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Anatomical Study of the Right Forearm and Hand of One Western Gorilla (*Gorilla gorilla*) for Comparison with Humans with Respect to Motions of the Thumb and Fingers

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Abstract The right forelimb of a western gorilla (*Gorilla gorilla*) was dissected with particular attention to the motor function of fingers of this species. The anatomical structure of the forearm and hand of our specimen of gorilla is not much different from that of the human. The palmar aponeurosis is absent. Ligamentous fibers, instead, extend to the palm from the flexor retinaculum to form the ligamentous septa along the flexor tendons. The short thumb seems to be carefully calculated to fulfill both roles of locomotion and feeding. The underdeveloped flexor pollicis longus muscle bifurcates from the flexor digitorum profundus muscle of the index finger. The extensor indicis is also underdeveloped; its tendon does not reach the index finger but attaches to the wrist. The extensor apparatus of the fingers composed of both the extrinsic and intrinsic systems is as well developed as in the human hand. During knuckle walking with the metacarpophalangeal joints in extension and the proximal interphalangeal joints in deep flexion, the former joint of each finger seems to be stabilized with integrated functions of the finger extensor, interosseous and lumbrical muscles, and sagittal bands as well as the groove at the metacarpal head. The ulnar antebrachial branch of the median nerve with a fine motor communicating branch from the ulnar nerve innervates the ulnar intrinsic muscles of the hand, which are innervated by the deep branch of the ulnar nerve in the human.

Key words: anatomy, gorilla hand, flexor pollicis longus, extensor indicis, median nerve, innervation of intrinsic muscles, all median hand.

Introduction

It is said that the human species had separated from the common ancestor of the human and the gorilla about ten to seven million years ago (Hayama, 1999; Watanabe, 2008). It is interesting to know how much difference has developed in the hands between two species for this period of many years. In this regard, we assume that the human evolved the hand into the work device and obtained the ability of precision grip while the gorilla uses the forelimb for locomotion and feeding and possesses the hand suitable for knuckle walking. Those differences between two species might result from the anatomical architecture possessed by the common ancestor of both species in the process of phylogeny. However, only a few comparative studies of motor functions of fingers between the gorilla and the human hands to explain this phylogenetic problem have been reported up to the present (Diago *et al.*, 2012), although Kaplan (1946) stated that this comparison might be extremely helpful for both the surgeon and the anthropologist.

In this connection, the author (H.S.). has seen the patients in clinical practice who cannot flex the thumb and the index finger individually (see also Fahrer, 1981), and also those who do not show any paralysis of the intrinsic muscles of the hand in spite of the injury of the ulnar nerve around the elbow suggesting variation in innervation of those muscles (see also Mannerfelt, 1966; Okubo *et al.*, 1977). Those are considered to be closely related to findings seen in this specimen of a gorilla: underdeveloped flexor pollicis longus muscle (uFPL) and innervation of intrinsic muscles of the hand by the ulnar antebrachial branch of the median nerve (UABMN).

In this paper, therefore, there are two objectives; one is to describe and show in figures the anatomical architecture of the forearm and hand of this specimen of a gorilla in detail, and the other is to correlate those with the hand functions of a gorilla, based on comparison with the human hand.

Material and Method

The right forelimb of a female western gorilla (*Gorilla gorilla*), estimated 40 years old that died at Ueno Zoo in Tokyo was used for dissection. The forelimb had been amputated at the level of the lateral margin of the cervical spines. Dissection was carried out under 3.5 times magnification of surgical loupes, and also 4–16 times magnification of an operating microscope especially for intraneural funicular dissection.

The findings were first compared with those described in Raven's book "The Anatomy of the Gorilla" (Gregory, 1950), to know whether the findings seen in this specific material are common or not in other materials of gorilla. Then those were compared with descriptions and figures in the established textbooks of the anatomy of the human (Lampe and Netter, 1951; Boileau Grant and Basmajian, 1965; Kaplan, 1965; Hollinshead, 1969; Lampe, 1974; Anderson, 1983).

The findings different from the human hand and forearm were analyzed from the viewpoint of phylogeny of the primates based on the pertinent papers and information available through the Internet. Relevant literature (Jones, 1946; Hayama, 1999; Yamagiwa, 2005; Shima, 2014) was consulted to consider the anatomical and functional significance of those.

For simplicity, the name of the thumb or fingers of the human hand substituted that of the corresponding digit of the gorilla.

Results

The findings described below are significantly different from those seen in the human hand and forearm.

1) Appearance

The thumb is short and thin. The tip of the thumb reaches only the distal margin of the palm while the human thumb can reach the distal portion of the proximal phalanx of the index finger (Fig. 1). The thumb is thinner than the index through little fingers. Both thenar and hypothenar eminences are a little hypoplastic compared to those in the human hand.

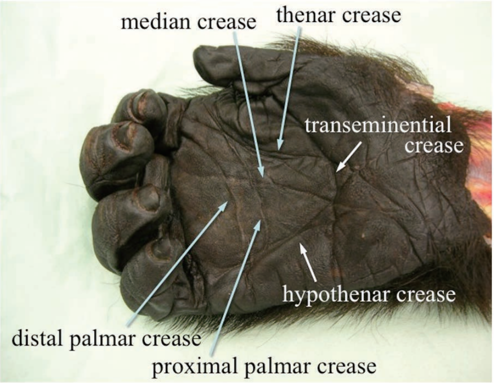

Fig. 1. The short and thin thumb, and two skin creases not seen in the human hand. It is different from the human hand to see the hypothenar and the transeminential creases.

2) Palmar aspect of the hand and forearm

Skin creases: The thenar crease exists along the thenar eminence and so do two distinct palmar creases, proximal and distal in the distal part of the palm. The single transverse line is not observed in the distal palm. It is occasionally seen in the human hand and called “simian crease” (Shiono and Azumi, 1981) as it is reported to be a characteristic skin crease in apes (van Mensvoort, 2002). The hypothenar crease along the hypothenar eminence and a transverse skin crease across the thenar and hypothenar eminences (“transeminential crease” coined by the author: H.S.) are skin creases not seen in the human hand (Fig. 1).

Palmaris longus and palmar aponeurosis: The palmar aponeurosis in the human hand is the subcutaneous aponeurotic structure spreading over the center of the palm in a fan shape extending from the tendon of the palmaris longus (PL). In this specimen of gorilla, there is not such a structure in the palm except for its most distal part called the natatory ligament that is the subcutaneous fibrous tissue in each interdigital web (McFarlane, 1985) (Fig. 2A). Neither the muscle nor tendon of PL is found in the forearm of this specimen.

Ligamentous fibers arising from the flexor retinaculum: The ligamentous bundles are found to arise from the distal margin of the flexor retinaculum* (transverse carpal ligament†). Those extend distally along flexor tendons of each digital ray and then dorsally on each side of the tendons attaching to the fasciae of the adductor pollicis and interosseous muscles to form ligamentous septa (Fig. 2B, C). This ligamentous structure covers the flexor tendons in the area between the digital sheath and the distal margin of the flexor retinaculum, where only the synovial sheath covers each flexor tendon underneath the palmar aponeurosis in the human hand.

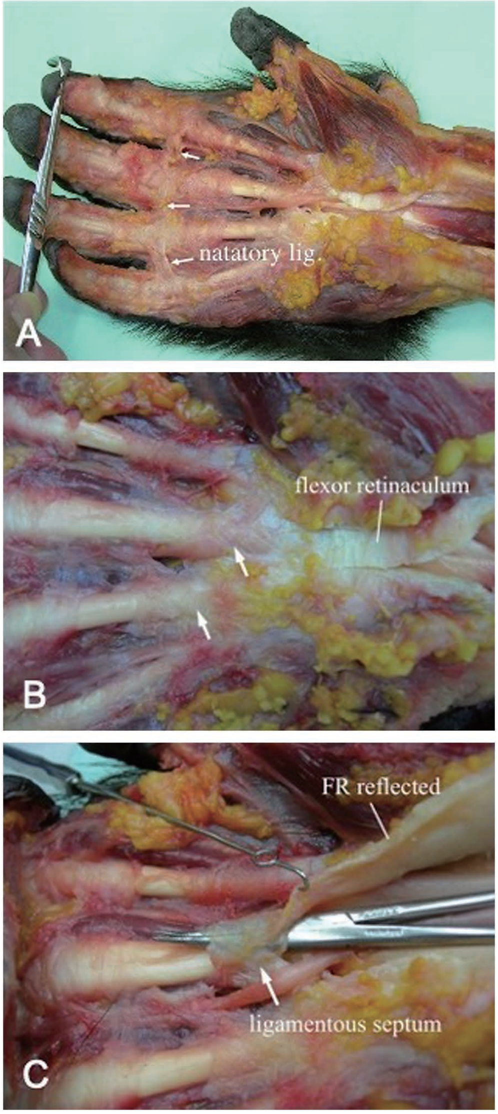

Fig. 2. The subcutaneous structures of the palm. A. The palmar aponeurosis is absent except for its most distal parts: natatory ligaments (white arrows); B. The ligamentous fibers (white arrows) arising from the distal margin of the flexor retinaculum; C. Ligamentous septum (a white arrow) along the flexor tendon formed with those ligamentous fibers.

Flexor pollicis longus: The flexor tendon of this short and thin thumb is much thinner than that of the flexor digitorum superficialis (FDS) or the flexor digitorum profundus (FDP) (Fig. 3A). Its proximal muscular portion bifurcates from the distal portion of the muscle of FDP of the index finger (Fig. 3B). Pulling FDP index finger proximally at its myotendinous junction by using a surgical retractor revealed that the thumb and the index finger were flexed simultaneously to make

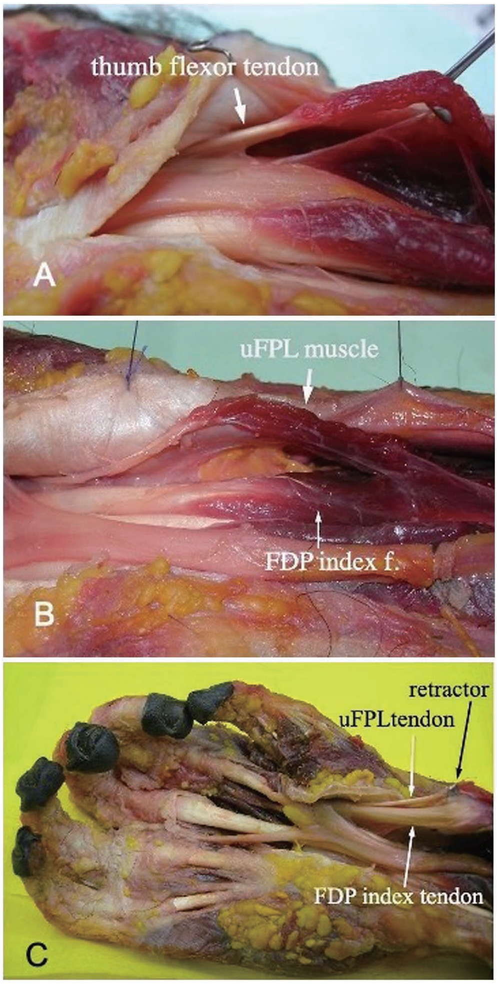

Fig. 3. Underdeveloped thumb flexor. A. The tendon of the thumb flexor is much thinner than that of FDS or FDP; B. Its muscle belly (uFPL) bifurcates from the distal portion of FDP muscle of the index finger; C. Pulling FDP index finger at its myotendinous junction with a retractor revealed that the thumb and the index finger were flexed simultaneously.

a tip pinch (Fig. 3C). So, the muscle bifurcating from the FDP muscle of the index finger is judged to be the underdeveloped flexor pollicis longus (uFPL).

Origin of FDP index finger muscle: The muscle of FDP of the index finger originates at the palmar aspect of the radius where FPL muscle does in the human forearm.

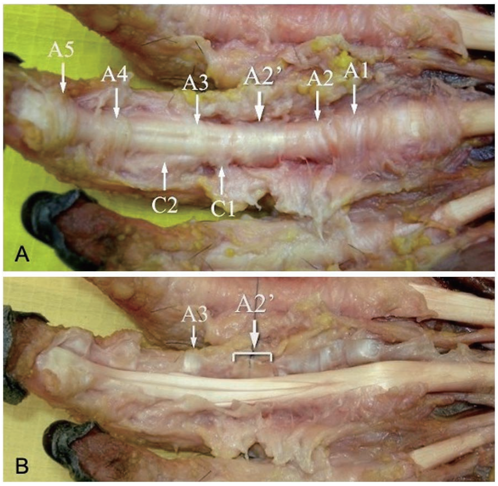

Fig. 4. Finger flexor sheath and pulley system. A. The entire sheath of the finger flexor of the ring finger is shown with the names of individual pulleys. The very thick and wide A2′ pulley (a white thick arrow) is located between A2 and C1; B. The inner surface of the sheath showing that A2′ pulley is twice as wide as A3.

Finger flexor sheath and pulley system: The thick parts of the tendon sheath of a finger flexor are called "pulley" which prevents the flexor tendon from bowstringing out when the flexor muscle contracts and the tendon gets tight on bending the finger. The thick ring-like pulley is called "annular pulley (A)" and relatively thinner and cruciate-form pulley is called "cruciate pulley (C)" in accordance with the pulley system in the human hand. Unlike the pulley system in the human hand described by Doyle (1988), there is another very thick and wide pulley between A2 at the proximal portion of the proximal phalanx and C1 pulley at its distal portion. This additional annular pulley found in this gorilla is tentatively termed A2′ (Fig. 4A). It is twice as wide as the A3 pulley located at the level of proximal interphalangeal (PIP) joint (Fig. 4B).

Palmar aspect of the proximal phalanx: Quite different from the human hand, there was an osseous crest along each edge of the palmar aspect of the proximal phalanx making the groove between those crests where the flexor tendon sits in (Fig. 5). The annular pulley mentioned above attaches to each crest of the proxi-

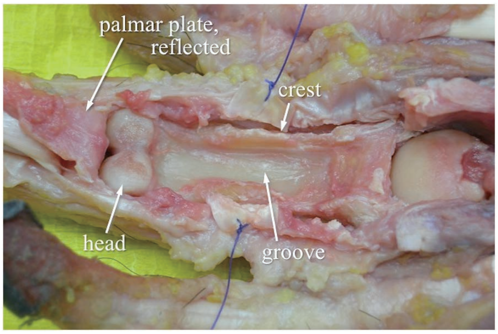

Fig. 5. Palmar aspect of the proximal phalanx. An osseous crest is seen along each edge of the palmar aspect of the phalanx and the groove is formed between those crests. The head of the proximal phalanx slants palmarward.

mal phalanx.

The head of the proximal phalanx slants palmarward so that the base of middle phalanx slides down deeply to increase the flexion angle of PIP joint while the extension angle is limited even when it slides up the proximal phalanx head dorsalward maximally.

Thenar muscles: The abductor pollicis brevis (APB) is well developed and its muscle belly extends as far as the midportion of the proximal phalanx of the thumb. By lifting that muscle, the opponens pollicis muscle is found to attach at the 1st metacarpal. The flexor pollicis brevis (FPB) muscle lies over the flexor pollicis longus tendon and attaches to the radial sesamoid at the palmar aspect of the metacarpophalangeal (MP) joint of the thumb. The inner head of this muscle described in Raven's book (Gregory, 1950) is not found in this specimen when it is defined to pass deep to the flexor pollicis longus tendon as in the human hand as described in Hollinshead's book (Hollinshead, 1969).

Motor branch of the thenar muscles: The common branch of the recurrent branch to innervate the thenar muscles and the radial palmar digital nerve of the thumb comes apart from the radial side of the median nerve in the distal portion of the carpal tunnel and then soon bifurcates. The recurrent branch penetrates through the very distal portion of the flexor retinaculum and goes deeply into the thenar muscles across the muscle fibers of APB. The branches coming from the ulnar nerve to communicate with the recurrent branch of the median nerve, called Riche-Cannieu anastomosis occasionally seen in the human hand (Mannerfelt, 1966; Spinner, 1972), are not present.

Ulnar antebrachial branch of the median nerve and innervation of intrinsic muscles: The most significant finding is that all intrinsic muscles other than three thenar muscles and radial two lumbrical muscles innervated by motor branches from the main trunk of the median nerve are innervated by the "ulnar antebrachial branch" of the median nerve, while those are innervated by the deep branch of the ulnar nerve in the human hand (Saito, 2020) ¶. In this specimen, the median nerve trifurcates at the level of the distal border of the pronator teres in the proximal forearm. The most radial one is the main trunk and the most ulnar one is the branch concerned. The latter is not seen in the human forearm and tentatively called the ulnar antebrachial branch of the median nerve (UABM) (Fig. 6 proximal). The branch between those two, the anterior interosseous nerve, comes off the radio-posterior portion of UABM. UABM runs radio-proximally to ulno-distally in the forearm and comes close to but does not unite with the ulnar nerve on the ulnar side of the wrist (Fig. 6 distal). It bifurcates there; its ulnar bundle goes distally along the hypothenar muscles, and the radial bundle goes radially as the deep branch of the ulnar nerve does in the human hand (Fig. 6 distal). The ulnar bundle further bifurcates, one being the ulnar digital nerve of the little finger and the other the 3rd common digital nerve going toward the 4th interdigital space. The radial bundle first branches off to the hypothenar muscles and then to the lumbrical muscles of the little and ring fingers, and then to both dorsal interosseous (DI) and palmar interosseous (PI) muscles (4th DI, 3rd PI and 3rd DI, 2nd PI) in the 4th and 3rd intermetacarpal spaces (Fig. 7). It goes further radially to give branches to both the transverse and the oblique heads of the adductor pollicis (ADP). The terminal branch of this bundle goes

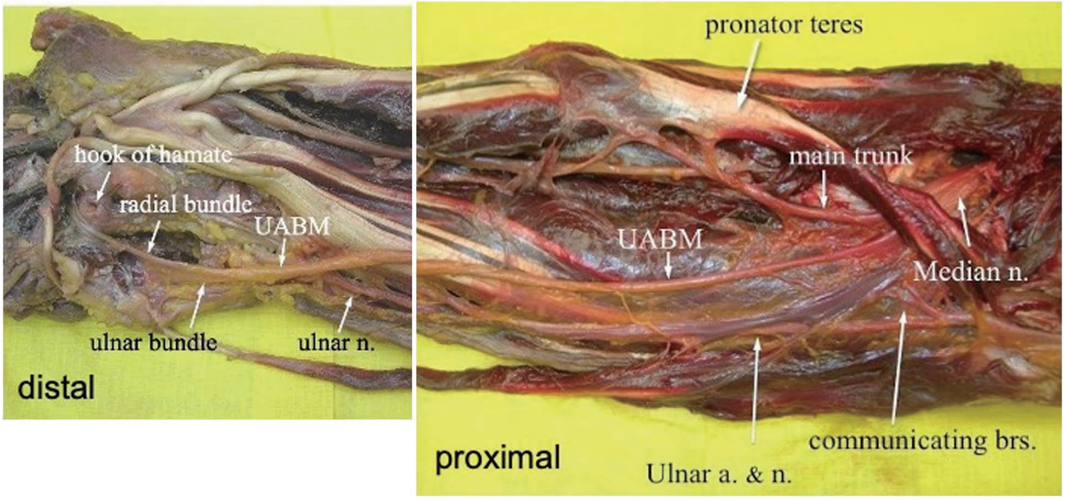

Fig. 6. The ulnar antebrachial branch of the median nerve (UABM). proximal: The median nerve trifurcates at the level of the distal border of the pronator teres. The most ulnar one is the branch UABM; distal: It runs ulno-distally in the distal forearm and comes close to but does not unite with the ulnar nerve on the ulnar side of the wrist. It bifurcates there to the radial and ulnar bundles.

through the interval between those two heads of ADP and comes out to the postadductor space to innervate both dorsal and palmar interossei (2nd DI, 1st PI) in the 2nd intermetacarpal space and finally both heads of the 1st DI in the 1st intermetacarpal space.

3) The dorsal aspect of the hand and forearm

Knuckle of the proximal interphalangeal joint (PIP joint): The skin at the dorsal aspect of the middle segment of each finger is thickened so as to make a 'knuckle pad' around PIP joint where chronic irritation has been inflicted by knuckle walking (Mackey and Cobb, 1994). The subcutaneous loose areolar tissue is also thickened to make a bursa. PIP joint of every finger is not fully extended passively. Maximum passive extension of PIP joint is limited in each finger, especially in the index finger where it is limited to −30 degrees.

Superficial extensor muscles: At the dorsoradial aspect of the proximal forearm, the extensor digitorum* (extensor digitorum communis†) (EDC) arises from the common muscle mass of the extensor-supinator group and then becomes a slightly thinner muscle bundle composed of proper muscles of individual tendons going to the index through the ring finger. EDC tendon going to the little finger (EDC$_{V}$) comes apart from the midportion of the one to the ring finger (EDC$_{IV}$) at the dorsum of the hand as seen in the human hand (Fig. 8A). This EDC$_{V}$ tendon connects EDC$_{IV}$ tendon with the extensor digiti minimi (EDM) tendon. A thin, oblique and short fibrous band is also seen between the distal portion of EDC$_{V}$ tendon and EDC$_{IV}$ tendon at MP joint level (Fig. 8B). There are no such transverse or oblique bands between EDC$_{II}$ and EDC$_{III}$, EDC$_{III}$ and EDC$_{IV}$ tendons known as the connexus intertendineus* (junctura tendinum†) in the human hand.

There is a very thin tendon slip along the ulnar margin of EDC tendon to the index finger (EDC$_{II}$), which is not the extensor indicis* (extensor indicis proprius†) (EIP) tendon but rather the additional tendon slip of the former.

Along the ulnar border of EDC muscle in the forearm, there is an independent muscle belly of the extensor digiti minimi (EDM), proper extensor of the little finger. There is a proper tendon sheath of this muscle at the dorsum of the hand a little distal to the distal margin of the extensor

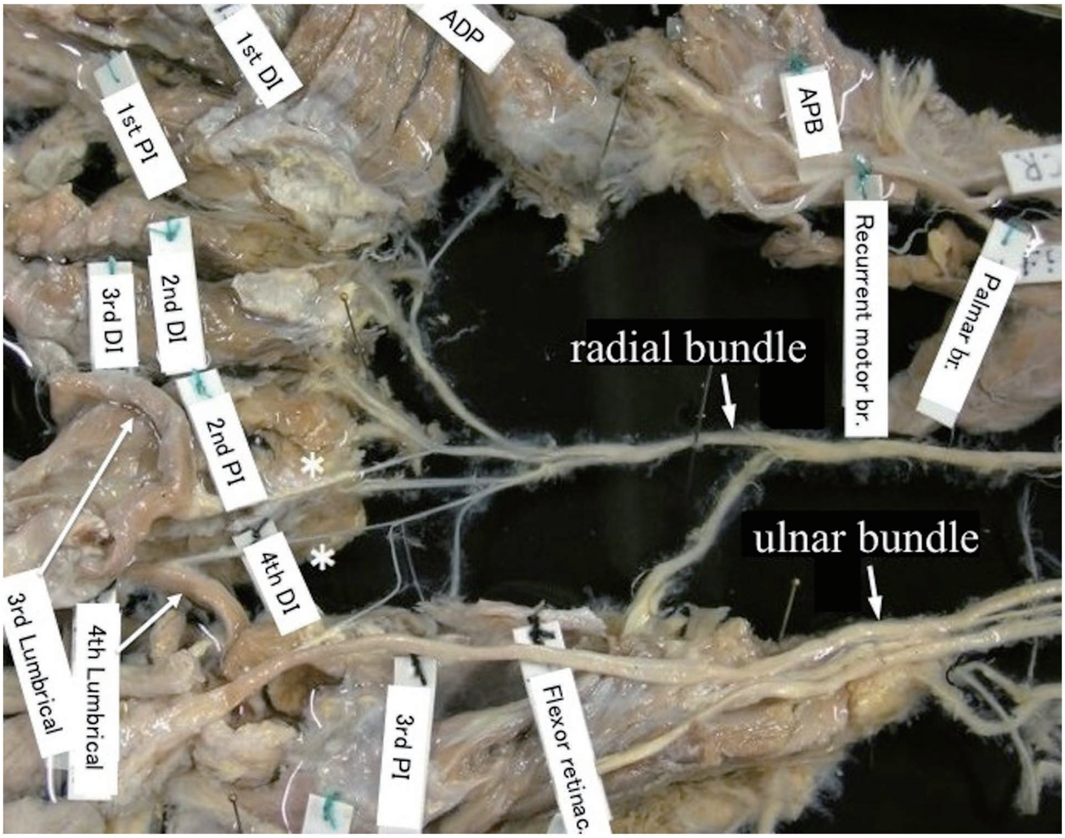

Fig. 7. Innervation of intrinsic muscles by the radial bundle of UABM. The radial bundle first gives off branches to the hypothenar muscles and to the lumbrical muscles of the little and ring fingers (marked with asterisks), and then to interossei (4th DI, 3rd PI and 3rd DI, 2nd PI).

retinaculum* (dorsal carpal ligament†) as seen in the human hand (Fig. 8A).

Deep extensor muscles: In the deep layer of forearm extensor muscles, the origin of the abductor pollicis longus muscle (APL) is identified at the proximal radius and ulna. An accessory muscle bundle coming from the common muscle mass of EDC was found to join this muscle at its myotendinous junction to give the appearance of the hemipennate muscle: tendinous at radial border and muscular at ulnar border. The tendon of this APL attaches to the radial part of the 1st metacarpal base and a thin tendinous slip coming off the ulnar margin of the main tendon extends more distally and attaches to the proximal phalanx base of the thumb (Fig. 8C). Either the muscle or tendon of the extensor pollicis brevis (EPB), distinct and independent from the above-mentioned APL, is not found. The extensor pollicis longus (EPL) muscle was found ulno-dstally to the muscle of APL. A small slender muscle is found at the dorsoradial aspect of the ulna, ulno-distally to the origin of the extensor pollicis longus (EPL). This muscle was judged to be the underdeveloped extensor indicis* (extensor indicis proprius†) muscle (uEIP) although its tendon did not reach the index finger, based on reasons described in the discussion section (Fig. 9).

Interosseous muscles: Dorsal and palmar interosseous muscles of the hand are as well developed in the specimen of our gorilla as in the human hand. The arrangement of each interosseous muscle corresponds to that in the human hand.

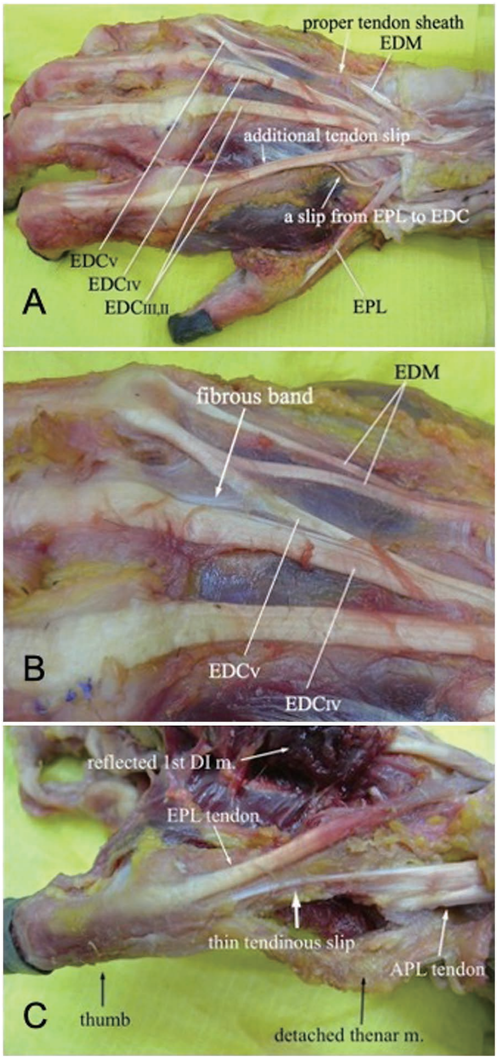

Fig. 8. Extensor tendons of the fingers and thumb. A. EDC_V tendon comes off EDC_{IV} tendon. The proper tendon sheath of EDM is seen. EIP tendon is not seen. Connexus intertendineus is not seen between EDC_{II} and ${}_{III}$, ${}_{III}$ and ${}_{IV}$ tendons; B. A thin and short fibrous band (a white arrow) is seen between the distal portion of EDC_V and EDC_{IV} tendons at MP joint level; C. APL tendon attaches to the radial part of the 1st metacarpal base. A thin tendinous slip of its ulnar margin extends more distally and attaches to the proximal phalanx (a thick white arrow).

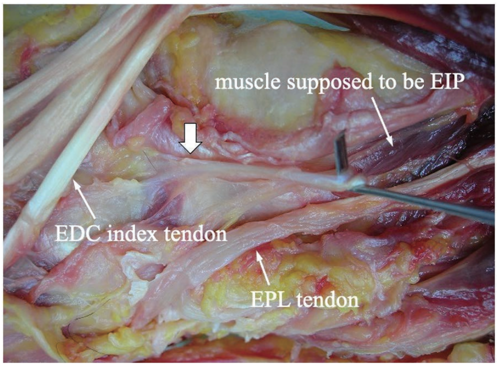

Fig. 9. Underdeveloped EIP. A small slender muscle sitting at the dorsoradial aspect of the ulna is judged to be underdeveloped EIP muscle although its tendon attaches to the dorsal aspect of the wrist (a white block arrow).

In the specimen of our gorilla, the proportion of the insertion either to the proximal phalanx base or to the interosseous hood (Tubiana and Valentin, 1964) in each interosseous muscle is shown in Table 1A. The 1st DI muscle inserts to the interosseous hood in the equal proportion to the proximal phalanx, quite different from the human hand (Fig. 10A, B). The proportion of the insertion of the abductor digiti minimi muscle (ADM) to the interosseous hood is as little as in the human hand (Table 1A, B).

Extensor apparatus of the finger: The anatomical structure of the extensor apparatus of each finger in the specimen of our gorilla nearly corresponds to that of the human hand shown by Tubiana and Valentin (1964) (Fig. 11A). In each finger, the muscle belly of DI or PI extends distally over the deep transverse metacarpal ligament (DTML) and converges with that of the lumbrical coming distally under the DTML to make the common tendinous band. From that band and the interosseous tendon itself, the membranous fibers expand dorsally to make a triangular aponeurotic sheet (Fig. 11B). The hood-like structure is formed together with the triangular sheet from the opposite side, incorporating EDC tendon at its central axis (Fig. 11B). Adherent to the proximal margin of this interosseous hood, there is a sagittal band on each aspect of MP joint. The sagittal band arises from DTML and extends dorsally and attaches to the margin of the extensor tendon.

Table 1. Proportion of the insertion either to the proximal phalanx or to the interosseous hood in each interosseous muscle of our gorilla (A) and human (Eyler & Markee) (B).

A. Our gorilla			B. Human (Eyler & Markee)*		
Muscle	Prox. phalanx	Inteross. hood	Muscle	Prox. phalanx	Inteross. hood
1st DI	5/10	5/10	1st DI	100%	0%
1st PI	3/10	7/10	1st PI	0	100
2nd DI	6/10	4/10	2nd DI	60	40
3rd DI	4/10	6/10	3rd DI	6	94
2nd PI	0/10	10/10	2nd PI	0	100
4th DI	5/10	5/10	4th DI	40	60
3rd PI	2/10	8/10	3rd PI	10	90
ADM	9/10	1/10	ADM	90	10

*Quoted from Hollinshead (1969)

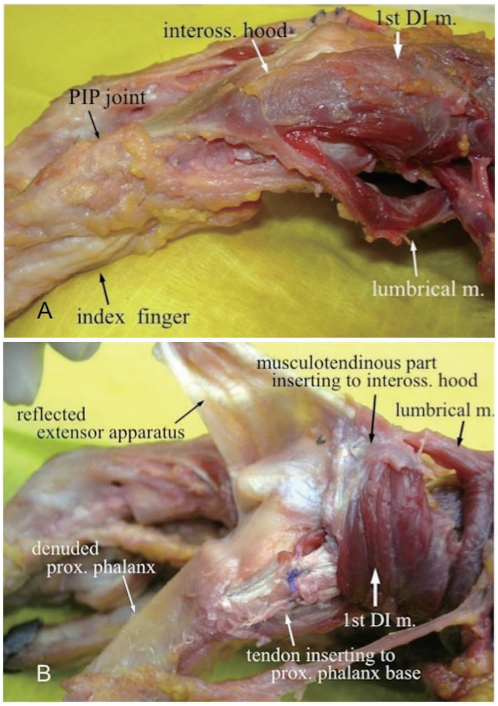

Fig. 10. The insertions of the first dorsal interosseous muscle. A. The distal portion of the 1st DI muscle is voluminously muscular and passes into the tendinous portion of the interosseous hood at the level of the proximal portion of the proximal phalanx; B. The tendinous insertion to the proximal phalanx base is exposed by reflecting the extensor apparatus. The tendon has been divided to explore the deeper structure and then re-sutured.

The oblique retinacular ligament (ORL) is developed enough to be identified in each finger, especially at the radial aspect (Fig. 11C). It originates from the lateral aspect of the proximal phalanx and extends distally and dorsally along the lateral band and then the terminal extensor tendon (Landsmeer, 1949; Milford, 1968).

Metacarpophalangeal joint: The extensor tendon sitting on the top of the MP joint of the middle finger is divided longitudinally and so is the dorsal capsule of the joint beneath it to expose the metacarpal head. There is a shallow groove along and a little proximal to the dorsal margin of the articular cartilage of the metacarpal head (Fig. 12A). It is observed that the dorsal edge of the proximal phalanx base sits in the groove by extending the MP joint passively (Fig. 12B).

Discussion

The anatomical structure of the hand of a gorilla was not much different from the human hand. Specific findings different from the human hand are discussed below.

Absence of palmaris longus muscle and palmar aponeurosis

According to Raven's book (Gregory, 1950), PL muscle is slender, measuring 12 cm, and is partly fused with the flexor carpi radialis and the pronator teres. This description, however, does not mean the existence of the palmar aponeurosis: the distal extension of PL. It is further stated that PL tendon fans out and mingles with the deep fascia of the forearm and attaches to the radius, and that very few of the tendinous fibers reach the lateral part of the transverse carpal liga-

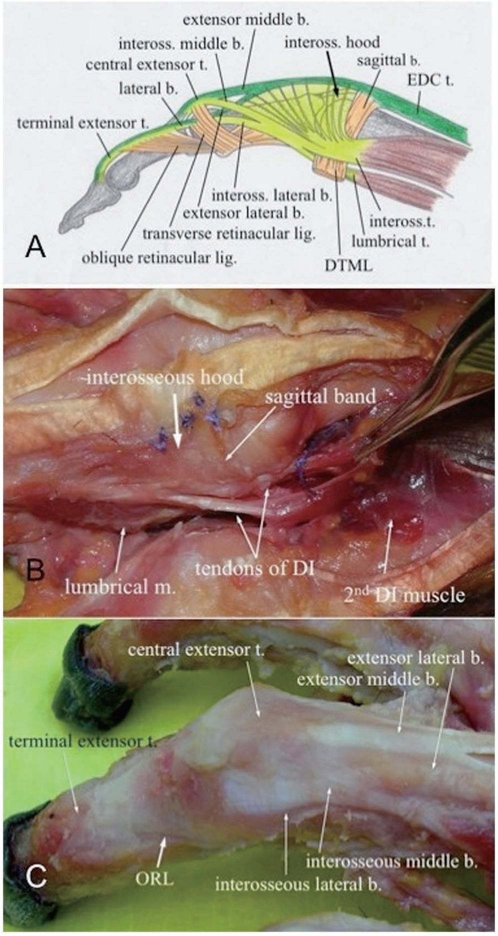

Fig. 11. Extensor apparatus and retaining ligaments. A. Extensor apparatus consists of two components: extrinsic compornent (dark green) and intrinsic component (light green). Ligamentous structures are shown in orange color. The interosseous hood is the proximal hood-like portion of the aponeurotic expansion of the interosseous tendon (a thick arrow). (modified from Tubiana and Valentin, 1964); B. On the radial side of the middle finger, the interosseous hood is shown. Adherent to the proximal margin of this interosseous hood, a sagittal band expands between DTML and EDC tendon; C. The oblique retinacular ligament (ORL) is well developed at the radial aspect.

ment[†] (flexor retinaculum[*]). This description in Raven's book suggests that there are no such aponeurotic fibers spreading over the palm as the palmar aponeurosis in the human hand. Chapman (1878) reported that PL was absent in a young male gorilla. Hepburn (1892) did dissections on four species of anthropoid, one each, and found that PL was present in the orangutan, the chimpanzee and the gibbon but not in the gorilla. Zihlman *et al.* (2011) reported that PL was absent in all five gorillas on which he did dissection.

Those descriptions suggest that both PL muscle and the palmar aponeurosis are usually absent in the gorilla (Diogo *et al.*, 2017). The palmar aponeurosis in the human is the structure that protects the finger flexor tendons and neurovascular bundles lying beneath it. It is thought that the ligamentous bundles arising from the flexor retinaculum and their extension: ligamentous septa covering the flexor tendons in this specimen substitute for the role of the palmar aponeurosis in the human hand (Fig. 2B, C).

In the human, the incidence of absence of PL muscle is reported to be 12.9% (Reimann *et al.*, 1944) or about 11% (Tountas and Bergman, 1993). Although the absence of PL muscle is considered to mean the absence of its distal extension: the palmar aponeurosis as well, Ghoshal *et al.* (2019) reported a case where the palmar aponeurosis arose from the distal border of the flexor retinaculum in spite of the absence of the muscle and tendon of PL.

The short and thin thumb, underdeveloped FPL and absence of EPB muscle

The short and thin thumb is a salient characteristic of the hand of a gorilla (Fig. 1). It is short enough to avoid the tip of the thumb hitting against the ground during PIP knuckle walking (Fig. 13A, B). The hands of a gorilla are not completely freed from the role of locomotion. The thumb length of the gorilla seems to be carefully calculated to fulfill both roles of locomotion and feeding.

Shima (2014) referred to the thickness index of the thumb proposed by Susman (1994). It is the proportion (percent) of the width of the head to the length of the thumb metacarpal. He measured the indices in early hominid fossils (*Austropithecus afarensis*, *Paranthropus robustus*, *Homo erec-*

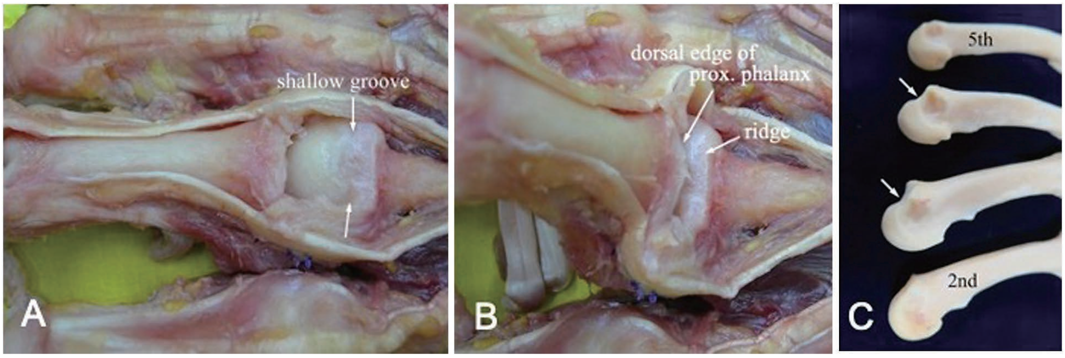

Fig. 12. Dorsal aspect of the metacarpophalangeal joint. A. A shallow groove (white arrows) is seen along the dorsal margin of the articular cartilage of the metacarpal head; B. The dorsal edge of the proximal phalanx base sits in the groove by extending the MP joint passively; C. Grooves are deep enough at the 3rd and 4th metacarpals (white arrows), but not at the 2nd and 5th in the skeletal specimen of another gorilla stored in National Museum of Nature and Science.

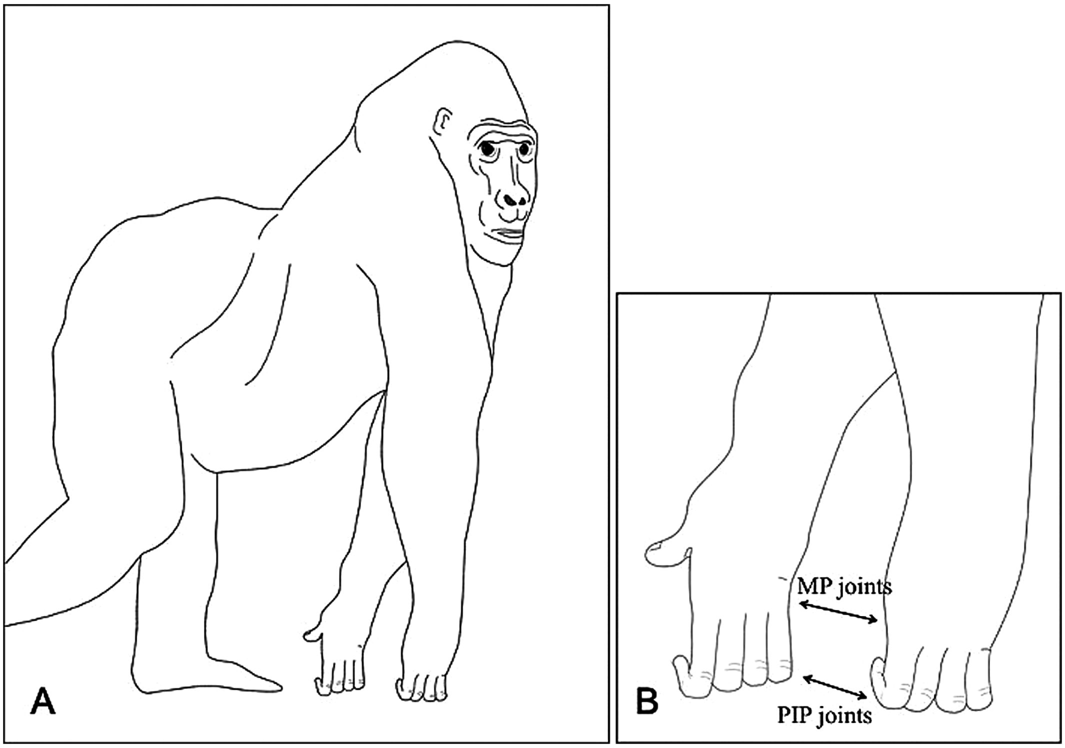

Fig. 13. Knuckle walk. A. The trunk tilts backward because of longer forelimbs; B. The knuckle walk of gorillas is walking with MP joints in extension and PIP joints in deep flexion bearing the weight on the dorsal aspects of the middle phalanges of the hands. Sketches are drawn imitating the walking style shown in movies of NHK BS TV program (Yamagiwa, 2012).

tus and *Homo sapiens neanderthalensis*), and compared their indices to those of two extant species: chimpanzees and modern humans. He confirmed that the three hominids (*P. robustus*, *H. erectus*, and *H. s. neanderthalensis*) found with stone and bone tools showed their thumb thick-

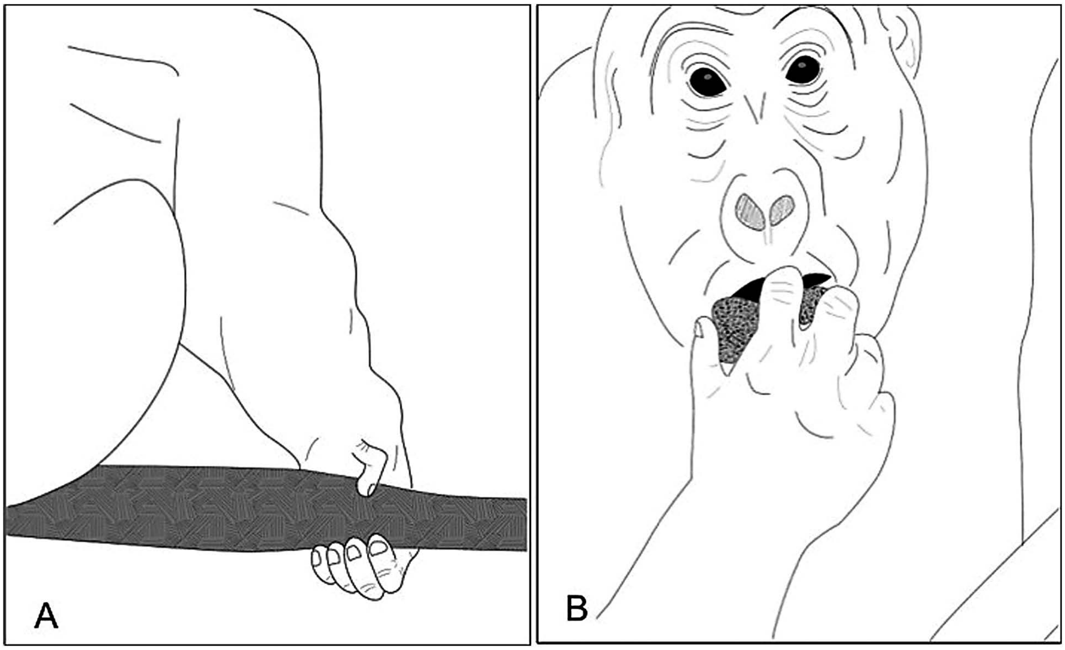

Fig. 14. Grasping pattern of the hand. A. Grasping a bough of the tree; B. Holding a piece of fruit. Sketches are drawn imitating the hand motion shown in movies of NHK BS TV program (Yamagiwa, 2012).

ness indices close to 30, similar to that of *Homo sapiens*. So, he insisted that this index could be one of criteria to detect the capability for refined, humanlike precision grasping in fossil hominid species of the Plio-Pleistocene. Contrary to his proposal, Ohman *et al.* (1995), who added the data of gorillas, claimed that the thumb thickness index indicated the strength of grasping rather than refined precision grasping essential for tool making, because the size of joint corresponds to how much stress is loaded on it.

Apart from this discussion, the thickness index of the thumb is the head width/length ratio of the first metacarpal sitting in the palm. It is not the index of the part projected out of the palm (MP joint to the thumb tip). So, this index does not correspond to the appearance of "short and thin thumb" of a gorilla.

The well-developed APB in the thenar eminence suggests that placing the thumb into palmar abduction or opposition is feasible as in the human hand. The pentadactyly with the thumb placeable into opposition was one feature in the evolution of the human hand (Hayama, 1999). Movies and photos taken during the fieldwork by Yamagiwa (2012) teach us how a gorilla uses the thumb when it grasps the bough of a tree or holds a fruit to eat. The pattern of grasping a bough is not the hook grip but the power grip in which the thumb is placed in the position of palmar abduction with a bough placed in the first interdigital space (Fig. 14A). The pattern of holding a fruit is the whole hand grasp with the thumb placed in opposition (Fig. 14B).

The relative segment length of the palm of a gorilla seems to be longer than that of the human hand. Feix *et al.* (2015) confirmed that the relative segment length of the 2nd metacarpal, and of the proximal and middle phalanges of the index finger was longer than that of the human hand. This makes the entire length of the index finger ray (2nd metacarpal plus three phalanges) long enough for the tip of the index finger to meet that of the short thumb (Fig. 3C). They estimated the thumb-index finger precision grip and manipulation potential in extant and fossil primates using a kinematic model based on the bony hand morphology. They described that gorillas have the closest workspace to humans. This study, however, assumes that the interphalangeal (IP) joint of the thumb moves actively in the same range as in humans. When FPL muscle is absent, active flexion of IP joint is not feasible. Thus, the workspace would be smaller than that calculated by the kinematic model mentioned above.

Chapman (1878) reported that FPL was entirely absent in a young male gorilla. Straus (1942) described, based on his own dissections and data in the literature available to him, that FPL tendon was absent in five, rudimentary and inutile in six and a half of 16 gorillas with the rate of absent plus non-functioning tendon being 71.9% in all. Diogo *et al.* (2012) reported the findings of their own dissections of five main groups of hominoids; FPL was absent in orangutans, gorillas and chimpanzees but present in hylobatids and humans. Diago *et al.* (2017) described that the tendon to digit I was present but this tendon mainly originated from the fascia lying over the thenar muscles in a great part of gorillas dissected by other authors as well as in four hands of their own gorillas.

In the specimen of our gorilla, the muscle of FDP of the index finger originates at the palmar aspect of the radius where FPL muscle does in the human forearm. It is considered that FDP muscle of the index finger occupied the empty place of the origin of FPL muscle.

Active flexion of the thumb IP joint is not feasible in those cases without FPL muscle. The motion of the thumb is controlled by thenar muscles and three forearm muscles of APL, EPL and EPB if present. Hepburn (1892) described a very interesting finding regarding FPL in a gorilla. There was a tendinous band occupying the position of the long flexor of the thumb, one end of which attached to the carpus and the other to the base of the distal phalanx. Bunnell (1956) described similar findings seen in the chimpanzee and the orangutan; there is only a narrow tendon from the distal phalanx of the thumb to the transverse carpal ligament[†]. In both cases of Hepburn and Bunnell, such a tendon acts as a tenodesis, flexing the thumb automatically on extension of the wrist or radial abduction of the thumb.

In the specimen of our gorilla, the muscle of uFPL comes off the distal portion of the muscle belly of FDP of the index finger (Fig. 3B). The own muscle belly of uFPL is much shorter than the fully developed FPL muscle. Its stretch-contraction amplitude must be short. However, this anatomical structure of uFPL muscle is a kind of digastric muscle. So, the insufficient amplitude of the distal muscle belly could be augmented by that of the proximal one common with FDP muscle of the index finger. This structure also lets the thumb and the index finger flex simultaneously and facilitates a pinch motion between those two digits (Fig. 3C). Phylogenetically, uFPL muscle bifurcating from the FDP index muscle is considered to be the incomplete form of individualization from the FDP muscle (Kodera, 2010). This hypothesis might be supported by the report of Diogo *et al.* (2012) that FDP muscle sends tendons to the first through the fifth digits in species of non-hominoid primates. Contrarily, it might be on the halfway to the complete absence of FPL as in most of gorillas reported above.

There are some persons who cannot flex the thumb and the index finger individually. Simultaneous flexion of both the thumb and the index finger by a common flexor muscle might be the character that the common ancestor of both the human and the gorilla had in the process of phylogeny.

Chapman (1878) described that there existed a distinct extensor primi internodii pollicis (Extensor pollicis brevis*: EPB) in a gorilla of his specimen. Straus (1941) casted some doubt on this description "distinct" because other authors such as Duckworth, Eisler, Hepburn, Pira and Sommer described that EPB merely was a derivative of the metacarpal division of the abductor. Gibbs *et al.* (2000) reported, based on the statistical analysis of soft tissue characters in higher primates by an extensive literature search, that EPB muscle with the tendon inserting on the base of the proximal phalanx of the thumb as in the human existed only in the gorilla out of four anthropoids: the gibbon, the orangutan, the gorilla and the chimpanzee. Straus (1941) described that such a part of the abductor muscle complex as inserts upon the phalangeal portion of the thumb seemed to have been found only in the gorilla (56%, 9/16) and the gibbon (7%, 1/15). He also referred to Keith who wrote that the tendon of APL sent a slip to the proximal phalanx of the thumb in one chimpanzee out of 20 reported, although he has not encountered such statement in any other publications. The finding seen at the dorsoradial aspect of the wrist in our gorilla is just the same as Keith's description of the tendon of the long abductor in that chimpanzee (Fig. 8C). Another unique finding in our specimen is that an accessory muscle bundle coming from the common muscle of EDC joins the muscle belly of APL at its myotendinous junction. We are not sure that this muscle bundle is the EPB muscle, because it comes off the superficial extensor mass rather than the deep one. Straus (1941) claims that EPB indubitably is a differentiated portion of APL, the tendon of which has migrated distally on to the proximal phalanx of the thumb. According to Tountas and Bergman (1993), EPB was reported absent only in 6.3% of cases in the human. So, the existence of EPB seems to be closer to the human hand.

Underdevelopment of both FPL and EPB muscles of the thumb seen in the specimen of our gorilla seems to be a transitional form between the hand of anthropoids and the human hand. This form, however, must be specifically evolved and adapted for gorillas to live in the wild.

Extensor apparatus, interosseous hood, sagittal band and oblique retinacular ligament

Tubiana and Valentin (1964) showed the anatomical structure of the extensor apparatus in the human hand schematically with precise names of each detailed component (Tubiana, 1981) (Fig. 11A). The extensor apparatus is composed of two muscular systems: the extrinsic system (EDC, EIP, EDM muscles arising from the forearm) and the intrinsic system (interosseous and lumbrical muscles originating from the hand proper). The aponeurotic expansion of the interosseous tendon forms a triangular sheet. The proximal transverse fibers of this triangular sheet form the interosseous hood together with those fibers from the opposite side (Tubiana and Valentin, 1964) (Fig. 11A, B). According to their description, the proximal portion of the entire dorsal expansion (extensor expansion) is called "interosseous hood". This hood-like structure covers the dorsal portions of the proximal phalanx and MP joint.

The anatomical structure of the extensor apparatus of each finger in the specimen of our gorilla nearly corresponds to that of the human hand shown by Tubiana and Valentin (1964) (Fig. 11A). The intrinsic components of the extensor apparatus in each finger arise mainly from both DI and PI muscles, and the lumbrical muscle on the radial side. The main role of each interosseous muscle depends on its location (Lampe and Netter, 1951; Lampe, 1974). The 1st DI muscle is located on the radial side of the 2nd MP joint in the 1st intermetacarpal space. In the human hand, it inserts entirely to the radiopalmar corner of the proximal phalanx base and works as abductor and flexor of the 2nd MP joint (Table 1B). In the specimen of our gorilla, however, one half of the component of 1st DI inserts to the proximal phalanx base and the other does into the interosseous hood. (Fig. 10A, B, Table 1A). In the human hand, the 3rd DI muscle located on the ulnar side of the 3rd MP joint inserts mostly (94%) to the interosseous hood while that of our gorilla sends only a little more than half of the insertion (6/10) to it (Table 1 A, B).

EDC tendon extends distally and trifurcates into the extensor middle band and, radial and ulnar extensor lateral bands at the level of the proximal phalanx (Fig. 11A). The extensor middle band extends distally and merges with the interosseous middle bands coming from both sides to make the central extensor tendon that attaches to the middle phalanx base. The extensor lateral band on each side merges into the interosseous lateral band described below.

The interosseous tendons on the both sides send the membranous fibers dorsally and the cord-like fibers distally (Fig. 11A, B). The cord-like portion bifurcates to the interosseous middle

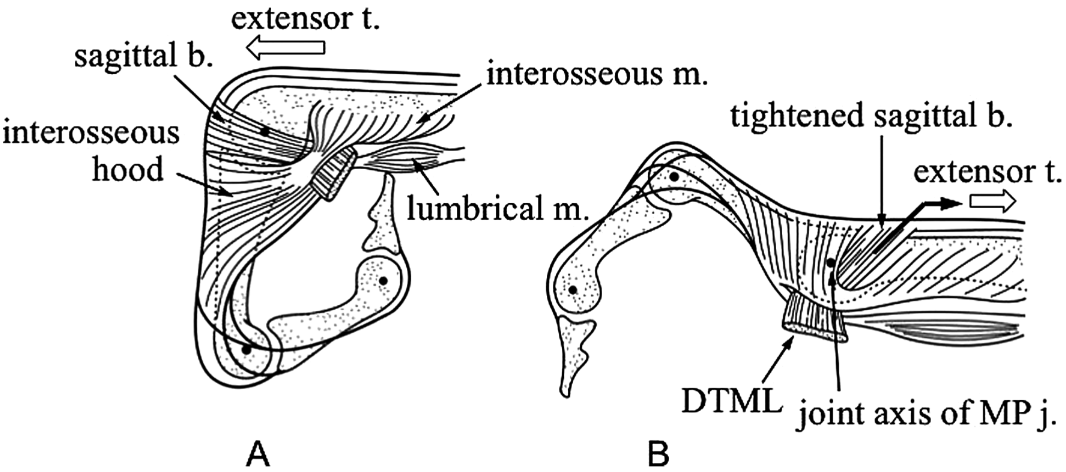

Fig. 15. The mechanism to block hyperextension of the MP joint with the function of the sagittal band. A. When the finger is flexed, the sagittal band passes over the joint axis of the metacarpal head in coordination with the distalward movement of the extensor tendon; B. When the MP joint is extended and surpasses the range of extension, the traction force of the finger extensor is blocked with the tightened sagittal band that transmits the force palmarward so that the proximal phalanx base does not move further to hyperextension.

band and the interosseous lateral band. The lumbrical muscle coming under DTML on the radial side of each finger joins the interosseous lateral band. The interosseous lateral band joins the extensor lateral band to make the lateral band. It extends further distally to unite with the lateral band coming from the other side to form the terminal extensor tendon that attaches to the distal phalanx.

In the human hand, the sagittal band arises from the DTML and extends dorsally and attaches to the margin of the extensor tendon. This band seen on each side of the MP joint connects the extensor tendon with DTML to stabilize the former on the top of the MP joint as described by Tubiana and Valentin (1964), and Milford (1968). The same aponeurotic band is also named the transverse lamina by Landsmeer (1955). In addition to stabilizing the extensor tendon on the top of MP joint, the sagittal bands have the other role to restrict the hyperextension of MP joint. The sagittal bands transmit the traction force of the finger extensor palmarward to DTML when the MP joint surpasses the range of extension (straight position) so that the proximal phalanx base does not move further to hyperextension (Fig. 15A, B). This anatomical structure also exists in the specimen of our gorilla. We consider that the same mechanism as in the human hand works in gorillas, especially on the MP joints with shallow metacarpal grooves.

Another noteworthy finding was that the oblique retinacular ligament (ORL), one of the retaining ligaments of the finger, was well developed in each finger especially at the radial aspect (Fig. 11C). It arises from the radial or ulnar aspect of the proximal phalanx along the attachment of the flexor sheath and extends distally and dorsally along the margin of the lateral band, and then merges into the terminal tendon at the dorsal aspect of DIP joint. This anatomical structure corresponds to ORL in the human hand (Landsmeer, 1949; Milford, 1968). As ORL passes palmar to the rotation axis of PIP joint and then dorsal to the rotation axis of DIP joint, it loses tension when PIP joint is flexed so that DIP joint becomes flexible. When PIP joint is extended, it tenses so that DIP becomes extended. So, ORL facilitates simultaneous extension or flexion of both PIP and DIP joints (Landsmeer, 1963). Haines (1951) called this ligament “link ligament”.

Those anatomical evidences of the extensor apparatus suggest that gorillas could use their fingers for manipulating, grasping or pinching objects in a similar manner to humans. It also supports that they could exert strong power on the finger pulps enough to hold the surface of the thick trunk of the tree while climbing it as shown by the fieldwork of Yamagiwa (2005, 2012).

Knuckle walk and stabilization of the MP joint

The skin at the dorsal aspect of the middle segment of each finger is so thick as to be called a 'knuckle pad', where chronic irritation had been inflicted (Mackey and Cobb, 1994). This is a proof that this gorilla had walked with knuckles. The knuckle walk of gorillas is walking with MP joints in extension and PIP joints in deep flexion bearing the weight on the dorsal aspects of the middle phalanges of the hands (Fig. 13A, B). Stability of both PIP and MP joints are secured mainly with coordination of the forces of the extensors and flexors during the stance phase of knuckle walking. The mechanism to stabilize the MP joints seems to be essential during knuckle walk in which the MP joints are stabilized in extension (straight position), and the PIP joints in over 90° flexion.

Tuttle (1969) listed major features associated with knuckle walking in the African apes as follows: (1) configuration of the carpal bones and the distal radius, (2) increased development of the wrist flexors, (3) extension of the articular cartilage onto the dorsal aspects of the 2nd through 5th metacarpal heads, (4) prominent ridges on the dorsal aspects of the metacarpal heads, (5) shortening of the long digital flexor muscles, (6) prominent development of the lumbrical and interosseous muscles and (7) friction skin over the dorsal aspects of the middle phalanges. The findings seen in the right hand of our gorilla correspond to the features: (3)(4)(6) and (7) described above. Items (1)(2)(5) are beyond the scope of this paper since we did not do any osteoarticular study of the wrist joint or any quantitative muscle study of wrist or finger flexors.

The groove and ridge located along the dorsal margin of the articular cartilage of the metacarpal head seen in our specimen correspond to the feature (4) listed above. The groove is called 'knuckle walking groove' that is the evidence of walking on knuckles (Fig. 12A). The role of the groove and the ridge behind it might be to prevent MP joints from going into hyperextension by bony blockage. It is observed in the middle finger of this specimen that the dorsal edge of the proximal phalanx base sits in the groove when MP joint is extended passively (Fig. 12B). This groove, however, seems to be too shallow to block the proximal phalanx base moving over the ridge of the groove into hyperextension. Observation of the skeletal specimen of another gorilla stored in National Museum of Nature and Science revealed that grooves are deep enough at the 3rd and 4th metacarpals but not at the 2nd and 5th (Fig. 12C).

The sagittal bands play a role to restrict hyperextension of MP joint in the human hand (Green, 1982). Those transmit the traction force of the finger extensor palmarward just when MP joint surpasses the range of extension so that the proximal phalanx base does not move to further hyperextension (Fig. 15A, B). This anatomical structure also exists in the specimen of our gorilla as described above. We consider that the same mechanism as in the human hand works in gorillas, especially on MP joints with shallow metacarpal grooves.

Retaining structures of the finger flexor

An osseous crest along each edge of the palmar aspect of the proximal phalanx and the groove between those crests make the place where the flexor tendon sits firmly (Fig. 5). Each pulley of the flexor tendon sheath attaches to the crests of the palmar aspect of the proximal phalanx. The thick and wide annular pulley A2′ of the flexor sheath, which is not seen in the human hand, is considered to reinforce the retaining structure of the flexor sheath to prevent the flexor tendon from bowstringing and slipping out of the osseous groove (Fig. 4A, B), when the flexor tendon gets extremely tight on powerful grasping such as climbing the tree or grasping a bough while living in the wild (Fig. 14A) (Jones, 1946; Yamagiwa, 2005, 2012).

Underdeveloped EIP and pointing

A small slender muscle sitting at the dorsoradial aspect of the ulna in the deep layer of the forearm extensors is judged to be the underdeveloped EIP (uEIP) muscle, although its thin tendon attaches to the dorsal aspect of the wrist joint (Fig. 9). The following descriptions support this judgment.

There is a description of M. extensor indicis proprius[†] (EIP) in the gorilla in Raven's book (Gregory, 1950), stating that it is a slender, spindle-shaped muscle existing between EPL muscle and the ulna, and that its tendon divides and most of it joins EDC_{II} tendon while the remainder consists of two slender tendons; one of these inserts on the dorsum of the hamatum and the other on the capitatum. It occupies the same location of the origin of EIP as in the human forearm described by Kaplan (1965). Ueba (1985) described that there is a variation of EIP in human specimens in whom the tendon does not reach the index finger but inserts to the dorsal aspect of the second metacarpal.

Chapman (1878) reported that the extensor indicis[*] (EIP) existed in a young male gorilla. Hepburn (1892) described, from the findings of his own dissection of four species of anthropoids, one of each species, that EIP muscle in the gorilla was as slender as in the human, while it showed a considerably greater development with plural tendons inserting to other digits as well as the second digit in other species of anthropoids: the chimpanzee, the orangutan and the gibbon. After extensively reviewing literature on soft tissue anatomy of the five extant hominoid genera, Gibbs *et al.* (2000) reported that the most common pattern of the insertion of EIP is to the second digit in the gorilla. Aversi-Ferreira *et al.* (2010) reported that EIP existed in the gorilla based on an extensive review of the literature and on the dissections by themselves. Diogo *et al.* (2017) showed in their atlas of gorilla that the tendon of this muscle attached to only the 3rd and 4th metacarpals on one side while to the index finger as well as to the 3rd and 4th metacarpals on the other side.

Tan and Smith (1999) stated, by reviewing literature of anomalous extensors muscles of the human hands, that the deep portion of the forearm extensors to which EIP belongs appears to be highly unstable and undergoes considerable evolutionary change in the great variation in different species of primates. They showed in the sketches the anomalous finger extensors in the human: the extensor digitorum brevis manus, the extensor medii proprius and the extensor indicis et medii communis. Yoshida (1995) also reported the anomalous extensors in the human such as the extensor pollicis et indicis accessories and extensor indicis radialis, both of them arising from the deep layer of the forearm extensors.

Considering those pieces of information, EIP muscle with the insertion to the index finger exists in most of gorillas but that of our gorilla is specifically underdeveloped; its tendon does not reach the index finger.

The fully developed EIP is essential to extend the index finger while other fingers being flexed in such a motion of pointing. When EIP is functioning, MP joint of the index finger is extended. When EIP muscle is underdeveloped and its tendon does not reach the proximal phalanx of the index finger as in our gorilla, theoretically, intrinsic muscles alone can extend both PIP and DIP joints but not MP joint. The question is whether a gorilla has the ability to point to the particular object. According to Leavens and Hopkins (1999), Patterson (1978) reported that a gorilla (born in captivity, initially mother reared and language trained) pointed to itself and the object or food placed at a distance. It is not clear which was used, the index finger alone or the whole hand with outstretched fingers. Pointing with all outstretched fingers is feasible mainly with the function of EDC even when EIP muscle or tendon is absent.

No connecting bands in the radial part of finger extensor tendon complex

Connexus intertendineus* (junctura tendinum†) in the human hand are transverse or oblique tendinous bands connecting individual EDC tendons between EDC index finger (EDC_{II}) and EDC middle finger (EDC_{III}), EDC_{III} and EDC ring finger (EDC_{IV}). There are no such connecting bands seen between each extensor tendon of the index through ring fingers in the specimen of our gorilla (Fig. 8A). EDC little finger (EDC_{V}) tendon coming apart from the midportion of EDC_{IV} tendon runs obliquely to the EDM tendon at the MP joint of the little finger. A thin, oblique and short fibrous band is also seen between the distal portion of EDC_{V} tendon and EDC_{IV} tendon at MP joint level (Fig. 8B). Those are considered to work as functionally as a part of connexus intertendineus.

Connexus intertendineus is not seen, although the intervening tissues between the individual tendons might have been excised during preparation of the specimen, in photos of finger extensors in the atlas of Diogo *et al.* (2017). This structure is also absent on the hand of a gorilla shown in the book of Kaplan (1965). He explains that absence of this structure between the individual tendons of EDC_{II} and EDC_{III} is 'advanced' isolation of those tendons, referring to Straus's (1941) observation in the series of primates. Straus described that the terminal tendons of EDC are intimately interconnected in the hand in most specimens of Tupaia, lemurs, Tarsius and both groups of monkeys, and sometimes also in gibbons, and that these connections are reduced to the so-called juncturae tendinum† in anthropoid apes and man. He also described that even these junctures were said to be entirely lacking in some examples of the anthropoids.

Connexus intertendineus of the human hand is considered to play a role in keeping the extensor tendons on the top of the knuckle of MP joints especially on making a tight fist, as explained below. The transverse arch of the human hand lengthens at the level of MP joints by making a tight fist because the 4th and 5th carpometacarpal joints (CM joint) flex and the knuckles of the ring and little fingers sink palmarward (Boileau Grant and Basmajian, 1965; Zancolli, 1979). This phenomenon also occurs on opposing the thumb to the little finger (Kapandji, 1970). Each tendon of EDC_{III} or EDC_{IV} consists of two slips in the human hand. So, connexus intertendineus connects EDC_{II} tendon with the radial slip of EDC_{III} tendon and, the ulnar slip of EDC_{III} tendon with the radial slip of EDC_{IV} tendon, leaving each cleavage between two slips of the individual tendons going to the middle or ring fingers not bound. The tension on the extensor tendons exerted by lengthening of the transverse arch of the hand is absorbed by widening each cleavage. Ulnarward pull of the extensor tendons transmitted through the connexus intertendineus is also restrained by the checkrein effects of the more fixed radial components of the extensor mechanism: the 2nd and 3rd CM and MP joints, and interosseous muscles, interosseous hoods, sagittal bands, collateral ligaments on the radial side of MP joints.

This functional role is the reason why connexus intertendineus is retained in the human hand. In the hand of our gorilla, there was not such a cleavage in each individual tendon going to the index through ring fingers, which consists of one slip.

The absence of connexus intertendineus in the gorilla suggests immobility of the 4th and 5th CM joints so that the transverse arch of the hand does not lengthen at the level of the MP joints on making a tight fist. Immobility of those joints might afford support to the ring and little fingers on pushing off the hand (Jones, 1946). Further study is needed to determine whether the 4th and 5th CM joints in the hand of the gorilla are mobile or not.

The ulnar antebrachial branch of the median nerve innervating the intrinsic muscles of the hand

The ulnar antebrachial branch of the median nerve (UABM) seen in our gorilla is the most significantly different anatomical structure from the human forearm (Fig. 6 proximal, distal). This branch conveys the motor fibers to all intrinsic muscles of the hand other than thenar muscles and radial two lumbricals innervated by motor branches from the main trunk of the median nerve (Fig. 7). In the human forearm, those motor fibers are conveyed through the ulnar nerve. We do not know whether the innervation of those intrinsic muscles through the median nerve seen in this specimen is the common pattern in the gorilla or not. “The ramus ulnaris of the nervus medianus” is described in the text and clearly shown in the plate 40 as “ramus anastomoticus n. medianus cum ulnaris” in Raven’s book (Gregory, 1950).

Martin-Gruber anastomosis connecting the median nerve with the ulnar nerve in the forearm is not so uncommon in the human. Gruber reported that the incidence of this anatomical variation was 17.9% in human cadavers (Leibovic and Hasting, 1992). Leibovic and Hasting (1992) analyzed the world literature of Martin-Gruber connections in the human forearm and classified them into four types. Type II is the connection sending motor branches from the median to the ulnar nerve that conveys motor fibers to “ulnar intrinsic muscles (interossei, ADP, FPB deep head, 3rd & 4th lumbricals and hypothenar muscles). UABM that conveys motor fibers to innervate ulnar intrinsic muscles, however, comes close to the ulnar nerve at the distal forearm but does not unite with it. In our gorilla, there are two thin connecting branches between the ulnar nerve and UABM in the proximal forearm. A very fine proximal branch connects the ulnar nerve with the radial bundle (motor fasciculi) of UABM and the other thicker distal one with its ulnar bundle (sensory fasciculi). Therefore, all ulnar intrinsic muscles are innervated by UABM although the very fine proximal branch coming from the ulnar nerve might take a part in innervating the intrinsic muscles. The motor branches coming from the main trunk of the median nerve innervate thenar muscles and two radial lumbricals. So, all intrinsic muscles of the hand of this gorilla are mainly innervated by the median nerve.

This innervation of all intrinsic muscles by the median nerve corresponds to the term “all median hand”, which Marinacci and von Hagen (1965) proposed. According to their report “the motor supply to the hypothenar-interosseous muscle group was travelling in the median nerve at the elbow and crossed to ulnar side to supply the muscles more usually innervated by the ulnar nerve” in a case of neurofibroma in the ulnar nerve above the elbow. In the human upper limb, there are other reports in which the intrinsic muscles are not paralyzed when the ulnar nerve is cut or anesthetized at the elbow or the proximal forearm (Mannerfelt, 1966; Okubo *et al.*, 1977). The explanation for this paradoxical phenomenon is that the motor fibers innervating those intrinsic muscles come through the median nerve in the arm and then the Martin-Gruber anastomosis in the forearm.

N.B.

Names marked with * correspond to P.N.A. (Paris Nomina Anatomica)

Names marked with † correspond to B.N.A. (Basel Nomina Anatomica)

¶: This part was submitted in a short message to American Society for Surgery of the Hand Perspectives, January 2020 edition.

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References

Anderson, J. E. 1983. Grant’s Atlas of Anatomy. 8th edition, Section 6. Fig. 6-1–124. Williams & Wilkins, Baltimore (no pagination in this book).

Aversi-Ferreira, T.A., R. Diogo, J. M. Potau, G. Bello, J. F. Pastor and M. A. Aziz 2010. Comparative anatomical study of the forearm extensor muscles of *Cebus libidinosus* (Rylands *et al.*, 2000; Primates, Cebidae), modern humans, and other primates, with comments on primate evolution, phylogeny, and manipulatory behavior. Anatomical Record 293: 2056–2070.

Boileau Grant, J. C. and J. V. Basmajian 1965. Grant's Method of Anatomy. 7th edition. pp. 75–196. Williams & Wilkins, Baltimore.

Bunnell, S. 1956. Bunnell's surgery of the hand. Fourth edition revised by Boyes, J. H. pp. 24–54 (Chapter 2. Phylogeny and comparative anatomy and embryology). J. B. Lippincott, Philadelphia, Toronto.

Chapman, H. C. 1878. On the structure of the gorilla. Proceedings of the Academy of Natural Science of Philadelphia. 30: 385–394. Available at https://www.jstor.org/stable/4060442 (Accessed 14 February 2020).

Diogo, R., B. G. Richmond and B. Wood 2012. Evolution and homologies of primate and modern human hand and forearm muscles: with notes on thumb movements and tool use. Journal of Human Evolution. 63: 64–78 (doi: 10.1016/j.jhevol.2012.04.001).

Diogo, R., J. M. Potau, J. F. Pastor, F. J. de Paz, E. M. Ferrero, G. Bello, M. Barbosa and B. A. Wood 2017. Photographic and Descriptive Musculoskeletal Atlas of Gorilla. pp. 34, 35, 45–46, 103. CRC Press, Boca Raton, London, New York.

Doyle, J. R. 1988. Anatomy of the flexor tendon sheath and pulley system. Journal of Hand Surgery 13A: 473–484.

Fahrer, M. 1981. Interdependent and independent actions of the fingers. In Tubiana R. (ed.): The Hand Vol. 1. pp.399–403. W.B. Saunders, Philadelphia, London, Toronto.

Feix, T., T. L. Kivell, E. Pouydebat and A. M. Dollar 2015. Estimating thumb–index finger precision grip and manipulation potential in extant and fossil primates. Journal of the Royal Society Interface 12: 2015.0176. Available at http://dx.doi.org/10.1098/rsif.2015.0176 (Accessed 22 February 2020).

Ghoshal, J. A., P. K. Sankaran, T. P. Manrya, V. Vishwakarma, R. Manivarshini and R. N. Malepati 2019. Bilateral agenesis of palmaris longus: A case report and its clinical significance. International Journal of Anatomy, Radiology and Surgery 8(2): AC01–AC02 (doi: 10.7860/IJARS/2019/40716:2469). Avialable at http://www.ijars.net/articles/PDF/2469/40716_CE%5bRa1%5d_F(SHU)_PF1(AG_SHU)_PFA(SHU)_PB(AG_SHU)_PN(SHU).pdf#search=%27Absence+of+palmaris+longs+muscle++palmar+aponeurosis%27 (Accessed 12 April 2020).

Gibbs, S., M. Collard and B. Wood 2000. Soft tissue characteristics in higher primates phylogenetics. Proceedings of the National Academy of Sciences of the United States of America 97(20): 11130–11132 (doi: 10.1073/pnas.190252697). Available at https://www.ncbi.nlm.nih.gov/pmc/articles/PMC27160/ (Accessed 28 February 2020).

Green, D. P. 1982. Operative Hand Surgery. pp. 1476–1479. Churchill Livingstone, New York.

Gregory, W. K. (ed.) 1950. The Anatomy of the Gorilla: The Henry Cushier Raven memorial volume. pp. 28–53, p. 134 (Plate 40). Columbia University Press, New York.

Haines, R. W. 1951. The extensor apparatus of the finger. Journal of Anatomy 85: 251–259.

Hayama, S. 1999. Birth of a human: Miracle species created by two-time revolutions of locomotion. pp. 51–81. PHP Institute, Tokyo (in Japanese).

Hepburn, D. 1892. The comparative anatomy of the muscles and nerves of the superior and inferior extremities of the anthropoid apes. Journal of Anatomy and Physiology 26: 149–186.

Hollinshead, W. H. 1969. Anatomy for Surgeons: Vol. 3 The Back and Limbs. 2nd edition. pp. 349–574. Harper & Row Publishers, New York.

Jones, F. W. 1946. The principles of anatomy as seen in the hand. pp. 60–73. Baillière, Tindall and Cox, London.

Kapandji, I.A. 1982. The Physiology of the Joints. 2nd edition. Vol. 1. Upper limb. pp. 178–179, 196–197, Churchill Livingstone, Edinburgh.

Kaplan, E. B. 1946. Notes on the upper extremity of the gorilla. American Journal of Physical Anthropology 4: 261.

Kaplan, E. B. 1965. Functional and Surgical Anatomy of the Hand. 2nd edition. pp. 68–71, 199–226. J.B. Lippincott, Philadelphia.

Kodera, H. 2010. Human body and the nervous system as acquired by human beings. Journal of Fossil Research 42: 216–221 (in Japanese).

Lampe, E. W. (Author) and F. H. Netter (Illustrator) 1951. Surgical Anatomy of the Hand: With special reference to infections and trauma. Ciba Clinical Symposia Vol. 3, No. 8. pp. 263–305. Ciba Pharmaceutical Products, Inc., Summit, New Jersey.

Lampe, E. W. (Translated into Japanese by Iwata, H. *et al.*) 1974. Surgical Anatomy of the Hand. Clinical Symposia Anthology: Musculo-Skeletal System. pp. 55–86. Ciba-Geigy, Takarazuka, Japan (in Japanese).

Landsmeer, J. M. F. 1949. The anatomy of the dorsal aponeurosis of the human finger and its functional significance. Anatomical Record 104: 31–44.

Landsmeer, J. M. F. 1955. Anatomical and functional investigations on the articulation of the human fingers. Acta Anatomica 25: Supplementum 24, pp.10–24.

Landsmeer, J. M. F. 1963. The coordination of the finger-joint motions. Journal of Bone and Joint Surgery 45A: 1654–1662.

Leavens, D. A. and W. D. Hopkins 1999. The whole-hand point: The structure and function of pointing from a comparative perspective. Journal of Comparative Psychology 113(4): 417–425. Available at https://www.

ncbi.nlm.nih.gov/pmc/articles/PMC2080771/ (Accessed 16 February 2020).

Leibovic, S. J. and H. II. Hasting 1992. Martin-Gruber revisited. Journal of Hand Surgery 17A: 47–53.

Mackey, S. L. and M. W. Cobb 1994. Knuckle pads. Cutis 54(3): 159–160.

Mannerfelt, L. 1966. Studies on the hand in ulnar nerve paralysis: A clinical-experimental investigation in normal and anomalous innervation. Acta Orthopaedica Scandinavica Supplementum No. 87, pp. 21–29.

Marinacci, A. A. and K. O. von Hagen 1965. Misleading "all median hand. " Archives of Neurology 12: 80–83.

McFarlane, R. M. 1985. The anatomy of Dupuytre's disease. In Hueston J.T. and R. Tubiana (eds.): Dupuytren's Disease. pp.55–72. Churchill Livingstone, Edinburgh, London, Melbourne, New York.

Milford, L. W. Jr. 1968. Retaining ligaments of the digits of the hand: Gross and microscopic anatomic study. pp. 21–27. W.B. Saunders, Philadelphia.

Ohman, J. C., M. Slanina, G. Baker and R. P. Mensforth 1995. Thumbs, tools, and early humans. Science 268: 587–589.

Okubo, K., Y. Itami, K. Murota, S. Morita and M. Kato 1977. Studies on an anastomosis between the median and ulnar nerve (Martin-Gruber anastomosis). Saigai-Igaku 20: 903–912 (in Japanese).

Patterson, F. 1978. Linguistic capabilities of a lowland gorilla. In Peng, F. C. C. (ed.): Sign Language and Language Acquisition in Man and Ape. New dimensions in comparative pedolinguistics. pp. 161–201. Westview Press, Boulder, CO. USA.

Reimann, A. F., E. H. Daseler, B. J. Anson and L. E. Beaton 1944. The palmaris longus muscle and tendon: A study of 1600 extremities. Anatomical Record 89: 495–505.

Saito, H. 2020. The nerve bundle via the median nerve innervating the intrinsic muscles of the hand in a gorilla. ASSH Perspectives, January 2020 edition. American Society for Surgery of the Hand. Available at http://asshperspectives.org/2020/01/the-nerve-bundle-via-the-median-nerve-innervating-the-intrinsic-muscles-of-the-hand-in-a-gorilla/ (Accessed 10 January 2020).

Shima, T. 2014. Why is the human thumb thick: Inquiring into the riddle of upright bipedal walking. 3rd edition. 277 pp. Chuokoron-Shinsha, Tokyo (in Japanese).

Shiono, H. and J. Azumi 1981. Simian line and Sydney line. Nipponijishinpo (Japan Medical Journal) No. 2998: 45–46 (in Japanese).

Spinner, M. 1972. Injuries to the Major Branches of Peripheral Nerves of the Forearm. p.106. W. B. Saunders, Philadelphia.

Straus, W. L. 1941. The phylogeny of the human forearm extensors. Human Biology 13: 23–50, 203–238.

Straus, W. L. 1942. Rudimentary digits in primates. The Quarterly Review of Biology 17: 228–43. Available at https://www.jstor.org/stable/2809086 (Accessed 21 March 2020)

Susman, R. L. 1994. Fossil evidence for early hominid tool use. Science 265: 1570–1573.

Tan, S. T. and P. J. Smith 1999. Anomalous extensor muscles of the hand: A review. Journal of Hand Surgery 24A: 449–455.

Tountas, C. R. and R. A. Bergman 1993. Anatomic variations of the upper extremity. pp. 129–130, 141–143. Churchill Livingstone, New York, Edinburgh, London, Melbourne, Tokyo.

Tubiana, R. and P. Valentin 1964. The anatomy of the extensor apparatus of the fingers. Surgical Clinics of North America 44: 897–906.

Tubiana, R. 1981. Architecture and functions of the hand. In Tubiana, R. (ed.): The Hand Vol. 1. pp.48–65. W. B. Saunders, Philadelphia, London, Toronto.

Tuttle, R. H. 1969. Quantitative and functional studies on hands of the anthropoidea I. The Hominoidea. Journal of Morphology 128: 309–363.

Ueba, Y. 1985. Hand: Its function and anatomy. Second edition. p. 123. Kinpodo, Kyoto (in Japanese).

van Mensvoort, M. 2002. Hand Lines; primate hand vs. human hand. Available at http://www.handresearch.com/diagnostics/palmar-creases-hand-lines-primatology.htm. (Accessed 16 December 2015).

Watanabe, M. 2008. Humans evolved too. In National Museum of Nature and Science, M. Watanabe and Yomiuri Shimbun Co. (eds.): The Exhibition of Charles Darwin (catalog raisonné), pp. 116–118. Yomiuri Shimbun Press, Tokyo (in Japanese).

Yamagiwa, J. 2005. Gorilla. 227 pp. Tokyo University Press, Tokyo (in Japanese).

Yamagiwa, J. 2012. NHK BS TV program (16 January). Wildlife: "Tropical rain forest in the central part of Africa; Unknown ties in a large family of gorilla".

Yoshida, Y. 1995. Anatomical study on the extensor pollicis et indicis accessories muscle and the extensor indicis radialis muscle in Japanese. Okajimas Folia Anatomica Japonica 71: 355–364.

Zancolli, E. 1979. Structural and dynamic bases of hand surgery. Second edition. pp. 12–37, 42–44, 325–338. J. B. Lippincott, Philadelphia.

Zihlman, A. L, R. K. McFarland and C. E. Underwood 2011. Functional anatomy and adaptation of male gorillas (*Gorilla gorilla gorilla*) with comparison to male orangutans (*Pongo pygmaeus*). Anatomical Record 294: 1842–1855 (https://doi.org/10.1002/ar.21449). Available at http://onlinelibrary.wiley.com/doi/10.1002/ar.21449/full (Accessed 30 August 2013).