Introduction

Primate hands have two main functions: locomotor/postural behavior and manipulation. Extant apes characteristically engage in forelimb-dominated orthograde arboreal locomotor behavior (Ward, 2007). In their suspensory behaviors, forelimbs must serve physically more demanding functions. Hook grips are predominantly used during suspensory behaviors in apes. Extant apes, except gorillas, have narrow and long hands compared to other primates (Schultz, 1956; Almécija et al., 2015). The pollical ray did not elongate, unlike rays 2–5 (ulnar rays) in orangutans and chimpanzees, resulting in a low pollical-to-ulnar ray length ratio (Almécija et al., 2015). The relative length of the fourth ray of the gorilla is comparable to that of modern humans, macaques, and some baboons when scaled on body mass, distinguishing gorillas from other extant apes (Almécija et al., 2015).

Hook grips greatly reduce the locomotor burden on the pollex and can produce potential for its functional reduction. Hylobatids are an exception to this in having a relatively long pollical digit and metacarpal (Straus, 1942; Almécija et al., 2015). Their pollical ray is separated from the second ray by a deep cleft that reaches the carpometacarpal joint level and can be tucked at the proximal palm so as not to hinder the hook grip (Straus, 1942). It seems probable that selective pressure is acting to maintain their long pollical ray for grasping during climbing and manipulation as it does not cost in brachiation. A functional decrease of the pollex is more evident in the muscular anatomy rather than its length (Straus, 1942; Tuttle, 1975). The tendon of flexor digitorum profundus (FPD) muscle to the pollical distal phalanx is often reduced or absent in extant great apes (Straus, 1942, 1949; Day and Napier, 1963; Tuttle, 1969a, 1975; Susman, 1998; Diogo et al., 2012: see figure 3 of Susman (1998) for various conditions in extant great apes). The FDP muscle has tendons linking to digits 1–5 in platyrrhines and cercopithec-
cids except some taxa that have a rudimentary pollex (Straus, 1942; Diogo et al., 2012). This muscle is the only extrinsic (= forearm) flexor of the pollex in these primates. However, loss of a functioning FDP tendon to the pollex enables muscular force to be allocated exclusively to the ulnar digits (Tuttle, 1969a). Release of the pollex from the concomitant flexion caused by the contraction of the FDP muscle might be adaptive for hook grips. In hylobatids and modern human, a muscle belly separate from the FDP muscle links via a tendon to the pollex, and is known as the flexor pollicis longus (FPL) muscle in human anatomy (although the separation of this muscle belly from the FDP muscle may be variable in hylobatids; see Payne (2001)). The pollical distal phalanges of the earliest hominids (= all members of the human lineage after the split from the Pan lineage), such as *Orrorin tugenensis* or *Ardipithecus ramidus*, bear evidence of the insertion of the long flexor tendon on their volar surface (Gommery and Senut, 2006; Lovejoy et al., 2009), showing the presence of a well-developed tendon of the extrinsic pollical flexor.

In a study on the evolution of manipulative ability in hominids, Susman (1994) claimed that the lack of a true FPL muscle in great apes correlated with the loss of sesamoid bones at the metacarpophalangeal joint of the pollex. Metacarpophalangeal joint sesamoids are small bones embedded in the volar plate (the fibrocartilaginous structure that stretches between the metacarpal head base and the base of the proximal phalanx distal to the joint) and articulate with the palmar surface of the metacarpal head (Calhoun, 1976; Le Minor, 1988: Figure 1, online supplementary item 1). In modern humans, a pair (radial and ulnar) of sesamoids form a groove through which the tendon of the flexor pollicis longus muscle passes. This groove contains the tendon and its fibrous sheath and is covered by an annular ligament (Goldberg and Nathan, 1987). This soft–hard tissue complex prevents subluxation and bowstringing of the FPL tendon that probably also functions like a pulley (Wood, 1984; Goldberg and Nathan, 1987). Thus, it is quite reasonable that Susman (1994) correlated the loss of sesamoids with the reduction/loss of the pollical FDP tendon. He noted that “these bones are generally lacking in the metacarpophalangeal joints of chimpanzees, gorillas, and orangutans” (p. 1572). However, this statement seems a little cursory because the loss of sesamoid bones from the pollical metacarpophalangeal joint of chimpanzees is not clear in the literature.

To date two studies have reported on the prevalence of pollical metacarpophalangeal joint sesamoids (hereinafter they are referred to as ‘pollical sesamoids’ for simplicity although the pollical interphalangeal joint may have a sesamoid) in extant apes (Calhoun, 1976; Le Minor, 1988: see Table 1). They reported consistent results regarding hylobatids (radial and ulnar sesamoids present 100%), and orangutans and gorillas (both sesamoids absent 100%). However, whereas Calhoun (1976) observed that both pollical sesamoids are missing in all his chimpanzee samples (n = 9), Le Minor (1988) observed that two out of three chimpanzee individuals had radial and ulnar sesamoids. This inconsistency, as well as the general paucity of observation of orangutans and gorillas, requires additional data for clarification. Thus, we newly examined 18 great ape cadavers and report on the result.

### Table 1. Prevalence of the pollical metacarpophalangeal joint sesamoid in extant apes

| Source            | Chimpanzee | Gorilla | Orangutan | Hylobatids | Note                                      |
|-------------------|------------|---------|-----------|------------|-------------------------------------------|
| Calhoun (1976)    | 0/9        | 0/3     | 0/2       | 6/6        | Dissection and X-ray photograph            |
| Le Minor (1988)   | 2/3        | —       | 0/2       | 7/7        | Skeletal observation (one chimp with radial and ulnar sesamoids, one with ulnar bone)    |
| This study        | 3/12       | 0/4     | 0/2       | —          | CT observation (two chimps with radial and ulnar sesamoids, one with ulnar bone)        |
| Total             | 20.8%      | 0%      | 0%        | 100%       | Chimps having radial and ulnar sesamoids: 12.5% (3/24)                                |

Hylobatids constantly have radial and ulnar sesamoids
Materials and Methods

Cadavers of 12 chimpanzees (central chimpanzee), four gorillas (western gorilla), and two orangutans (Bornean and Sumatran orangutans) at the Primate Research Institute, Kyoto University (Table 1) were scanned using medical computed tomography (CT) (Asterion, Toshiba Medical Systems). The scanning and reconstruction parameters were as follows: beam collimation, 1.0 mm; slice increment, 0.3 mm; image reconstruction kernel, FC03 ('bone filter'). Because some of the specimens have been partially dissected or formalin fixed with postures that limit CT scanning, we did not unify the side for investigation. As a result, we obtained volumetric data of 7 right hands and 11 left hands. The hard-tissue morphology was visualized as three-dimensional (3-D) surface using Amira version 5 (Thermo Fisher Scientific). Human pollical sesamoids complete ossification by 10–12 years in males and 11–15 years in females (Yammine, 2014). Thus, we did not include juveniles in which cartilaginous epiphyseal plates of forearm and hand long bone are observable (space exists between the epiphysis and the metaphysis after segmentation). Because a small sesamoid bone might be overlooked, we cautiously applied a relatively low threshold for the bone tissue segmentation even if parts of the heavily keratinized skin, nails, ligaments, and tendons were not erased totally.

Bony measurements were taken on 3-D solid models of hand skeletons reconstructed from CT data. The maximum diameter of the sesamoid was measured irrespective of its orientation in the coronal plane (e.g. radioulnarly or proximodistally). To assess whether a presence/absence of sesamoid(s) is associated with variation of pollex robusticity, the biarticular length and radioulnar breadth (at mid-length) of the pollical proximal phalanx were measured and shaft robusticity was evaluated.

Results

Table 1 summarizes the results of observation of the pollical sesamoid in living apes. As in previous studies, we did not observe any pollical sesamoid in orangutans (n = 2) and gorillas (n = 4). On the other hand, 3 out of 12 chimpanzee specimens had single or double pollical sesamoid(s) (Figure 2, online supplementary item 2). Two of them (PRI 9803 and PRI 10049) had ulnar and radial sesamoids and the rest only ulnar sesamoid. In one of these chimpanzees (PRI 9803), the ulnar and radial sesamoids were similar in size (maximum diameter = 4.0 mm); in the other (PRI 10049), the ulnar sesamoid was larger than the radial one (3.9 mm vs 3.0 mm). In the chimpanzee (PRI 8533) that had a single sesamoid on the ulnar side, its maximum diameter was 5.4 mm.

The morphology of the volar articular surface of the metacarpal head did not differ markedly between chimpanzees.

Figure 2. Three-dimensional renderings of the right hands of chimpanzee skeletons. Left hands are reversed for comparison. Only 3 out of 12 examined chimpanzees had single or double pollical sesamoid(s). PRI 10049 showed larger ulnar sesamoids and a smaller radial sesamoid. PRI 9803 displayed ulnar and radial sesamoids that are similar in size. PRI 8533 had only the ulnar sesamoid. (Inset A) Proximopalmar view of the pollical metacarpophalangeal joint of PRI 9803. A space between the sesamoids is narrow and shallow unlike the case in humans (see Figure 1). (Inset B) Close-up view of the pollical metacarpophalangeal joint of PRI 9803 after removing the sesamoids. (Inset C) An equivalent view of chimpanzee, which had no sesamoid. There is no feature in the distal articular surface of pollical metacarpal to infer the presence/absence of sesamoid bone. Proximal extension of the palmar articular surface on the radial side (Inset B) is variably observed among chimpanzees regardless of sesamoid bone. Three-dimensional solid models (STL format) of these hand skeletons are available as supplementary material (online supplementary item 2).
with double sesamoids and those with no sesamoid (Figure 2). Shaft robusticity was compared between pollicies with and without sesamoid(s) to explore whether there is any relation between the pollex robusticity and prevalence of the pollical sesamoid. The mean percent breadth was 26.6% (SD = 3.57%) in the non-sesamoid group. Values for specimens PRI 9803, PRI 10049, and PRI 8533 were 26.4%, 28.3%, and 27.0%, respectively. Apparently, the shaft robusticity does not correlate with the presence of sesamoid bone.

Discussion

Ancestral mammals had a pair of sesamoids on the radial and ulnar sides of the metacarpophalangeal joint in all rays (Le Minor, 1988). This pattern is rather conservative in non-hominoid primates. Le Minor (1988) investigated skeletons of over 30 genera of strepsirrhines, Tarsius, and monkeys (total sample = 249) and observed no variation. Although sample size for each genus was generally small (n = 1–3), some genera involved relatively many individuals: Nycticebus (n = 6), Callithrix (n = 6), Cercopithecus (n = 15), Cercopithicus (n = 30), Macaca (n = 30), Papio (n = 30). Hylobatids also retain two pollical sesamoids (100%, n = 14) (Calhoun, 1976; Le Minor, 1988). Modern humans consistently have two pollical sesamoids (>99.93%; Yammine, 2014). Among fossil apes, the pollical metacarpals of the 15 Ma old Nacholapithecus kerioi, a putative great ape (Kunimatsu et al., 2019), show two sesamoid grooves on its volar surface of the head (two of the two existing specimens; Nakatsukasa, unpublished data: see Figure 3).

We observed pollical metacarpophalangeal joint sesamoids in only 3 out of 12 chimpanzees (25%). This result differs from both of the two previous studies but is closer to Calhoun (1976) in supporting an outstanding tendency of pollical sesamoid loss in chimpanzees. Thus, a higher occurrence (67%) in Le Minor (1988), based on a limited observation (n = 3), should be regarded as a result of sampling bias. Summing up counts in three studies, 21% of chimpanzees (5/24) retained single or double pollical sesamoid(s). None of the gorilla (n = 7) or orangutan (n = 6) specimens studied to date have shown the presence of pollical sesamoids. Therefore, extant great apes show a remarkable trend of pollical sesamoid loss, endorsing Susman’s (1994) claim that the loss of the FDP tendon and pollical sesamoids in extant great apes are interrelated.

It is important to note that both the prevalence of a functioning FDP tendon to the pollex and the prevalence of pollical sesamoids are higher in chimpanzees than in gorillas and orangutans. Straus (1942) calculated frequencies of individuals that have no functioning tendon (absence or rudimentary) as 96% in orangutans (n = 27), 72% in gorillas (n = 16), and 52% in chimpanzees (n = 47). From the current and previous studies, the percentages of individuals retaining pollical sesamoid were 0% in orangutans, 0% in gorillas, and 21% in chimpanzees. If the last common ancestor of the extant great apes (hereinafter OLCA) had lost the pollical FDP tendon and pollical sesamoids, why do chimpanzees show such higher frequencies compared to orangutans and gorillas? These higher frequencies (of functioning tendon and sesamoids) in chimpanzees are probably not a coincidence. We are not able to answer whether these two traits occur independently or are associated in chimpanzees (i.e. sesamoids are developed with a higher frequency among chimpanzees that retain a functional FDP tendon). However, the much lower frequency of sesamoid formation relative to a functioning FDP tendon to the pollex (21% vs 48%; or 13% vs 48% if only double sesamoid cases are counted) suggests the functional importance of sesamoids as a tendon guide is negligible in chimpanzees. In fact, it is impossible to predict the absence or presence of the pollical sesamoids from the morphology of the metacarpal head (Figure 2) or pollical phalangeal robusticity in chimpanzees. Clearly, in chimpanzees the function of the sesamoid(s), if it exists, to prevent subluxation and bowstringing of the FPL tendon is greatly reduced.

Thus, we suggest that these structures were released from stabilizing selection in extant apes and that relatively higher frequencies in chimpanzees reflect a shorter time period since the split from the human lineage on the premise that the sesamoids/FPL tendon were lost in the lineages of three extinct great ape genera in parallel as further discussed below.

To explain the reduction of the pollical FDP tendon in the extant great apes, Diogo et al. (2012) hypothesized that reduction of this tendon occurred in three stages (Hypothesis 1) rather than a single reduction of the tendon in the OLCA and redevelopment of this tendon in the human lineage (Hypothesis 2). Although Hypothesis 1 is less parsimonious (three changes) than Hypothesis 2 (two changes), they regarded the first one as more likely because this tendon is highly variable in the extant great apes and the attachment site of the FPL tendon is identifiable in the pollical distal

![Figure 3. Right pollical metacarpal of Nacholapithecus kerioi (KNM-BG 48089) in volar and distal views. Although this specimen is dorsopalmarly squashed, two distinct sesamoid grooves are observed on the volar surface of the distal joint. R, radial; U, ulnar.](image-url)
phalanges of earliest hominids such as Orrorin tugenensis and Ardipithecus ramidus (Gomery and Senut, 2006; Lovejoy et al., 2009), a fact that would require a rapid reacquisition of the functional tendon of the pollical extrinsic flexor in the human lineage to maintain Hypothesis 2. Recently, van Leeuwen et al. (2018) reported that bonobos have a well-developed FDP tendon of the pollex as thick as that of other digits (unfortunately, we had no access to bonobo cadavers). Thus, to support Hypothesis 2, an additional character change (reversal) must be presumed in the bonobo lineage.

Hypothesis 2 requires that the FDP tendon to the pollex re-evolved in hominids to form the true FPL and that two pollical sesamoids re-evolved to form a guide for the FPL tendon in hominids. Reversals that violate Dollo’s law of irreversibility are recognized in primate myology (Diogo and Wood, 2012). The presence of two pollical sesamoids is highly consistent in extant humans (Yammine, 2014), which suggests strong genetic control over the formation of these bones. It may be possible that reuse of an ancestral developmental pathway helped the reversal of pollical sesamoids once a re-evolved FPL tendon induced adaptive value to have a robust tendon guide. However, if this is the case, those sequential (muscular then osteological) changes need to have occurred after the split of the Pan-human lineages prior to the emergence of Ardipithecus ramidus (>4.4 Ma), which has two pollical sesamoids (Lovejoy et al., 2009). A. ramidus relied on both arboreal and terrestrial environments and its hands had to play important locomotor roles in trees (Lovejoy et al., 2009; White et al., 2015). Thus, increased selective pressure for skillful manipulation (which causes redevelopment of the FPL tendon and its sesamoids) is doubtful in the stage of pre-A. ramidus hominids on the premise that OLCA hands were specialized for hook grips. Overall, current evidence favors loss (or reduction) of this tendon and concomitant loss of pollical sesamoids at least three times. This conclusion is consistent with the view that the human-like or gorilla-like hand proportion (relationship between the pollical and manual fourth ray lengths) is plesiomorphic for living hominoids and that orangutans and chimpanzees independently acquired an elongated hand (Almécija et al., 2015).

Although we think our conclusion is reasonably well supported, room for further clarification remains. Compared to the total sample of chimpanzees, that of gorillas and orangutans is much smaller. Their sample size should be augmented to confirm whether pollical sesamoids are completely missing or still appear at low frequencies. In addition, interspecific variation in each genus should be considered in the future. In fact, van Leeuwen et al. (2018) reported that bonobos, unlike chimpanzees, did not show a remarkable tendency of reduction of the FDP tendon of the pollex. Almécija et al. (2014) noted that the gorilla’s pollical distal phalanx (including western and eastern gorillas) is the most human-like among extant great apes in terms of proportions and the presence of anatomies, suggesting that a flexor tendon is inserting there (see their figure 2). Although it is not documented which species of gorilla Calhoun (1976) used ($n = 3$), ours are all western gorillas ($n = 4$). Since western gorillas are more arboreal than eastern gorillas (Remis, 1998), species-level analyses would be adequate for gorillas when possible. Unfortunately, congeneric interspecies variation of hand muscular anatomy is not well examined for Gorilla and Pongo. Such studies are awaited to corroborate the causal link between pollical sesamoid loss and reduction of FDP tendon of the pollex.

Finally, we note an enigma of the evolution of the gorillas’ hand. The pollical FDP–sesamoid complex of gorillas is derived like that of other great apes that are adapted for hook grips. However, the gorillas’ hand proportion is similar to that of humans (Almécija et al., 2015), and their proximal and middle phalanges of the ulnar digits are stout and lack longitudinal curvature (Susman, 1979). Gorillas (mountain gorillas) use their pollex for power grips in adducted or opposing ways during climbing (Neufuss et al., 2017). The gorillas’ pollical metacarpal head is significantly wider than that of chimpanzees and bonobos, partially overlapping with that of humans when standardized by pollical metacarpal length (Hamrick and Inouye, 1995), which may be related to this active involvement of the pollex in locomotor behavior. What, then, made it advantageous for gorillas to lose (or reduce) the commitment of a powerful extrinsic muscle to pollical flexion?

We speculate that the current manner of hand usage and present hand bony (metacarpals and phalanges) features of gorilla may not be a simple retention from the last common ancestor of extant African apes (GLCA). This is not a new idea. Tuttle (1967, 1969a, b, 1975) hypothesized that knuckle walking has originated as a solution for apes that had flexible and long-fingered hands to travel quadrupedally on the ground. Tuttle (1969a) wrote that: “Gorillas probably evolved from chimpanzee-like knuckle-walking troglodytians through advanced adaptation for terrestrial foraging and feeding” (p. 961), which implies that the gorillas’ lineages had a long hand which was adaptive for hook grip in its early evolutionary phase (it should be noted that we think that a long hand was acquired independently in each of the extant great ape genera). On this assumption, the derived tendon–sesamoid complex of the pollical extrinsic flexor in gorillas is explained as a past evolutionary scar. On the other hand, a recent study of evolutionary modeling of anthropoid hand proportions (Almécija et al., 2015) concluded that gorillas had experienced a comparatively small proportional change from the GLCA, namely a modest reduction of the pollical ray and a slight reduction of the fourth ray. This hypothesis, by extension, means that the hook grip was not the only selective regime for the reduction of the pollical extrinsic flexor in extant great apes. In this regard, it is important to decide whether bonobos have retained the primitive condition of the FDP muscle from the OLCA. Either way, this enigma is unanswered and requires further evidence for clarification.

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