending as far as the wrist and ball of the thumb.

Median Nerve.—This large and important nerve had many points of similarity with its fellows throughout the series of dissections. In every case it commenced its course external to the axillary and brachial arteries; in all, it passed subjacent to the brachial artery in the lower part of the arm—a condition of parts which has been seen in the human subject; in all, it entered the forearm between the superficial and deep groups of flexor muscles; in all, it was responsible for the same general supply of muscles and skin. But there were points of difference to be observed in the different animals. Thus, in the Gorilla, at the point where the median nerve crossed beneath the brachial artery, viz., in the lower third of the upper arm, it gave off a branch which was joined by one from the musculo-cutaneous nerve, and together they entered the lower part of the brachialis anticus muscle, and probably reached the elbow-joint. This afforded the only instance of a branch arising from the median nerve above the level of the elbow-joint.

Again, in the Gorilla, Chimpanzee, and Gibbon, distinct branches of communication existed between the median and ulnar nerves as these main trunks lay upon the deep stratum of muscles in the forearm. In the Chimpanzee the nerve formed by communicating branches from median and ulnar gave off a twig for the ulnar segment of the deep flexor and then joined the ulnar nerve. In connection with the study of the great deep flexor we have already seen that the ulnar segment of the muscle ultimately provided the tendons for the three inner digits, while the radial or humero-radial segment provided tendons for the thumb and index fingers. The nerve-supply of these segments is most interesting. We find that the radial segment is always supplied entirely from the median nerve, either directly, or indirectly through its anterior interosseous branch. The ulnar segment, on the other hand, receives nerve-supply from two sources—(*a*) the median or its anterior interosseous branch (sometimes both, as in the Orang), and (*b*) the ulnar nerve. Now, a careful examination shows that the portion of the ulnar segment supplied by the median nerve is readily separable from the rest of the segment, and the tendon which the part in question provides is distributed to the medius digit. Here, then, we have proof that this deep flexor stratum cleaves into two unequal portions so far as nerve-supply is concerned, and muscular substance corresponding with the three radial tendons—(pollex, index, and medius)—is supplied by the median nerve, while the remainder of the muscle for annularis and minimus is supplied by the ulnar nerve. We have already indicated how the increased development and specialisation of that portion of the radial segment, associated with the pollex, causes the remainder of the radial segment to approximate more closely to the ulnar segment, until ultimately it assumes the appearance of an inherent part thereof.

The following scheme will serve to illustrate the transformation and the homologies :—



Coming now to the consideration of the median nerve as distributed in the palm of the hand, we find that in the Gorilla and Orang the cutaneous and muscular supply were exactly the same as in Man. In the Chimpanzee, the cutaneous supply resembled that found in Man; but in regard to the supply of muscles, it had the 3rd lumbrical muscle supplied by the median nerve, while all the other muscles were supplied just as in Man. The greatest variety, however, existed in the Gibbon. In it the median nerve merely supplied the two and a half radial digits with digital cutaneous branches; and of muscles, it supplied the two outer lumbricales, the abductor pollicis (brevis), the opponens pollicis, and both heads of the flexor brevis pollicis, the latter supply being very distinct.

As already indicated, in discussing the posterior interosseous nerve, there was no trace of any branch from the anterior interosseous (median) to the pronator quadratus muscle of the Gibbon.

Ulnar Nerve.—This nerve commenced its course external to the great vessels of the upper arm, and crossed them superficially to reach the inner side of the limb, along which it descended behind the internal condyle of the humerus to the interval between it and the olecranon process, where it entered the forearm between the heads of the flexor carpi ulnaris. In the forearm it formed communications with the median nerve as already mentioned. In the forearm it supplied the customary branches—articular, muscular, and cutaneous. On entering the palm superficial to the anterior annular ligament, it distributed itself exactly as in Man by dividing into a superficial and a deep part. The superficial part provided the cutaneous supply left blank by the median nerve, *i.e.*, one and a half digits in the Gorilla, Chimpanzee, and Orang, and two and a half digits in the case of the Gibbon. From the deep branch twigs were supplied to all the interossei and contrahentes muscles (including the adductor pollicis obliquus and transversus) to the two inner lumbricales of the Gibbon and Orang; one (the inner) lumbrical of the Chimpanzee; the three inner lumbricales of the Gorilla, which had therefore a double nerve-supply (median and ulnar) for the 2nd lumbrical muscle. We must also note that the inner head of the flexor brevis pollicis of the Orang was supplied by the deep branch of the ulnar nerve. In addition to these palmar branches, the ulnar nerve supplied dorsal cutaneous branches, which were distributed to the back of the forearm in its lower part, and to those parts of the dorsum of the hand and digits left unsupplied by the radial and posterior interosseous nerves.

In each animal the inner cord, *i.e.*, the lowest part of the plexus, supplied internal cutaneous branches, which had the usual distribution to the skin of the inner aspect of arm and forearm.

In the Chimpanzee there was only one intercosto-humeral nerve, and that emerged from the second intercostal space; but in each of the other animals (Gorilla, Gibbon, and Orang) lateral branches emerged from the 1st and 2nd intercostal spaces, and descended as cutaneous branches to the skin on the inner side of the upper arm, usually extending almost to the elbow-joint.

(*To be continued.*)

[EXPLANATION OF PLATE III.

EXPLANATION OF PLATE III.

Fig. 1. Radial view of the hand and lower part of the forearm of the Gibbon (Hylobates ?). (The index digit was rudimentary, probably owing to injury.) *a.p.l.*, abductor pollicis longus; *a.p.b.*, abductor pollicis brevis; *e.p.b.*, extensor pollicis brevis; *e.l.p.*, extensor pollicis longus; *d.*, dorsal interosseous I.

Fig. 2. Radial view of the hand and lower part of the forearm of the Gorilla (Gorilla Savagei). The lettering bears the same significance as in Fig. 1.

Fig. 3. Palmar surface of hand of Gibbon (Hylobates ?).

Fig. 4. Palmar surface of hand of Orang-utan (Simia Satyrus).

Fig. 5. Palmar surface of hand of Chimpanzee (Anthropopithecus troglodytes).

Fig. 6. Palmar surface of hand of Gorilla (Gorilla Savagei). In each of these figures the lettering has the same significance. *a.l.*, anterior annular ligament; *n.ul.p.*, ulnaris profunda nerve; *c.*, contrahentes; *f.l.p.*, flexor longus pollicis; *f.b.p.* (*o*), outer head of flexor brevis pollicis; *f.b.p.* (*i*), inner head of flexor brevis pollicis; *ad.p.*, adductor pollicis (fig. 3); *ad.ob.*, adductor obliquus pollicis; *ad.tr.*, adductor transversus pollicis; *ab.m.d.*, abductor minimi digiti; *f.b.m.d.*, flexor brevis minimi digiti.

EXPLANATION OF DIAGRAMS IN TEXT.

Fig. 1. Brachial plexus of Gorilla.
Fig. 2. " " " Chimpanzee.
Fig. 3. " " " Orang-utan.

C. IV.–VIII.	Cervical nerves (ant. primary divisions).
D. I. .	Dorsal nerve.
m.c. .	Musculo cutaneous nerve.
M. .	Median "
m.s. .	Musculo spiral "
Cx. .	Circumflex "
U. .	Ulnar "
i.c. .	Internal Cutaneous "
l.i.c. .	Lesser do. " "
Ant. Thor. .	Anterior Thoracic "
P.th. .	Posterior " "
S.sc. .	Supra-scapular "
S.s. .	Sub-scapular "
N. to *C.B.*	Nerves to coracobrachialis muscle.