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# Form, function and evolution of the human hand

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## Funding information

H2020 European Research Council,  
Grant/Award Number: 819960

## Abstract

The modern human hand is an intriguing mix of primitive morphology and derived function. Traditionally, its form and function are explained as a functional “trade-off” between the requirements of locomotion and manipulation, but recently acquired comparative, experimental and fossil evidence suggests that this functional trade-off is more complex than conventional wisdom suggests. Moreover, when studying hand evolution within the hominin clade, the only morphological evidence comes from the hard-tissues, and evidence about hand function must be inferred indirectly from the archaeological record. We lack information about critical aspects of hand form (e.g., soft tissues) and function (e.g., neurology) as well as non-lithic evidence about behavior. Thus, comparative anatomical, experimental and ethological studies of modern humans and other primates are critical to making more informed inferences about hand use in the past. We review the relevant fossil and archaeological evidence within the relevant comparative context (e.g., other extant apes and dexterous monkeys) in an attempt to reconstruct hand evolution within the hominin clade. We conclude by summarizing our current understanding—or lack thereof—of the evolutionary history of the modern human hand.

## KEYWORDS

African apes, dexterity, hominin, locomotion, tool use

*The morphology of the hand has been prominent for three centuries in debates on the relationship of [humans] to other primates. But there never has been an attempt to go beyond the selection of evidence favorable to particular theories to analyze the total morphological pattern and functions of primate hands with a view toward tracing the origin of the human hand.*

(Marzke, 1971, p. 61)

## 1 | INTRODUCTION

The capabilities of the modern human hand epitomize the distinctiveness of modern humans. Unlike other primates, modern humans only

rarely use their hands for locomotion. Instead, they use them for a range of tasks subsumed under the general heading of exploring and modifying the environment, and for communication. Jean-Baptiste Lamarck recognized a transition from a *quadrumanes* primate in the trees to a *bimanes* form that was “obliged to use their feet only in walking, and cease using their hands as feet.” (Lamarck, 1809, p. 326; see also Keith (1923)). In the *Descent of Man*, Charles Darwin also drew attention to the importance of the shift to an upright posture and a bipedal gait, writing that “the hands and arms could hardly have become perfect enough to have manufactured weapons, or to have hurled stones and spears with a true aim, as long as they were habitually used for locomotion and for supporting the whole weight of the body, or as long as they were especially well adapted, as previously remarked, for climbing trees” (Darwin, 1871, p. 141). When Raymond Dart introduced what was then

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called the Taungs child's skull to the world, he also emphasized the importance of the change in the role played by the hand. Dart was convinced the skull belonged to a “man-ape” with an upright posture, which meant the “hands were being freed from their more primitive function of accessory organs of locomotion” and “were assuming a higher evolutionary rôle not only as delicate tactual, examining organs which were adding copiously to the animal's knowledge of its physical environment, but also as instruments of the growing intelligence in carrying out more elaborate, purposeful, and skilled movements” (Dart, 1925, p. 197), suggesting the Taungs child and its ilk “handled objects with greater meaning and to fuller purpose than the corresponding organs in recent apes” (Dart, 1925, p. 198).

The modern human hand is distinctive and primitive. Bell's early comparative anatomical studies described it as “the consummation of all perfection as an instrument” (Bell, 1833, p. 209) whereas Wood Jones and others (e.g., Straus, 1942) summarized the structure of the modern human hand as “a very slight departure from the condition of the manus that we have every justification for believing is the most primitive form of vertebrate hand known to us” (Wood Jones, 1946, p. 36). For example, the retention of five separate digits in most primates is a form shared with the earliest mammals (e.g., Ji et al., 2002), making the underlying structure of the modern human hand primitive relative to many other mammals (e.g., cetaceans, chiropterans, artiodactyls and perissodactyls) (Wood Jones, 1916; Lewis, 1989). Napier (1956, 1980) echoed Wood Jones' view, with both researchers emphasizing that the hand's neurological connections, rather than its general form, are responsible for its remarkable manipulative abilities. While acknowledging its primitive *Bauplan*, Lewis suggested that “the [human] hand has its full quota of apomorphic features contained within its complex assembly of joints, which are finely attuned to its specialized role as a delicate manipulative organ” (Lewis, 1989, p. 89). This combination of primitive and derived features is also emphasized by researchers who focus on reconstructing the hand morphology of the most recent common ancestor (MRCA) of hominins and panins (e.g., Alba et al., 2003; Almécija et al., 2015; Prang et al., 2021; Rolian et al., 2010; and see below).

Of all the structures that make up the modern human hand, the bones are arguably less informative about function than are the soft-tissues. Think of the nerve endings that provide modern human fingertips with exquisite sensitivity, the muscles that act on the hand, and the tendons and ligaments that convert those movements into the manipulative ability that underpins the exceptional dexterity of modern humans. Paleoanthropologists are forced to view hand evolution primarily through the lens of the hard tissues, but to understand hand function researchers need to find creative ways to incorporate the morphology of the soft tissues that make the modern human hand functionally distinctive. It is also important to appreciate that modern human hand function depends on specializations in the regions of the central nervous system that monitor the environment through sensory receptors, or exert control over fine movements via the extrinsic and intrinsic muscles. But none of these soft-tissue features fossilize, so the external and internal morphology of hand bones, plus indirect evidence of hand function—such as durable artifacts—are currently the most reliable ways we can track the evolution of the hand in and around the hominin clade.

This review summarizes the form, function and evolution of the human hand within a comparative primate context. We start with how the hand is defined and what its components are. We then discuss the form of the modern human hand relative to other great apes and dexterous monkeys, including hard and soft tissues, intrinsic hand proportions, and the relevant neuroanatomy. Regarding hand function, we review hominoid hand use and its biological role, the basic biomechanics of the modern human hand and that of other apes, and our current understanding (or lack thereof) about the sensory and motor control of the hand. In the final section we review the evolution of the hominin hand and what is known about form and what can be inferred about function from both the fossil and archaeological records. We conclude with a summary of what we currently can, and cannot, know or infer about the form, function and evolution of the hominin hand.

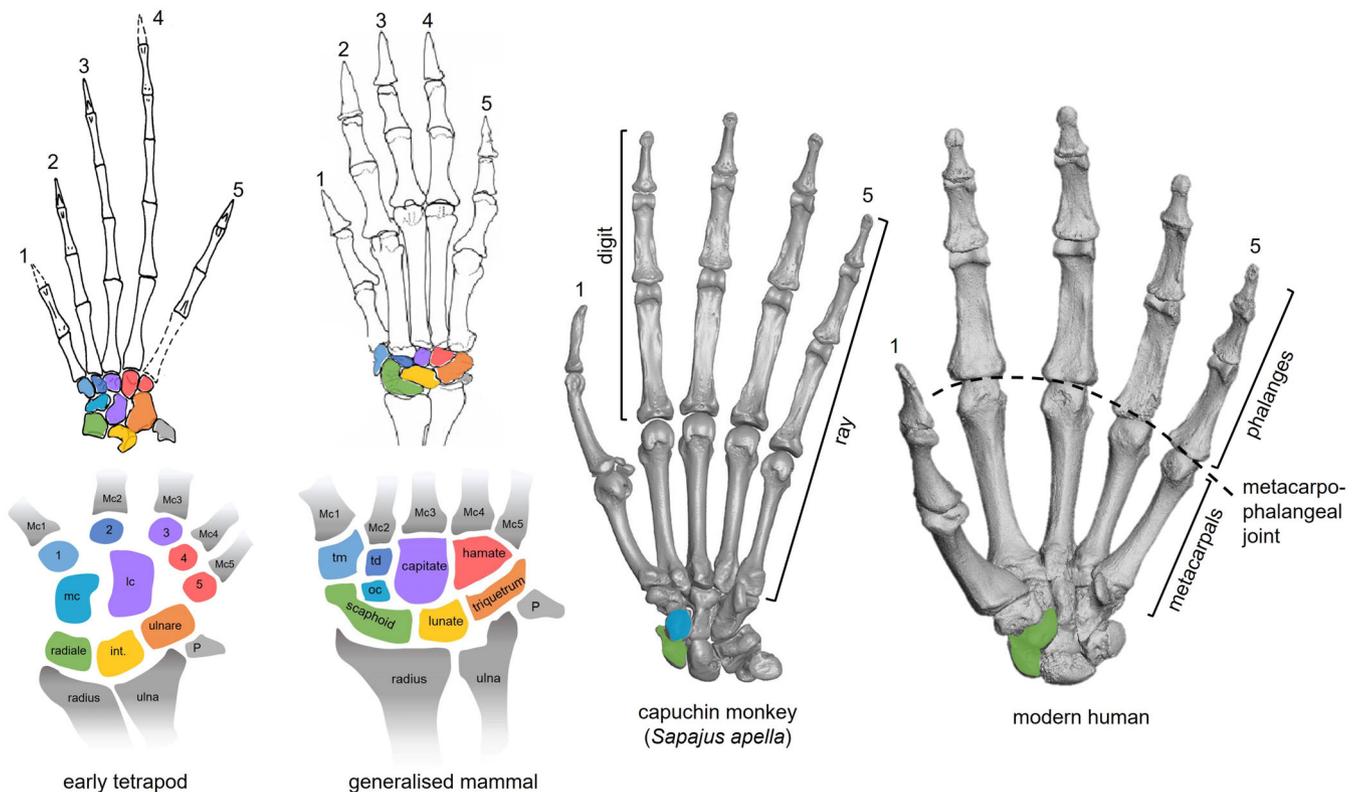
## 2 | PART 1: FORM

### 2.1 | Definition

The limbs of tetrapods consist of three linked segments: the proximal (i.e., closest to the point of attachment to the axial skeleton) segment is the stylopod, which is connected to the zeugopod, with the autopod (Gk *autos* = self and *pod* = foot) the most distal (i.e., furthest from the point of attachment to the axial skeleton) segment. The autopod can be further divided into the mesopod and acropod (Wagner & Chiu, 2001). This basic limb structure dates back to the origin of tetrapods at least 375 million years ago (Ahlberg, 1995; Ahlberg & Milner, 1994), with the earliest known autopod-like structure appearing in the pectoral fin of an elpistostegalian—a tetrapod-like fish—in the Upper Devonian (Cloutier et al., 2020). In the pectoral limb of primates, these three main segments are called, respectively, the upper arm, the forearm, and the hand.

What is it about the autopod of the pectoral limb of a primate that would lead us to refer to it as having two hands, instead of four feet? Humphry (1861) suggested that the determining factor is the nature of the first digit, writing that “when this digit stands apart from the others, and can be moved independently of them, we call the member a Hand” (Humphry, 1861, p. 109). Humphry (1861), however, also recognized that this definition does not work for primates with a grasping first digit on the foot, thus distinguishing “quadrumanus” nonhuman primates from “bimanus” modern humans. Others (e.g., Cloutier et al., 2020) use the term “hand” more inclusively for the autopods of the pectoral limbs of all tetrapods, regardless of the similarities or differences in overall structure and function across both sets of autopods (i.e., hands and feet).

The primate hand, which typically consists of the palm proximally and the five digits distally, begins at the skin crease at the base of the palm on the anterior aspect of the distal end of the forearm. The term “wrist” is not used in official anatomical terminology but informally it can refer to either the synovial joint between the forearm and the hand (i.e., radiocarpal joint or, in non-hominoid primates, antebrachiocarpal joint) or the radiocarpal joint plus the “carpus” comprising eight or nine carpal bones and their multiple articulations. The carpal bones, which are immediately distal to the radiocarpal joint, make up the most proximal part



**FIGURE 1** Comparison of the hand skeletons of an early tetrapod, a generalized mammal, a monkey and a modern human. The early tetrapod carpus included three proximal carpals [radiale, intermedium (int.) and ulnare], two centrale bones [medial (mc) and lateral (lc)] and five distal carpals, combined with five rays. The early tetrapod example (left, above) is that of early sauropsid *Paleothyris* from approximately 300 Ma (image adapted from Carroll (1969)). The generalized mammal carpus is arranged roughly into proximal [scaphoid, os centrale (oc), lunate, triquetrum and pisiform (P)] and distal [trapezium (tm), trapezoid (td), capitate and hamate] carpal rows. The generalized mammal example (second from left, above) is that of an extant shrew [*Cryptotis meridensis*, image adapted from Woodman and Morgan (2005)]. Most primates, including modern humans, retain a generalized mammalian wrist and hand skeleton, with examples of a capuchin monkey (image adapted from Boyer et al., 2013), which retains a separate scaphoid and os centrale, and a modern human, in which the os centrale is fused to the scaphoid. Carpal bones have been color-coded to represent *potential* homologies between the early tetrapod and generalized mammalian wrist (see Kümmel et al. (2020) for more details and alternative homologies)

of the palm. The digits are referred to colloquially as the thumb, or pollex, and, from radially (laterally) to ulnarly (medially), as the “index,” “middle,” “ring” and “little,” fingers. In this review we will refer to the thumb as either the pollex, or digit 1, and the fingers by their number, from digit 2 to digit 5. A “ray” is a digit plus the metacarpal with which it articulates.

## 2.2 | Hard tissues

In primates, the primitive condition for the endoskeleton of the proximal part of the pectoral autopod is nine carpal bones, which are typically described as forming two rows—a proximal and distal row each with four carpals, plus a centrale (Figure 1). In the living members of the African ape clade, as well as some lemurs, the centrale nearly always fuses with—and becomes incorporated into—the scaphoid (Jouffroy, 1975; Kivell & Begun, 2007; Mivart, 1867; Schultz, 1936). The fusion process seems to be the same in modern humans and the African apes, with the only difference being that fusion occurs earlier in ontogeny in modern humans than it does in *Pan* and *Gorilla* (Hita-Contreras et al., 2012; Kivell & Begun, 2007; Schultz, 1936).

Distal to the carpal bones, but still in the palm of the hand, are the five metacarpal bones, one each for the four fingers and the pollex (Figure 1). Multiple fibrous ligaments connecting the distal heads of metacarpals 2–4 prevent them from moving independently. The ulnar-most (ray 5) is linked to metacarpals 2–4 by a single ligament giving it more independence than the other metacarpals, but not as much as the pollex (ray 1). Distal to the metacarpals are the digits. The endoskeleton of the digits consists of the phalanges; two in the thumb (proximal and distal), and three in each of the four fingers (proximal, intermediate and distal). The only other bones of the hand are the sesamoids, small bones that develop entirely within their associated tendon (Standing, 2020). Pairs of sesamoid bones are variably present on the palmar aspect of the metacarpal heads. Although they can occur in all five rays in modern humans, they are only commonly found at the metacarpophalangeal and interphalangeal joints of the pollex and, less often, the fifth ray (Yamine, 2014). Sesamoids are usually absent in the first ray in gorillas, and they have been found in only 20% of the chimpanzee hands that have been investigated (Nakatsukasa et al., 2019).

All the joints between the bones in the hand are synovial. Joint mobility is determined and constrained by the shape of the articular

surfaces and the surrounding ligaments (Lewis, 1989). Joint motion consists mainly of rotation, with translation also occurring at joints with complex articular surfaces. Some joints—such as those between the phalanges—can only move along one axis (i.e., one degree of freedom). At the interphalangeal joints, the single transverse axis allows primarily for flexion and extension, with minimal rotation (Hess et al., 2013) that facilitates their ability to meet the tip of the thumb during the movement known as opposition. The metacarpophalangeal joints between the distal ends, or heads, of the metacarpals and the proximal ends of the proximal phalanges, are biaxial (i.e., two degrees of freedom) allowing movement in two axes (i.e., flexion/extension and abduction/adduction). Joint surfaces with even more complex shapes are polyaxial (i.e., three degrees of freedom). For example, the capitate head at the center of the midcarpal joint allows for flexion/extension, abduction/adduction and rotation.

### 2.3 | Soft tissues

Most of the soft-tissue volume of the modern human hand is made up of muscles and tendons; the only muscle bellies belong to the intrinsic muscles (i.e., short muscles whose attachments are within the hand). Extrinsic muscles whose muscle bellies are in the forearm (i.e., long muscles) reach the hand as tendons that either move the whole hand at the radiocarpal joint (e.g., flexion and adduction), the midcarpal joint (e.g., extension and abduction), or they act on one or more of the more distal synovial joints within the hand (Lewis, 1989). Both types of hand muscles perform different roles—prime mover, antagonist, fixator or synergist—depending on the movement being undertaken. Synergists are particularly important when muscles cross several joints, as is the case for the muscles that act on the distal interphalangeal joints. For example, if you want to play a quiet note on the piano with your extended index finger, digit 2, by flexing the metacarpophalangeal joint, the long and short flexors of that digit will act as prime movers, the long and short extensors will act as antagonists, and the flexors and extensors of the wrist will act as fixators. In addition, other muscles will act as synergists to prevent unwanted flexion at the interphalangeal and the radiocarpal joints.

The rest of the soft tissues in the hand consist of the skin and its appendages (e.g., nails), dense connective tissues (e.g., ligaments, the palmar fascia, and the “extensor hoods” that cover the dorsal aspect of the digits), looser connective tissues (e.g., fat pads in the palm and at the palmar surface at the tip of each digit), sensory nerves that transmit sensory information from receptors in the skin, muscles and joints, motor nerves that activate and control the activity of the intrinsic muscles of the hand, and last, but not least, the blood vessels that sustain all of these components.

Among extant hominoids, the relatively few differences in the extrinsic and intrinsic hand musculature are found primarily in the muscles of the pollex (Diogo et al., 2012; Jacofsky, 2009; Marzke et al., 1999). Modern humans, as well as hylobatids (Susman, 1998), are the only extant hominoids to consistently have a separate and functionally-independent pollical long flexor, called the flexor pollicis

longus (FPL). This distinct FPL muscle inserts at the distal pollical phalanx, facilitating the flexion of the interphalangeal joint that is critical to forceful opposition in modern humans (Hamrick et al., 1998; Marzke, 1997; Marzke et al., 1998). Bonobos have a well-developed tendon that splits off from the flexor digitorum profundus muscle belly, while in chimpanzees the long tendon to the pollical distal phalanx is vestigial or even absent (Tuttle, 1969; Van Leeuwen et al., 2018). In *Pan*, the shared muscle belly between the pollex and second ray limits the amount of independent movement of these digits compared with modern humans.

In addition to an independent FPL, the pollical musculature of modern humans differs from most other primates in having: (1) a separate extrinsic extensor pollicis brevis muscle (also found in hylobatids; Diogo et al., 2012); (2) a separate intrinsic deep head of the flexor pollicis brevis muscle, and (3) distinct fibers for a first palmar interosseous (sometimes referred to as “pollical palmar interosseous of Henle” [e.g., Susman et al., 1999] or *musculus adductor pollicis accessorius* [Bello-Hellegouarch et al., 2013]), which have likely become differentiated from the oblique adductor pollicis (Marzke et al., 1999; Susman et al., 1999).

These soft tissue differences, plus changes in joint morphology and orientation (Marzke et al., 1999; Tocheri, 2007; Tocheri et al., 2008), enable modern humans to use the pollex independently of the fingers as well as providing greater force and precision relative to other apes. Some of the intrinsic pollical muscles shared between modern humans and chimpanzees have different actions due to the more supinated position of the trapeziometacarpal joint in modern humans, which alters the course of the muscle tendons (Marzke et al., 1999). For example, the opponens pollicis muscle flexes and *abducts* the pollex in modern humans, whereas it flexes and *adducts* it in chimpanzees, and the adductor pollicis (both heads) *flexes* the pollex in modern humans, but in chimpanzees it (variably) *extends* it (Marzke et al., 1999; Tocheri et al., 2008). The enhanced power of the modern human pollex derives primarily from longer muscle moment arms rather than the greater physiological cross-sectional area (i.e., the muscle's capacity to generate force) of the thenar (i.e., pollical) musculature (Marzke et al., 1999; Ogihara et al., 2005).

The other main difference in intrinsic musculature between modern humans and the other African apes involves the muscles that lie between the metacarpal bones, most notably the distinct intermetacarpals and flexor brevis profundus muscles in *Pan* and *Gorilla* that in modern humans combine to form the dorsal interossei muscles (Diogo et al., 2012; van Leeuwen et al., 2018). The differences between the hand muscles of modern humans and other great apes translate into relative differences in the mass of muscles in the regions of the hand (Table 1). Modern humans have a relatively larger extrinsic and intrinsic muscle mass linked to the pollex, but a relatively smaller proportion of muscle mass in the palm, primarily due to a reduction in the size of the lumbricals and dorsal interossei compared with the apes (Tuttle, 1969). In contrast, non-human great apes have greater relative extrinsic flexor mass to the fingers (Tuttle, 1969). However, it is important to note the substantial inter-individual variation in forearm and hand musculature in apes, including modern humans (Diogo et al., 2012; Linburg & Comstock, 1979; van Leeuwen et al., 2018).

**TABLE 1** Relative mass of different muscles or muscle groups within the forearm and hand across hominoids

Muscle group	<i>Homo</i>	<i>Pan</i> <sup>a</sup>	<i>Gorilla</i>	<i>Pongo</i>	<i>Hylobatids</i>	Source
<b>Extrinsic muscles</b>						
Extrinsic extensors relative to total forearm musculature	35%	26%		28%	23%	Tuttle (1969)
Wrist extensors (ECRL, ECRB, ECU) relative to total forearm musculature	17%	12%		13%	9%	
Digital extensors to rays 2–5 relative to total forearm musculature	11%	9%		10%	8%	
Total extrinsic flexors relative to total extrinsic extensors	1.5× greater	2.3× greater		2× greater	2.8× greater	
Extrinsic flexors relative to total forearm musculature	51%	60%		56%	64%	
Wrist flexors (FCR, FCU, PL) relative to total forearm musculature	14%	16%		14%	14%	
Digital flexors (FDS, FDP, FPL) relative to total forearm musculature	37%	43%		42%	50%	
FDP relative to FDS	1.6× greater	1.4× greater		1.4× greater	1.1× greater	
<b>Intrinsic muscles</b>						
Thenar musculature relative to total intrinsic hand musculature	39%	24%		24%	33%	Tuttle (1969)
		23%	22%	28%	28%	Zihlman and Underwood (2019)
Adductor pollicis muscles relative to total intrinsic hand musculature	18%	11%		9%	11%	Tuttle (1969)
Adductor pollicis muscles relative to total thenar musculature	45%	45%		37%	34%	Tuttle (1969)
Hypothenar musculature relative to total intrinsic musculature	16%	16%		13%	11%	Tuttle (1969)
		14%	21%	13%	13%	Zihlman and Underwood (2019)
Palm musculature relative to total intrinsic hand musculature	45%	60%		63%	55%	Tuttle (1969)
		62%	57%	59%	59%	Zihlman and Underwood (2019)

Abbreviations: ECRB, m. extensor carpi radialis brevis; ECRL, m. extensor carpi radialis longus; ECU, m. extensor carpi ulnaris; FCR, m. flexor carpi radialis; FCU, m. flexor carpi ulnaris; FDP, m. flexor digitorum profundus; FDS, m. flexor digitorum superficialis; FPL, m. flexor pollicis longus; PL, m. palmaris longus.

<sup>a</sup>Note that Tuttle (1969) included both *Pan troglodytes* and “*Pan gorilla*” within his “*Pan*” category.

The extent to which the digits can move independently is partially determined by the extent to which the muscle bellies of the extrinsic flexors and extensors of the digits are independent. For example, in African apes and modern humans, the flexor digitorum profundus muscle belly (and consequently, the tendon) associated with the second digit is largely independent from the muscle belly of the third, fourth, and fifth digits. As a result, the second digit has a greater degree of independence, particularly at the proximal interphalangeal joint, compared with the more medial digits (Schieber, 1995; van Leeuwen et al., 2018). Other primates without separate muscle bellies to the digits produce movement of an individual digit by activating multiple muscles as antagonists or synergists to restrict the movements of other digits (Schieber, 1995).

## 2.4 | Hand proportions

Differences in the relative lengths of the five digits (i.e., intrinsic hand proportions) among primates are a major determinant of hand function. The impressive manipulative abilities of the modern

human hand are, in part, linked to a long thumb relative to the fingers, which facilitates bringing together the tips—and particularly the palmar pads—of the thumb and one or more digits in the movement known as opposition. The functional significance of modern human intrinsic hand proportions has been recognized for at least nearly two centuries (e.g., Bell, 1833), and arguably since da Vinci's anatomical drawings (Clayton & Philo, 2010) over 500 years ago.

Assessments of intrinsic hand proportions typically consider first ray length relative to length of the second or third ray, and first-second ray relationship is often the focus of clinical (e.g., McDonnell et al., 2006), ergonomic (e.g., Chen et al., 2020; Kuo et al., 2009), behavioral or experimental (e.g., Christel et al., 1998; Vigouroux et al., 2011) studies given the importance and frequency of precision pollex-index finger grasping in modern humans and other primates. In contrast, comparative morphological studies, including those of both extant and fossil primates, typically focus on first ray length relative to the third ray because the latter is a better proxy for overall hand length (e.g., Alba et al., 2003; Marzke, 1971; Schultz, 1930). Others, dictated by what elements are best preserved in the hominin

TABLE 2 Primate intrinsic hand proportions

Taxon	As % of total hand length <sup>a</sup>			As % of total ray 3 length <sup>b</sup>						
	Carpus	Metacarpus (ray 3)	Phalanges (ray 3)	%Mc3	%PP3	%IP3	Ray 1/Ray 2	Mc1/Mc2	Ray 1/Ray 3	Mc1/Mc3
Modern human	18% <sup>c</sup>	34% <sup>c</sup>	48% <sup>c</sup>	47%	32%	22%	67%	67%	62%	68%
<i>Pan</i>	14%	38%	48%	49%	30%	21%	46%	45%	42%	46%
<i>Gorilla</i>	17%	35%	48%	48%	31%	22%	48%	51%	47%	53%
<i>Pongo</i>	13%	37%	51%	45%	34%	22%	38%	45%	34%	44%
<i>Hylobates</i> sp.	11%	35%	54%	43%	33%	24%	44%	55%	44%	61%
<i>Symphalangus</i>	-	-	-	44%	36%	23%	-	-	42% <sup>b</sup>	59% <sup>b</sup>
<i>Cebus</i>	-	-	-	42%	34%	24%	64%	71%	60%	71%
<i>Macaca</i>	-	-	-	45%	32%	23%	53%	61%	46%	61%
<i>Papio</i>	-	-	-	52%	29%	19%	60%	66%	54%	64%

Note: Ray 1/Ray 2 and Ray 1/Ray 3 ratio includes total lengths of metacarpal, proximal, intermediate (ray 2 or 3 only) and distal phalanges of the respective ray. See Tables 9 and 10 and Figure 9 for additional data and comparisons.

Abbreviations: IP, intermediate phalanx; Mc, metacarpal; PP, proximal phalanx.

<sup>a</sup>Data from Zihlman and Underwood (2019).

<sup>b</sup>Data from Patel and Maiolino (2016).

<sup>c</sup>Data collected from a sample of adult, healthy modern human radiographs ( $n = 28$ ) from the Radiological Society of North America (RSNA) open-access database.

fossil record, use the length of the first ray relative to the fourth ray (Almécija et al., 2015).

The modern human first ray averages ~62%–66% of the length of the third ray (Patel & Maiolino, 2016; Schultz, 1930; Table 2), making it substantially longer, on a relative basis, than that of other hominoids (*Gorilla* is the closest at 46% [Patel and Maiolino (2016)]) and more similar to the relative pollex length of monkey species known to be especially dexterous (e.g., *Cebus* at 60% or *Papio* at 54%). The same relative pattern is true for the length of the first ray to the second ray in modern humans relative to other hominoids and monkeys (Table 2).

## 2.5 | Neuroanatomy

Among the many factors contributing to the exceptional functional capabilities of the modern human hand is its innervation. We begin this survey of the somatic innervation of the modern human hand by considering the structures concerned with its various sensory modalities, and then consider the structures involved with controlling motor activity. Both of these topics have been intensively investigated in modern humans, but there is much less information about the innervation of the hands of non-human primates. For those wanting a more detailed review of these topics, Verendeev et al. (2016) provides an excellent starting point.

### 2.5.1 | Sensation

The hand in general, and the digit pads in particular, are densely populated with receptors that can sense touch, temperature,

vibration and pain. Although there are several types of tactile mechanoreceptors in the skin of the modern human hand, the majority in the palm and on the digit pads are tactile corpuscles (eponymously called Meissner's corpuscles) (Purves et al., 2008). These receptors, which are particularly responsive to shear stress on the skin, are thought to play an important role in ensuring the hand maintains a grip on an object. The cell bodies of the neurons that innervate the skin of the hand are in the posterior root ganglia of the last two cervical and the first thoracic spinal nerves (i.e., C7, C8 and T1 [Strandberg, 2020]). The tactile information travels up the central processes of these neurons in the spinal cord, where it relays first in the medulla oblongata and then in the thalamus before reaching the primary somatosensory region (S1) of the opposite side, which is situated in the postcentral gyrus of the cerebral cortex. The other sensory modalities take a slightly different route through the central nervous system, but they make the same number of relays as the tactile information. The hand represents approximately 1% of the total body surface area (Sheridan et al., 1995) yet, along with the tongue and the lips and the rest of the face, the palmar aspect of the hand—and the pollex in particular—occupies a disproportionately large percentage of the surface area of the primary somatosensory cortex, resulting in a grossly distorted sensory homunculus (Catani, 2017; Penfield & Boldrey, 1937).

There are sensory inputs from parts of the hand other than the skin. Mechanically-sensitive neurons called proprioceptors located within muscles, tendons, and synovial joint capsules provide information about position sense. Precise proprioception is particularly important for the fine motor control of the digits, and other circuits involving intrafusal fibers help generate and monitor tone within the extrinsic and intrinsic muscles of the hand.

## 2.5.2 | Motor control

The motor pathways controlling the extrinsic and intrinsic muscles of the hand are made up of two neurons (i.e., they are mono-synaptic). The cell bodies of the upper motor neurons are in the primary motor area (M1) within the precentral gyrus of the cerebral cortex. The motor homunculus features the same distorted inverted representation of the body as the sensory homunculus, with the number of upper motor neurons devoted to supplying the intrinsic muscles of the hand disproportionate to the volume of those muscles (Catani, 2017; Penfield & Boldrey, 1937). Each upper motor neuron synapses with a lower motor neuron in the spinal cord at the same levels (i.e., C7, C8 and T1) as the dorsal root ganglia involved with the sensory innervation of the hand. Each lower motor neuron innervates multiple muscle fibers within a single muscle, but the fibers innervated by a single lower motor neuron are not necessarily contiguous. The lower motor neuron and the muscle fibers it innervates are referred to as a motor unit. The number of fibers innervated by a single lower motor neuron varies from muscle to muscle. In general, the larger the muscle the larger the size of the motor unit, so that in the large limb muscles (e.g., gluteus maximus) and the extensor muscles of the back a single neuron may innervate several hundred muscle fibers. In much smaller muscles involved in precise movements, such as the muscles that move the eyeball, the muscles that control the vocal cords and the intrinsic muscles of the hand, a single lower motor neuron may innervate ~10 muscle fibers, providing for much finer motor control.

## 2.5.3 | Comparative context

Working out what aspects of the innervation of the hand summarized above are peculiar to modern humans and what are shared with non-human primates is a challenge. The evidence for cortical representation of the modern human hand resulted from developments in anesthesia that allowed surgeons to stimulate the surface of the cerebral cortex in patients undergoing neurosurgery. Today, ethical considerations thankfully prevent the types of invasive experimental research that could throw light on cortical representation of the hand in apes, but such experiments were conducted in the past in the laboratory of Sir Charles Sherrington while he was at The University of Liverpool in the UK. The brains of anesthetized apes were exposed, and groups of neurons accessible on the surface of the cerebral cortex were either stimulated or ablated. The first brief publication (Grünbaum & Sherrington, 1902), which reported the results of experiments conducted on 10 apes, included an illustration of the motor homunculus of a chimpanzee; the results of experiments conducted on five additional chimpanzees and one orangutan were reported soon after (Grünbaum & Sherrington, 1904). Additional experiments were conducted subsequently, and a final comprehensive report summarized the results of experiments conducted on “twenty-two chimpanzees, three gorillas and three orang-utan” (Leyton & Sherrington, 1917, p. 136), with observations being made at a maximum of nearly 400 locations on the motor cortex. It is difficult to make

an accurate comparison of the relative size of the area of the motor cortex devoted to the hand in modern humans and in chimpanzees, but a subjective impression suggests it is relatively larger in modern humans than in the chimpanzees investigated by Sherrington and his collaborators.

## 3 | PART 2: FUNCTION

### 3.1 | Hand function

We make a distinction between hand movements and hand use. Hand movements refer to the various ways anatomical components or features are combined to generate a motion sequence that allows an individual to explore, or apply force to, external objects (e.g., a precision grip). Hand use refers to the behaviors (e.g., feeding, grooming, stone tool manufacture) that one—or more—hand movements make possible. The combined degrees of freedom at the shoulder, elbow and radiocarpal joints allow the hands of the members of the African ape clade to move anywhere within—literally—arms reach. The main differences in how modern humans and African apes use their hands involve the movements that take place within the hand.

The first section of Bock and von Wahlert (1965) presents a useful framework for thinking about how form can be related to function in a complex structure like the hand. In their scheme, each component or feature—be it a bone, muscle or ligament—has a form and a basic function, which, in combination, is that structure's faculty. Several features (e.g., the pollical carpometacarpal joint and the intrinsic and extrinsic muscles acting on the pollex) are combined into a functional complex, and that functional complex can have an emergent function, or biological role, which is more than a combination of the individual functions of its components. For example, within the pollex, abduction, flexion and conjunct rotation at the carpometacarpal joint, plus flexion and some rotation at the metacarpophalangeal joint, and flexion at the interphalangeal joint combine to produce opposition, which together with movements at the target digit, result in the emergent function of enabling a pad-to-pad precision grip.

Napier (1956) outlines the two main ways the hand can be used (see also Jones and Lederman (2006)). Non-prehensile hand use involves using individual digits—or the whole hand—to move an object. Prehensile hand use involves grasping an object with more than one digit, or between one or more digits and the palm. For example, sliding a piece of paper across a table with the palmar pad of one finger would be considered non-prehensile hand use, whereas opposing the palmar pads of digits 1 and 2 to lift the corner of the piece of paper off the table would be considered prehensile hand use.

If you rest your hand on a table, with the palm facing up, you will notice a difference in the orientation of the fingers and the pollex. The palmar pads of digits 2–5 face upwards, whereas the pollical palmar pad faces sideways. When you flex the fingers, the fingertips touch the palm, but when you flex the pollex it moves across the base of the digits without making contact with the palm. The approximate 90° difference in the orientation of the fingers and the pollex, plus the

ability to abduct, flex and rotate the pollex, allows the pollical palmar pad to touch any of the palmar pads at the ends of the fingers. The extant African apes have muscles that can abduct-adduct and flex-extend the pollex to facilitate precision grasping but short pollical length relative to the length of the fingers, the shape and orientation of the carpometacarpal joint, and differences in musculature, preclude forceful pad-to-pad opposition. However, during food processing and organic tool manufacture, wild chimpanzees have been observed infrequently using seemingly high-force (e.g., pulling against resistance by the teeth) pad-to-side grips (Marzke et al., 2015). Opposability in the modern human hand refers to the ability to flex and abduct, with conjunct pronation, the pollex toward one or more of the fingers (Napier, 1961; Marzke et al., 2010; Tocheri, 2007). However, it is important to distinguish this particular compound movement from the more inclusive notion of an “opposable thumb” that characterizes extant hominoids and most cercopithecoids (see Lemelin and Schmitt (2016) for further discussion).

A long pollex relative to the fingers enhances opposability (Bardo et al., 2018; Feix et al., 2015; Hu et al., 2018; Marzke, 1971; Napier, 1961). Kinematic modeling shows that primates with relatively shorter thumbs—such as *Pongo* and *Pan*—have a smaller “manipulation workspace” than that of modern humans, particularly when grasping small objects (Feix et al., 2015; Hu et al., 2018). However, kinematic modeling also shows that the majority of nonhuman primates share a similar manipulation workspace despite substantial differences in intrinsic hand proportions in taxa such as *Pongo*, *Papio* and *Loris* (Feix et al., 2015). Thus, it is not intrinsic hand proportions alone, nor a high range of mobility in the pollex, but the combination of both factors that provide a kinematic “balance” to facilitate the enhanced precision manipulation capacity of the modern human hand (Feix et al., 2015). Indeed, modern human hand proportions are not “optimal” in terms of the potential manipulative workspace, suggesting that precision dexterity was not the only functional selective pressure acting on hominin hand proportions (Hu et al., 2018; also see Rolian et al. (2010)).

The rest of this section will focus primarily on prehensile hand use, but it is important to bear in mind non-prehensile hand use when considering how modern humans and nonhuman primates interact with their environments. Moreover, although most research has focused on locomotor and manipulative food processing or tool-use in apes—and this will be our focus below as well—apes also use their hands for grooming (Fragaszy & Crast, 2016; McGrew et al., 2001), to carry objects between locations (Carvalho et al., 2012; Prime & Ford, 2016), and for communication (Hobaiter & Byrne, 2014; Pika et al., 2003).

### 3.2 | Prehensile hand use

The Merriam-Webster dictionary defines grip as “to seize or hold firmly” (Merriam-Webster.com 2022). There have been several grip classifications. One of the earliest was by Schlesinger (1919), who divided modern human grips into six types: cylindrical, tip, hook, palmar, spherical, and lateral. Griffiths' (1943) ontogenetic-based scheme recognized two grips; the initial cylinder/grasp reflex grip used by

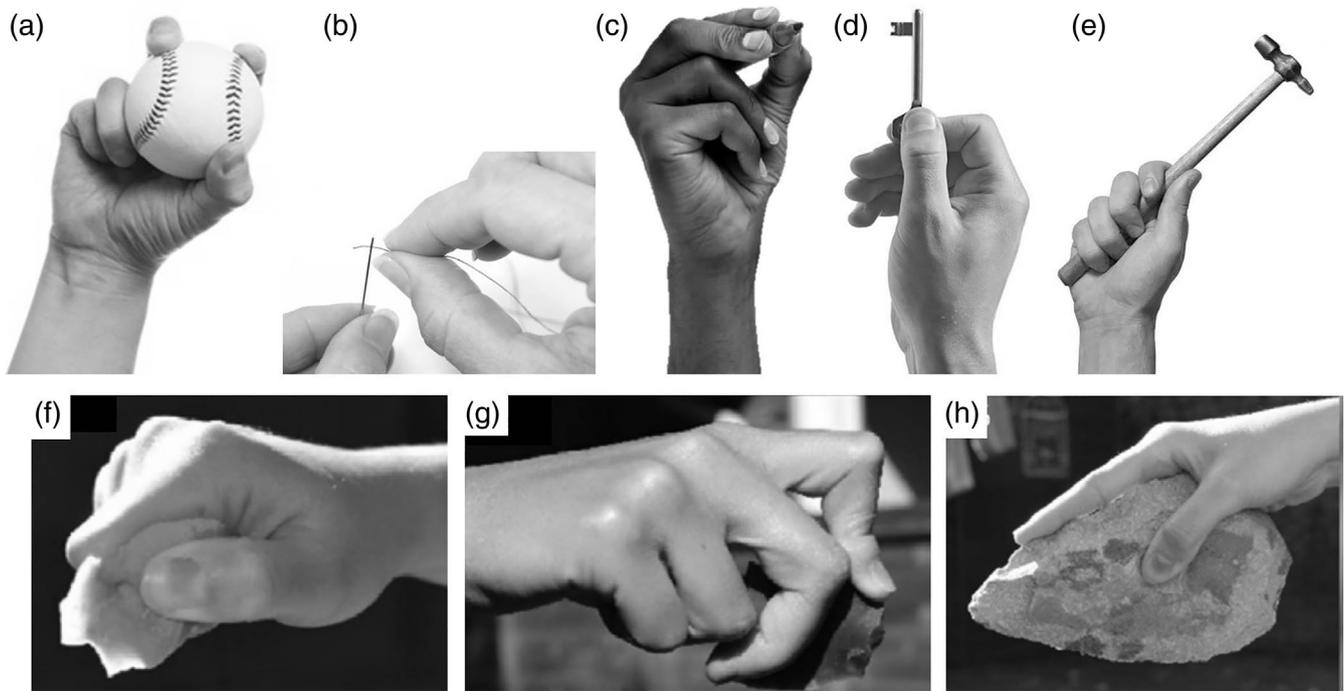
infants, which later in ontogeny transforms into the ball-grip reflex grip by the conscious recruitment of the thumb.

The classification suggested by Napier (1956) divides prehensile hand function into two main categories of grip—power and precision—plus hook and scissor grips. Napier's (1956) scheme, and adaptations of it (e.g., Marzke, 1997; Marzke et al., 1992; Marzke et al., 2009), formed the foundation of hand use and grip studies within biological anthropology, including studies of living primates (e.g., Bardo et al., 2017; Byrne et al., 2001; Christel & Fragaszy, 2000) and modern human stone tool use (e.g., Key et al., 2018; Marzke & Wullstein, 1996). In power grips the object is held between the pollex and fingers against the palm, whereas in precision grips the object is secured between one or more the palmar pads of the fingers and the opposed pollex. Elements of power and precision grips can be combined. In the hook grip, an object is manipulated with the flexed digits 2–5 only, with digit 1 remaining passive; in a scissor grip it is held between the sides of adjacent fingers. Others have added subcategories of power and precision grips based on the number and positioning of the digits involved, passive use of the palm, or the size and shape of the object being grasped, both in modern humans and other apes (e.g., Bardo et al., 2017; Key et al., 2018; Marzke, 1997; Marzke et al., 1992; Marzke et al., 2015; Neufuss et al., 2019).

Modern humans and other primates are not necessarily unique in their prehensile grasping abilities. Prehensile grasping, including either or both power and precision grasping, is common across many mammalian and non-mammalian clades and it likely originated in the earliest tetrapods (Fragaszy & Crast, 2016; Iwaniuk & Whishaw, 2000). For example, animals as distantly related as the marsupial woolly opossum (*Caluromys*) (Lemelin, 1999) and some tree frogs (e.g., *Phyllomedusa*, *Chiromantis* [Manzano et al., 2019]) have opposable digits and extrinsic extensor and flexor muscles acting on the digits. These enhanced grasping abilities are often (but not always) associated with living in an arboreal environment (Lemelin, 1999; Manzano et al., 2019; Sustaita et al., 2013).

#### 3.2.1 | Modern humans

Healthy modern humans use a variety of different prehensile grips during activities of daily living (e.g., cleaning, cooking, personal care), but a few grips are dominant (at least in WEIRD [Western, educated, industrialized, rich and democratic] populations, which provide most study samples; see also Clancy and Davis (2019)). This research—which ranges across clinical, ergonomic and robotics disciplines—varies greatly in its grip categorizations and level of detail, but the most frequent grips used by healthy adults during daily household activities are: pinch grips between the pad of the pollex and pads of one or more finger (i.e., two- to five-jaw pad-to-pad grips; Figure 2a), or between the pad of the pollex and the radial side of the index finger (Figure 2d); grasping between the pollex and palm with an extended digit 2; power grips involving all digits and the palm with the pollex opposed to the fingers; and power “squeeze” grips in which the object is held diagonally across the palm and pollex is positioned



**FIGURE 2** Common hand grips used by modern humans. (a) Three-jaw full-finger pad-to-pad grip; (b) two-jaw pad-to-pad precision grip; (c) tripod precision grip; (d) two-jaw pad-to-side precision grip; (e) power “squeeze” grip. During modern human stone tool use, the most common grips are (f) two-jaw chuck pad-to-side of entire digit 2; (g) three-jaw chuck pad-to-side with digit 2 used in forceful opposition to the cutting edge; (h) five-jaw buttressed pad-to-pad, including all five digits and an active palm (latter three images adapted from Key et al. (2018))

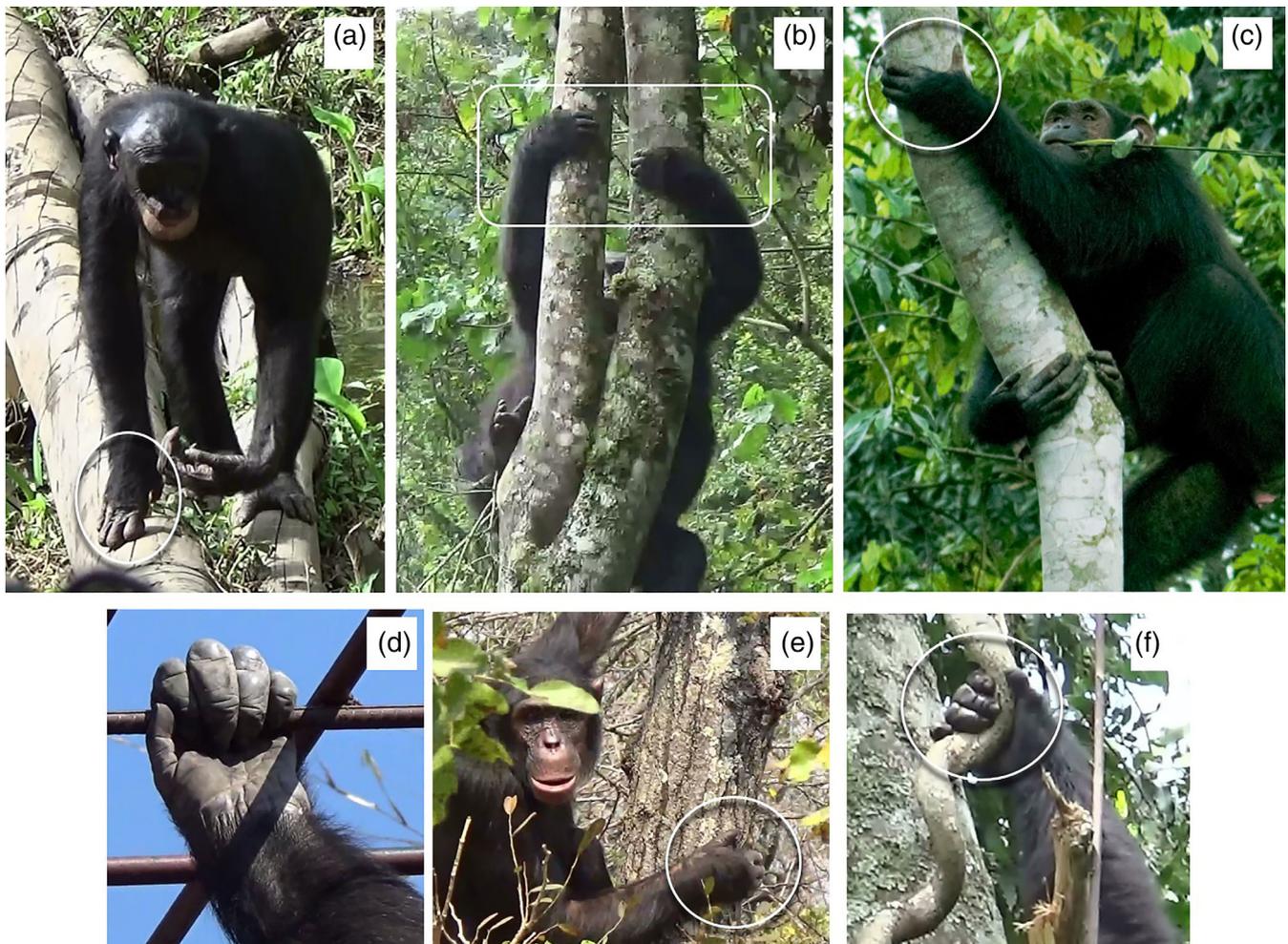
obliquely (Figure 2e) (Dollar, 2014; Kilbreath & Heard, 2005; Marzke et al., 1992; Vergara et al., 2014; Zheng et al., 2011). The most frequent grips used by modern pastoralists (the Dassanach in Kenya) during butchering with stone flakes and cores are either gripping the flake between pad of the pollex and the radial side of digit 3, with the pad of digit 2 on top of the tool (i.e., three-jaw chuck pad-to-side; Figure 2g), or gripping the core between the pad of the pollex, the sides of the digits 3–5 and the palm, with an extended digit 2 along the top of the tool (i.e., buttressed five-jaw chuck with active palm; Figure 2h) (Key et al., 2018).

### 3.2.2 | Gorillas

Gorillas (both western and eastern) use their hands for terrestrial and arboreal locomotion (Figure 3). Terrestrial knuckle-walking makes up approximately >90% of locomotor activity in mountain gorillas while western gorillas are thought to be more arboreal (Doran, 1996, 1997; Masi, 2004; Remis, 1994, 1995, 1998; Schaller, 1963; Tuttle & Watts, 1985). However, detailed locomotor frequency studies are limited to only one community of western lowland gorillas (Bai Hokou, Central African Republic; Remis, 1994, 1995, 1998; see also a preliminary study by Masi (2004)) and three groups of mountain gorillas (Parc National des Volcans, Rwanda; Doran, 1996, 1997; Tuttle & Watts, 1985), making general statements about differences in degree of

arboreality tenuous, especially in light of variation in landscape and ecology. When zoo-housed gorillas knuckle-walk, their similar-length ulnar rays typically are aligned in a palm-back posture and the intermediate phalanges of digits 2–5 contact the substrate (Inouye, 1992, 1994; Matarazzo, 2013). However, in the wild, mountain gorillas use a range of hand postures during terrestrial locomotion, including loading the dorsum of the proximal phalanges and the dorsal and palmar aspects of the hand (Thompson et al., 2018). Mountain gorillas also engage in vertical climbing on arboreal substrates of varying sizes (Doran, 1996; Neufuss, Robbins, et al., 2017), typically using power grips, with an adducted pollex, on large-sized supports (c. >11 cm diameter) (Figure 3b), and diagonal power grips, with the pollex opposed to the fingers, on medium-sized supports (c. 6–10 cm diameter) (Neufuss, Robbins, et al., 2017).

The way gorillas use their hands for the limited tool use that has been observed in the wild (Breuer et al., 2005; Grueter et al., 2013; Kinani & Zimmerman, 2015; Masi et al., 2022) differs from the way chimpanzees use their hands to modify and use tools. Gorillas use larger sticks than chimpanzees, holding them using a power grip, with the pollex either adducted or opposed to the other digits (see figures in Breuer et al. (2005) and Grueter et al. (2013)). Zoo-based experimental studies shed light on gorilla dexterity (Bardo et al., 2017; Pouydebat et al., 2005). For example, during the manufacture and use of tools for extractive foraging, gorillas used both power grips and precision grips between the phalanges of



**FIGURE 3** Hand postures and grips during African ape locomotion. (a) Knuckle-walking hand posture—the most common locomotor behavior in all African apes—in a bonobo; (b) mountain gorilla using power grip with pollex adducted to digit 2 while climbing; (c) chimpanzee using diagonal power grip with pollex opposed to fingers, common on medium-sized substrates; (d) chimpanzee using hook grip; (e) chimpanzee using power grip with pollex abducted from digit 2, common on large- and extra large-sized substrates; (f) mountain gorilla using power grip while climbing a liana. For more information, see Neufuss, Robbins, et al. (2017); Neufuss et al. (2019). All photos taken by Johanna Neufuss

digits 2–5 to manipulate tools small enough to fit into 1 cm-diameter holes (see Figure 1 in Pouydebat et al. (2005)). When gorillas performed a maze task to extract food with a tool, they always used unimanual (as opposed to bimanual) grips, most often holding the stick between their fingers without using the pollex (Bardo et al., 2017).

Gorillas in the wild have been observed using precision, power, and hook grips for feeding and food processing (Byrne et al., 2001; Neufuss et al., 2019; Figure 4). The most common precision grips used during feeding include approximating the tips of the digits, or a tip to the side of a digit, or the sides of two digits (Byrne et al., 2001). The tip-to-tip grip was observed occasionally in the Virunga gorilla population during food processing (Byrne et al., 2001), whereas in the Bwindi gorilla population the two-jaw chuck pad-to-side grip was the most frequently used (Neufuss et al., 2019; Figure 4a). When power grips are used during thistle processing the thumb is adducted (Byrne et al., 2001).

### 3.2.3 | Chimpanzees

Knuckle-walking is the predominant form of locomotion for chimpanzees (Doran, 1993, 1996; Hunt, 1991; Sarringhaus et al., 2014). Chimpanzee rays 2–5 differ in length more than those of gorillas (Inouye, 1992) and zoo-based studies show they typically use a “rolling” palm-in hand posture in which ray 5 touches down first, followed by the fourth, third and second rays (Matarazzo, 2013; Wunderlich & Jungers, 2009). Recent studies have quantified the 2D kinematics of chimpanzee (as well as bonobo and gorilla) knuckle-walking hand postures in zoo-based studies, highlighting a limited range of wrist extension throughout the stance phase (Finestone et al., 2018; Pontzer et al., 2014). Thompson (2020) quantified for the first time the 3D kinematics of wrist, palm and fingers during adult chimpanzee knuckle walking. He showed that two adult chimpanzees used a palm-in hand posture with high ulnar deviation of the wrist, both at touch-down and during the stance phase (see also Jenkins and Fleagle (1975)), and



**FIGURE 4** Hand grips during manipulative activities in African apes. Food processing in mountain gorilla showing (a) a power pad-to-side grip, in which food is held within the palm with the pollex adducted to the radial side of digit 2; (b) a interdigital 2–3 grip in which food is held between the intermediate phalanges of digits 2 and 3; (c) a transverse hook grip, in which food is only held within the fingers; (d) a palm grip used to counter pulling of food with the teeth. Manipulation in chimpanzees showing (e) pad-to-side precision grip; (f) a scissor grip between sides of digits 2 and 3; (g) three-jaw chuck grip using the full palmar surface of the fingers (right hand); (h) tip-to-tip precision grip used during grooming (all photos taken by Johanna Neufuss)

a much higher degree of metacarpophalangeal joint extension ( $26^{\circ}$ – $59^{\circ}$ ) than is typically depicted in schematics of knuckle-walking postures (e.g., Kivell & Schmitt, 2009; their Figure 3). Importantly, this research has highlighted greater similarities between gorilla and chimpanzee knuckle-walking hand kinematics than previously hypothesized (cf. Kivell & Schmitt, 2009) as well as notable intraspecific variation, making clear that the dichotomy of “palm-in” (chimpanzees) vs. “palm-back” (gorillas) hand postures is an oversimplification (Finestone et al., 2018; Thompson, 2020).

Chimpanzees spend between 33% and 68% of their locomotor time in trees, with habitat and sex both influencing the frequency of arboreal behaviors (Crompton et al., 2010; Doran, 1996; Hunt, 1991). Vertical-climbing chimpanzees, like gorillas, have been observed using diagonal power grips, often with the pollex opposed to the fingers, on medium-sized (c. 6–10 cm in diameter) supports (Figure 3c), and power grips, typically with an abducted pollex, on extra large supports (>50 cm diameter) (Neufuss, Robbins, et al., 2017; Figure 3e).

Regarding manipulation during tool use, chimpanzees have received the most attention, beginning with Darwin in *The Descent of Man* (1871, p. 81): “It has often been said that no animal uses any tool; but the chimpanzee in a state of nature cracks a native fruit, somewhat like a walnut, with a stone.” Zoo-based experiments offer

detailed information on the grips commonly used by chimpanzees during particular types of tool use or when manipulating objects of different sizes (e.g., Foucart et al., 2005; Hopkins et al., 2002; Hopkins et al., 2005; Pouydebat et al., 2005; Tbnooka & Matsuzawa, 1995), including how grips change throughout ontogeny (Crast et al., 2009; Jones-Engel & Bard, 1996; Pouydebat et al., 2011). The most common precision grips observed among chimpanzees are those in which the tip of the pollex is opposed to either the tip, or the radial side, of digit 2 (Jones-Engel & Bard, 1996; Pouydebat et al., 2011). These grips are frequently used when manipulating a small object like a grape, whereas power grips involving the palm are common when manipulating a larger object like an apple (Pouydebat et al., 2011). Experimental studies also demonstrate that captive chimpanzees are capable of in-hand manipulative movements (i.e., “precision handling”) in which an object is moved within one hand via manipulation of the digits (Crast et al., 2009), an ability previously considered to be unique to modern humans (Marzke, 1997).

Studies of wild habituated chimpanzees have focused on feeding and tool manufacture and use (Boesch & Boesch, 1993; Dominy et al., 2016; Lesnik et al., 2015; Marzke et al., 2015). When Tai forest chimpanzees nut-crack, they use one hand, both hands, or one or more hands and a foot, to hold wooden or stone hammers.

The grips used are related to the size and weight of hammer (Boesch & Boesch, 1993). For example, when using smaller hammers (i.e., 300–600 g), they use six different variations of power grips involving the palm and varied number of digits, yet when they manipulate nuts they mostly do so by holding them between the tip of the pollex and the tip of digit 2 (Boesch & Boesch, 1993; Figure 4h). During food processing, the most common grips used by the Mahale chimpanzees are the two-jaw chuck pad-to-side (Figure 4e), which was used for all plant food types, and an extended transverse hook grip, which was used to remove meat from a carcass (Figure 4c) (Marzke et al., 2015). Mahale chimpanzees also used novel grips not previously observed in captivity, including full-pollical grips (e.g., the V-pocket grip between the full pollex and second ray) and the use of an opposed pollex during an extended transverse hook grip (Marzke et al., 2015). The opposed pollex, which likely offers greater force to resist pulling by the teeth or the other hand, was also observed in gorillas (Byrne, 1994) and in giant pandas, though the latter uses an extended sesamoid for this grip rather than its pollex (Endo et al., 1999). Mahale chimpanzees also occasionally use a precision two-jaw chuck pad-to-side grip with seemingly high force when grasping slender objects that are too small to use strong hook grips (Marzke et al., 2015). Previously, forceful precision grips traditionally have been considered unique to modern humans (Marzke et al., 2015).

### 3.2.4 | Bonobos

Bonobos, which are traditionally considered to be more arboreal than chimpanzees, use more palmigrade hand postures in arboreal settings, but the frequency of arboreality is likely biased by the degree of bonobo habituation (Doran, 1993; Susman et al., 1980). A recent study of bonobo positional behavior shows that bonobos are most similar to chimpanzees from west Africa (*P. t. verus*) (Ramos, 2014) in terms of how much time they spend on the ground. An experimental study of zoo-housed bonobos showed that during arboreal knuckle-walking the third and fourth digits touched down first, with the fifth digit rarely making contact with the substrate (Samuel et al., 2018). This pattern differs from the “rolling” touch down of digits 5 through 2 documented in captive chimpanzees (Matarazzo, 2013; Wunderlich & Jungers, 2009). During suspension and vertical climbing, the whole hand, including the pollex, was in contact with the support, but pressures incurred by the pollex were most often too low to register on the pressure mat (Samuel et al., 2018). Although it remains unclear how bonobo hand grips and pressure vary on supports of different diameters, these results suggest that the pollex may be functionally less important during locomotion than during manipulation (Marzke et al., 2015; Samuel et al., 2018).

Compared with chimpanzees, bonobos use tools in the wild far less and typically not for foraging (Hohmann & Fruth, 2003; Samuni et al., 2021). However, studies in zoo-settings and sanctuaries suggest that bonobos are capable of a similar level of dexterity as chimpanzees (Bardo et al., 2016; Neufuss, Humle, et al., 2017; Toth et al., 1993). Like chimpanzees, zoo-housed bonobos most commonly

use a two-jaw chuck pad-to-side grip (Figure 4e) and V-pocket grips, but they are also capable of one-handed in-hand movements (Bardo et al., 2016). During feeding, the power and precision grip manipulative repertoire of zoo-housed bonobos is similar to that seen in chimpanzees, with the pad-to-side of digit 2 and a power grip with the pollex being two of the most common grips used (Gérard et al., 2022). Sanctuary bonobos are as efficient at nut-cracking with stone hammers as wild Bossou chimpanzees, and when the former cracked nuts they used a variety of precision and power grips to manipulate the hammers, some of which have not been described previously in other apes (Neufuss, Humle, et al., 2017; Figure 5a,b). There are no studies focusing on how bonobos use their hands during food processing.

### 3.2.5 | Orangutans

Orangutans spend the majority of their time in the trees (Manduell et al., 2011; Thorpe & Crompton, 2006), using their hands to engage in a range of locomotor and postural behaviors, including suspension, above- and below-branch quadrupedalism, hand-assisted bipedalism, and vertical climbing (Thorpe & Crompton, 2006). Napier (1960) emphasized the “double-locked” grip used by orangutans when grasping small-diameter supports. In this grip, the combination of long proximal phalanx length and high flexion ability of the digits 2–5, allows orangutans to “lock” their distal phalanx against the metacarpal head (see also Rose (1988)), but in a preliminary study of hand (and foot) postures in wild orangutans the double-locked grip was rarely used (McClure et al., 2012). Despite the conventional wisdom that the orangutan pollex is too short to be used effectively during arboreal grasping (Alexander, 1994; Sarmiento, 1988), the same preliminary study found that during locomotion orangutans use grips involving the pollex five times more frequently than finger-only grips (McClure et al., 2012). A comprehensive analysis of hand postures during locomotor or manipulative activities in wild orangutans has yet to be conducted, likely in part due to limited visibility in the tree canopy (Thorpe & Crompton, 2006). When orangutans travel terrestrially in zoo environments, they typically use palmigrade and fist-walking hand postures (Sarmiento, 1988; Tuttle, 1967), although one obese captive orangutan has been observed engaging in “facultative” knuckle-walking (Susman, 1974; Tuttle & Beck, 1972).

Though not as common as in chimpanzees, tool manufacture and use has been observed in wild orangutans (van Schaik et al., 1996). Zoo-based studies confirm observations made in the wild that suggest orangutans make more use of their mouth and foot to reposition food, and they use power grips more frequently than African apes and modern humans (Bardo et al., 2017, 2018).

### 3.2.6 | Hylobatids

Compared with the other hominoids, hand use in gibbons and siamangs has received less attention (Cunningham et al., 2006; Prime & Ford, 2016; van Horn, 1972). The elongated digits 2–5 are thought to



**FIGURE 5** Hand grips used during tool use in primates. (a) Power grip used to hold a large hammerstone during nut-cracking, here in a sanctuary-living bonobo but power grips involving the palm and 2–5 digits are also most common in wild nut-cracking chimpanzees using both wood or stone hammers (Boesch & Boesch, 1993) (photo credit: Johanna Neufuss); (b) precision grip with active palm, in which small hammerstone is held between distal tip of the adducted pollex and palmar aspect of digit 2 and is supported by the distal region of the palm, a novel grip seen in sanctuary-living bonobos (photo credit: Johanna Neufuss); (c) pad-to-side of digit 2 grip used during termite fishing in wild chimpanzees (photo credit: Alex Piel, GMERC); (d) power grips used to hold large hammerstone in capuchin (*Sapajus libidinosus*) during nut-cracking (adapted from Frigaszy et al., 2013); (e) precision grip with passive palm use by *Macaca fascicularis* to hold an axe hammer, in which the pollex appears to press tool firmly against ulnar fingers with extended digit 2 on top of the tool (image adapted from Gumert et al., 2009); (f) precision grip used by *M. fascicularis* with the pollex opposed to fingers in a three-jaw chuck (image adapted from Gumert et al., 2009)

facilitate brachiation, with the pollex playing a minimal role during locomotion (Pocock, 1925; Sarmiento, 1988; Straus, 1942). Although the pollex is relatively long, its more proximal placement within the hylobatid hand creates a cleft separating the pollex from the other digits (Lorenz, 1971; Straus, 1942; Tuttle, 1969; Table 2). This morphology, combined with the high degree of mobility from its unique ball-and-socket first carpometacarpal joint, allows for such a large degree of abduction that the palmar surface of the pollex is able to fully oppose the palmar surface of the index finger (Lewis, 1989; van Horn, 1972). During vertical climbing, hylobatids grasp the substrate with the pollex widely opposed to the fingers (Prime & Ford, 2016; Straus, 1942; van Horn, 1972), while during brachiation, the pollex is either adducted to the radial side of the hand or, surprisingly, positioned onto the dorsum of the hand (van Horn, 1972).

The manipulative abilities of hylobatids have only been studied in zoo environments (Christel, 1993; Lorenz, 1971; Prime & Ford, 2016). When manipulating different-sized food items, gibbons most often use their fingers and pollex together, rather than fingers alone, with the most common grip holding the food item between the pollex and the palm and digit 2 (Prime & Ford, 2016). Because of the deep cleft between the pollex and the ulnar rays, by using their long fingers and

highly opposable pollex, gibbons are able to grip much larger objects than the average modern human hand can grasp (Prime & Ford, 2016).

### 3.2.7 | Dexterous macaques, baboons and capuchin monkeys

This review focuses on hominoids, but the intrinsic hand proportions of modern human hands are more similar to those of many extant monkeys than they are to apes (Table 2). Furthermore, several genera within both cercopithecines and platyrrhines use organic and stone tools in their natural environments (e.g., Chiang, 1967; Ottoni & Izar, 2008; Tan et al., 2015). Thus, dextrous palmigrade or digitigrade monkeys, including baboons, macaques and capuchin monkeys, are relevant and valuable comparators.

Tool use has been observed in wild long-tailed macaques (*Macaca fascicularis*) (Gumert et al., 2009; Luncz et al., 2017; Tan et al., 2015), capuchin monkeys (*Sapajus*) (Ottoni & Izar, 2008; Westergaard & Suomi, 1997) and baboons (*Papio*) (van Lawick-Goodall et al., 1973; Oyen, 1979). Long-tailed macaques typically use power grips when using pounding hammers to crush shellfish or nuts on anvils, as do

chimpanzees and capuchins (Gumert et al., 2009) (Figure 5e). When using small axe hammers to perform tasks that require greater precision (e.g., picking or chipping at an oyster attached to a rock using the point of the tool), they use precision grips between the palmar surfaces of their pollex and digits without active use of the palm (Gumert et al., 2009; Tan et al., 2015) (Figure 5f). Gelada baboons (*Theropithecus gelada*) and Japanese macaques (*Macaca mulatta*) have been reported to use pad-to-pad precision grips during food processing and grooming (Maier, 1993; Tanaka, 1998).

Capuchin monkeys (*Sapajus apella* and *Sapajus libidinosus*)—along with other platyrrhines and strepsirrhines—are often described as having a “pseudo-opposable” pollex (Costello & Fragaszy, 1988; Fragaszy & Crast, 2016; Jouffroy & Lessertisseur, 1979; Napier, 1961; Ziemer, 1978) in contrast to the fully “opposable” thumb of catarrhines. A pseudo-opposable thumb has a trapeziometacarpal joint that is hinge-like, rather than saddle-shaped, which inhibits the flexion, abduction and conjunct rotation of the pollex needed to make pad-to-pad contact with the fingers (Napier, 1961). However, capuchins, as well as many other platyrrhines and strepsirrhines (Boyer et al., 2013; Etter, 1974; Rafferty, 1990; Rose, 1992) have a saddle-shaped trapeziometacarpal joint, which may be the basal condition for all primates (Lemelin & Schmitt, 2016; Lewis, 1977; Rafferty, 1990). Capuchins are capable of several precision grips, including pad-to-side grips between the pollex and digit 2, during daily activities (Costello & Fragaszy, 1988; Westergaard & Suomi, 1997). During nut-cracking, capuchins typically use power grips involving 3–5 digits depending on the size of the hammer stone (Costello & Fragaszy, 1988; Westergaard & Suomi, 1997; Figure 5d) and also inadvertently produce Oldowan-like stone flakes (Falótico, Proffitt, Ottoni, Staff, & Haslam, 2019; Proffitt et al., 2016).

Much of what we know (or assume) about non-human ape and monkey hand use is based on zoo-based studies of a limited number of individuals (e.g.,  $n = 2$  in Wunderlich & Jungers; Thompson, 2020) and species (e.g. only *G. g. gorilla*), and the majority of these studies have focused on tool-use or small-object manipulation (e.g., Bardo et al., 2016; Christel et al., 1998; Pouydebat et al., 2005). Far fewer have studied hand use during locomotion (e.g., Matarazzo, 2013; Samuel et al., 2018; Thompson, 2020; Wunderlich & Jungers, 2009). Among non-human apes, hand use in natural environments—be it sanctuaries or habituated wild groups—is limited to only a few communities, and yet has revealed far greater diversity in locomotor hand use than zoo-based studies have documented (e.g., Byrne et al., 2001; Marzke et al., 2015; Neufuss, Humle, et al., 2017). Moving forward, studies of hand use across multiple manual behaviors (i.e., locomotor, postural and a variety of manipulative activities) in natural environments should be a priority.

### 3.3 | Biomechanics of the hominoid hand

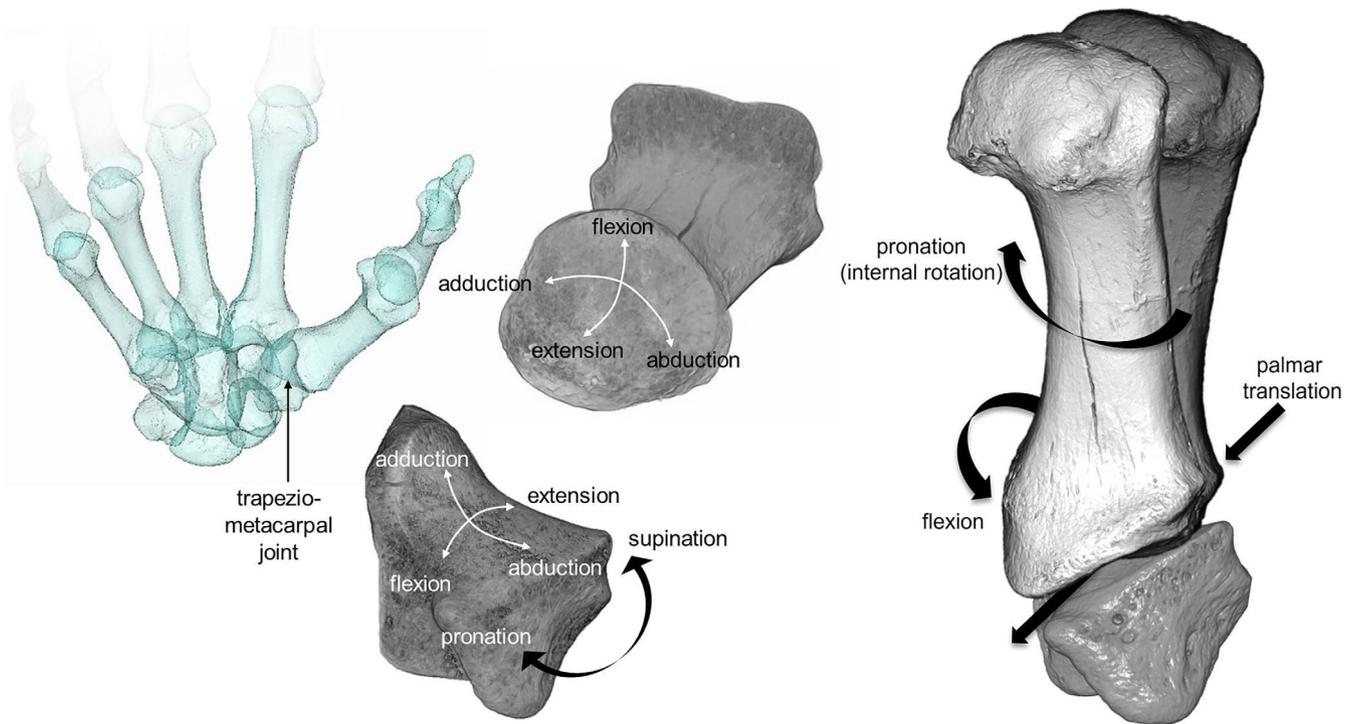
Understanding how hominoids perform the manual activities and grips described above is a challenge. The biomechanics of the modern human hand have been well-studied, including several books on the

topic (e.g., Chao, 1989; Schuind et al., 2013). Kinematics and loading of joints within the digits that have one or two degrees of freedom (the interphalangeal and metacarpophalangeal joints, respectively) are straightforward compared to the intercarpal and carpometacarpal joints, but the former are more complex than one might expect. For example, due to the asymmetrical shape of the metacarpal head, the center of rotation at the metacarpophalangeal joint shifts as the finger flexes, which, in turn, alters the direction and distribution of loads incurred at the joint (Ishii et al., 2020; Pagowski & Piekarski, 1977).

The biomechanics of the pollex have received particular attention due to its importance in modern human hand function and the complexity of the trapeziometacarpal joint (e.g., Cooney & Chao, 1977; D'Agostino et al., 2017; Kawanishi et al., 2018). A seminal study by Cooney and Chao (1977) using human cadavers and 3D modeling quantified the static external and internal (muscle tendon) forces acting on the thumb during different pinch grips (e.g., pad-to-pad and pad-to-side of digit 2) and a power grip. They showed that during a pinch grip, 1 kg (~10 N) of force incurred at the thumb tip resulted in 12 kg (~117 N) of force at the trapeziometacarpal joint, and force at the latter could be as high 120 kg (~1180 N) during power grasping (Cooney & Chao, 1977).

The complementary concavoconvex articular surfaces of the trapezium and Mc1 create two axes of rotation (i.e., two degrees of freedom): flexion-extension axis of the trapezium's dorsopalmar curvature and abduction-adduction axis of the Mc1's radioulnar curvature (Crisco et al., 2015; D'Agostino et al., 2017; Hollister et al., 1992; Kuczynski, 1974; Marzke et al., 2010). However, because these axes are not orthogonal to each other, movement at the joint necessitates rotation and translation of the Mc1 on the trapezium (Hollister et al., 1992; Marzke et al., 2010). Thus, as the pollex moves from extension to flexion, the Mc1 rotates internally (i.e., pronates); conversely, as the pollex moves from abduction to adduction, the Mc1 rotates externally (i.e., supinates) (Crisco et al., 2015) (Figure 6). Because this rotation is coupled with, or determined by, the two axes of this joint, it is called “conjunct rotation.” When the pollex is opposed to digit 2, the Mc1 is abducted and flexed (with conjunct pronation) in a “screw-home” mechanism (D'Agostino et al., 2017; Edmunds, 2011; Kawanishi et al., 2018). In the screw-home mechanism, the palmar portion of the Mc1 base rotates and translates into the most palmar portion of the trapezium recess, causing tension on the dorsal ligament complex and creating stability at the joint during forceful precision or power grasping (D'Agostino et al., 2017; Edmunds, 2011; Kawanishi et al., 2018; Figure 6).

Kinematic studies of ape trapeziometacarpal joints are limited (van Leeuwen et al., 2019; van Leeuwen et al., 2021; van Leeuwen et al., 2022). Bonobos have a similar range of motion at the trapeziometacarpal joint as modern humans, with the latter having a notably larger range of Mc1 extension (van Leeuwen et al., 2019). The dorso-palmar radius of curvature on the trapezium is similar in bonobos and modern humans, so the more limited extension in bonobos is likely due to its more well-developed palmar ligaments (van Leeuwen et al., 2019).



**FIGURE 6** Kinematics of the modern human trapeziometacarpal joint in the pollex. Left, showing transparent model of a modern human hand, highlighting the trapeziometacarpal joint. Middle (below), showing distopalmar view of the trapezium, highlighting the concavoconvex Mc1 facet and direction of motions facilitated by this facet shape. Middle (above), showing distal view of Mc1 with the complementary concavoconvex trapezium facet. Right, schematic of “screw-home” mechanism during opposition of the pollex to digit 2 in which the non-orthogonal axes of flexion-extension and abduction-adduction mean that as the pollex flexes at the trapeziometacarpal joint, the Mc1 pronates (via conjunct rotation) and palmarly translates on the trapezium’s articular surface (see text for details)

The modern human carpus is traditionally considered to be distinct in its out-of-plane movement when, for example, modern humans use a hammer, throw a baseball, or throw a dart, with the latter being the source of its namesake: the dart thrower’s motion (Fisk, 1981). The dart thrower’s motion describes a functional axis of the modern human midcarpal joint in which the hand moves from extension with radial deviation to flexion with ulnar deviation (Crisco et al., 2005; Palmer et al., 1985). This motion, which increases accuracy and force, is used during modern human stone tool knapping, suggesting it may have evolved as an adaptation for this behavior (Williams et al., 2014). However, the ability of nonhuman apes to use the dart thrower’s motion (i.e., for their carpus to move in an out-of-plane motion) has yet to be investigated. The underlying hard and soft tissue structures of the modern human carpus that facilitate this movement may be plesiomorphic and exapted for tool-related behaviors (Wolfe et al., 2006).

Carpal kinematic studies in nonhuman apes have focused on the range of motion at the midcarpal joint (Orr, 2017; Orr et al., 2010). Movement at the midcarpal joint of chimpanzees follows a “screw-clamp” mechanism during extension, whereby the “centrale portion” of the scaphoid quickly shifts into the recess between the radially-expanded capitate head and the trapezoid, while at the same time the lunate is pinned between the scaphoid and triquetrum. Altogether, this movement “close-packs” the carpals to create stability in this posture

(Orr, 2017; Orr et al., 2010). In contrast, orangutans with a separate centrale and scaphoid have a “looser-packing” to the carpus that allows for a greater ranges of motion between the scaphoid and lunate, and between the lunate and triquetrum, which facilitate a higher degree of wrist extension than in chimpanzees (Orr, 2017; Orr et al., 2010).

## 4 | PART 3: EVOLUTION

### 4.1 | Hominin hand fossils

Hand fossils discovered at early hominin fossil sites in southern (e.g., Sterkfontein and Kromdraai, South Africa) and eastern Africa (e.g., Hadar, Ethiopia; South Turkwel, Kenya) are typically found in isolation, which makes it challenging to reconstruct hand function and the potential locomotor or manipulative behaviors of early hominin taxa (e.g., Domínguez-Rodrigo et al., 2015; Susman, 1989; Ward et al., 1999). As we will see below, despite its small size, the hand shows a remarkable degree of variation in morphology. Previous work has shown high modularity (e.g., the Mc1 vs. the ulnar metacarpals in modern humans; Morrish & Hlusko, 2014) and limited morphological integration within the wrist (Williams, 2010) that can differ across hominines (Bardo et al., 2020; Bucchi et al., 2022). Exactly how

**TABLE 3** Fossil hominin associated hand remains

Specimen	Taxon	Age (Ma)	Elements preserved	Source
ARA-VP-6/500	<i>Ar. ramidus</i>	4.4	A relatively complete hand comprising (from left and right sides) all carpals, excluding the pisiform; Mc1, partial Mc2 and Mc3, Mc4 and Mc5; PP3 and PP4 plus partial PP2 and PP5; all IPS; DP1 and two non-pollical DPs from rays 2–4	Lovejoy et al. (2009)
StW 573	<i>Australopithecus</i> sp.	3.67?	Complete left hand, excluding one non-pollical DP; also preserves a pollical sesamoid and several bones from the associated right hand	Clarke (1999)
L.H. 21	<i>Au. afarensis</i>	3.7	Proximal fragment of a Mc2 or Mc3, two proximal phalanges and one intermediate phalanx, all associated with ~3 year-old juvenile partial skeleton	White (1980)
DIK-1-1	<i>Au. afarensis</i>	3.3	Associated proximal, intermediate and distal phalanges from one ray and a proximal phalanx from an adjacent ray, all associated with the partial juvenile skeleton of ~3 year-old	Alemseged et al. (2006)
A.L. 288-1	<i>Au. afarensis</i>	3.2	Left capitate and one proximal phalanx	Johanson et al. (1982)
A.L. 333 composite	<i>Au. afarensis</i>	3.2	Associated Mc2–Mc5 likely from one individual, while Mc1, all phalanges and carpals are unassociated and derive from A.L. 333 and A.L. 333 w	Alba et al. (2003); Bush et al. (1982); Marzke (1983)
A.L. 438-1	<i>Au. afarensis</i>	~3.0	Associated left and right Mc2 and left Mc3	Drapeau et al. (2005)
MH 2	<i>Au. sediba</i>	1.98	Complete right hand, excluding the trapezium, trapezoid, pisiform and all non-pollical DPs; also associated with capitate, hamate and PP1–PP4 from left hand and complete upper limb	Kivell et al. (2011); Kivell, Churchill, et al. (2018); Kivell, Rosas, et al. (2018)
OH 7	<i>H. habilis</i>	1.85	Partial right scaphoid, trapezium and possible capitate; proximal epiphysis of Mc2; two proximal portions of PPs (possibly PP2 and PP3); IP2–IP5 missing their proximal epiphyses; DP1 and two non-pollical DPs	Napier (1962); Susman and Creel (1979)
KNM-ER 47000	<i>P. boisei</i>	1.5	Right associated hand including Mc1 missing its head, complete Mc3, and Mc4 shaft; complete PP4, and a PP3 and PP5 both missing distal ends	Richmond et al. (2020)
KNM-WT 15000	<i>H. erectus</i>	1.6	One PP1, one intermediate phalanx and possible juvenile left and right Mc1; all associated with relatively complete juvenile skeleton	Walker and Leakey (1993)
Dinaledi hand 1	<i>H. naledi</i>	0.24–0.34	Complete right hand, excluding the pisiform; distal Mc4 and PP5 are fragmentary; plus several hand bones from the associated left hand	Kivell et al. (2015)
LB 1	<i>H. floresiensis</i>	0.10–0.06	Left hand preserving scaphoid, lunate, trapezoid, capitate, hamate; a metacarpal fragment; three PPs, one IP, DP1 and one non-pollical DP	Larson et al. (2009); Tocheri et al. (2007)
LB 6	<i>H. floresiensis</i>	0.10–0.06	Partial capitate; metacarpal shaft; two PPs, two IPs and three DPs	Larson et al. (2009); Orr et al. (2013)

Abbreviations: DP, distal phalanx; IP, intermediate phalanx; Mc, metacarpal; PP, proximal phalanx.

TABLE 4 Fossil hominin carpal bone remains

Carpal	Taxon	Specimen number	Source
Scaphoid	<i>Ar. ramidus</i>	ARA-VP-6/500-072	Lovejoy et al. (2009)
		ARA-VP-6/500-085	
		ARA-VP-7/2 E	
	<i>Australopithecus</i> sp.	StW 573	Clarke (1999)
	<i>Australopithecus</i> sp.	StW 618	Kibii et al. (2011)
	<i>Au. sediba</i>	MH 2 U.W. 88-158	Kivell et al. (2011, 2018)
	<i>H. habilis</i>	OH 7 FLK-NN-P	Napier (1962), Susman and Creel (1979), Tocheri et al. (2007)
	<i>H. naledi</i>	U.W. 101-807	Kivell et al. (2015)
		U.W. 101-1624	
		U.W. 101-1639	
Hand 1 U.W. 101-1726			
<i>H. floresiensis</i>	U.W. 102a-117	Hawks et al. (2017)	
	LB1/44	Tocheri et al. (2007), Larson et al. (2009)	
Lunate	<i>Ar. ramidus</i>	ARA-VP-6/500-034	Lovejoy et al. (2009)
		StW 573	Clarke (1999)
	cf. <i>Au. afarensis</i>	KNM-WT 22944-J	Ward et al. (1999)
	<i>Au. afarensis</i>	A.L. 444-3	Ward et al. (2012)
	<i>Au. sediba</i>	MH 2 U.W. 88-159	Kivell et al. (2011, 2018)
	<i>H. erectus</i>	<i>Sinathropus</i> ' from Zhoukoudian	Weidenreich (1941)
	<i>H. naledi</i>	U.W. 101-418B	Kivell et al. (2015)
		U.W. 101-1546	
		Hand 1 U.W. 101-1732	
	<i>H. floresiensis</i>	U.W. 102a-477	Hawks et al. (2017)
LB1/60		Larson et al. (2009)	
Triquetrum	<i>Ar. ramidus</i>	ARA-VP-6/500-029	Lovejoy et al. (2009)
		ARA-VP-6/500-068	
	<i>Au. sediba</i>	MH 2 U.W. 88-157	Kivell et al. (2011, 2018)
	<i>P. robustus</i> or early <i>Homo</i> ?	SKX 3498	Kivell (2011)
	<i>H. naledi</i>	U.W. 101-1702	Kivell et al. (2015)
Hand 1 U.W. 101-1727			
Pisiform	<i>Au. afarensis</i>	A.L. 333-91	Bush et al. (1982)
	<i>Australopithecus</i> sp.	StW 573	Clarke (1999)
Trapezium	<i>Ar. ramidus</i>	ARA-VP-6/500-087	Lovejoy et al. (2009)
	<i>Au. afarensis</i>	A.L. 333-80	Bush et al. (1982); Tocheri et al. (2003)
	<i>Australopithecus</i> sp.	StW 573	Clarke (1999); Crompton et al. (2021)
	<i>H. habilis</i>	OH 7 FLK-NN-Q	Napier (1962), Susman and Creel (1979), Tocheri et al. (2003, 2007)
	<i>H. naledi</i>	U.W. 101-916	Kivell et al. (2015)
		U.W. 101-1580	
Hand 1 U.W. 101-1731			

(Continues)

TABLE 4 (Continued)

Carpal	Taxon	Specimen number	Source
Trapezoid	<i>Ar. ramidus</i>	ARA-VP-6/500-027	Lovejoy et al. (2009)
		ARA-VP-6/500-101	
	<i>H. naledi</i>	U.W. 101-1545	Kivell et al. (2015)
		Hand 1 U.W. 101-1728	
<i>H. floresiensis</i>	LB1/47	Tocheri et al. (2007), Larson et al. (2009)	
Capitate	<i>Ar. ramidus</i>	ARA-VP-6/500-020	Lovejoy et al. (2009)
		ARA-VP-6/500-058	
		ARA-VP-7/2F	
	<i>Au. anamensis</i>	KNM-KP 31724	Ward et al. (2001)
	<i>Au. afarensis</i>	A.L. 288-1 w	Johanson et al. (1982); McHenry (1983)
		A.L. 333-40	Bush et al. (1982); McHenry (1983)
	cf. <i>Au. afarensis</i>	KNM-WT 22944-H	Ward et al. (1999)
	<i>Australopithecus</i> sp.	StW 573	Clarke (1999)
	<i>Au. africanus</i>	TM 1526	McHenry (1983)
	<i>Au. sediba</i>	MH 2 U.W. 88-105	Kivell et al. (2011, 2018)
		MH 2 U.W. 88-156	
	<i>H. habilis</i>	OH 7 FLK-NN-R	Napier (1962), possible capitate or hamate
	<i>H. naledi</i>	U.W. 101-930	Kivell et al. (2015)
		U.W. 101-1385	
		Hand 1 U.W. 101-1730	
U.W. 102a-476		Hawks et al. (2017)	
<i>H. floresiensis</i>	LB1/45	Tocheri et al. (2007), Larson et al. (2009); Orr et al. (2013)	
	LB20	Orr et al. (2013)	
Hamate	<i>Ar. ramidus</i>	ARA-VP-6/500-071	Lovejoy et al. (2009)
		ARA-VP-6/500-080	
		ARA-VP-7/2D	
	<i>Au. afarensis</i>	A.L. 333-50	Bush et al. (1982)
	cf. <i>Au. afarensis</i>	KNM-WT 22944-I	Ward et al. (1999)
	<i>Australopithecus</i> sp.	StW 573	Clarke (1999)
		<i>Au. sediba</i>	MH 2 U.W. 88-95
	<i>H. naledi</i>	MH 2 U.W. 88-106	
		U.W. 101-713	Kivell et al. (2015)
		U.W. 101-1640	
<i>H. floresiensis</i>	Hand 1 U.W. 101-1729		
	LB1/46	Tocheri et al. (2007), Larson et al. (2009); Orr et al. (2013)	
	LB21	Orr et al. (2013)	
	LB22	Orr et al. (2013)	

modularity or morphological integration factor into the mosaic morphologies documented among hominin hands remains unclear. This means that predicting the overall morphology of the hand on the basis

of only one bone—or from only one region of the hand—is fraught with problems. Thus, associated fossils, which provide information about several regions of the same hand are especially valuable.

**TABLE 5** Fossil hominin metacarpal (Mc) remains

Metacarpal	Taxon	Specimen number	Source
<b>Mc1</b>			
	<i>Ar. ramidus</i>	ARA-VP-6/500-015 ARA-VP-6/1638	Lovejoy et al. (2009)
	<i>Au. afarensis</i>	A.L. 333 w-39 A.L. 333-58	Bush et al. (1982)
	<i>Australopithecus</i> sp.	StW 573	Clarke (1999)
	<i>Au. africanus</i>	StW 418 StW 583	Green and Gordon (2008); Kivell et al. (2020); Ricklan (1987)
	<i>P. robustus</i> or early <i>Homo</i>	SK 84 SKX 5020	Susman (1989); Susman et al. (2001); Trinkaus and Long (1991)
	<i>P. boisei</i>	KNM-ER 47000 E	Richmond et al. (2020)
	<i>Au. sediba</i>	MH2 U.W. 88-119	Kivell et al. (2015, 2018, 2018)
	<i>H. erectus</i>	KNM-WT 15000-BU & -BV	Walker & Leakey (1993); possibly not Mc1s
	<i>H. naledi</i>	U.W. 101-007 Hand 1 U.W. 101-033 U.W. 101-270 U.W. 101-401 U.W. 101-917 U.W. 101-1282 Hand 1 U.W. 101-1321	Bowland et al. (2021); Kivell et al. (2015)
<b>Mc2</b>			
	<i>Ar. ramidus</i>	ARA-VP-6/500-001a & 001b ARA-VP-6/500-014	Lovejoy et al. (2009)
	<i>Au. afarensis</i>	A.L. 333-15 A.L. 333-48 A.L. 333 w-23 A.L. 438-1f A.L. 438-1 e	Bush et al. (1982); Ward et al. (2012)  Drapeau et al. (2005)
	<i>Australopithecus</i> sp.	StW 573	Clarke (1999)
	<i>Au. africanus</i>	StW 382 StW 664	Green & Gordon (2008); Kivell et al. (2020); Ricklan (1987) Pickering et al. (2018)
	<i>P. robustus</i> or early <i>Homo</i>		Susman (1989); Susman et al. (2001)
	<i>Au. sediba</i>	MH2 U.W. 88-115	Kivell et al. (2015, 2018, 2018)
	<i>H. habilis</i>	OH 7 FLK-NN-O	Napier (1962); Susman and Creel (1979)
	<i>H. naledi</i>	U.W. 101-512 Hand 1 U.W. 101-1320 U.W. 101-1650	Kivell et al. (2015)
<b>Mc3</b>			
	<i>Ar. ramidus</i>	ARA-VP-6/500-006	Lovejoy et al. (2009)
	<i>Au. afarensis</i>	A.L. 333-16 A.L. 333-65 A.L. 333 w-6 A.L. 438-1d	Bush et al. (1982); Ward et al. (2012)  Drapeau et al. (2005)
	<i>Australopithecus</i> sp.	StW 573	Clarke (1999)

(Continues)

TABLE 5 (Continued)

Metacarpal	Taxon	Specimen number	Source
	<i>Au. africanus</i>	StW 27 StW 64 StW 68 StW 394	Green & Gordon (2008); Kivell et al. (2020); Ricklan (1987)
	<i>P. robustus</i> or early <i>Homo</i>	SKX(W) 3646	Susman (1989); Susman et al. (2001)
	<i>P. boisei</i>	KNM-ER 1500m KNM-ER 47000F	Day et al. (1976) Richmond et al. (2020)
	<i>Au. sediba</i>	MH1 U.W. 88-112 MH2 U.W. 88-116	Kivell et al. (2018, 2018) Kivell et al. (2015, 2018, 2018)
	<i>H. naledi</i>	U.W. 101-559 U.W. 101-517 + 721 Hand 1 U.W. 101-1319 U.W. 101-1651 + 1628	Bolter et al. (2020); Kivell et al. (2015)
	<i>H. erectus</i>	KNM-WT 51260	Ward et al. (2014)
<b>Mc4</b>			
	<i>Ar. ramidus</i>	ARA-VP-6/500-010 ARA-VP-7/2G	Lovejoy et al. (2009)
	<i>Au. afarensis</i>	A.L. 333-18 A.L. 333-56 A.L. 333-122	Bush et al. (1982)
	<i>Australopithecus</i> sp.	StW 573	Clarke (1999)
	<i>Au. africanus</i>	StW 26 StW 65 StW 292 StW 330 StW 552	Green & Gordon (2008); Kivell et al. (2020); Ricklan (1987)
	<i>P. robustus</i> or early <i>Homo</i>	SK 85 SKX 2954	Susman (1989); Susman et al. (2001)
	<i>P. boisei</i>	KNM-ER 47000G	Richmond et al. (2020)
	<i>Au. sediba</i>	MH2 U.W. 88-117	Kivell et al. (2015, 2018, 2018)
	<i>H. naledi</i>	Hand 1 U.W. 101-1318 U.W. 102a-028	Kivell et al. (2015) Hawks et al. (2017)
<b>Mc5</b>			
	<i>Ar. ramidus</i>	ARA-VP-6/500-019 ARA-VP-6/500-036	Lovejoy et al. (2009)
	<i>Au. afarensis</i>	A.L. 333-14 A.L. 333-17 A.L. 333-27 A.L. 333-89 A.L. 333-144 A.L. 333-153 A.L. 333-163 A.L. 333 w-5 A.L. 333 w-26 A.L. 333 w-35	Bush et al. (1982); Ward et al. (2012)  Ward et al. (2012)  Bush et al. (1982)

TABLE 5 (Continued)

Metacarpal	Taxon	Specimen number	Source
	<i>Australopithecus</i> sp.	StW 573	Clarke (1999)
	<i>Au. africanus</i>	StW 63	Green & Gordon (2008); Kivell et al. (2020); Ricklan (1987)
		StW 639	Pickering et al. (2018)
	<i>P. robustus</i> or early <i>Homo</i>	SK(W) 14147 (SKW 27)	Susman (1989); Susman et al. (2001)
	<i>Au. sediba</i>	MH2 U.W. 88-118	Kivell et al. (2015, 2018, 2018)
	<i>H. naledi</i>	Hand 1 U.W. 101-1309	Kivell et al. (2015)
<b>Unidentified</b>			
	<i>Au. afarensis</i>	L.H. 21z, proximal fragment of juvenile Mc2 or Mc3	White (1980)
	<i>Au. africanus</i>	StW 673	Pickering et al. (2018)
	<i>H. naledi</i>	Several metacarpal shafts, including several juvenile specimens, some of which are thought to be associated to one individual (DH 7)	Bolter et al. (2020); Kivell et al. (2015)
	<i>H. floresiensis</i>	LB1/59	Larson et al. (2009)
		LB5/2	
		LB6/5	

For some early hominin taxa, such as *Ardipithecus ramidus* (Lovejoy et al., 2009), *Australopithecus afarensis* (Bush et al., 1982; Ward et al., 2012) and (what is assumed to be) *Australopithecus africanus* at Sterkfontein (Kivell et al., 2020; Ricklan, 1987), hand fossils make up a large proportion of the skeletodental fossil evidence (McRae & Wood, 2022) (Tables 3–8). These hypodigm contrast with the paucity of evidence about the hand for *Homo habilis* (Napier, 1962; Susman & Creel, 1979) and *Homo erectus* (Domínguez-Rodrigo et al., 2015; Walker & Leakey, 1993; Lordkipanidze et al., 2007; Ward et al., 2014; Weidenreich, 1941) (Tables 3–8). Below, we briefly review the hominin hand fossil record, starting with the earliest putative hominins and ending with early *Homo* (including recent taxa that present primitive morphology; Figure 7). Later *Homo* hand fossil evidence is extensive and thus we encourage readers to consult morphological descriptions for: *Homo antecessor* (Lorenzo, 2007; Lorenzo et al., 1999), *Homo heidelbergensis* (Lorenzo, 2012), Neandertals (e.g., Kivell, Churchill, et al., 2018; Kivell, Rosas, et al., 2018; Mersey et al., 2013; Musgrave, 1977; Niewoehner, 2006; Niewoehner et al., 1997; Trinkaus, 1982, 1989; Trinkaus & Walker, 2017) and fossil *H. sapiens* (e.g., Trinkaus & Jelínek, 1997; Trinkaus & Svoboda, 2006; Trinkaus et al., 2010).

#### 4.1.1 | *Orrorin tugenensis*

Two hand phalanges are associated with Late Miocene *Orrorin tugenensis* (6 Ma): a distal pollical phalanx and a proximal phalanx—although the latter was found at a different locality to that of the femur and humerus (Gomery & Senut, 2006; Senut et al., 2001; Tables 6 and 8). The proximal phalanx is described as curved and similar to that of “extant climbing primates as well as *Au. afarensis*” (Senut et al., 2001, p. 141). The distal pollical phalanx is interpreted as having a modern

human-like morphology associated with a (presumably) well-developed FPL suggesting precision grip abilities for non-tool related activities, such as climbing and balancing (Gomery & Senut, 2006) or the manipulation of natural objects (Almécija et al., 2010). However, it is difficult to determine FPL development based on the morphology of the pollical distal phalanx (Shrewsbury et al., 2003; also see Williams-Hatala et al. (2016)).

#### 4.1.2 | *Ardipithecus*

Two manual phalanges are attributed to *Ardipithecus kadabba* (~5.6 Ma; Haile-Selassie, 2001), but the best evidence for this genus derives from the *Ar. ramidus* (4.4 Ma) ARA-VP 6/500 hand fossils, which include a well-preserved carpus, metacarpus (although Mc2 and Mc3 are quite fragmentary) and several phalanges (including distal phalanges) (Lovejoy et al., 2009) (Tables 3–8). Apart from the pollical proximal phalanx (which derives from ARA-VP 7/2), all are considered to belong to a single individual (Lovejoy et al., 2009). Descriptions of the carpus emphasize the enigmatic notion of a “central joint complex” (CJC), comprising the trapezoid, capitate and their articulations with the proximal Mc2 and Mc3 (Lovejoy et al., 2009). Unlike the more stable CJC of the African apes—which the authors suggest is able to resist metacarpal rotation through a “screw-like” configuration of articular facets—*Ar. ramidus* is described as having simple, planar joints and a CJC most similar to palmigrade cercopithecines, which permits flexibility at the wrist, particularly in extension (Lovejoy et al., 2009). However, the morphology underpinning this interpretation—including a radioulnarly broad and spherical lunate—is most similar to *Pongo* (see Lovejoy et al. (2009); their figures S23–S25). The *Ar. ramidus* centrale is fused with the scaphoid as in extant African apes and humans, and the scaphoid tubercle, trapezium

TABLE 6 Fossil hominin proximal phalanx (PP) remains

Taxon	Specimen number	Ray	Source
<i>O. tugenensis</i>	BAR 349'00	PP2-5	Senut et al. (2001)
<i>Ar. kadabba</i>	DID-VP-1/80	PP2-5	Haile-Selassie (2001); Haile-Selassie et al. (2009)
<i>Ar. ramidus</i>	ARA-VP-6/500-022	PP4	Lovejoy et al. (2009)
	ARA-VP-6/500-030	PP3	
	ARA-VP-6/500-043	PP2	
	ARA-VP-6/500-046	PP5	
	ARA-VP-6/500-061	PP3	
	ARA-VP-6/500-069	PP4	
	ARA-VP-7/2H	PP2	
	ARA-VP-7/2I	PP1	
	ARA-VP-6/507	PP2-5	
<i>Au. anamensis</i>	KP 30503	PP2-5	Ward et al. (2001)
<i>Au. afarensis</i>	A.L. 288-1x	PP2-5	Johanson et al. (1982)
	A.L. 333-19	PP4?	Alba et al. (2003); Bush et al. (1982); Marzke (1983); Ward et al. (2012)
	A.L. 333-20	PP2-5	
	A.L. 333-19	PP2-5	
	A.L. 333-31	?	
	A.L. 333-33	PP2-5	
	A.L. 333-49	PP2-5	
	A.L. 333-57	PP2-5	
	A.L. 333-62	PP5	
	A.L. 333-63	PP3?	
	A.L. 333-69	PP1	
	A.L. 333-93	PP2?	
	A.L. 333 n-2	PP4?	
	A.L. 333 w-4	PP2-5	
	A.L. 333 w-20	PP2-5	
	A.L. 333 w-25	PP2-5	
	A.L. 333 w-29	PP2-5	
	A.L. 333 w-51	PP2-5	
	A.L. 333 w-54	PP2-5	
	A.L. 333x-13a	PP2-5	
	A.L. 438-4	PP1	
	A.L. 444-4	PP4?	
	A.L. 724-3	PP2-5	
	A.L. 1044-1	PP2?	
	DIK-1-1	PP2-5	Almeseget et al. (2006)
	DIK-1-1	PP2-5	
	L.H. 21x	PP2-5	White (1980)
	L.H. 21z	PP2-5	

TABLE 6 (Continued)

Taxon	Specimen number	Ray	Source	
<i>Australopithecus</i> sp.	StW 573	PP1	Clarke (1999)	
		PP2		
		PP3		
		PP4		
		PP5		
<i>Au. africanus</i>	StW 28	PP5	Kivell et al. (2020)	
	StW 29	PP3 or 4		
	StW 122	PP2-4		
	StW 293	PP4		
	StW 400	PP3 or 4		
	StW 478	PP1		
	StW 575	PP1		
	StW 597	PP5?		Pickering et al. (2018)
	StW 605	PP2?		Partridge et al. (2003)
	StW 662	PP2?		
	StW 663	?		
	StW 668	?		Stratford et al. (2016)
<i>P. robustus</i> or early <i>Homo</i>	SKX 5018	PP2 or 4?	Susman (1989); Susman et al. (2001)	
	SKX 10641	PP2 or 4?		
	SKX 15468	PP2-4		
	SKX 19576	PP5?		
	SKX 22511 + 30220	PP2-4		
	SKX 22741	PP2 or 4?		
	SKX 27431	PP2-4		
	SKX 35822	PP2-5		
<i>Au. sediba</i>	MH 2 U.W. 88-91	PP1	Kivell et al. (2015, 2018, 2018)	
	MH 2 U.W. 88-108	PP4		
	MH 2 U.W. 88-109	PP2		
	MH 2 U.W. 88-110	PP4		
	MH 2 U.W. 88-120	PP3		
	MH 2 U.W. 88-121	PP5		
	MH 2 U.W. 88-160	PP1		
	MH 2 U.W. 88-164	PP2		
<i>H. habilis</i>	OH 7 FLK-NN-H	PP3?	Napier (1962); Susman & Creel (1979)	
	OH 7 FLK-NN-I	PP2?		
<i>H. erectus</i> (?)	OH 86	PP5	Dominguez-Rodrigo et al., (2015)	
	KNM-WT 15000-O	PP1	Walker & Leakey (1993)	
<i>H. naledi</i>	U.W. 101-120	PP1	Bolter et al. (2020); Kivell et al. (2015)	
	U.W. 101-168	PP2-5		

(Continues)

TABLE 6 (Continued)

Taxon	Specimen number	Ray	Source
	U.W. 101-175	PP2-5	
	U.W. 101-428	PP1	
	U.W. 101-554	PP2-5	
	U.W. 101-558	PP3 or 4?	
	U.W. 101-720	PP1	
	U.W. 101-754	PP2 or 4?	
	U.W. 101-913	PP3 or 4?	
	U.W. 101-923	PP2-5	
	U.W. 101-1025	PP2-5	
	U.W. 101-1055	PP1	
	U.W. 101-1247 + 1630	PP5?	
	Hand 1 U.W. 101-1326	PP4	
	Hand 1 U.W. 101-1327	PP3	
	Hand 1 U.W. 101-1328	PP2	
	U.W. 101-1348	PP2-5	
	U.W. 101-1380	PP2-5	
	U.W. 101-1454	PP5	
	U.W. 101-1460	PP2 or 4?	
	Hand 1 U.W. 101-1464	PP3	
	U.W. 101-1478	PP5?	
	U.W. 101-1516	PP2-5	
	U.W. 101-1539	PP2-5	
	U.W. 101-1552	PP2-5	
	U.W. 101-1620	PP2-5	
	U.W. 101-1635	PP2-5	
	U.W. 101-1642	PP1	
	U.W. 101-1643	PP3	
	U.W. 101-1644	PP4	
	U.W. 101-1645	PP5	
	U.W. 101-1708	PP2-5	
	U.W. 101-1709	PP2-5	
	Hand 1 U.W. 101-1721	PP1	
	Hand 1 U.W. 101-1725	PP5	
<i>H. floresiensis</i>			
	LB1/61	PP2-5	Larson et al. (2009)
	LB1/62	PP2-5	
	LB6/8	PP2-5	
	LB6/16	PP2-5	

tubercle and hamate hamulus are all well-developed, suggesting a deep carpal tunnel and powerful flexion of the digits.

The metacarpals of *Ar. ramidus* are short relative to extant nonhuman hominoids, while the phalanges of digits 2–5 are similar in length (relative to body size) to those of gorillas (Lovejoy et al., 2009) (Table 9). When considering finger proportions relative to body size [whether one estimates *Ar. ramidus* body size to be *c.* 36 kg or *c.*

51 kg (Grabowski et al., 2018)], *Ar. ramidus* has a ray 4 length—the best-preserved ray—that is longer than *Gorilla*, and intermediate between modern humans and chimpanzees; among fossil hominoids it is most similar to *Proconsul* (Almécija et al., 2015) (Table 10). A separate analysis of the length of digit 3 phalanges relative to body size found that *Ar. ramidus* is most similar to *Pan* and the Miocene apes *Hispanopithecus* and *Pierolapithecus* (Prang et al., 2021) (Figure 8).

**TABLE 7** Fossil hominin intermediate phalanx (IP) remains

Taxon	Specimen number	Ray	Source
<i>Ar. kadabba</i>	ALA-VP-2/11	IP2-5	Haile-Selassie et al. (2009)
<i>Ar. ramidus</i>	ARA-VP-6/500-002	IP5	Lovejoy et al. (2009)
	ARA-VP-6/500-055	IP4	
	ARA-VP-6/500-059	IP3	
	ARA-VP-6/500-078	IP4	
	ARA-VP-6/500-092	IP3	
	ARA-VP-6/500-107	IP2	
<i>Au. afarensis</i>	A.L. 333-25	IP2-5	Alba et al. (2003); Bush et al. (1982); Marzke (1983); Ward et al. (2012)
	A.L. 333-32	IP2-5	
	A.L. 333-46	IP2-5	
	A.L. 333-64	IP5?	
	A.L. 333-88	IP3?	
	A.L. 333-148	IP2-5	
	A.L. 333-149	IP2 or IP4	
	A.L. 333-150	IP5?	
	A.L. 333-151 <sup>a</sup>	IP2-5	
	A.L. 333 w-7	IP2?	
	A.L. 333 w-38	IP2-5	
	A.L. 333 w-53	IP2-5	
	A.L. 333x-13b	IP2-5	
	A.L. 333x-18	IP2-5	
	A.L. 444-5	IP2-5	
	DIK-1-1	IP2-5	Alemesged et al. (2006)
	L.H. 21 w	IP2-5	White (1980)
<i>Australopithecus</i> sp.	StW 573	IP2 IP3 IP4 IP5	Clarke (1999)
<i>Au. africanus</i>	StW 331	IP2-4	Kivell et al. (2020)
	StW 620	IP2-5	Pickering et al. (2018)
	StW 635	IP2-5	
	StW 657	IP2-5	
<i>Au. sediba</i>	MH 2 U.W. 88-122	IP4	Kivell et al. (2015, 2018, 2018)
	MH 2 U.W. 88-123	IP2	
	MH 2 U.W. 88-161	IP3	
	MH 2 U.W. 88-162	IP5	
<i>P. robustus?</i>	TM 1517 n	IP2-5	Day (1978); Skinner et al. (2013)

(Continues)

TABLE 7 (Continued)

Taxon	Specimen number	Ray	Source
<b><i>P. robustus</i> or early <i>Homo</i></b>			
	SKX 5019	IP2-5	
	SKX 5021	IP2-5	
	SKX 5022	IP2-5	
	SKX 9449	IP2-5	
	SKX 13476	IP2-5	
	SKX 33355	IP2-5	
	SKX 35439	IP2-5	
	SKX 36712	IP2-5	
	SKX 38653	IP2-5	
<b><i>H. habilis</i></b>			
	OH 7 FLK-NN-D	IP2?	Napier (1962); Susman & Creel (1979)
	OH 7 FLK-NN-E	IP3?	
	OH 7 FLK-NN-F	IP4?	
	OH 7 FLK-NN-G	IP5	
<b><i>H. erectus</i></b>			
	KNM-WT 15000	IP2-5	Walker & Leakey (1993)
<b><i>H. naledi</i></b>			
	U.W. 101-178	IP5?	Bolter et al. (2020); Kivell et al. (2015)
	U.W. 101-381	?	
	U.W. 101-603	?	
	U.W. 101-665	?	
	U.W. 101-777	IP5?	
	U.W. 101-924	IP3 or 4?	
	U.W. 101-982	?	
	U.W. 101-1027	IP3 or 4?	
	U.W. 101-779		
	U.W. 101-780		
	U.W. 101-781		
	Hand 1 U.W. 101-1308	IP4	
	Hand 1 U.W. 101-1310	IP3	
	Hand 1 U.W. 101-1311	IP2	
	Hand 1 U.W. 101-1325	IP5	
	U.W. 101-1379	?	
	U.W. 101-1440	IP5?	
	U.W. 101-1455	IP3 or 4?	
	U.W. 101-1479	?	
	U.W. 101-1619	?	
	U.W. 101-1637	?	
	U.W. 101-1660	IP2 or IP4?	
	U.W. 101-1646	IP3	
	U.W. 101-1647	IP4	
	U.W. 101-1648	IP5	
	U.W. 101-1664	?	
	U.W. 101-1704	?	
	U.W. 101-1705	?	

TABLE 7 (Continued)

Taxon	Specimen number	Ray	Source
	U.W. 101-1706	?	
<i>H. floresiensis</i>			
	LB1/40	IP2-5	Larson et al. (2009)
	LB1/42	IP2-5	
	LB1/48	IP2-5	
	LB6/9	IP2-5	
	LB6/10	IP2-5	

<sup>a</sup>A.L. 333-151 identified in Ward et al. (2012) as a manual intermediate phalanx, but likely a PP1 from a cercopithecoid.

The proximal phalanges are robust with well-developed flexor sheath ridges and their curvature is most similar to suspensory *Pongo* and atelines (Prang et al., 2021). Overall, the *Ar. ramidus* ray morphology suggests the frequent use of arboreal locomotor behaviors, including strong flexion of the digits as occurs in extant apes during vertical climbing and suspension (Prang et al., 2021; but see Lovejoy et al. (2009)).

Relative to *Pan*, the first metacarpal of *Ar. ramidus* is robust—particularly at its distal end, with a large enthesal attachment for the abductor pollicis longus tendon (Lovejoy et al., 2009). The distal pollical phalanx is described as having a “rugose” and “clearly marked insertion gable” for the FPL like that of modern humans (Lovejoy et al., 2009, p. 70e1-2), although this “gable” is not obvious on the fossil specimen (T.L.K., pers. observation). The pollex to digit 4 relative length is similar to that of gorillas and hylobatids and shorter than that of modern humans (Almécija et al., 2015).

The *Ar. ramidus* carpus and hand, together with its preserved upper limb elements, were originally described as being unlike that of extant apes, with neither knuckle-walking, vertical climbing or suspension being part of the *Ar. ramidus* locomotor repertoire (Lovejoy et al., 2009). Instead, *Ar. ramidus* is attributed new (and somewhat vague) modes of locomotion. Lovejoy et al. (2009) described *Ar. ramidus* locomotion as “careful climbing,” combining bipedalism on the ground, with above-branch palmigrade quadrupedalism in the trees. Later, due to the challenges of classifying fossil hominin positional behaviors by existing categories used to describe living primates, White and colleagues described *Ar. ramidus* positional behavior as “arboreal multigrady” (White et al., 2015). This term reflects the use of arboreal orthograde and pronograde postures, deliberate climbing and clambering, but a lack of dependence on forelimb-dominated suspension and vertical climbing (White et al., 2015). Others, however, have highlighted morphological similarities in hand morphology between *Ar. ramidus* and African apes (or all nonhuman hominoids) that are most parsimoniously interpreted as functional indications of vertical climbing and suspension (Prang et al., 2021), and preliminary analyses of the capitate cast doubt on inferences of habitual palmigrady (Orr, 2013). Practically, one may question how a potentially c. 50 kg hominin is able to engage in above-branch palmigrady without the means to vertically climb into the tree.

#### 4.1.3 | *Australopithecus anamensis*

Little is known about the hand of *Au. anamensis*. To date, only a capitate (KNM-KP 31724) and an incomplete proximal phalanx (KNM-KP 30503) have been attributed to this taxon (Ward et al., 2001) (Tables 4 and 6). The capitate has a notably radioulnarly broad head for articulation with the scaphoid and lunate. The capitate's Mc2 facet is radially-oriented as in African apes and unlike humans, suggesting a limited ability to pronate the second ray (Ward et al., 2001). The proximal phalanx is described as having clear flexor sheath ridges, a markedly curved shaft and overall most similar to *Au. afarensis* (Ward et al., 2001).

#### 4.1.4 | *Australopithecus afarensis*

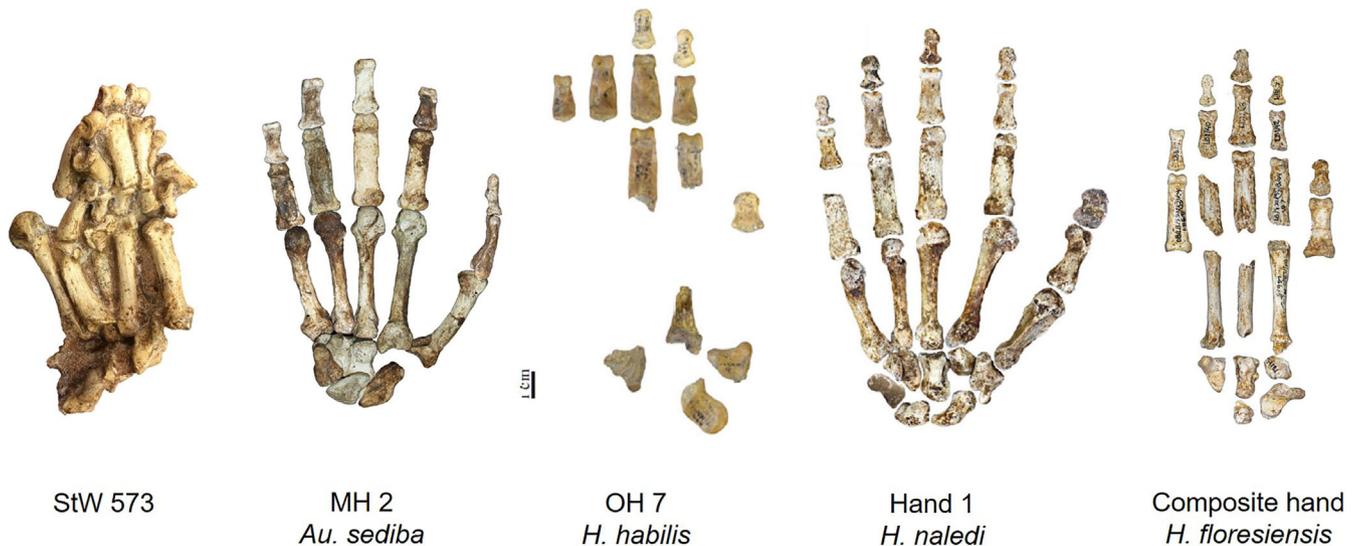
Numerous hand bones are attributed to *Au. afarensis*, including carpals, metacarpals and phalanges, most of which were recovered from Hadar, Ethiopia (Bush et al., 1982; Drapeau et al., 2005; Johanson et al., 1982; Ward et al., 2012), as well as remains from South Turkwel, Kenya (KNM-ER 22944) that are not notably distinct from *Au. afarensis* (Ward et al., 1999) (Tables 3–8). However, of the remains, only two sets of metacarpals can be associated to individuals: the Mc2–Mc5 of the *Au. afarensis* “composite hand” (Marzke, 1983; Kivell et al., 2015) and a right and left Mc2 and left Mc3 associated with the A. L. 438-1 associated forelimb (Drapeau et al., 2005). Estimates of intrinsic hand proportions range from potentially gorilla-like (Rolian & Gordon, 2013) to similar to (Marzke, 1983), if not equal to that of modern humans (Alba et al., 2003; Almécija & Alba, 2014) (Tables 9 and 10, Figures 8 and 9). The *Au. afarensis* trapezium is similar to that of modern humans in having an articulation for the Mc2 that is more palmarly oriented than that of African apes, suggesting the ability to pronate ray 2 (Tocheri et al., 2003). The capitate-Mc3 facet shape is more similar to cercopithecines than that of modern humans and lacks a Mc3 styloid process, suggesting greater mobility at this joint than in later hominins (Rein & Harvati, 2013). The Mc1 is gracile relative to modern humans and the phalanges are curved with well-developed flexor sheath ridges, suggesting frequent use of power grasping (Bush et al., 1982; Ward et al., 2012). A distal pollical phalanx has a gable for the attachment of flexor pollicis longus tendon and a radioulnarly-broad apical tuft as in modern humans (Ward et al., 2012).

TABLE 8 Fossil hominin distal phalanx (DP) remains

Taxon	Specimen number	Ray	Source
<i>O. tugenensis</i>	BAR 1901'01	DP1	Gommery & Senut (2006)
<i>Ar. ramidus</i>	ARA-VP-6/500-049	DP1	Lovejoy et al. (2009)
	ARA-VP-6/500-050	DP3?	
	ARA-VP-6/500-053	DP4?	
	ARA-VP-6/500-060	DP2?	
<i>Au. afarensis</i>	A.L. 333-159	DP1	Bush et al. (1982); Ward et al. (2012)
	A.L. 333 w-11	DP2-5	
	A.L. 333 w-50	DP2-5	
	DIK-1-1	DP2-5	Alemesged et al. (2006)
<i>Australopithecus</i> sp.	StW 573	DP1 DP2-5 DP2-5 DP2-5	Clarke (1999)
<i>Au. africanus</i>	StW 294	DP1	Kivell et al. (2020)
	StW 661	DP2-5	Pickering et al. (2018)
<i>Au. sediba</i>	MH 2 U.W. 88-124	DP1	Kivell et al. (2015, 2018, 2018)
<i>P. robustus?</i>	TM 1517k	DP1	Day (1978); Skinner et al. (2013)
	TM 1517o	DP2-5	
<i>P. robustus</i> or early <i>Homo</i>	SKX 5016	DP1	
	SKX 8963	DP2-5	
	SKX 27504	DP3?	Almecija et al. (2010); Susman (1989)
<i>H. habilis</i>	OH 7 FLK-NN-A	DP1	Napier (1962); Susman & Creel (1979)
	OH 7 FLK-NN-B	DP3?	
	OH 7 FLK-NN-C	DP2?	
<i>H. erectus</i>	D2679	DP?	Lordkipanidze et al. (2007)
	D3480	DP?	
<i>H. naledi</i>	U.W. 101-604	DP2-5	Bolter et al. (2020); Kivell et al. (2015)
	Hand 1 U.W. 101-1329	DP2	
	Hand 1 U.W. 101-1351	DP1	
	U.W. 101-1453	DP1	
	U.W. 101-1527	DP2-5	
	U.W. 101-1582	DP2-5	
	U.W. 101-1590	DP2-5	
	U.W. 101-1607	DP2-5	
	U.W. 101-1649	DP2-5	

TABLE 8 (Continued)

Taxon	Specimen number	Ray	Source
	U.W. 101-1703	DP2-5	
	U.W. 101-1718	DP2-5	
	Hand 1 U.W. 101-1722	DP3	
	Hand 1 U.W. 101-1723	DP4	
	Hand 1 U.W. 101-1724	DP5	
<i>H. floresiensis</i>			
	LB1/49	DP2-5	Larson et al. (2009)
	LB1/55	DP1	
	LB6/7	DP2-5	
	LB6/11	DP2-5	
	LB6/12	DP2-5	
	LB12	DP2-5	



**FIGURE 7** Fossil hominin hand skeletons. From left to right, StW 573 hand still articulated within breccia; MH2 *Au. sediba* (photo credit: Peter Schmid); OH 7 hominin hand bones in approximate anatomical position, showing the radioulnarly-broad juvenile intermediate phalanges with a distinctive shape described as “bottle-shaped” (Susman & Creel, 1979); hand 1 *H. naledi* (photo credit: Peter Schmid); composite hand skeleton of *H. floresiensis*, primarily comprising LB1 and LB6 hand bones (photo credit: Matt Tocheri). All images scaled to the same 1 cm scale

The juvenile phalangeal remains from DIK-1-1 and L.H. 21 associated skeletons, both estimated to be approximately three years of age, are described as long and curved (Alemseged et al., 2006; White, 1980) but to our knowledge comparison of how their curvature compares to adult phalanges has not yet been conducted.

Functional interpretations based on the differences in estimated intrinsic hand proportions, as well as other wrist and hand morphology, vary: some conclude that *Au. afarensis* could not have produced precision grips with the same efficiency as modern humans (Rolian & Gordon, 2013); others suggest *Au. afarensis* was capable of pad-to-side as well as three-jaw chuck precision grips, but likely had less effective precision handling and power squeeze grips (Marzke, 1983, 1997; Tocheri et al., 2003); while still others allow for the distinctly modern human-like pad-to-pad precision grips (Alba et al., 2003;

Almécija & Alba, 2014). While it is important to recognize that precision grip abilities in *Au. afarensis* (and earlier hominins) may have evolved in response to non-lithic tool behaviors or other manipulative behaviors (e.g., food processing), the discovery of the Lomekwian (Harmand et al., 2015) and evidence of tool-use behaviors (McPherron et al., 2010) contemporary with *Au. afarensis*, suggest lithic behaviors may have been part of the behavioral repertoire of this taxon.

#### 4.1.5 | StW 573

In 1999, a remarkably well-preserved hand and upper limb of the StW 573 skeleton from Sterkfontein (3.67 Ma; Bruxelles et al., 2019; Granger et al., 2015; but see Pickering and Kramers (2010) and

TABLE 9 Total length measurements of metacarpals and phalanges in associated fossil hominin and extant ape hand skeletons (all values in mm)

Species	Specimen	Mc1	PP1	DP1	Mc2	PP2	IP2	DP2	Mc3	PP3	IP3	DP3	Mc4	PP4	IP4	DP4	Mc5	PP5	IP5	DP5
<i>Ar. ramidus</i>	ARA-VP-6/500 (L)	35.2	[25.7]	14.6*	-	[43.0]	-	-	-	52	37	-	[59.5]	47.1	35	-	55.3	-	24.4	-
<i>Australopithecus</i> sp.	StW 573 (L)	[41.3]	[27.5]	[16.2]	[62.6]	[37.2]	26.4*	[15.0]	[60.5]	40.5*	[27.5]	[15.9]	[51.7]	39.5*	[27.2]	14.2?	[47.4]	[35.3]	19.4*	[14.1]?
<i>Au. afarensis</i>	A.L. 333 <sup>a</sup>	39.5	26.0	19.2	61.5	37.4	20.8	-	60.2	40.5	25.8	13.7	54.7	38.4	-	-	51.5	35.0	21.3	-
<i>Au. sediba</i>	MH 2 (R)	39.4	24.1	15.1	52.8	31.2	[16.4]	-	48.3	34.7	21.6	-	44	33.4	20.4	-	41.6	27.2	16.8	-
<i>H. habilis</i>	OH 7	-	-	17.2	-	-	20.1	14.7?	-	-	26.8	16.0?	-	-	26.6	-	-	-	18.7	-
<i>H. naledi</i>	Hand 1 (R)	37.4	24.5	15.2	53.7	32.2	17.8	12.7	49	35.9	22.6	[14.4]	42.7	33.1	22.1	14.1	40.7	[26.5]	15.6	12.4
Neandertals	Kebara 2 (L)	46.4	31.4	26.6	70.4	43.7	25.9	21.6	71.2	48.3*	31.9	23.0	60.9	46.6	31.0	23.7	-	37.3	-	21.9
	Tabun C1 (L)	40.7	26.2	-	[65.2]	[38]?	24.6?	-	62.8	[42.0]?	-	[18.6]?	[53.3]	-	25.2?	-	[46.5]	-	-	-
Fossil <i>H. sapiens</i>	Qafzeh 9 (R)	45.4	33.5	23.8	[65]	41.7	26.2	18.3*	62.1	46.4	-	19.7*	53.1	43.7	-	18.2*	52.2	35.8	22.5	17.9
	Ohalo II H2 (R)	46.0	32.5	21.8	73.8	41.3	25.6*	16.9	69.5	46.7*	31.4*	20.1*	63.1	41.8*	30.2*	17.7*	56.0	34.0	22.0	-
<b>Extant</b>																				
Modern human	Mean	44.9	30.8	22.9	67.6	40.4	23.8	17.8	67.0	45	29.5	19	57.0	42.0	28.1	18.7	52.6	33.1	20.2	16.6
	SD	3.3	2.7	2.0	4.6	2.8	2.1	1.7	4.6	3.1	2.2	1.5	4.0	2.9	2.1	1.6	3.4	2.3	2.0	1.9
Small-bodied modern human	Mean	41.5	28.0	19.9	60.7	36.3	21.1	15.5	60.0	40.5	26.0	16.7	51.2	38.0	24.8	16.7	46.6	29.7	17.7	15.0
	SD	4.5	2.8	1.7	5.2	3.1	2.5	1.4	4.5	3.9	2.9	1.8	4.8	3.7	2.6	1.6	4.3	3.1	2.4	1.7
<i>Pan</i>	Mean	39.9	26.3	18	87.1	47.9	31.2	-	86.3	56.4	40.5	20.7	78.9	52.3	37.9	-	70.6	39.8	26.9	-
	SD	2.0	1.8	2.7	3.9	3.1	2.8	-	3.5	3.6	3	0.9	3.9	3.8	2.2	-	3.4	5.1	2.6	-
<i>Gorilla</i>	Mean	48.6	27.3	-	91.5	51.4	32.7	-	91.4	58.6	40.9	-	84.6	56.1	37.6	-	81.2	46.7	30.1	-
	SD	5.6	4.2	-	12.2	6.4	4.4	-	11.7	6.3	4.4	-	10.7	6.2	4.2	-	11.4	5.9	3.6	-

Note: Values in [x] are estimated; values marked with \* indicate measurements taken from opposite side due to preservation; values marked with “?” indicate that bone may not be associated to the correct ray. The *Ar. ramidus* PP1 is from ARA-VP 7/21, a different and smaller individual and the measurement is scaled to 6/500 size to 25.7 mm following Almerica et al. (2015); some values differ from those of Lovejoy et al. (2009) following repeat measurements of fossils by T.L.K. and G. Suwa, with approval from T. White. The StW 573 values are estimated lengths taken from fossil while still articulated within breccia and should be interpreted with caution. The *Au. afarensis* is a composite hand (?) comprising bones from A.L. 333 and A.L. 333 w sites; only Mc2–Mc5 articulate well together are likely from the same individual; DP3 length is mean of only two known DPs (A.L. 333 w-11 and 333 w-50). In OH 7 all intermediate phalanges are missing their proximal epiphysis and values represent preserved juvenile lengths. Abbreviations: DP, distal phalanx; IP, intermediate phalanx; Mc, metacarpal; PP, proximal phalanx.

**TABLE 10** Intrinsic hand proportions in fossil hominin and extant ape associated hand skeletons

Species	Specimen	Ray 1:Ray 2 excl. DPs	Ray 1:Ray 2 with DPs	Ray 1:Ray 3 excl. DPs	Ray 1:Ray 3 with DPs	Ray 1:Ray 4 excl. DPs
<i>Ar. ramidus</i>	ARA-VP-6/500 (L)	-	-	-	-	43.0
<i>Australopithecus</i> sp.	StW 573 (L)	54.5	48.7	53.5	58.9	58.1
<i>Au. afarensis</i>	A.L. 333*	54.8	49.5	52.1	60.7	56.0
<i>Au. sediba</i>	MH 2 (R)	63.1	56.5 <sup>^</sup>	60.7	67.0 <sup>^</sup>	64.2
<i>H. naledi</i>	Hand 1 (R)	59.7	53.2	57.6	63.2	63.2
Neandertal	Kebara 2 (L)	55.6	48.1	51.4	59.9	56.2
Fossil <i>H. sapiens</i>	Qafzeh 9 (R)	59.4	52.2	56.6	64.5 <sup>^</sup>	61.7
	Ohalo II H2 (R)	56.0	49.9	52.8	59.5	58.1
<b>Extant</b>						
Modern human	Mean	57.3	66.6	53.5	61.3	59.3
<i>n</i> = 23 F; <i>n</i> = 19 M	SD	1.8	1.9	2.0	1.8	2.0
Small-bodied modern human	Mean	59.0	67.1	54.9	62.4	61
<i>n</i> = 13 F; <i>n</i> = 12 M	SD	2.1	1.8	2.1	1.8	2.1
<i>Pan</i>	Mean	40.0	-	36.3	<b>41.0</b>	39.9
<i>n</i> = 10 F; <i>n</i> = 12 M	SD	1.2	-	0.9	<b>2.4</b>	3.2
<i>Gorilla</i>	Mean	48.9	-	39.7	<b>45.9</b>	41.9
<i>n</i> = 3 F; <i>n</i> = 6 M	SD	1.6	-	1.4	<b>3.8</b>	2.0

Note: Ratios of ray 1 (pollex) to other rays, either excluding the distal phalanges (DPs) or with the distal phalanges, shown as a percentage. Values based on data presented in Table 3, apart from values in bold are taken from Patel and Maiolino (2016). Note that *Au. afarensis* is a composite hand from multiple individuals and measurements in *Australopithecus* sp. StW 573 are estimates so both should be interpreted with caution. *Au. sediba* MH 2 does not preserve distal non-pollical phalanges so lengths are estimated following human scaling in Feix et al. (2015) at 12.7 mm (DP3) and 11.7 mm (DP2). Similarly, Qafzeh 9 does not preserve an IP3 and is estimated to be 31.0 mm following proportions in Ohalo II H2.

Abbreviation: SD, standard deviation.

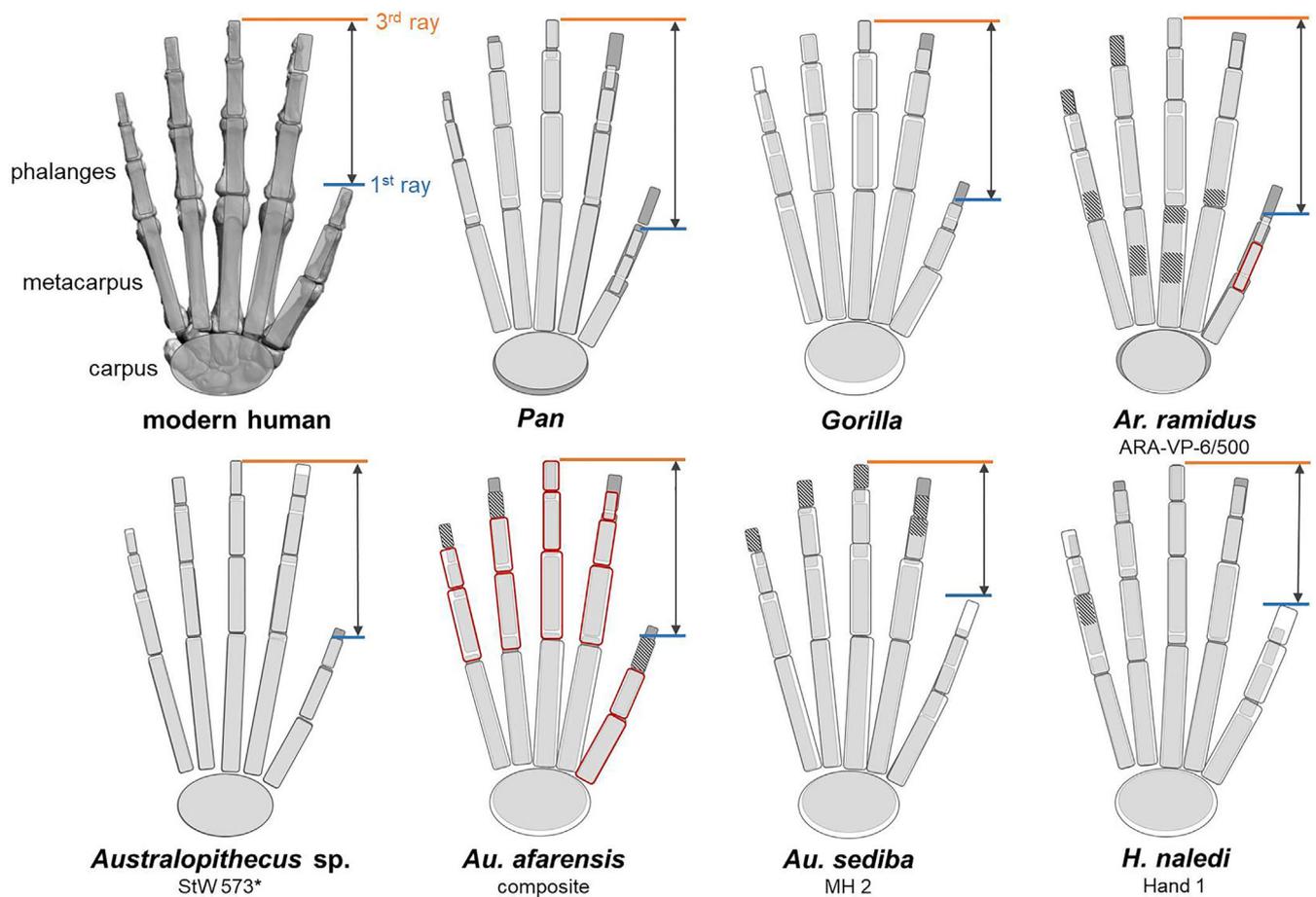
Frost et al. (2022) was announced (Clarke, 1999). StW 573 preserves a complete (excluding one distal non-pollical phalanx) articulated left hand including, remarkably, a pollical sesamoid, along with several elements from the right hand (Figure 7). The hand is described as combining modern human-like intrinsic hand proportions with an African ape-like “ridge” on the trapezium's first metacarpal facet that would have stabilized the pollex in abducted pinch grips (Clarke, 1999, 2002; Crompton et al., 2021). Although the hand remains articulated within the breccia (Figure 7), making morphological analyses challenging, our own study of the fossils based on caliper linear measurements (T.L.K.) estimates pollex length (Mc1 + PP1 + DP1) to be approximately 60% the length of the third digit (Mc3 + PP3 + IP3 + DP3), which is similar to the intrinsic hand proportions of modern humans (mean 61%) (Tables 9 and 10; Figures 8 and 9). The estimated relative pollex length of StW 573 is similar to that for the *Au. afarensis* composite hand (61%), but is shorter than the pollex of *Homo naledi* (Hand 1, 63%) and, especially, *Australopithecus sediba* (MH2, 67%) (Table 9; Figure 9). The StW 573 trapezium's first metacarpal facet shows strong dorsopalmar convex curvature like that of African apes and unlike the flatter, broader facet of modern humans, but no “ridge”—which would prohibit mobility at this joint—is present (T.L.K., pers. observation). Phalangeal morphology is difficult to assess, but the isolated right third, fourth and, especially, fifth proximal phalanges show well-developed flexor sheath ridges and the dorsal curvature appears

similar to that of other hominin phalanges from Sterkfontein (Kivell, Churchill, et al., 2018). Overall, this morphology is consistent with detailed morphological assessments of the StW 573 upper limb that indicate climbing and/or suspension were part of its locomotor repertoire (Carlson et al., 2021; Crompton et al., 2021; Heaton et al., 2019).

#### 4.1.6 | *Australopithecus africanus*

Several hominin carpal, metacarpal and phalangeal fossils from Sterkfontein, South Africa are attributed to *Au. africanus* (Tables 4–8). The majority of these fossils were found in Member 4 of Sterkfontein, while a few come from Member 5, Jacovac Cavern and Milner Hall from this cave system (Kivell et al., 2020; Partridge et al., 2003; Pickering et al., 2018; Stratford et al., 2016). All of these fossils are isolated remains (i.e., cannot be associated to particular individuals; but see Ricklan (1987)) and while most are considered *Au. africanus*, some are conservatively attributed to *Australopithecus* sp. given the lack of association with taxonomically-informative morphology and the presence of multiple hominin species at Sterkfontein (e.g., Kibii et al., 2011).

The scaphoid (StW 618) has a large tubercle that, together with the orientation of the trapezium-trapezoid facet, suggest a more pronated thumb and deep carpal arch (Kibii et al., 2011). The capitate (TM 1526) retains a dorsally-positioned trapezoid facet as in *Pan* and



**FIGURE 8** Schematic of differences in intrinsic hand proportions in modern humans, African apes and fossil hominins. Each schematic of *Pan troglodytes*, *Gorilla gorilla* or fossil hominin (light gray) is scaled to the length of the modern human third ray and overlaid on the modern human hand proportions (dark gray). Elements or regions that are not preserved or poorly preserved shown with slanted lines; elements that are not associated to the same individual are outlined in red. The *Australopithecus* sp. StW 573 proportions are based on estimated lengths from fossil while still articulated within the breccia and should be interpreted with caution

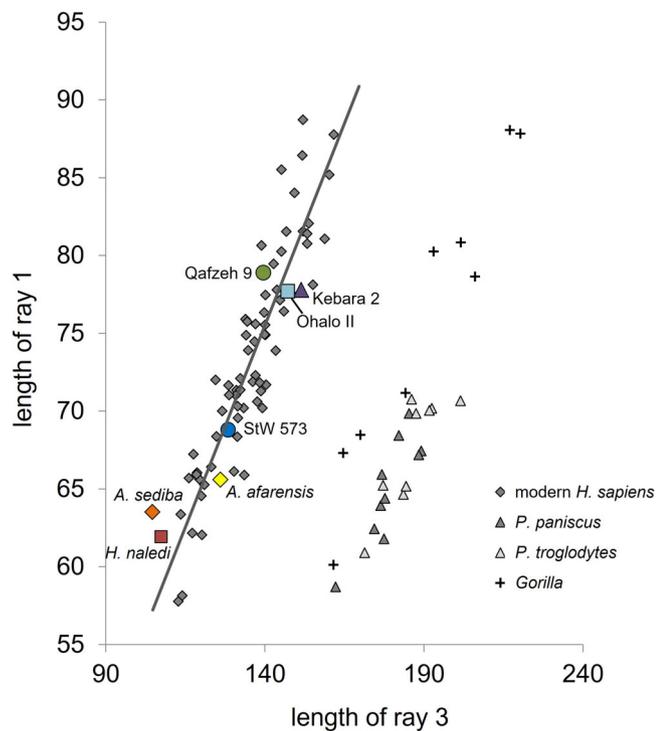
*Au. afarensis*, as opposed to palmarly-positioned in modern humans, and overall shows a morphology that is intermediate between African apes and modern humans (McHenry, 1983; Tocheri et al., 2007). The only complete Mc1 (StW 418) has a gracile shaft, but has a distinct opponens pollicis tendon entheses not seen in *Au. afarensis*. Given the lack of associated fossils, a resampling approach shows that the Mc1 is narrow and ape-like but its relative length to the other metacarpals is modern human-like (Green & Gordon, 2008; Ostrofsky & Richmond, 2015). The relative proportions of the phalanges and metacarpal lengths within each ray are also modern human-like (Kivell et al., 2020; Ostrofsky & Richmond, 2015). The phalanges combine an intermediate degree of curvature and robust shafts, but the flexor sheath ridges are weakly developed (Kivell et al., 2020; Pickering et al., 2018).

The metacarpals and phalanges from Sterkfontein vary substantially in size: StW 382 Mc2, StW 478 pollical proximal phalanx and StW 331 intermediate phalanx are the largest specimens not only among the *Au. africanus* sample, but also compared to all current fossils known from Swartkrans, *Au. sediba* and *H. naledi*. If we assume all

of the Sterkfontein fossils currently attributed to *Au. africanus* are from that taxon, then *Au. africanus* likely had a large degree of sexual dimorphism (as well as potential temporal variation in size) (Ricklan, 1987; Kivell et al., 2020).

#### 4.1.7 | *Australopithecus sediba*

Two partial skeletons from Malapa, South Africa—MH1, a late juvenile, likely male and MH2, an adult, likely female—date to 1.977 Ma (Berger et al., 2010; Pickering et al., 2011). While MH1 currently only preserves a third metacarpal missing its distal (unfused) epiphysis, a relatively complete right hand, plus a few bones from the left hand, is associated with a complete right upper limb in MH2 (Churchill et al., 2013; Churchill et al., 2018; Kivell et al., 2011; Tables 3–9; Figure 7). The MH2 carpus shows a mix of ape-like and modern human-like features, as well as a distinctive, radioulnarly-narrow lunate, which suggests a greater range of abduction at the radiocarpal joint, and perhaps less central-axis loading of the radiocarpal and



**FIGURE 9** Length of the first ray (pollex) to the third ray (middle finger) in extant African apes, modern humans and fossil hominins. Ratio does not include distal phalanges; total length of first ray (Mc1 + PP1)/total length of third ray (Mc3 + PP3 + IP3)

midcarpal joints, than is interpreted for other early hominin taxa [e.g., *Ar. ramidus* (Lovejoy et al., 2009); *Australopithecus* sp., KNM-WT 22944J (Ward et al., 1999)] and modern humans (Kivell et al., 2011; Kivell, Churchill, et al., 2018; Kivell, Rosas, et al., 2018). The metacarpals, including the Mc1, are gracile, which, in combination with the (albeit poorly preserved) radial carpometacarpal region, suggests limited force production by the pollex. However, intrinsic hand proportions reveal a pollex that is surprisingly long relative to the fingers, and longer than in our sample of modern humans (Table 10; Figures 8 and 9), which would have facilitated opposition of the pollex to the fingers and pad-to-pad precision gripping that is typical of later *Homo* (Kivell et al., 2011; Kivell, Churchill, et al., 2018; Kivell, Rosas, et al., 2018).

The MH2 proximal phalanges show moderate curvature and both the proximal—and unusually the intermediate—phalanges have well-developed flexor sheath ridges (Kivell et al., 2015). This phalangeal morphology in combination with a palmarly-projecting hamate hamulus, suggests powerful flexion of the fingers during grasping (Kivell et al., 2011; Kivell, Churchill, et al., 2018; Syeda et al., 2021). Strong grasping of the fingers, which is consistent with the well-developed humeral epicondyles and the shoulder girdle morphology, suggests the habitual use of overhead arm postures (Churchill et al., 2013, 2018). Analyses of the metacarpal internal trabecular structure support this functional interpretation, showing a *Pongo*-like grasping signal within the fingers combined with a modern human-like loading pattern within the first metacarpal (Dunmore et al., 2020).

The MH1 Mc3 is notably larger (despite missing its epiphyseal head) and more robust than the gracile Mc3 of MH2 (Kivell, Churchill, et al., 2018; Kivell, Rosas, et al., 2018). The “adult” length of the MH1 Mc3 is estimated to be about 8% longer than that of the MH2 Mc3, which is similar to the degree of sexual dimorphism in small-bodied modern humans (male Mc3s are, on average, 7.5% longer than those of females; Kivell, Churchill, et al., 2018; Kivell, Rosas, et al., 2018). Relative to length, the MH1 and MH2 Mc3 midshaft breadth fall on the opposite extremes of modern human variation, suggesting caution should be applied when drawing functional inferences from robusticity, especially on limited samples. The differences in the *Au. sediba* Mc3s—which fit comfortably within the sexual dimorphism documented in other fossil hominins and modern humans—does not necessarily reflect differences in function or hand use (Kivell, Churchill, et al., 2018; Kivell, Rosas, et al., 2018).

#### 4.1.8 | *Homo habilis*

The OH 7 hand bones uncovered at site FLKNN I announced by Leakey (1960) were described by Napier (1962) and included in the formal definition of *Homo habilis* by Leakey et al. (1964). The OH 7 late juvenile hand has played an historically influential role in our understanding and perceptions of the evolution of hominin tool use, and how the genus *Homo* is defined. The only well-preserved elements of the OH 7 hand are the intermediate phalanges 2–5, which are missing their proximal epiphyses, and three distal phalanges, one of which is pollical (Day, 1976, 1978; Napier, 1962; Susman & Creel, 1979; Tables 3–9; Figure 7). These are associated with three fragmentary carpal bones (scaphoid, trapezium and what is described as a capitate), the base of the Mc2, and two fragmentary proximal phalanges. None show clear indications of their developmental age, but they are considered to come from the same individual, as were two adult proximal phalanges since recognized as cercopithecine (Day, 1976, 1978; Napier, 1962; Susman & Creel, 1979).

Napier's (1962) initial description of the OH 7 hand emphasized its mosaic morphology (e.g., the ape-like curvature of the phalanges with well-developed flexor tendon attachments combined with a modern human-like radioulnarly-broad distal pollical phalanx). Within the carpus, the trapezium has a large and mildly-curved saddle-shaped Mc1 facet that is more modern human-like, but Napier (1962) suggests it is “set” within the carpus like that of gorilla. Overall, Napier interpreted the hand bones as showing the greatest similarity to juvenile *Gorilla* and to adult modern humans in that the pollex was powerful, opposable but possibly short (Napier, 1962). Napier's (1962, p. 410) functional interpretation emphasized “there is no doubt that the Olduvai hand was sufficiently advanced in terms of the basic power and precision grips to have used naturally occurring objects as tools” but “[t]here is less certainty about tool-making” and the possibility that a “more advanced [hominin] form was the toolmaker and the known incumbents [OH 7] of the floor were its victims”. This initial interpretation contrasts with that of Leakey et al. (1964), even though their *H. habilis* species definition includes the same anatomical

features. Leakey et al. (1964, p. 9), incorporating inferences drawn from brain size as well, emphasized that “[w]hile it is possible that *Zinjanthropus* and *Homo habilis* both made stone tools, it is probable that the latter was the more advanced tool maker and that the *Zinjanthropus* skull represents an intruder (or a victim) on a *Homo habilis* living site.”

The most detailed assessment of the OH 7 hand morphology was by Susman and Creel (1979). They highlighted the robusticity of the phalanges, with the proximal phalanges described as most chimpanzee-like, while the intermediate phalanges are unusually radioulnarly broad and “bottle-shaped” (i.e., notably broad at the proximal- and mid-shaft and narrowing distally; see Figure 7) and most similar to gorilla (Susman & Creel, 1979). Overall, Susman and Creel (1979) concluded that the modern human-like features of the distal phalanges reflect precision grip abilities, while the African-ape like features reflect the frequent use of climbing. A more recent study of the phalangeal morphology highlighted similarities in morphology to phalanges putatively associated with *Paranthropus*, calling into question the taxonomic attribution of the OH 7 hand (Moyà-Solà et al., 2008). Morphological and cladistic analyses of the OH 8 foot—assumed to belong to the same individual as OH 7 and also assigned to *H. habilis*—suggest that it should be attributed to *Paranthropus boisei* (Wood, 1974; DeSilva et al., 2019). In addition, there is debate over whether the OH 8 foot is the same developmental age as the OH 7 hand and mandible (DeSilva et al., 2010; Susman et al., 2011), further confounding the association and taxonomic attribution of these fossils.

The perception that the OH 7 hand belonged to an individual that was highly dexterous and capable of tool-making has persisted (e.g., Boesch & Boesch, 1993; Lieberman, 2014; Potts, 2018; Tobias, 1991; Wilson, 1999) despite its poor preservation and the several ape-like aspects of its morphology. For example, the shape of the OH 7 scaphoid, although it does not preserve its tubercle, is most similar to *Pan* (Tocheri et al., 2007). The OH 7 trapezium has a remarkably flat and broad Mc1 facet, which is derived relative to australopiths and more similar to Neandertals than to modern humans (Trinkaus, 1989), whereas the Mc2 facet is radioulnarly oriented as in African apes and more primitive than that of *Au. afarensis* (Tocheri et al., 2003, 2008).

#### 4.1.9 | *Paranthropus*

Until recently, there has been limited definitive evidence of *Paranthropus* hand morphology. Several isolated hand fossils from Swartkans have been provisionally attributed to *Paranthropus robustus* based the preponderance of craniodental remains (Susman, 1989; Susman et al., 2001) (Tables 4–8). However, given that early *Homo* is also found at Swartkans, taxonomic attribution of the hand fossils remains uncertain (Susman, 1988, 1991; Trinkaus & Long, 1991). The best-studied of these fossils are two Mc1 specimens (SK 84 and SKX 5020); they are both robust with well-developed muscle entheses, but they differ in overall size (Susman, 1988, 1991; Trinkaus & Long, 1991). Several hand fossils associated with the TM 1517 craniodental remains may be more confidently attributed to *P. robustus*, but most of the original list of

hand remains (Broom, 1942) have since been identified as cercopithecoïd. Only two distal phalanges remain: TM 1517-k that is likely from the hallux (rather than the pollex) and TM 1517-o that was originally described as also being pedal (Broom, 1942) but is possibly manual from rays 2–5 (Day, 1978; Skinner et al., 2013).

The best evidence of the *Paranthropus* hand is the recently-discovered associated upper limb and partial hand of KNM-ER 47000 (1.5 Ma) from Ileret, Kenya, which was attributed to *P. boisei* on the basis of distal humeral morphology (Richmond et al., 2020) (Table 3). This specimen preserves Mc1, Mc3 and Mc4 and three proximal phalanges. The Mc1 is described as gracile and narrow with a saddle-shaped trapezium facet that is more curved than in modern humans and similar to australopiths (Richmond et al., 2020). The Mc3 lacks a styloid process, like australopiths and *H. naledi*, but the length of the Mc1 relative to the Mc3 is modern human-like. The phalanges are short, but show similar curvature to that of *Orrorin* and *Au. afarensis* (Richmond et al., 2020). The overall gracile morphology of KNM-ER 47000 hand combined with an extremely robust humerus and ulna, contrasts with what is known of these regions in *H. erectus* (Richmond et al., 2020; Walker & Leakey, 1993).

#### 4.1.10 | *Homo erectus*

Surprisingly little is known about the *H. erectus* hand (and foot) given the wealth of the cranial evidence for this taxon (Tables 4–8). The relatively complete KNM-WT 15000 skeleton (~1.5 Ma) preserves a partial proximal pollical phalanx, one intermediate phalanx, and two bones tentatively identified as left and right Mc1s (KNM-WT 15000-BU and -BV) missing their proximal epiphyses (Walker & Leakey, 1993), which is consistent with the juvenile status of this skeleton [i.e., this epiphysis fuses by 15–17 years of age in humans (Scheuer & Black, 2000) and estimated age at death is 8–13.5 years old for KNM-WT 15000 (Smith, 1993; Dean & Smith, 2009)]. However, one specimen (-BU) also preserves what appears to be a developing distal epiphysis, which is inconsistent with hominoid developmental osteology (Scheuer & Black, 2000). One of us (T.L.K.) doubts both the identification and attribution of these two specimens.

The remaining hand bones (potentially) associated with *H. erectus* include a partial lunate from Zhoukoudian (Weidenreich, 1941), two distal phalanges from Dmanisi (Lordkipanidze et al., 2007), neither of which have been formally described, a >1.84 Ma year-old proximal phalanx (OH 86) from Olduvai (Domínguez-Rodrigo et al., 2015; although the authors do not attribute this specimen to a particular taxon), and a recently-discovered complete Mc3 (~1.42 Ma) from Kaitio, Kenya (Ward et al., 2014). The Mc3 (KNM-WT 51260) is large, robust and, most notably, shows the earliest evidence of a styloid process in hominin fossil record (Ward et al., 2014). The functional morphology of the styloid process of modern humans (and Neandertals) is interpreted as providing stability at the carpometacarpal joints when large forces from the pollex are experienced across the palm during tool-related behaviors (Marzke & Marzke, 1987). The presence of a styloid process in KNM-WT 51260 suggests a modern-human-like

reorganization of the wrist that coincides with the increase in Acheulian tools in the archaeological record, but prior to changes in the Acheulian that occur around 1.2 Ma (Beyene et al., 2013; Ward et al., 2014).

#### 4.1.11 | *Homo naledi*

Over 1500 hominin fossils from deep within the Rising Star Cave system, South Africa, dated to 236–335 Ka (Dirks et al., 2017) were attributed to a new species *Homo naledi* (Berger et al., 2015; Hawks et al., 2017) (Tables 3–8). The collection includes a semi-articulated complete right hand (Hand 1) missing only its pisiform, as well as hand elements from at least six other adult individuals and several juveniles (Berger et al., 2015; Bolter et al., 2020; Hawks et al., 2017; Kivell et al., 2015) (Table 9, Figure 7). The radial carpus preserves a suite of features, including a trapezium-trapezoid facet extending onto the scaphoid tubercle and a palmarly-expanded trapezoid (Kivell et al., 2015), that is only found in taxa (e.g., Neandertals and modern humans) that manufacture and use complex tools (Tocheri, 2007). The first metacarpal is unusual in having a robust shaft with well-developed entheses for the intrinsic pollical muscles and a radioulnarly broad distal head, combined with a surprisingly small carpometacarpal articulation with the trapezium (Bowland et al., 2021; Kivell et al., 2015). The distal pollical phalanx is radioulnarly broad with a clear gable for the FPL tendon attachment. The length of the pollex relative to the third ray falls within the upper range of modern human variation found in s (Kivell et al., 2015) (Figures 8 and 9). The morphology indicates a long, robust and potentially powerful pollex capable of pad-to-pad forceful precision grips, but how this force is accommodated by such a relatively small Mc1-trapezium articulation is puzzling (Kivell et al., 2015).

The *H. naledi* pollex and palm morphology is combined with curved proximal and intermediate phalanges, the former resembling the curvature found in *Pan*, *Au. afarensis* and OH 7, while the intermediate phalangeal curvature is most similar to *Pongo* and hylobatids, and more curved than any hominin in the comparative sample, and the *H. naledi* phalanges are longer relative to their respective metacarpals than all early hominins (apart from *Ar. ramidus*) (Kivell et al., 2015). Given the strong correlation between phalangeal curvature and frequency of arboreality in extant primates (Jungers et al., 1997), and the biomechanical role of curvature to reduce overall strain experienced by the phalanx (Richmond, 2007; Nguyen et al., 2014), the *H. naledi* phalangeal curvature suggests they were using their hands for locomotor grasping (Kivell et al., 2015; but see Wallace et al. (2020)). This functional interpretation is consistent with *H. naledi*'s cranially-oriented shoulder and extremely low humeral torsion, both of which are advantageous for climbing (Feuerriegel et al., 2017).

#### 4.1.12 | *Homo floresiensis*

The announcement of a new, diminutive hominin species, *H. floresiensis*, on the island of Flores, Indonesia, by Brown et al. (2004) was based on

the relatively complete LB1 skeleton dated to between approximately 100–60 Ka (Sutikna et al., 2016). The LB1 skeleton includes well-preserved lower limbs and feet, but the upper limbs and hands are less complete. The hand remains currently include a complete left scaphoid, trapezoid, capitate, a partial left lunate and hamate, and proximal, intermediate and distal phalanges, including a distal pollical phalanx, but only one metacarpal fragment (Crevecoeur et al., 2012; Larson et al., 2009; Tocheri et al., 2007) (Tables 3–8; Figure 7). Currently it is not possible to assess the intrinsic hand proportions, but *H. floresiensis* is associated with Oldowan-like stone tool technology providing archaeological evidence of its manual dexterity (Brumm et al., 2006; Moore et al., 2009). The carpal morphology, however, suggests *H. floresiensis* was making and using tools in a different way to that of other hominins. The morphology of the scaphoid, trapezoid and capitate is surprisingly *Pan*-like, showing none of the features associated with committed tool use in Neandertals or modern humans (Orr et al., 2013; Tocheri et al., 2007). The hamate has a long, well-developed hamulus most similar to African apes and *Au. afarensis* (Orr et al., 2013). The proximal phalanges preserved in both LB1 and LB6 are robust with radioulnarly broad proximal bases and well-developed flexor sheath ridges (Larson et al., 2009). Proximal phalangeal curvature in LB6 is similar to *Au. afarensis* and falls within the range of variation in *Gorilla* and the upper extreme of modern humans (Larson et al., 2009). The distal pollical phalanx of LB1, in contrast, shows a modern human-like morphology with radioulnarly broad apical tuft and clear gable for the FPL tendon attachment (Crevecoeur et al., 2012; Larson et al., 2009).

#### 4.1.13 | Hominin hand evolution

From the above review, it is clear that evolution of hominin hand morphology is not linear, and nor should we expect it to be. For example, current evidence shows a more modern human-like distal pollical phalanx in *Orrorin* (Gommery & Senut, 2006) compared to the 2.5 Ma-younger *Ardipithecus* (Lovejoy et al., 2009) and several later hominins (Almécija et al., 2010), similarities in primitive carpal morphology between *Au. sediba* and *H. floresiensis* despite being 2 Ma apart (Kivell et al., 2011, 2015; Tocheri et al., 2007), and the presence of ape-like phalanges in *Au. afarensis* and *H. naledi*, even though they are 3 Ma apart (Bush et al., 1982; Kivell et al., 2015). The presumably primitive characters in recent taxa like *H. naledi* and *H. floresiensis*, and the fact that more basal taxa can persist through time, make clear that we cannot rely on chronology to reconstruct hominin hand evolution. Instead, it must be interpreted within a phylogenetic context, as difficult as that is.

The paucity of fossil evidence of the hominin hand means there are notable gaps in our understanding of hand morphology in important taxa, such as *Paranthropus boisei*, whose upper limb morphology suggests a significant degree of arboreality (Dominguez-Rodrigo et al., 2013; Lague et al., 2019), or *Homo habilis* and *Homo erectus*, whose respective temporal spans coincide with critical transitional periods in stone tool technologies. Although there is general consistency in hand morphology across committed stone tool users

(*Homo antecessor*, *H. heidelbergensis*, Neandertals, and *H. sapiens*; e.g., Lorenzo, 2012; Lorenzo et al., 1999, Niewoehner, 2006), we do not know when this suite of traits first evolved (Tocheri et al., 2008). Moreover, the discovery of stone tools at 3.3 Ma (Harmand et al., 2015), evidence of possible tool use at 3.4 Ma (McPherron et al., 2010), and the association of Oldowan-like tools with *H. floresiensis* (Brumm et al., 2006; Moore et al., 2009), make clear there are multiple hominin hand morphologies capable of stone tool-related behaviors, and that these manipulative abilities can apparently coexist with potentially habitual locomotor hand use.

## 4.2 | Understanding hand function and anatomy from the archaeological record

Paleoanthropology is unique among the paleosciences because of the rich, extended record of material—mostly lithic—culture (also see Falóitico et al. (2019), Mercader et al. (2007), and Proffitt et al. (2016)). The earliest potential artifacts in the archaeological record belong to the Lomekwian industry, dating to ~3.3 Ma (Harmand et al., 2015; but see Dominguez-Rodrigo and Alcalá (2019)) while the earliest definitive artifacts are from the Oldowan industry, dating to ~2.6 Ma (Braun et al., 2019; Semaw, 2000; Semaw et al., 1997). Artifacts from both traditions are dominated by tools that can be loosely described as unifacial cores with invasive feathered, hinged and/or stepped flake removals and the associated simple flakes. Though the tools share some morphological characteristics, the Lomekwian is distinguished by the presence of significantly larger cores with high frequencies of unifacial flaking, relatively larger flakes, some of which show evidence of prior use as a percussive object, and a high proportion of large percussive tools (Harmand et al., 2015; Lewis & Harmand, 2016). The Oldowan, on the other hand, is known for its simple core technology dominated by flaked cobbles, the resultant flakes—including retouched pieces—and debitage, and percussive objects (e.g., hammerstones) (Schick & Toth, 2006; Toth, 1982, 1985). Oldowan tools have been classified according to a number of different typologies, including Mode I (Clarke, 1968), heavy-duty, light-duty, utilized and waste (Leakey, 1971), and Modes A-D (Shea, 2013), alluding to the morphological, chronological, and geographic diversity encompassed within the industry. Similar to the tools, the hypothesized production methods of the two industries overlap to some extent (e.g., the use of bipolar reduction, in which a core is positioned on an anvil and flaking occurs with a hammer stone) and diverge in other respects (Braun et al., 2019; Harmand et al., 2015). Given the large size of the Lomekwian tools, Harmand et al. (2015) proposed that they were produced using passive hammer and bipolar techniques, to the exclusion of direct freehand percussion. A greater diversity of techniques has been associated with the Oldowan, including bipolar reduction, striking a core against an anvil, direct hard hammer percussion, and throwing one rock against another (e.g., Braun et al., 2019; de la Torre & Mora, 2018; Stout et al., 2010).

It has long been hypothesized that the production and use of these early tools played a role in selecting the morphology and functional abilities of the modern human hand. Coupled with experimental

biomechanics research, the archaeological record provides paleoanthropologists with a unique window into the functional anatomy of the upper limb of early hominins. In combination, they provide a nearly unparalleled opportunity to test adaptive hypotheses, akin to how fossilized footprints preserve kinematic snapshots that enable the testing of hypotheses related to locomotion of extinct organisms (Falkingham & Gatesy, 2014; Hatala et al., 2021). Yet, despite this opportunity and abundant research in the area, major questions remain unaddressed by experimental biomechanics studies about the functional adaptations of the hominin hand to tool-making, and even less is known in regard to potential adaptations to tool using (and given ethnographic accounts of the use-life of stone tools [e.g., Sahle et al., 2012] the biomechanics of stone tool use may be more relevant than those of tool production). Most of the focus of experimental biomechanics and biomechanical modeling has been limited to the radial side of the hand (i.e., pollex and radial carpals) during the production of stone tools (e.g., Rolian et al., 2011; Tocheri et al., 2003, 2005). More recently, progress has been made on the functional role of the second and fifth rays (e.g., Key et al., 2019), but the midline and ulnar side of the hand remains largely uninvestigated.

Lomekwian tools are hypothesized to have been made using passive-hammer and bipolar techniques (Harmand et al., 2015; Lewis & Harmand, 2016). Both methods were also used during the Oldowan, as well as free-hand direct-hammer percussion (Schick & Toth, 2006; Semaw et al., 2009; Stout et al., 2010). Limited experimental biomechanical information (i.e., kinetics, kinematics, EMG) is available on passive-hammer and bipolar techniques (Macchi et al., 2021 is the exception), and even less is known about the biomechanics of the hand during these behaviors. Musculoskeletal modeling of the hand of *Au. afarensis* suggests that the morphology of the articular surface on the hamate for the fifth metacarpal would have inhibited this species' ability to rotate the fifth digit in a palmar-radial direction and to use that digit to apply a strong grip force to any large object held in the hand (Domalain et al., 2017). This aligns with earlier functional conclusions based on the articular morphology of the hamate (Marzke, 1983), but is contrary to conclusions based on the morphology of the fifth metacarpal head (Marzke, 1997), demonstrating the difficulty of reconstructing functional patterns from joint surfaces of fossil remains. Domalain et al. (2017) concluded that the morphology of the fifth carpometacarpal joint may have made it difficult for *Au. afarensis* to produce the Lomekwian tools. However, the authors also acknowledge two critical limitations of their model: (1) the need for additional in vivo data and (2) muscle attachment locations have a significant impact on the modeling outcomes (Domalain et al., 2017). Given the dearth of the former and the difficulty of interpreting muscle attachment sites (i.e., entheses), their combination may have a significant impact on the accuracy of the model. At present, kinematic, kinetic, and EMG data associated with the production of Lomekwian tools are lacking. However, experimental tool use data demonstrate that the palmar surface of the fifth distal phalanx is used to help secure large Lomekwian-style flakes during cutting behaviors (Key et al., 2018). Whether the fifth ray is used passively, or in a more active manner that would necessitate rotation and

pulp-to-object contact to counter large loads, has yet to be determined.

The biomechanics of the type of free-hand knapping used for making the core tools and flakes that typify the Oldowan has received more attention (e.g., Bril et al., 2010; Hamrick et al., 1998; Key & Dunmore, 2015; Marzke & Shackley, 1986; Marzke et al., 1998; Mateos et al., 2019; Williams et al., 2010), but research focused on the hand is comparatively limited, making it difficult to evaluate functional and adaptive hypotheses. What we do know regarding hand function during free-hand knapping is that a wide variety of grips are used, with a significant emphasis on precision grips (Key et al., 2018; Williams-Hatala et al., 2021). Loads tend to be concentrated on the pollex in both the dominant (Rolian et al., 2011; Williams-Hatala et al., 2018; Williams-Hatala et al., 2021, *contra* Williams et al., 2012) and non-dominant hands (Key & Dunmore, 2015), followed by the second ray, whereas the ulnar rays on both hands experience significantly lower loads (Key et al., 2019; Williams-Hatala et al., 2018, 2021). High loads on the first ray correlate with increased flexor pollicis longus (FPL) activity in other behaviors (Basmajian & De Luca, 1985; Hamrick et al., 1998), which was confirmed by two studies of muscle activity during free-hand knapping (Hamrick et al., 1998; Marzke et al., 1998). The biomechanics of knapping coupled with the large size of the FPL muscle in modern humans (it constitutes ~22% of the total thumb muscle PCSA [Marzke et al., 1999] and ~26.5% of the total deep flexor muscle mass [Lieber et al., 1992]) results in significant stress across the pollical joints.

Many aspects of the anatomy of the pollex seem to exist as a direct response to the biomechanical demands of stone tool production, making this region perhaps the best candidate for a manual adaptation for this specific behavior (Marzke, 2006). Kinematic computer modeling demonstrates that command of precision grips in modern humans is facilitated by our relatively long pollex and short fingers (Feix et al., 2015; Hu et al., 2018). Solid evidence also indicates that the enhanced pollical musculature (Lieber et al., 1992; Marzke et al., 1999; Susman, 1994), proportionately larger articular surface areas on the trapezium for the first metacarpal and the scaphoid (Marzke et al., 2010; Tocheri et al., 2005), reduced curvature of the trapeziometacarpal joint surface (Marzke et al., 2010), and the broad pollical metacarpal head relative to length (Susman, 1994) enable the pollex to generate and withstand the high forces associated with stone tool behaviors. We currently lack evidence that other aspects of the derived pollex anatomy (e.g., broad apical tufts, unguis fossa and spines to support increased unguis pulp) of modern humans have functional significance during stone tool production.

The modern human second metacarpal is also derived relative to the hypothesized primitive condition. It is the second most robust metacarpal (other than the pollical metacarpal), in contrast to the nonhuman great ape condition (Susman, 1979). The orientation of the articular surfaces on the trapezium and the capitate for the second metacarpal also reflect an enhanced ability relative to the nonhuman apes to distribute forces radioulnarly from the pollex through the trapezium-trapezoid and trapezoid-capitate joints (Tocheri et al., 2003, 2007), as occurs during stone tool production (and use) (Rolian et al., 2011;

Williams-Hatala et al., 2018, 2021). Additionally, the loads experienced by the second digit during tool behaviors are the second highest other than those on the pollex in both the dominant and non-dominant hands, and the second digit plays an important role in stabilizing hammerstones, cores, and cutting implements (Key et al., 2019; Williams-Hatala et al., 2018, 2021). It is possible these demands may have resulted in the distinctive morphology we see in modern humans, but the evidence is not as strong as the evidence for the pollex.

The presence of several features in the fifth ray of modern humans, including its relative independence and robusticity (Marzke et al., 1992), has prompted hypotheses that it may also reflect functional adaptations toward stone tool behaviors (Marzke, 2006, 2013). Indeed, new insights regarding the contributions of the fifth ray toward stone tool behaviors are coming to light, highlighting its role in stabilizing the core in the non-dominant hand (e.g., Key et al., 2019; Marzke et al., 1998) and buttressing the hammerstone in the dominant hand (Williams-Hatala et al., 2018, 2021). A recent study on the role of the non-dominant fifth digit during knapping (Key et al., 2019) reported that the majority of the time (~85% of all Oldowan and Early Acheulean strikes and ~78% of all Late Acheulean strikes) loads on the fifth distal phalanx, which experiences the greatest loads of all of the phalanges of the smallest finger, are similar to those experienced on the dominant hand's fifth digit during nut-cracking performed by modern humans (Williams-Hatala et al., 2018). Western chimpanzees (*P. troglodytes verus*) also engage in hammerstone mediated nut-cracking behaviors (Boesch & Boesch, 1993; Sakura & Matsuzawa, 1991) using grips that include the fifth ray (Boesch et al., 2017). Though we lack the data to evaluate the specifics of the grips used and the associated loads, we know that western chimpanzees lack modern human-like fifth ray morphology. Perhaps most importantly, they lack a robust fifth metacarpal (Marzke et al., 1992) that would help reduce joint stress incurred during percussive behaviors (Marzke et al., 1998; Susman, 1994). Thus, it is questionable whether the relatively low loads experienced during the tested percussive behaviors—be it knapping or nut-cracking—would be sufficient to elicit a selective response (e.g., increased robusticity) in the hominin Mc5.

The analysis of entheses (muscle attachment site) morphology is a commonly used though contentious alternative method for reconstructing the function and anatomy of fossil hominins hands. Entheses are thought to provide a direct record of muscle recruitment over the life of an individual, making them particularly compelling to paleontologists. Enthesis morphology has been cited as evidence of muscle presence and gross morphology (and by association, repeated and/or heavy muscle recruitment) for a number of hand muscles, including the flexor pollicis longus (e.g., Almécija & Alba, 2014; Susman, 1998), the opponens pollicis (e.g., Kivell et al., 2015; Maki & Trinkaus, 2011), and the flexor digitorum superficialis (e.g., Drapeau et al., 2005; Ricklan, 1987).

Popularized following Hawkey and Merbs (1995), early attempts to analyze enthesal morphology were based on qualitative scoring of the enthesal surface. More recently, methods have been developed to extract quantitative data describing aspects of the enthesal

surface (e.g., area, rugosity) thought to be informative of muscle architecture and recruitment patterns from high resolution three-dimensional models (e.g., Karakostis & Lorenzo, 2016; Turcotte et al., 2020). Multiple validation studies have generated evidence that it is not yet possible to reconstruct any aspect of muscle anatomy from the surface morphology of a single enthesis (e.g., Karakostis, Wallace, et al., 2019; Rabey et al., 2015; Williams-Hatala et al., 2016; Zumwalt, 2006, *contra* Karakostis et al., 2021) and two notable studies demonstrated that presumed enthesal surface morphology (e.g., a bony crest) is at times present in areas where the associated muscle does not actually attach (Marzke et al., 2007) or where there is no muscle at all (Eliot & Jungers, 2000). However, internal enthesal morphology may be more informative of behaviors when recorded from juvenile individuals (Turcotte et al., 2022). Another promising line of research has demonstrated that groups of entheses can be used to separate individuals into behavioral groups (e.g., occupation, walking patterns) on the basis of muscle synergies (e.g., Karakostis & Lorenzo, 2016; Karakostis, Wallace, et al., 2019; Karakostis, Jeffery, & Harvati, 2019). Though it is rare to find multiple associated hand bones from a single individual, there are notable exceptions (e.g., Kivell et al., 2011, 2015), making this a potentially fruitful avenue for reconstructing hand use in at least those species for which the relevant data are available, such as *Au. sediba* and *H. naledi*.

To summarize, the most convincing candidate for an adaptive response to stone tool production and use in the hand is the osteology and muscular anatomy of the pollex, including the first carpometacarpal joint. Moving forward, more data are needed on the kinematics, kinetics, and EMG of the digits, palm, and their muscles during both tool production and tool use, as well as a validated and accurate method for interpreting what signal, if any, is present in muscle entheses. Even then, the task of accurately reconstructing function, be it in extant or extinct organisms, is not trivial. New insights gained through the application of novel techniques for reconstructing joint mobility, such as bi-planar X-ray with X-ROMM (X-ray reconstruction of moving morphology) demonstrate it is essential to consider all six degrees of freedom and soft-tissue parameters when estimating joint mobility functions from the articular surfaces of fossil bones (Manafzadeh & Gatesy, 2021; Manafzadeh & Padian, 2018). Such realizations highlight the difficulty of assigning functional roles to individual anatomical components, such as the styloid process on the base of the third metacarpal (Marzke & Marzke, 1987), in the absence of direct experimental observation or high-resolution computer modeling of those components. Given the appearance of different combinations of derived features at various times throughout prehistory and the problems of equifinality with respect to behavior (Marzke, 2013; Weiss, 2012), a conservative approach toward interpreting hand function is warranted.

### 4.3 | Reconstructing the hand morphology of the most recent common ancestor of panins and hominins

Reconstructing the hand morphology of the most recent common ancestor (MRCA) of the panin/hominin clade is highly dependent on

which late Miocene and early Pliocene fossils are considered to be hominin (e.g., Daver et al., 2022; Macchiarelli et al., 2020; Sarmiento, 2010), and which taxa are included in the comparative sample (e.g., Almécija et al., 2015; Lovejoy, 2009; Prang et al., 2021). It is critical to recognize the paucity of the fossil record between 8 and 4 Ma for both hominins (Bobe & Wood, 2022) and African apes (McBrearty & Jablonski, 2005), and that the few fossils we have from this time period may fall within the hominin clade, or the panin clade, or in any number of extinct clades (Wood & Harrison, 2011). Among the earliest putative hominins, only *Orrorin* and *Ardipithecus* preserve hand elements, with the former restricted to two phalanges, and the only common element between the taxa is the distal pollical phalanx. That the older *Orrorin* has a more modern human-like morphology than the more recent *Ardipithecus* (Almécija et al., 2010; Lovejoy et al., 2009; but see Bobe and Wood (2022)), suggests that the evolution of grasping and enhanced manipulation within the earliest hominins may have followed several different trajectories. Furthermore, there are currently three different functional interpretations of *Ardipithecus* hand morphology (Almécija et al., 2015; Lovejoy et al., 2009; Prang et al., 2021), confounding inferences about the MRCA morphotype.

Given the functional importance of intrinsic hand proportions to locomotor and, especially, manipulative precision grasping, reconstructing the intrinsic hand proportions of the MRCA is an important first step. Do the relatively long fingers of extant *Pan* represent the hand proportions of the MRCA, or are *Pan* hand proportions uniquely derived (i.e., an autapomorphy)? Did hominins elongate their thumbs, shorten their fingers or both? And how have selective pressures on intrinsic foot proportions influenced the intrinsic proportions of the hand (Prang et al., 2021; Rolian, 2009; Rolian et al., 2010)? The inclusion of Miocene apes is essential for addressing these questions, but it does not always provide the desired resolution. For example, a phylogenetic analysis of intrinsic hand proportions including Miocene apes and *Ardipithecus* found that while *Pan* and *Pongo* share convergently-derived elongated fingers, the MRCA morphotype is reconstructed as being more *Gorilla*-like (Almécija et al., 2015; also see Drapeau and Ward (2007)). In this scenario, changes in intrinsic hand proportions are more marked among nonhuman apes, while modern human and fossil hominin hand proportions, which are convergent with dexterous monkeys (i.e., *Sapajus*, *Cebus*, *Theropithecus*), are closer to the MRCA morphotype (Almécija et al., 2015; see also Figure 9). Based solely on intrinsic hand proportions (which is not the only anatomical requirement for precision manipulation; Feix et al., 2015), the MRCA may have had more enhanced precision grip abilities (i.e., similar to dexterous monkeys and gorillas) than *Pan*. The *Gorilla*- or monkey-like intrinsic hand proportions some have proposed (see above) for the MRCA may have enabled food processing or organic/stone tool use that were later exapted for stone tool production. However, it is important to recognize that gorillas and monkeys differ notably in their hard and soft tissue anatomy, and thus are not equivalent MRCA reconstructions.

In contrast, a recent phylogenetic and morphometric analysis of intrinsic hand proportions together with metacarpal and phalangeal

shape that used a similar comparative fossil sample as the analysis discussed above, reconstructed the MRCA—as well as that of *Ardipithecus*—as a *Pan*-like hand that would have enabled below-branch suspension and vertical climbing (and potentially knuckle-walking) (Prang et al., 2021; *contra* Lovejoy et al., 2009). This analysis also found a notable transition in hand morphology between *Ardipithecus* and *Australopithecus* around 3.5 Ma, consistent with stone tool production being the driver for modern human-like intrinsic hand proportions (Prang et al., 2021). These two studies highlight the challenges of reconstructing the MRCA morphotype based on the current patchy fossil evidence, and show how a particular MRCA reconstruction is consistent with a range of inferences about evolutionary mechanisms and selective pressures (i.e., exaptation vs. adaptation). If *Ardipithecus* is not a hominin, then we have even less evidence to go on (see Wood & Harrison (2011), Sarmiento (2010) vs. Kimbel et al. (2014) and Mongle et al. (2019)).

#### 4.4 | Reconstructing the past through the lens of extant primates

The goal of paleoanthropologists and functional morphologists is to infer how variation in morphology (e.g., joint shape, length or robustness of a bone) provides information about performance, how this performance can be linked to biological role(s) and, ultimately, how those biological role(s) influences fitness (Arnold, 1983; Daegling, 2022). However, this is not an easy task, in part because it is challenging to understand how hard tissue morphology links with performance when soft tissues are not preserved, how potential variation in performance may have a positive or negative selective force in a particular environmental context (i.e., the *umwelt*; Bock & von Wahlert, 1965), and multiple aspects of morphology may covary and/or be influencing the same or different biological roles that also contribute to fitness (Daegling, 2022). Because of these challenges, many paleoanthropologists simply forego considering biological roles or fitness, and instead link morphological variation directly to behavioral variation (e.g., Kivell et al., 2011, 2015), which is far from ideal but often seems like necessity. However, new methods or advances on traditional methods applied to extant primates may help us do a better job of linking morphology and fitness.

Experimental biomechanical data can help us better understand how particular behaviors in extant primates are reflected (or not) in their hand morphology, and thus generate more informed behavioral reconstructions from the fossil evidence. Experimental evidence of the pressures incurred by the digits during modern human stone tool production and use (Key & Dunmore, 2015; Williams-Hatala et al., 2018, 2021; see above), bonobo arboreal locomotion (Samuel et al., 2018) and modern human arboreal locomotion (Lockwood et al., 2019, 2022), reveal interesting patterns. During modern human tool-related behaviors, pressures experienced are always highest on the pollex (Key & Dunmore, 2015; Williams-Hatala et al., 2018, 2021; *contra* Williams et al., 2012), while pressures during suspension and climbing, both in modern humans and bonobos, are highest on the

fingers, particularly digit 3 (Samuel et al., 2018; Lockwood et al., 2019, 2022). We will likely never have the equivalent biomechanical data for non-human ape tool use, however the relative patterns across the digits may tell us where to look for evidence of particular behaviors. With respect to the external and internal morphology, the larger loads experienced by the fingers from locomotion may override any functional signal from manipulation, whereas because the pollex is potentially not as functionally important for locomotion, its morphology may preserve functional signals of manipulative grasping (Samuel et al., 2018). Indeed, the internal bone structure of *Au. sediba* metacarpals show this dual functional signal; trabecular distribution in the Mc2-5 suggests loading of the fingers in a manner most similar to *Pongo* while the Mc1 suggests loading of the pollex was modern human-like (Dunmore et al., 2020).

From the external morphology of fossilized hand bones, we may not be able to tell whether a hominin was using a power grip to grasp a large hammer stone, a branch during suspension, or a rock face during climbing, or whether a precision grip was being used for tool use, grooming, or food processing. Musculoskeletal (e.g., Bardo et al., 2018; Domalain et al., 2017; Synek, Lu, et al., 2019) and finite-element modeling (e.g., Christen et al., 2015; Nguyen et al., 2014; Synek, Dunmore, et al., 2019) and the analysis of internal bone structure (e.g., Barak et al., 2017; Chirchir et al., 2017; Dunmore et al., 2019; Dunmore et al., 2020) can provide more nuanced interpretations of hand use from fossils. However, the musculoskeletal models that are developed and validated use scarce and difficult-to-collect biomechanical and anatomical data from extant primates, and are applied to the fossil evidence using a range of assumptions about soft tissue anatomy. Finite element modeling can provide refined information about how bone shape (both external and internal) experiences specific loads, and inverse bone remodeling allows researchers to use bone morphology to predict joint loading history (Christen et al., 2015; Synek, Dunmore, et al., 2019). Musculoskeletal and finite-element modeling require information about internal bone structure as well as loading and kinematics in relevant extant primate taxa, and both methods are computationally time-consuming. Moreover, there remains much we do not fully understand about the influences of factors beyond external and internal loads (e.g., genetics, sex, hormones, age, microbiome) on bone structure (see review in Kivell, 2016).

There are substantial gaps in our knowledge about how extant primates use their hands to interact with their environments. Although Darwin (1871) acknowledged tool use in chimpanzees and several monkeys, it is only in the last quarter century that researchers have conducted systematic analyses of food- and tool-related behaviors (Gumert et al., 2009; Marzke et al., 2015; Neufuss, Humle, et al., 2017; Tan et al., 2015) including their kinematics (Liu et al., 2009; Sirianni et al., 2018). Recent advances in primate archaeology, combined with ethological studies of a broader range of tool-using primate species, provide an invaluable source of information for how non-human primates, especially those with intrinsic hand proportions similar to that of hominins (e.g., *Macaca*, *Papio*) grip and use tools (Luncz et al., 2019; Tan et al., 2015). Primate archaeology is also our best bet for identifying archaeological signatures of the earliest forms

of hominin tool use, including organic tool use, in the archaeological record (Haslam et al., 2017; Luncz et al., 2019; Luncz et al., 2020; Mercader et al., 2002; Mercader et al., 2007).

We also require more research on how nonhuman apes and other primates grasp and load their hands during locomotor behaviors, particularly in non-terrestrial contexts (Neufuss, Humle, et al., 2017). Studies of African ape locomotor behaviors have to date been almost solely focused on forest-dwelling communities (e.g., Doran, 1993, 1996; Ramos, 2014; Remis, 1995; Sarringhaus et al., 2014; Susman et al., 1980). Chimpanzees, however, live in a variety of landscapes, ranging from dense rainforest to arid savannas (Lindshield et al., 2021). Understanding how ape locomotor or manipulative behaviors vary within and among different landscapes offers a unique opportunity to investigate the potential ecological drivers of bipedalism, arboreality, or changes in foraging strategy in a large-bodied, semi-arboreal ape that cannot be investigated from fossil evidence alone. This is particularly true of chimpanzees living in savanna-mosaic landscapes that are analogous to those reconstructed for early hominins (e.g., Senut et al., 2001; Su & Haile-Selassie, 2022; White et al., 2009), such as Issa Valley, Tanzania (Drummond-Clarke et al., 2022; Giuliano et al., 2022; Piel et al., 2017) or Fongoli, Senegal (Pruetz et al., 2015; Wessling et al., 2018). The chimpanzees in the Issa Valley occasionally climb steep, rocky outcrops (Drummond-Clarke et al., 2022), offering a valuable opportunity to investigate the potential influence that petrous climbing may have played in hominin locomotion and hand morphology (also see Everett et al. (2021)).

Improving our understanding of how extant primates use and load their hands with their associated hard and soft tissue anatomies in a variety of natural and experimental contexts can help infer the potential biological roles of fossil hominin hands, and what abilities are autapomorphic to the modern human hand. One can envision the fitness benefits of more forceful and precise grip abilities, if they facilitate even basic and inefficient (compared to modern humans and/or extant primates) use of stone tools, or the processing of organic materials if they allowed a particular hominin to access new and valuable food resources. One can also envision how features of hand morphology that facilitate stronger power grips or faster climbing would enhance fitness by avoiding terrestrial predators or falls from the canopy, especially as the hominin lower limb morphology continued to change in response to the bipedal biological role (Sylvester, 2006). Thus, hominin hand morphology may have facilitated (at least) two distinct biological roles that each contributed to fitness. However, partitioning between the two or determining how specific features or forms of the hominin hand that make up the functional complex that facilitates precision or power grip abilities may relate to fitness is far more challenging.

## 4.5 | Overview and summary

The recovery of each new hand fossil, especially associated hand elements, allows for greater insight into how extinct hominins used their hands. Fossil discoveries have provided evidence of combinations of modern human-like, nonhuman ape-like and autapomorphic morphology

not found in extant primates. Unlike Cuvier's (1812) dictum, finding one element or region of the early hominin hand does not predict the morphology of the remaining hand skeleton; the fossil record and, more so, extant primates demonstrate that extant hominoid hand morphology only scratches the surface of the diverse and often unpredictable combinations of carpal, metacarpal and phalangeal morphology that are possible within the same hand of extinct taxa. Fossil evidence of the hominin hand (combined with evidence from the remainder of the postcranial skeleton) makes it clear that facultative bipedalism, and even obligate bipedalism, did not entirely “free” the hands from the functional constraints of locomotion, nor did the use of the forelimb for locomotion exclude enhanced dexterity. Hominin hand morphology from the late Miocene to late Pleistocene shows features that are typically considered advantageous for arboreal locomotion in combination with features typically considered adaptive for forceful and precise manipulation. There is evidence in the fossil hominin record of multiple “solutions” to accommodating both of these functional requirements. Equifinality is rife.

## ACKNOWLEDGMENTS

We dedicate this review to the seminal work of Professor Mary Marzke (1937–2020), whose comparative anatomical, experimental, and evolutionary research on the hand laid the foundation for much our current understanding of all that is unique about the modern human hand and what is shared with our primate cousins. We thank Alastair Key, Johanna Neufuss, Alex Piel and Matt Tocheri for sharing images. We are grateful to Caley Orr, John Shea and two anonymous reviewers whose efforts improved our manuscript. This work is supported by the European Research Council (ERC) under the European Union's Horizon 2020 research and innovation program (grant 819960) (T.L.K.).

## DATA AVAILABILITY STATEMENT

Data sharing is not applicable to this article as no new data were created or analyzed in this study.

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**How to cite this article:** Kivell, T. L., Baraki, N., Lockwood, V., Williams-Hatala, E. M., & Wood, B. A. (2023). Form, function and evolution of the human hand. *Yearbook Biological Anthropology*, 1–52. <https://doi.org/10.1002/ajpa.24667>