

Entheseal Patterns Suggest Habitual Tool Use in Early Hominins

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ABSTRACT

Systematic tool use is a central component of the human niche. However, the timing and mode of its evolution remain poorly understood. A newly developed method for the analysis of muscle recruitment patterns (Validated Entheses-based Reconstruction of Activity - V.E.R.A.) has recently been experimentally shown to provide clear and reliable evidence of habitual activity during life from skeletal remains. It is thus ideal to investigate the emergence of tool-related behaviors in the human fossil record. Here, we investigate this question by applying V.E.R.A. to the attachment proportions of thumb (first metacarpal) muscles considered crucial for tool use, in combination with a geometric morphometric analysis of bone shape. Our sample comprises modern humans, extant great apes, Neanderthals, *Homo naledi*, three *Australopithecus* species (*A. afarensis*, *A. africanus* and *A. sediba*) and a taxonomically unassigned fossil hominin from Swartkrans, South Africa. Results show that modern humans are distinct from extant non-human great apes in the recruitment patterns of the thumb muscles examined, as expected. Importantly, all hominins except *A. africanus* exhibit human-like thumb muscle use irrespective of the overall shape of their first metacarpal. This pattern supports habitual tool-related behaviors in these early taxa—excluding *A. africanus*—despite their lack of skeletal adaptations for efficient tool use observed in the first metacarpals of later *Homo*. Our findings strongly suggest habitual tool use by early hominins, and indicate an early, mosaic establishment of this behavior among *Australopithecus* taxa, preceding the evolution of tool-related biomechanical adaptations of the hominin hand and consistent with recent archaeological discoveries.

INTRODUCTION

Habitual stone tool use is a fundamental element of the hominin adaptive niche and a cornerstone of human bio-cultural co-evolution. However, the time and mode of its emergence remain elusive. Since chimpanzees, our closest living relatives, are known to engage in stone hammer-and-anvil nut-cracking and plant-tool use (Haslam et al. 2009; Whiten et al. 1999), it is considered reasonable to suggest some form of tool-use in our last common ancestor (Kivell 2015; Panger et al. 2002). However, this view does not take into account several million years of independent chimpanzee evolution. To reliably assess early hominin behavior, therefore, we must turn to the direct evidence from the archaeological and fossil record.

The currently available evidence is inconclusive—the recently discovered lithic industry from Lomekwi, Kenya, dated to as early as 3.3 Ma (Harmand et al. 2015), is controversial, as both its artifactual character and its chronology have been questioned (Archer et al. 2020; Domínguez-Rodrigo and Alcalá 2016), while proposed 3.39 my-old cut-marks from Dikika, Ethiopia, (McPherron et al. 2010) may have been produced through taphonomic processes or bite marks rather than hominin activity (Domínguez-Rodrigo et al. 2012; Sahle et al. 2017). The hand anatomy of early fossil hominins has been used to infer their mechanical abilities and manual dexterity (Alba et al. 2003; Galletta et al. 2019; Green and Gordon 2008; Kivell et al. 2011; 2015; 2018; Marchi et al. 2017; Marzke 1983; Marzke et al. 2010; Ricklan 1987; Susman 1988, 1994). Current consensus of this work describes early hominins as showing a mosaic of human- and ape-like features, which may or may not be consistent with systematic tool use. However, while manual biomechanical dexterity and skeletal morphology are important indicators of evolutionary adaptation potentially related with tool-using skills, they cannot be used to directly infer the habitual performance of tool-related behaviors during life. Due to its importance for functional and motoric aspects, gross bone shape is considered to be genetically regulated, reflecting evolutionary adaptation, and thus less subject to change through physical activity during life (Currey 2002; Kivell 2016; Parfitt et al. 2000; Wallace et al. 2020). Bone shape, therefore, may inform on movements a taxon is adapted for, but may also reflect the retention of ancestral features which have little or no bearing on an individual's actual behavior in life. To overcome this problem researchers have turned to the analysis of trabecular features. Differences in trabecular bone architecture are often thought to inform on different loading regimes during life and thus to be a possible proxy for activity (Barak et al. 2011; Biewener et al. 1996; Kivell 2016; Ruff et al. 2006; Scherf et al. 2013; 2016; Stephens et al. 2018; Tsegai et al. 2013). Studies of trabecular bone in *Australopithecus sediba* and *A. africanus* suggested the possibility of frequent forceful opposition of the thumb in these taxa, possibly indicating a human-like use of the hand (Dunmore et al. 2020; Skinner et al. 2015b), despite their observed low manual biomechanical efficiency (Galletta et al. 2019; Karakostis et al. 2021b; Marchi et al. 2017). While the exact factors driv-

ing variation in trabecular features can often be difficult to assess (e.g., Alméjija et al. 2015; Carlson et al. 2008; Judex and Carlson 2009; Kivell 2016; Robling 2009; Skinner et al. 2015a), such results still hint at a discrepancy between biomechanical efficiency inferred by bone functional anatomy and reconstructions of habitual behavior based on analyses of structures more responsive to mechanical loading.

Another approach to reconstructing habitual activity is the analysis of muscle recruitment patterns. As the interface of soft and hard tissue, muscle attachment sites (entheses) experience mechanical stress through muscle activation and dissipate it across larger areas, resulting in remodeling of the bone surface (Benjamin et al. 2002; Cashmore and Zakrzewski 2013; Foster et al. 2014; Schlecht 2012). The analysis of enthesal morphology has been plagued by important methodological shortcomings in the past, including a former lack of supportive experimental evidence that enthesal surfaces are affected by physical activity (Rabey et al. 2015; Wallace et al. 2017; Williams-Hatala et al. 2016; Zumwalt 2006). The Tübingen University Validated Entheses-based Reconstruction of Activity (V.E.R.A.) method, however, which focuses on muscle recruitment patterns—as revealed by the relative proportions of muscle attachment sites on bone through multivariate analysis of enthesal 3D surface areas (rather than individual entheses per se)—has overcome many of these difficulties, providing a reliable way to reconstruct habitual activity in the past (Karakostis and Lorenzo 2016). Since the development of V.E.R.A. by one of us (FAK; Karakostis and Lorenzo 2016; Karakostis and Harvati 2021 and references therein), it has been validated both in documented human samples and several independent animal experimental models, and shown to reliably discern habitual muscle coordination using multiple anatomical regions and associated groups of muscles (Castro et al. 2021; Karakostis et al. 2017; Karakostis et al. 2019a; 2019b). It can therefore shed light on habitual performance of specific body movements, and thus specific behaviors, in the past (Karakostis et al. 2017; 2018; 2020; 2021a; Karakostis and Lorenzo 2016). In a recent review dedicated to previous applications of this method, Karakostis and Harvati (2021) provided a more detailed step-by-step protocol for applying V.E.R.A., to facilitate its broader application.

Here we apply this novel method for the first time to hand bones of early hominins to help elucidate the origins of human-like tool using behavior. We investigate recruitment patterns of thumb muscles important for these behaviors across hominin species in a comparative framework to help reconstruct their habitual manual activities and shed light on their potential tool use. We focus on the first metacarpal and its three attachment sites for the muscles: *opponens pollicis* (OP), *abductor pollicis longus* (APL), and first dorsal *interosseous* (DI1) (Figure 1). These muscles, which are important for human tool use (Table 1 and Materials and Methods), are thought to share key functions across humans and apes (Diogo et al. 2013; Lemelin and Diogo 2016; Vereecke and Wunderlich 2016), enabling their comparison across taxa—the OP flexes the thumb at the carpo-metacarpal joint (Netter et al. 2019) and plays a central role

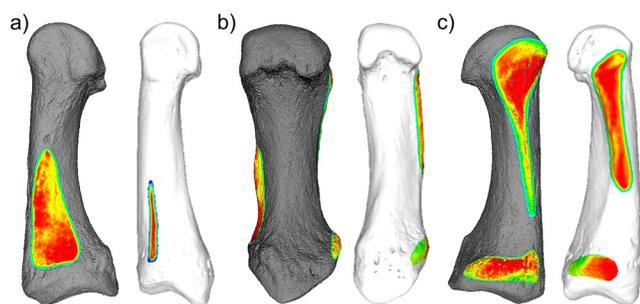


Figure 1. Depiction of the three entheses delineated on the right first metacarpal of Basel 264 (left), recent modern human, and Pan troglodytes 176229 (right) following the V.E.R.A. method developed by one of us (FAK; Karakostis and Lorenzo 2016; Karakostis and Harvati 2021 and references therein). a) medial view with the delineation of the D11 entheses; b) palmar view; c) lateral view with the delineations of the OP and APL entheses.

in precision grasping, which places the thumb in an opposing position to the palm and the remaining fingers (Napier 1956). Therefore, this muscle is often associated with human-like manual dexterity (Feix et al. 2015; Karakostis et al. 2021b; Marzke 1997) and tool-use (Kivell 2015; Marzke 2013; Marzke et al. 1998). The APL is also activated during thumb opposition and precision grasping through thumb abduction at the carpometacarpal joint (Napier 1956; Netter et al. 2019). Finally, the D11 abducts the second digit at the metacarpophalangeal joint (Netter et al. 2019), which is critical for habitual tool production (Williams-Hatala et al. 2020), and is also thought to stabilize the thumb (Marzke et al. 1998). Previous work has found that this muscle is less developed in great apes compared to modern humans (Jacofsky 2009; Tocheri et al. 2008). Importantly, electromyographic work has shown that the D11 is consistently activated together with the *flexor pollicis longus* (FPL) during human-like stone tool use irrespective of tool type, as well

as during hard hammer percussion manufacture (which involves both the dominant and the non-dominant hand), underlining the importance of this muscle for tool-related behaviors in general (Key et al. 2020; Marzke et al. 1998). Similar to the other muscles analyzed here, the FPL is generally thought to play a major role in human-like object manipulation, and particularly in tool use (Hamrick et al. 1998; Kivell 2015; Susman 1988, 1994). However, it is usually either absent or not a distinct muscle in the non-human great apes (Diogo et al. 2012). Its insertion ridge on the first distal phalanx is therefore typically not discernible in these species and, as a result, could not be included here.

In addition to the recruitment patterns of these muscles, we analyze the overall 3D shape of the first metacarpal including the shape of its entheses (see Supplementary Online Material (SOM); the terms ‘overall shape’ or ‘overall morphology’ will be used throughout the paper to refer to the shape of the bone, its head and base, as well as of the respective muscle attachment sites) to assess whether differences in muscle recruitment are independent of gross external morphology of the bone. The latter is generally assumed to reflect genetic adaptation directly associated with biomechanical efficiency (including morphological characters across the bone diaphysis and articular surfaces; see, e.g., Galletta et al. 2019; Kivell 2015; Marchi et al. 2017; Marzke 2013).

Overall, we expect that habitual human-like tool users (later *Homo*, here comprising fossil and recent *Homo sapiens* and *Homo neanderthalensis*) will differ in their overall first metacarpal shape from the non-human great apes, reflecting genetic adaptation and possibly biomechanical efficiency related to tool use in the former (e.g., Karakostis et al. 2021b). At the same time, we predict muscle recruitment patterns showing proportionately larger D11 entheses in species with human-like tool use (recent and fossil *Homo sapiens*, *Homo neanderthalensis*), and proportionally smaller D11 attachments in the non-human great apes. Because

TABLE 1. DETAILS ON EARLY FOSSIL HOMININ SAMPLE
(references are provided for the dating of the fossil or the respective site).

ID	Species	Date	Location*	Reference
A.L. 333w(-39)	<i>Australopithecus afarensis</i>	~3.2 mya	Hadar, ET	Walter 1994
StW 418	<i>Australopithecus africanus</i>	1.95–2.95 mya	Sterkfontein, SA	Pickering et al. 2011
UW 88-119	<i>Australopithecus sediba</i>	1.78–1.95 mya	Malapa, SA	Pickering et al. 2011
SK 84	early <i>Homo</i> / <i>Paranthropus robustus</i> [†]	1.8–1.9 mya	Swartkrans, SA	Pickering et al. 2011
UW 101-1321	<i>Homo naledi</i>	241–335 kya	Rising Star Cave, SA	Robbins et al. 2021

*Abbreviations following ISO 3166 country codes.

[†]See Susman (1988) and Trinkaus and Long (1990).

of the reported importance of the DI1 across tool-related behaviors irrespective of tool type or industry (Key et al. 2020; Marzke et al. 1998), we consider it to reflect generalized tool-related tasks. If early hominins already practiced generalized human-like tool use habitually, we expect them to also exhibit proportionally larger DI1 attachments, irrespective of human- or ape-like overall bone shape. Finally, the muscles OP and APL are also essential for human precise thumb manipulatory activities (e.g., Clarkson 2000; Marzke 1997, 2013), with recent biomechanical research demonstrating the substantial contribution of OP to the adaptive evolution of increased thumb efficiency in hominins after approximately 2 Ma (Karakostis et al. 2021b). Since more developed tool-related thumb use is thought to have emerged among later hominins (e.g., Karakostis et al. 2021b; Marzke 1997; also see Shea 2016), we would not necessarily expect early hominins to exhibit a human-like pattern in the entheses of these two pollical muscles, even if they show evidence for habitual generalized tool-use as reflected by proportionally larger DI1 attachments.

MATERIALS AND METHODS

Our sample comprises *Australopithecus*, *Homo naledi*, and SK 84 (an unassigned specimen from Swartkrans, South Africa) (see Table 1), as well as fossil and recent *Homo sapiens*, *Homo neanderthalensis*, and the three great ape genera (*Pongo pygmaeus*: n=7, *Pongo abelii*: n=2, *Gorilla gorilla*: n=7, *Pan troglodytes*: n=9) (Tables 2, 3). Our analysis focuses on the first metacarpal, as preservation of complete hand skeletons is rare in the fossil record (Kivell et al. 2011; 2018). Additionally, the first metacarpal contains three muscle attachment sites (see Figure 1), among which the OP and the DI1 are thought to play an important role during human-like tool use (Key et al. 2020; Marzke et al. 1998). Details on muscle function and location of the attachment sites can be found in Table 4.

The muscles examined here (OP, APL, DI1) share important corresponding functions across humans and the great apes (Diogo et al. 2013; Lemelin and Diogo 2016; Vereecke and Wunderlich 2016). It has been reported that OP serves as a flexor both in humans and *Pan troglodytes*, whereas it functions as an adductor rather than an abductor of the thumb in the latter species (Karakostis et al. 2021b; Marzke et al. 1999). Although the dorsal *interossei* have been reported absent in *Pan troglodytes*, in fact they present a plesiomorphic state, where the *intermetacarpales* 1 to 4 are not fused with the *flexores brevis profundi* 3, 5, 6 and 8 to form the dorsal *interossei* (Diogo et al. 2012). However, since *intermetacarpalis* 1 attaches in the same exact bone areas as DI1 (Diogo et al. 2013), it is assumed here that it has a similar function (i.e., contraction of the muscle would naturally lead to abduction of the index finger) (Lemelin and Diogo 2016; van Leeuwen et al. 2018; Vereecke and Wunderlich 2016). Most critically for our study, the attachment site of the DI1 can be identified reliably across all taxa in the form of a bone modification at the basal medial aspect of the first metacarpal, predominantly in the form of a depression in the area of muscle attachment (see Figure 1),

indicating the presence of biomechanical stress associated with muscle pull.

During data collection, the right anatomical side was generally prioritized. However, the left metacarpal was used if the right side was damaged. In our analyses, all bones associated with the same species consistently plotted together irrespective of anatomical side (see Figure 4 below), indicating that any bilateral differences were not considerable compared to interspecies variation.

ENTHESIS IDENTIFICATION AND DELINEATION

Previous work has shown that multivariate analyses of the proportions among different entheses can be used to reconstruct habitual activity and are not influenced by systemic factors such as body size or genetics (Castro et al. 2021; Karakostis et al. 2017; 2018; 2019a; 2019b; 2020; Karakostis and Lorenzo 2016). We applied this new, experimentally verified method (V.E.R.A.) to the analysis of the enthesal proportions of the first metacarpal muscles OP, DI1 and APL (see Table 4). The entheses were delineated on three-dimensional surface models of the bones using tools provided by Meshlab (CNR, Rome; version 2016.12 for Windows, Cignoni et al. 2008). The identification of the entheses and subsequent delineation followed the published V.E.R.A. protocols (Karakostis and Harvati 2021; Karakostis and Lorenzo 2016; Karakostis et al. 2020). Briefly, different filters in Meshlab (e.g., the ‘Discrete Curvatures’, ‘Equalize Vertex Color’ and ‘Principal Directions of Curvature’ filters) were applied to the 3D models of the bones to identify differences in elevation—including both projection and depression—coloration, and surface complexity in the area of muscle attachment. Based on these criteria, the enthesal surfaces were delineated and then separated from the surrounding bone. Afterwards, the 3D surface areas of the entheses were measured in square millimeters by the tools provided by Meshlab, to be used as variables in the V.E.R.A. analysis (Karakostis and Lorenzo 2016). Our measuring protocol allowed for minimal taphonomic damage of the entheses, which is common in fossil and archaeological specimens, so as to maximize the fossil hominin samples. Minimal damage on one enthesis was exhibited by La Chapelle-aux-Saints, La Ferrassie 1, Qafzeh 9, Villabruna, and Grevenmacher 93. These specimens nonetheless plotted close to other individuals of their respective taxa, suggesting that our analysis is robust towards slight taphonomic damage. This allowed us to confidently include early fossil hominin UW 88-119 (*A. sediba*) that presents slight damage on its DI1 muscle attachment site.

PRECISION TEST

The entheses of all australopithecids, *H. naledi*, and one randomly selected individual each of Neanderthals and early modern humans (La Ferrassie 1, Ohalo 2) were delineated twice by the same observer (JK), leaving at least one month between the first and the second observation. Precision was calculated by taking the mean of the two measurements and dividing it by their standard deviation. The result was

TABLE 2. DETAILS ON LATER *HOMO* SAMPLE
(references are provided for the dating of the fossil or the respective site).

ID	Species	Age	Sex	Date	Location*	Reference
Abri Pataud 1	fossil <i>H. sapiens</i>	20–29	Female	26–28 kya	France	Villotte et al. 2015
Abri Pataud 3	fossil <i>H. sapiens</i>	adult	Female	26–28 kya	France	Villotte et al. 2015
Arene Candide 2	fossil <i>H. sapiens</i>	~25	Male	11–12 kya	Italy	Sparacello et al. 2018
Ohalo 2	fossil <i>H. sapiens</i>	~35–40	Male	ca. 19 kya	Israel	Hershkovitz et al. 1995
Qafzeh 9	fossil <i>H. sapiens</i>	15–19	Female	90–100 kya	Israel	Valladas et al. 1988
Villabruna	fossil <i>H. sapiens</i>	~25	Male	ca. 14 kya	Italy	Vercellotti et al. 2008
Amud 1	<i>H. neanderthalensis</i>	~25	Male	53±8 kya	Israel	Rink et al. 2001
La Chapelle-aux-Saints	<i>H. neanderthalensis</i>	~60–70	Male	47–56 kya	France	Raynal 1990
Kebara 2	<i>H. neanderthalensis</i>	25–30	Male	60–64 kya	Israel	Szwarcz et al. 1989
La Ferrassie 1	<i>H. neanderthalensis</i>	Adult	Male	43–45 kya	France	Guérin et al. 2015
Shanidar 4	<i>H. neanderthalensis</i>	30–45	Male	60–100 kya	Iraq	Trinkaus 1983
B 137	modern <i>H. sapiens</i>	31	Male	19th century AD	Basel, CH	Hotz and Steinke 2012
B 211	modern <i>H. sapiens</i>	21	Male	19th century AD	Basel, CH	Hotz and Steinke 2012
B 264	modern <i>H. sapiens</i>	41	Male	19th century AD	Basel, CH	Hotz and Steinke 2012
GV 12	modern <i>H. sapiens</i>	30–40	Female	13th–14th/15th century AD	Grevenmacher, LU	Trautmann 2012
GV 29	modern <i>H. sapiens</i>	30–40	Female	13th–14th/15th century AD	Grevenmacher, LU	Trautmann 2012
GV 31	modern <i>H. sapiens</i>	20–25	Female	13th–14th/15th century AD	Grevenmacher, LU	Trautmann 2012
GV 46	modern <i>H. sapiens</i>	30–40	Male	13th–14th/15th century AD	Grevenmacher, LU	Trautmann 2012
GV 72	modern <i>H. sapiens</i>	20–30	Male	13th–14th/15th century AD	Grevenmacher, LU	Trautmann 2012
GV 93	modern <i>H. sapiens</i>	20–25	Female	13th–14th/15th century AD	Grevenmacher, LU	Trautmann 2012
GV 105	modern <i>H. sapiens</i>	30–40	Female	13th–14th/15th century AD	Grevenmacher, LU	Trautmann 2012
GV 112	modern <i>H. sapiens</i>	30–40	Male	13th–14th/15th century AD	Grevenmacher, LU	Trautmann 2012)
GV 117	modern <i>H. sapiens</i>	20–25	Male	13th–14th/15th century AD	Grevenmacher, LU	Trautmann 2012
GV 121	modern <i>H. sapiens</i>	20–25	Female	13th–14th/15th century AD	Grevenmacher, LU	Trautmann 2012
GV 132	modern <i>H. sapiens</i>	40–50	Male	13th–14th/15th century AD	Grevenmacher, LU	Trautmann 2012
GV 143	modern <i>H. sapiens</i>	30–40	Male	13th–14th/15th century AD	Grevenmacher, LU	Trautmann 2012

*Abbreviations following ISO 3166 country codes.

TABLE 3. DETAILS ON GREAT APE SAMPLE.

ID*	Species	Age [†]	Sex	Wild-caught / Captive	Provenance [‡]	Location
1784	<i>Gorilla gorilla</i>	Adult	Female	Wild-caught	Gabon	State Museum of Natural History Stuttgart, Germany
6294	<i>Gorilla gorilla</i>	Adult	Male	Wild-caught	Gabon	Natural History Museum Basel, Switzerland
7464	<i>Gorilla gorilla</i>	Subadult	Male	Wild-caught	Gabon	State Museum of Natural History Stuttgart, Germany
10429	<i>Gorilla gorilla</i>	Adult	Male	NN	NN	Natural History Museum Basel, Switzerland
38230	<i>Gorilla gorilla</i>	Adult	Female	Captive	Wilhelma Zoo Stuttgart, DE	State Museum of Natural History Stuttgart, Germany
167368	<i>Gorilla gorilla</i>	NN	NN	Wild-caught	Cameroon	American Museum of Natural History, NY, New York, USA [§]
176225	<i>Gorilla gorilla</i>	Adult	Male	Wild-caught	Gabon	National Museum of Natural History, Washington, DC, USA
1794	<i>Pan troglodytes</i>	Adult	Male	Wild-caught	Gabon	State Museum of Natural History Stuttgart, Germany
2738	<i>Pan troglodytes</i>	Adult	NN	Wild-caught	Southern Cameroon	State Museum of Natural History Stuttgart, Germany
7597	<i>Pan troglodytes</i>	Adult	NN	NN	NN	Natural History Museum Basel, Switzerland
8869	<i>Pan troglodytes</i>	Adult	Male	Captive	Zoological garden Basel, CH	Natural History Museum Basel, Switzerland
10449	<i>Pan troglodytes</i>	Adult	Male	Wild-caught	Ivory Coast	Natural History Museum Basel, Switzerland
10824	<i>Pan troglodytes</i>	Adult	Female	Captive	Zoological garden Basel, CH	Natural History Museum Basel, Switzerland
51376	<i>Pan troglodytes</i>	NN	Female	Wild-caught	DR Congo	American Museum of Natural History, NY, New York, USA [§]
176229	<i>Pan troglodytes</i>	NN	Female	Wild-caught	Cameroon	National Museum of Natural History, Washington, DC, USA [§]
2488	<i>Pan troglodytes</i>	NN	NN	NN	NN	Duke University, Evolutionary Anthropology Department, Durham, NC, USA [§]
1687	<i>Pongo pygmaeus</i>	Adult	Male	Wild-caught	Borneo	State Museum of Natural History Stuttgart, Germany
2190	<i>Pongo pygmaeus</i>	Adult	Female	Wild-caught	Borneo, MY	State Museum of Natural History Stuttgart, Germany
6286	<i>Pongo abelii</i>	NN	Male	Wild-caught	Sumatra	Natural History Museum Basel, Switzerland
7457	<i>Pongo pygmaeus</i>	Adult	Male	Wild-caught	Northern Borneo	State Museum of Natural History Stuttgart, Germany
10002	<i>Pongo abelii</i>	NN	Female	Wild-caught	Northern Sumatra	Natural History Museum Basel, Switzerland

TABLE 3. DETAILS ON GREAT APE SAMPLE (continued).

ID*	Species	Age [†]	Sex	Wild-caught / Captive	Provenance [‡]	Location
10965	<i>Pongo pygmaeus</i>	NN	Female	Captive	Zoological garden Basel, CH	Natural History Museum Basel, Switzerland
142169	<i>Pongo pygmaeus</i>	Young adult	Female	Wild-caught	Borneo, ID	National Museum of Natural History, Washington, DC, USA
145302	<i>Pongo pygmaeus</i>	Adult	Female	Wild-caught	Borneo, ID	National Museum of Natural History, Washington, DC, USA
200900	<i>Pongo pygmaeus</i>	NN	Female	Wild-caught	Borneo, ID	American Museum of Natural History, NY, New York, USA [§]

*Museum inventory numbers.

[†]The bones of all individuals were fused, including specimens with unknown exact age, indicating adult or near-adult status.

[‡]Abbreviations following ISO 3166 country codes.

[§]Specimens were downloaded from MorphoSource.

then multiplied by a hundred. The resulting number depicts the percentage of error for each enthesis. Precision was generally high among all entheses and individuals, as error rates were consistently below 5% (ranging from 0.7% to 4.61%), in broad agreement with the error tests previously reported for V.E.R.A. in its first publication (Karakostis and Lorenzo, 2016).

STATISTICAL ANALYSES

Principal Components Analysis

The surface area measurement of each enthesis was size-adjusted by dividing it by the geometric mean (e.g., Elewa 2010; Lycett et al. 2006), calculated using all three enthesal measurements of each individual. This standardization process, which constitutes part of the V.E.R.A. protocols (e.g., Karakostis et al. 2017), is shown to adequately control for the effects of bone dimensions and body size on the multivariate proportions among muscle attachment sites (Karakostis et al. 2017; 2019a; 2021a; Karakostis and Harvati 2021). The resulting values represent the propor-

tions of the entheses among each other for each individual (SOM Table 1). These values are irrespective of total bone size (whose variability might be affected by other potential systemic factors not associated with overall enthesal size variation), as they represent the proportion of each enthesis compared to the individual’s geometric mean of the enthesal surfaces on the first metacarpal. They signify whether the measurement of the enthesis is larger (value >1) or smaller (value <1) than the geometric mean of all three entheses. These size-adjusted enthesal measurements were analyzed in a Principal Components Analysis (PCA) based on a correlation matrix using PAST 3.25 (Hammer et al. 2001). This analysis does not assume *a priori* assignment of specimens to groups and is used to find the main axis of variance among the individuals. The absence of outliers was confirmed using the z-score approach (Field 2017). Relevant principal components (PCs) were selected for plotting following the scree-plot approach (Field 2017). Since the early fossil hominins were not included in the original PCA, their PC scores were calculated in R (RStudio Inc., Boston; R version 3.6.2 for Windows, R Core Team 2021)

TABLE 4. CHARACTERISTICS OF MUSCLES AND ATTACHMENT SITES (bold) USED IN THIS ANALYSIS*.

Muscle	Origin	Insertion	Muscle function
<i>Opponens pollicis</i>	Trapezium bone	Radial diaphysis of MC1	Abducts, rotates, and flexes the thumb
<i>Abductor pollicis longus</i>	Radius, ulna, scaphoid, trapezium, transverse carpal ligament	Base of MC1	Abducts the thumb at the carpometacarpal joint, abducts the wrist radially
<i>First dorsal interosseous</i>	Diaphyses of MC1 and MC2	Base of PP2	Abducts the 2nd digit

*After Netter et al. (2019).

TABLE 5. EIGENVALUES AND FACTOR LOADINGS OF PC1-3 OF THE ANALYSIS OF ENTHESEAL PROPORTIONS.

Principal component	Eigenvalue	% of variance	Factor loadings		
			OP	APL	DI1
PC1	1.86	62.06%	0.71	0.62	-0.99
PC2	1.1	36.52%	-0.7	0.78	-0.01
PC3	0.04	1.42%	0.11	0.1	0.14

using the 'predict' function and then projected onto the PC plot. PC loadings are reported in Table 5.

Discriminant Function Analysis

We conducted a discriminant function analysis (DFA) using the IBM SPSS software package v.25 (IBM Corp. 2017) to assess whether differences in enthesal proportions serve to reliably differentiate between tool-users and non-tool-users. The sample was divided into two groups: The first encompassed the tool-users *Homo neanderthalensis* and *Homo sapiens*, designated as 'Later Homo', and the second included all great apes. Additionally, the fossil hominins were entered with unknown group membership to predict their classification with 'Later Homo' or great apes. The assumptions of the DFA were met (Field 2017). Since the Box's M test was non-significant, indicating homogeneity of covariance matrices (Field 2017), the within-groups covariance matrix was used for developing the discriminant functions. The variables were entered stepwise and the robustness of the classification was validated through Leave-one-out classification (SOM Tables 2 and 3). The analysis was performed using the size-adjusted measurements of all three entheses as variables. However, the stepwise procedure only retained the adjusted DI1 measurement in the analysis, as an analysis based only on this variable provides the best separation of the two groups. It should be highlighted that this variable represents the DI1 enthesal surface areas adjusted using the geometric mean, which is a measure of the DI1's proportion compared to the other entheses in each individual (i.e., their geometric mean; e.g., Elewa 2010; Lycett et al. 2006). Details on DFA statistics, including percentages of correct original and cross-validated group classification, are reported in the Supplementary Online Material (see SOM Tables 2 and 3).

OVERALL 1ST METACARPAL 3D SHAPE ANALYSIS

The analysis of overall bone shape was conducted using geometric morphometrics. A brief description of the procedure will be provided here, while details on the statistical analysis and the precision test can be found in the Supplementary Online Material.

In cases where the right first metacarpal was not sufficiently preserved, the left side was mirrored for the geometric morphometric shape analysis. Due to preservation

issues, the Amud 1 Neanderthal and one *Pan* specimen had to be removed for this analysis.

The .ply files of the metacarpal surface models and of the entheses were imported into RStudio. The landmarks for the muscle attachment sites were not placed on the 3D models of the metacarpal, but on the separately imported models of the entheses, to minimize potential sources of error. Consequently, centering the models prior to digitization had to be disabled, so that the 3D model of the overall bone and the models of the corresponding entheses were still in the same coordinate system. As a result, the landmarks could later be combined for the analysis, despite being placed on separate models. Before landmarks were digitized, the entheses were placed in their correct anatomical position. For this, Meshlab was opened in a second window. Here, the 3D models of the entheses were placed on top of the models of their corresponding bone. Using this as a reference, the orientation of the entheses could be adjusted to properly match their position on the bone. For the landmark digitization in RStudio, the package geomorph (Adams and Otárola-Castillo 2013) was used to place fixed landmarks on the bone and enthesal surfaces, registered in geometrically corresponding positions. Six landmarks were placed on each enthesis, 9 landmarks were used to capture the shape of the bone, 3 landmarks were placed on the proximal, and 7 on the distal articular surface. Detailed landmark descriptions and illustrations are reported in SOM Table 4 and Figure 2.

RESULTS

Results of the overall shape analysis are reported in the Supplementary Online Material (SOM text). As expected, recent and fossil *H. sapiens* and *H. neanderthalensis* are well-differentiated from non-human great apes on PC1 of the PCA, showing minimal overlap with *Pan* and no overlap with *Gorilla* or *Pongo* (Figure 3, SOM Figure 1). All australopiths in our sample plot with the non-human great apes and away from later *Homo*. In contrast, *H. naledi* and SK 84 fall with later *Homo*.

The results of the muscle recruitment pattern analysis (Methods; see Table 5 and SOM Table 1) are depicted in Figure 4. The variation on PC1 (62.02% of variance) indicates differences in the proportionate size of the DI1 enthesis (loading negatively; see Table 5). In close agreement with our predictions, this axis clearly separates great apes

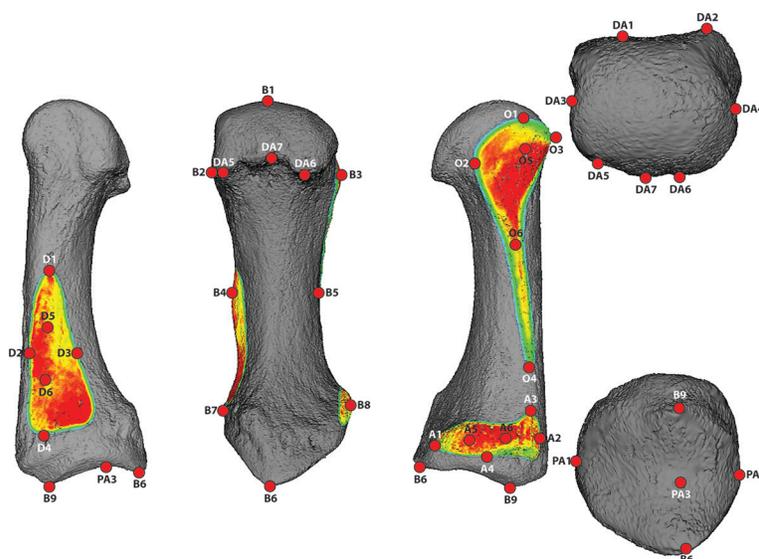


Figure 2. Location of the fixed landmarks depicted on the first metacarpal of a recent *H. sapiens* from Basel (B 264). Landmark descriptions are reported in SOM Table 4.

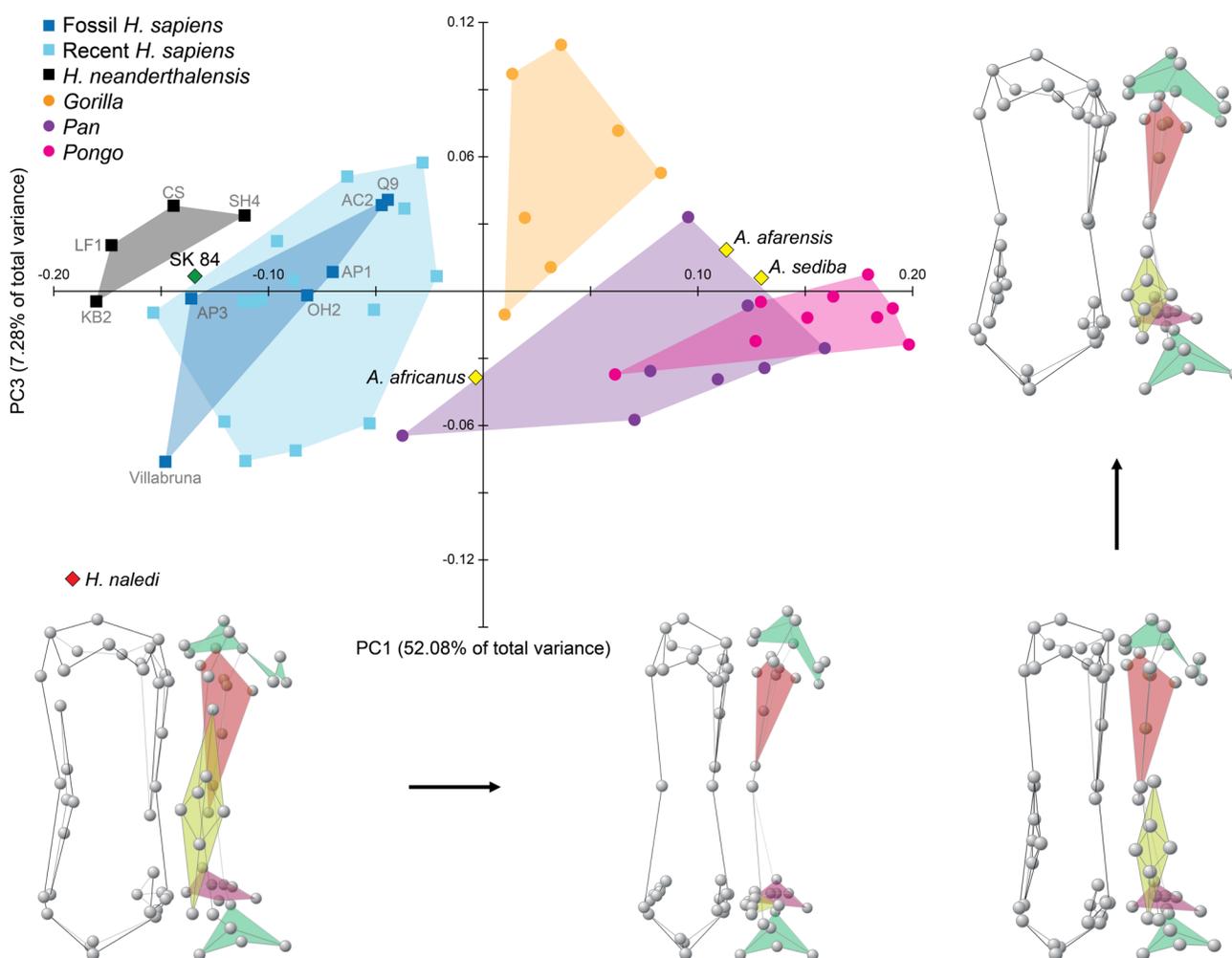


Figure 3. PCA of Procrustes-superimposed landmarks of the first metacarpal without a priori group association, PC1 compared to PC3. Shape changes along PC1 and PC3 are illustrated below and to the right of the plot, respectively. OP: red; DI1: yellow; APL: purple; articular surfaces: green. Abbreviations: OH: Ohalo; AP: Abrí Pataud; AC: Arene Candide; Q: Qafzeh; KB: Kebara; CS: Chappelle-aux-Saints; LF: La Ferrassie; SH: Shanidar.

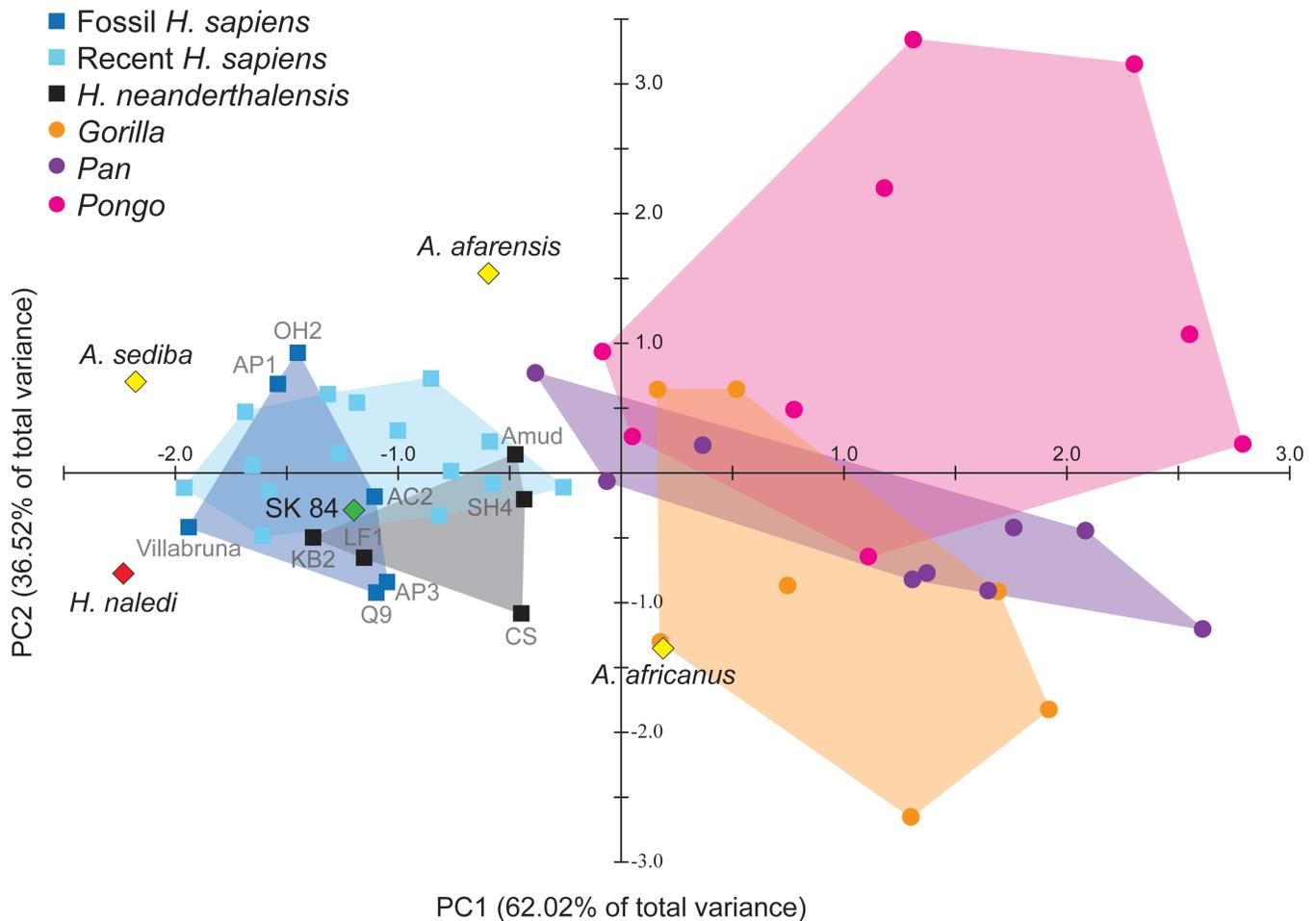


Figure 4. PCA on size-adjusted enthesal measurements without a priori group association, PC1 compared to PC2. Abbreviations: OH: Ohalo; AP: Abri Pataud; AC: Arene Candide; Q: Qafzeh; KB: Kebara; CS: Chapelle-aux-Saints; LF: La Ferrassie; SH: Shanidar.

(more positive scores, indicating proportionally smaller DI1 attachments) from later *Homo* (more negative scores, reflecting proportionally larger DI1 entheses), with minimal overlap with *Pan* (one specimen) and no overlap with *Gorilla* or *Pongo*. All earlier fossil hominins except *A. africanus* show negative PC1 scores and plot close to later *Homo* when projected into the PC plot, indicating human-like DI1 proportions. *H. naledi* plots towards the negative extreme of PC1, indicating an unusually proportionally large DI1 entheses. The only individual with similarly large DI1 proportions is *A. sediba*, plotting between early *H. sapiens* and *H. naledi*. *A. africanus* is the only hominin that clusters with the great apes, falling within the PC1 ranges of all great ape genera, indicating a proportionally smaller DI1 attachment for this taxon.

PC2 (36.52% of variance), on the other hand, differentiates specimens with a proportionally larger OP entheses (loading negatively; see Table 5) from those with a proportionally larger APL attachment site (loading positively; see Table 5). On this axis, later *Homo* cluster tightly around 0, with scores mainly between -1 and 1, indicating a relative balance in the proportions of their OP and APL attachments, in line with the importance of both these muscles for

precise thumb movements fundamental to specialized tool use. The great apes, on the other hand, show great variation and widely contrasting patterns in the relative proportions of these two entheses. While *Pan* is similar to *Homo* in its PC2 scores (clustering mainly between -1 and 1), *Pongo* plots on the positive side of PC2 with proportionally larger APL and smaller OP entheses compared to all other samples; and *Gorilla* on the negative side, showing the inverse pattern. Among earlier hominins projected into the plot, *H. naledi*, SK 84, and *A. sediba* overlap with later *Homo*, also clustering tightly around 0 in their PC2 scores. In contrast, *A. afarensis* shows a more positive PC2 value than all other hominins, similar only to *Pongo*, and *A. africanus* a more negative score, overlapping with *Gorilla*.

The discriminant function analysis (DFA) classified later *Homo* vs. the great ape genera with an accuracy of 100% and 96% respectively (see SOM Tables 2 and 3). Early hominins were treated as unknown. *A. africanus* was the only hominin classified with the great apes (posterior probability 70%, Table 6). All other hominins, including *A. afarensis*, *A. sediba*, *H. naledi*, and SK 84 were classified with later *Homo*.

TABLE 6. PREDICTED GROUP/POSTERIOR PROBABILITY VALUES OF THE DISCRIMINANT FUNCTION ANALYSIS*.

Enthesal proportions	
<i>A. afarensis</i>	Later <i>Homo</i> / 0.95
<i>A. africanus</i>	great apes / 0.70
<i>A. sediba</i>	Later <i>Homo</i> / 1
<i>H. naledi</i>	Later <i>Homo</i> / 1
SK 84	Later <i>Homo</i> / 0.99

*Later *Homo* comprises *H. sapiens* and *H. neanderthalensis*.

DISCUSSION

As expected, later *Homo* differs from the non-human great apes in the overall shape of the first metacarpal. Consistent with findings from previous studies of this bone (e.g., Karakostis et al. 2021b; Kivell et al. 2018; Marzke 2013; Susman 1988), all australopiths exhibited multiple ape-like features suggesting low biomechanical efficiency, while *H. naledi* and SK 84 were more similar to later *Homo* (see Figure 3, SOM Figure 1).

In terms of the recruitment pattern of the DI1, we predicted that the relative proportions of this muscle's enthesal would differentiate between later *Homo* and the other great apes, in part due to its importance for generalized human-like tool-related behaviors. The critical role of the DI1 was recently highlighted by experimental electromyographic work (Key et al. 2020), which reported high levels of activation of this muscle during the use of all stone tool types. On this basis, we consider that a contraction of the DI1, strongly pressing tools between the abducted index finger and the thumb's distal pad, without necessarily fully opposing or abducting the thumb (and therefore without involving systematic co-recruitment of OP and APL, respectively), as a shared component in human tool-use, which can be used to assess the origins of this behavior in the fossil record. Consistent with our prediction, we found a strong differentiation between later *Homo* and the non-human great apes, with proportionally larger DI1 muscle attachments in the former. Furthermore, all fossil hominins investigated except *A. africanus* showed DI1 proportions similar to those of later *Homo*, indicating that these taxa likely exhibited habitual tool-related behavior (see Figure 4, see Table 6).

Among australopiths, *A. sediba* and the earlier *A. afarensis* present human-like DI1 relative proportions consistent with habitual tool-use, despite both showing a clearly ape-like overall shape of the first metacarpal. *A. afarensis* has been proposed as one of the most likely potential makers of the Lomekwian due to its spatiotemporal range (Harmand et al. 2015). Although our study cannot confirm an association between this taxon and Lomekwian lithics, our results are consistent with this hypothesis. Our findings also support tool-related behaviors in *A. sediba*, previously

proposed on the basis of its trabecular bone structure and its unusually long thumb (Dunmore et al. 2020; Kivell et al. 2011; 2018). While tools have not been recovered in association with this species, they have been found at nearby contemporaneous sites (Backwell and d'Errico 2001; d'Errico and Backwell 2003; Kuman and Clarke 2000; Susman 1988). Previous analyses have found that both these australopith taxa are characterized by low thumb opposition efficiency (Karakostis et al. 2021b)—as also indicated by their overall bone morphology (see Figure 3, SOM Figure 1). Therefore, while these individuals recruited the DI1 more frequently than non-human great apes, this should not be taken to suggest a human-like level of thumb dexterity. On the contrary, our findings indicate that these early hominins were likely habitual tool users *even though* their hand anatomy lacked several key adaptations for efficient tool manipulation seen in later *Homo* (e.g., see Karakostis et al. 2021b; Kivell et al. 2018). Unlike all other hominins included here, *A. africanus* was similar to the great apes in both overall first metacarpal shape and its enthesal patterns. Its proportionally small DI1 attachment indicates a less frequent use of this muscle. *A. africanus* was also the only hominin classified with the non-human great apes in our discriminant analysis (see Table 6). Our results therefore do not support habitual human-like tool use in *A. africanus*, *contra* previous interpretations of trabecular bone distribution in this specimen (Almécija et al. 2015; Skinner et al. 2015a, 2015b).

The Swartkrans specimen SK 84 was similar to later *Homo* in both overall shape and muscle recruitment patterns. Its enthesal proportions indicate frequent recruitment of the DI1, consistent with habitual tool use. This specimen is dated to ca. 2.0–1.8 Ma and is attributed to either early *Homo* or *Paranthropus* (Susman 1988; Trinkaus and Long 1990). It was found in association with bone tools (Backwell and d'Errico 2001; d'Errico and Backwell 2003), and its morphology and thumb opposition efficiency, as well as overall first metacarpal shape, point to increased manual dexterity relative to earlier hominins (Karakostis et al. 2021b; Skinner et al. 2015b; Susman 1988; Tocheri et al. 2008; Trinkaus and Long 1990). *H. naledi* was characterized by the proportionally highest observed activation levels

of DII. While this taxon has not been found in association with lithic artifacts (Kivell et al. 2015), its human-like overall first metacarpal shape (see Figure 3, SOM Figure 1), and the derived morphology of its thumb and wrist (Kivell et al. 2015) also support considerable thumb opposition and tool-using efficiency (Galletta et al. 2019; Karakostis et al. 2021b).

Finally, later *Homo* consistently presented similar relative proportions between the entheses of the other two muscles investigated here, OP and APL (reflected in the PC2 axis; see Figure 4). We interpret these findings as suggesting a similarly frequent recruitment of the OP and APL, possibly due to the important role of both muscles in precision grips. Such a relatively balanced relationship between the OP and APL entheses was also found in most hominins investigated, with the exception of the earlier *Australopithecus* specimens—*A. afarensis* was similar to *Pongo* in its relatively greater proportion of the APL, while *A. africanus* clustered with *Gorilla* in showing a relatively greater proportion of the OP. While our results do not support habitual tool use for *A. africanus*, the comparatively lower biomechanical efficiency of the muscle OP in *A. afarensis* (Karakostis et al. 2021b) makes it likely that this muscle's contribution was less important than that of DII—whose function is proposed to be essential for all types of human-like tool use (Key et al. 2020)—for any tool-related activities of this taxon. Therefore, the combination of human-like DII proportions with ape-like OP / APL proportions in *A. afarensis* suggests simple tool use, without more specialized, precision-based behaviors observed in later species. In the case of *A. sediba*, both enthesal patterns (i.e., relative DII size and OP / APL proportions) are strikingly human-like (see Figure 4), despite the overall ape-like shape of its first metacarpal (see Figure 3, SOM Figure 1) and its relatively low biomechanical efficiency for thumb opposition (Karakostis et al. 2021b). Compared to the earlier *A. afarensis*, this finding is consistent with a more human-like and specialized pattern of tool using behavior in this taxon, preceding the evolution of heightened manual biomechanical efficiency observed in later *Homo* (see Kivell et al. 2011; Kivell et al. 2018). In contrast to *Homo* and most hominins, the great ape taxa were characterized by widely diverging patterns in their relative OP / APL proportions. At present it is unclear whether these proportional differences can be attributed to different locomotor or manipulative behaviors in these taxa, and this should be investigated further in the future.

Our proposed interpretation that some of the observed enthesal patterns in our study likely reflect habitual tool use largely relies on previous EMG experiments (e.g., Key et al. 2020; Marzke et al. 1998), which highlighted the importance of the DII muscle for stone tool-related activities in humans. Nonetheless, an alternative interpretation of our results would be that these enthesal proportions in early hominins may reflect the habitual performance of more generalized human-like hand use, for diverse types of object manipulation (which may or may not include stone tool-use in particular). This possibility cannot be dismissed, especially considering that these early hominin fossils were

not found in association with stone tools. The hypothesis of tool use in these early taxa can be further tested by investigating additional attachment sites and other aspects of bone morphology. For example, while the thumb plays an important role in human-like tool use, recent studies have shown the relevance of the second and fifth digit for this behavior, which should be further assessed (Key et al. 2019; Williams-Hatala et al. 2020). Furthermore, here we only investigated the thumb metacarpal, excluding muscles that attach to the phalanges of this ray, such as the FPL. Like the DII, the FPL is frequently activated during human-like tool use (Key et al. 2020), rendering the investigation of the interaction between these two muscles an intriguing objective. Future studies should therefore expand the analysis to additional bones of the thumb as well as to the remaining hand elements, to further assess how the pattern revealed in this study may interact with the enthesal proportions of other muscles that closely coordinate for human-like tool use.

CONCLUSION

Our analysis of thumb muscle attachment patterns supports an early emergence of habitual simple tool use, long before the evolution of early *Homo*, consistent with recent archaeological hypotheses. However, not all early hominins showed this pattern, underscoring the mosaic nature of the emergence of these behaviors, perhaps in a manner similar to cultural differences observed today between different chimpanzee societies (Whiten et al. 1999). Furthermore, the combination of ape-like manual dexterity (Karakostis et al. 2021b) with the human-like muscle use observed here in australopiths suggests that habitual tool use was established before the evolution of biomechanical adaptations of the human thumb, likely acting as selective pressure spurring their development, and highlighting the role of manual behavior as a leading factor in human bio-cultural evolution (Karakostis et al. 2021b). Future investigation of the hand musculature in these taxa will help further illuminate their behavior.

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