

## ANTHROPOLOGY

## Evidence for precision grasping in Neandertal daily activities

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Neandertal manual activities, as previously reconstructed from their robust hand skeletons, are thought to involve systematic power grasping rather than precise hand movements. However, this interpretation is at odds with increasing archeological evidence for sophisticated cultural behavior. We reevaluate the manipulative behaviors of Neandertals and early modern humans using a historical reference sample with extensive genealogical and lifelong occupational documentation, in combination with a new and precise three-dimensional multivariate analysis of hand muscle attachments. Results show that Neandertal muscle marking patterns overlap exclusively with documented lifelong precision workers, reflecting systematic precision grasping consistent with the use of their associated cultural remains. Our findings challenge the established interpretation of Neandertal behavior and establish a solid link between biological and cultural remains in the fossil record.

## INTRODUCTION

Reconstructing the habitual behaviors of fossil hominins is vital for understanding the biocultural factors driving human evolution. Manual activities specifically hold particular interest, as they provide insights into the evolution of tool making and use, an essential human adaptation. A fundamental objective of human evolutionary research therefore addresses the manipulative capacities and behaviors of fossil hominins compared with modern humans [for example, (1–8)]. The latter are characterized by the ability to perform various precision grips crucial for the production of sophisticated artifacts and tool use (3, 5, 8). Among archaic humans, Neandertal hands have been interpreted as showing overall muscle hypertrophy and frequent performance of transverse power grips (1, 2, 7), suggesting that their habitual manual activities mainly relied on sustained high grip force, without the systematic use of fine-tuned hand movements. Therefore, despite being anatomically capable of performing modern human-like precision grips using their thumb and index finger (3, 7, 8), previous analyses of Neandertal hand remains found no evidence for habitual use of precision grasping (1, 2, 7). This finding was, in turn, interpreted as indicating major behavioral differences with early modern humans, perhaps centering on a decreased reliance on composite tools and hafting (2), considered important components of behavioral modernity (9). However, this commonly accepted view of Neandertal behavior is difficult to reconcile with a growing body of archeological evidence documenting a wide range of activities that require relatively high levels of manual precision (for example, the production and use of specialized bone tools for hide processing, the making of cordage and fire-aided adhesives, etc.) (10–12), with the frequent “microlithic” character of Mousterian assemblages (13) and with the use of composite artifacts (14). Here, we reevaluate the manipulative activities of Neandertals and early modern humans using a new three-dimensional (3D)

method of analysis of hand enthesal surfaces and a uniquely documented comparative sample. Results show that Neandertals systematically performed precision grips, in agreement with their associated cultural remains. In contrast, early modern humans present a greater variability of manual grips, consistent with the hypothesis that intensified division of labor emerged among Upper Paleolithic modern humans (15).

Entheses (muscle attachment scars) are the only skeletal markers directly associated with the musculotendinous system (16). Their morphology is commonly considered to reflect biomechanical stress and habitual activities (see Materials and Methods) (4, 7, 17–23). However, their understanding has been limited in the past by low measuring repeatability, lack of rigorous statistical analysis, and—most importantly—the absence of a clear link between enthesal anatomy and physical activity [for example, (24)]. Although multiple studies suggest an association between particular aspects of enthesal variability and biomechanical forces [for example, (4, 7, 17–23)], recent work has questioned this relationship (25–28). Specifically, recent work on human cadavers found no linear correlation between muscle architecture and hand enthesal form (27). Furthermore, recent experimental studies on various nonprimate animals (25, 26, 28) reported no significant metric differences in certain entheses between independent groups of specimens (exercised versus control groups). Nevertheless, these studies suffer from important limitations (see Methods). For instance, they all focused on single entheses rather than the pattern among muscle attachments and often ignored factors known to greatly influence enthesal morphology [see (19, 22, 29, 30)], such as advanced age [for example, (27)]. All previous anthropological studies evaluating the link between entheses and activity relied on occupation at death, which is known to provide inadequate information on habitual, long-term activities [see (31)]. Moreover, past experimental work has relied on relatively short experimental sessions (lasting a few months) involving various nonprimate species (25, 26, 28), even though the threshold of biomechanical strain required to form a significant amount of new bone is unknown (25) and could vary greatly across taxa.

In contrast, our approach is based on the widely proposed notion that enthesal variability is mainly driven by a complex interaction between lifelong bone degeneration and long-term habitual physical activity [for example, (19, 22, 30)]. Rather than

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anticipating a statistically significant metric difference between independent groups of individuals after relatively short experimental sessions, we use a unique historical comparative sample with fully documented lifelong occupational activity and life history (22), which can capture the gradual effects of this interaction on the multivariate proportions among entheses. The nature of long-term occupational activities in this sample was determined on the basis of both the highly detailed archival information on each individual as well as the rich historical sources describing the exact manual tasks performed and mechanical equipment used in each occupation [see cited literature in (22)]. The power grip subsample mainly includes long-term heavy construction workers (bricklayers, stonemasons, and carpenters), while the precision grip group mainly comprises individuals with verified semimechanized activities of lower physical intensity (tailors, shoemakers, joiners, a silk-dyer, a writer, a painter, etc.) (22). We overcome the limitations of subjective evaluation, or “scoring,” of enthesal development by using a repeatable quantification of 3D hand enthesal surface areas (21). Finally, we identified morphometric patterns of entheses reflecting functionally significant muscle synergies relating to power versus precision grips (21, 22), for the first time providing an appropriate toolkit for reliable reconstructions of habitual physical activities in the past. The muscles involved in the observed power grasping pattern act together to move the thumb (extension of its proximal phalanx and flexion of the distal one), the fifth digit (abduction and flexion of the fifth finger), and the wrist (extension of the wrist and ulnar deviation of the hand). By contrast, the synergistic muscles of the observed precision grip pattern position the thumb (thumb opposition, adduction, abduction, and/or flexion) and the index finger (abduction and/or adduction). The primary function of each muscle and the biomechanical literature describing the above-mentioned muscle synergies are presented in Table 1. The enthesal patterns corresponding to these particular muscle groups were previously shown to differ across individuals with distinct long-term occupations (22).

We applied our innovative approach to a fossil sample of Neandertals and early modern humans from the Late Middle to Late Pleistocene of Europe, Western Asia, and, in one case, North Africa (table S1). Both groups were represented by a total of six individuals each, whose manual entheses were adequately preserved so as to be included in our study (see Methods).

## RESULTS

We quantified the enthesal surface areas (in square millimeters) of the two synergistic muscle groups related to precision (coordinated actions of thumb thenar and forefinger muscles) and power (application of high grip force by engaging specific thumb and fifth ray muscles; cf., literature cited in Table 1). After adjusting these measurements for overall size based on a geometric mean of all enthesal measurements (cf., Materials and Methods and table S2), we conducted a principal components analysis (PCA) without a priori group categorization to investigate the patterns of variance shown by our sample. We also performed a discriminant function analysis (DFA) to assign each specimen to a functional grip category (Materials and Methods). We conducted cross-validation classification to evaluate the robustness of the results. We performed two analyses for both PCA and DFA, so as to accommodate the incompleteness of the fossil record: the first maximized variables by using

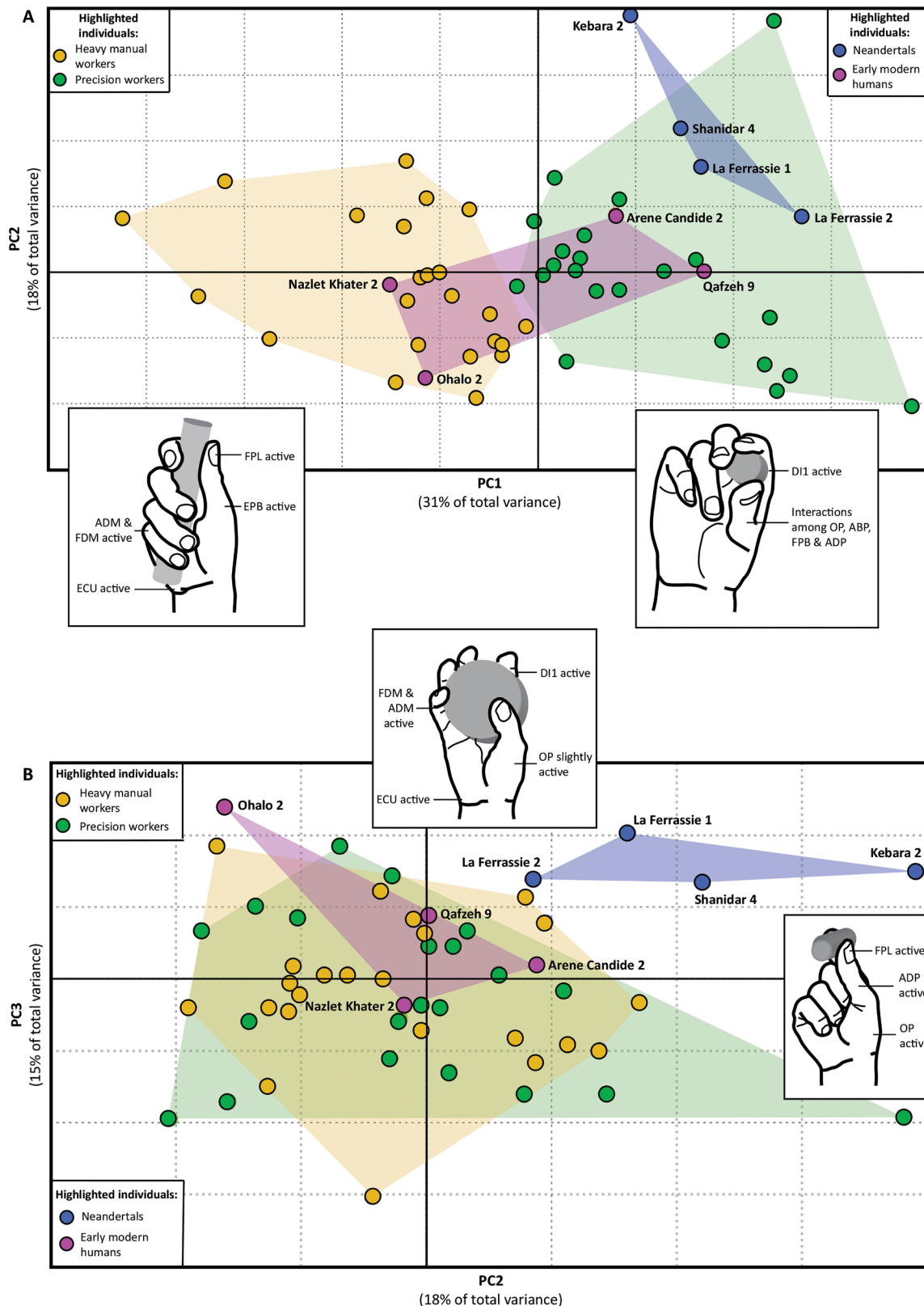
**Table 1. Two synergistic muscle groups reflected on the multivariate patterns among hand enthesal surfaces (21, 22).**

Muscles	Primary function (16)	Insertion site analyzed (16, 21, 22)
<b>Muscles coordinated for precision grasping using the thumb and index finger (21, 52–55)</b>		
Abductor pollicis	Abducts the thumb	Radial base of the first proximal phalanx
Adductor pollicis	Adducts the thumb	Ulnar base of the first proximal phalanx
First dorsal interosseus	Abducts the second finger	Radial base of the second proximal phalanx
First palmar interosseus	Draws the second finger toward the third finger	Ulnar base of the second proximal phalanx
Flexor pollicis brevis	Flexes the first metacarpophalangeal joint	Radial base of the first proximal phalanx
Opponens pollicis	Abducts, rotates, and flexes the thumb	Radial diaphysis of the first metacarpal
<b>Muscles coordinated for producing sustained power grasping (21, 53–55)</b>		
Abductor digiti minimi	Abducts the fifth finger	Ulnar base of the fifth proximal phalanx
Extensor carpi ulnaris	Extends the wrist and adducts hand	Ulnar base of the fifth metacarpal
Extensor pollicis brevis	Extends the thumb	Dorsal base of the first proximal phalanx
Flexor digiti minimi	Flexes the fifth finger	Ulnar base of the fifth proximal phalanx
Flexor pollicis longus	Flexes the first distal phalanx	Palmar diaphysis of the first distal phalanx

a data set of nine hand entheses and the second used three entheses to maximize the fossil sample. After establishing that left and right hand bone sets behaved similarly in all samples (Materials and Methods and figs. S1 to S3), we combined entheses from the right and left hands of fossil individuals, so as to include as many fossil specimens as possible. Our comparative sample includes 45 relatively young adult males (<50 years) with no direct genetic relationships, for which long-term occupational activities, exact manual tasks, official medical records, and socioeconomic characteristics have been documented (22).

## Results of the PCAs

Principal component 1 (PC1) (31% of total variance) of the first PCA separated individuals whose long-term occupational and socioeconomic characteristics required systematic precision grasping (high PC1 scores) from those whose long-term job positions demanded power grips (low PC1 scores) (Fig. 1A), as previously reported (22). The four Neandertals that could be included here exhibited high PC1 scores, overlapping exclusively with the former group. High PC1 scores correspond to strong correlations among specific thumb and index finger enthesal variables (that is, surface area measurements adjusted for the effects of overall size) of muscles whose coactivation is fundamental for human precision grasping



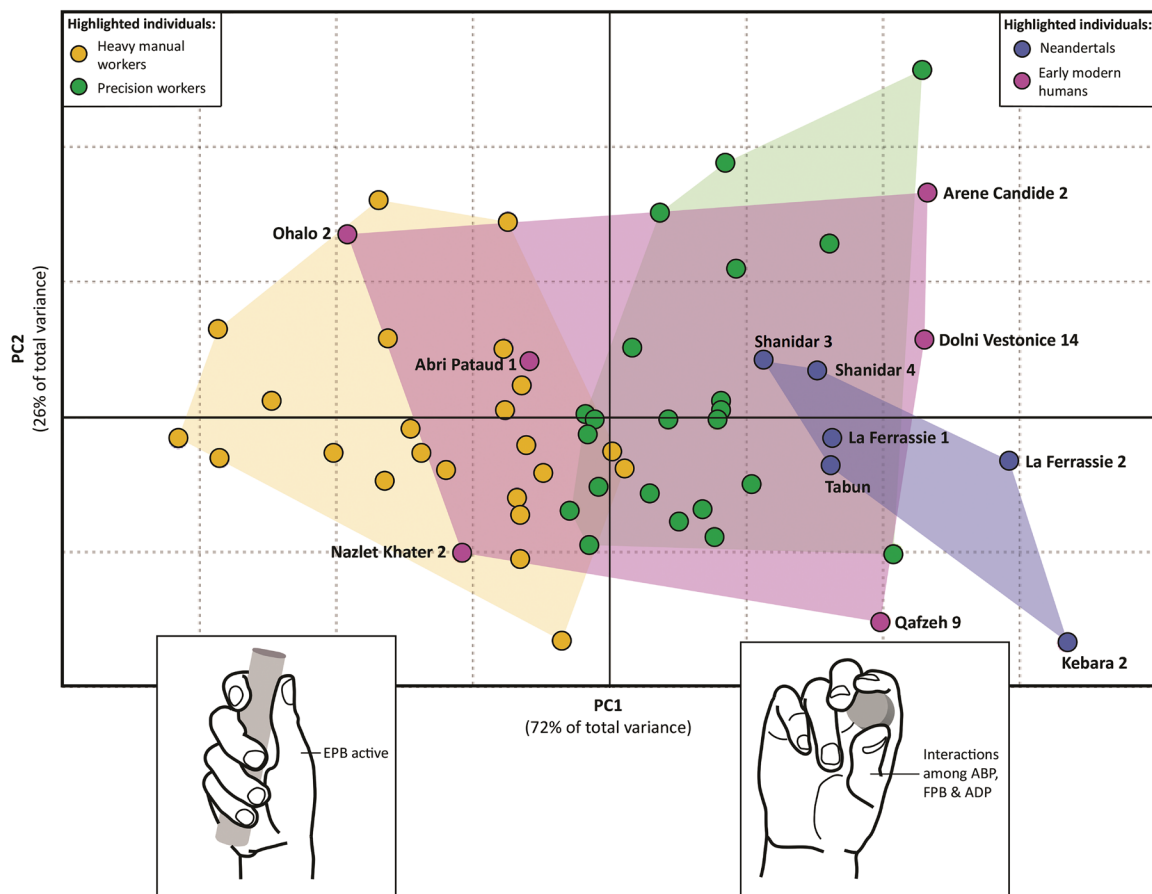
**Fig. 1. PCA (nine entheses) without a priori group categorization.** (A) PC1 versus PC2; (B) PC2 and PC3. The side figures in each plot demonstrate muscle entheses with high factor loadings (see Statistical analysis in Materials and Methods), describing the two opposite enthesal patterns of PC1 (A) and the enthesal pattern (that is, high values in both PC2 and PC3) separating Neandertals from all modern humans (B). FPL, flexor pollicis longus; ADM, abductor digiti minimi; FDM, flexor digiti minimi; ECU, extensor carpi ulnaris; EPB, extensor pollicis brevis; OP, opponens pollicis; FPB, flexor pollicis brevis; ABP, abductor pollicis; ADP, adductor pollicis; DI1, first dorsal interosseus.

(Fig. 1A; see also Table 1 for muscles involved in the described precision grip pattern) (5, 6, 8, 21, 22, 32). More specifically, higher scores on this PC indicate that the entheses of the precision grasping pattern present proportionally larger surface areas than those of the power grip pattern. Inversely, lower scores represent individual hands with proportionally larger entheses of muscles coordinated for power grasping using the thumb, the fifth ray, and the wrist (Table 1). Neandertals also presented high scores on PC1 (72% of total variance) of the second PCA (Fig. 2), which included six Neandertal individuals (table S1) and only three entheses. These results show that additional, less well-preserved Neandertal specimens, which could not be included in the initial analysis of nine entheses, also present a distinctive precision grasping enthesal pattern. Moreover, the second PCA results demonstrate that the two enthesal tendencies (power grasping versus precision grasping) are also observable using the three entheses of isolated thumb proximal phalanges.

By contrast, early modern humans' PC1 scores reflected both power and precision grasping. In the first analysis, two individuals (Ohalo 2 and Nazlet Khater 2) presented an enthesal pattern consistent with power grasping (Fig. 1A), with PC1 scores similar to those of lifelong heavy manual workers (22), while two others (Qafzeh 9 and Arene Candide 2) showed a precision grasping enthesal pattern, plotting together with Neandertals and precision

workers. The second analysis included six early modern human specimens, showing similarly variable PC1 scores (Fig. 2).

The first PCA also separated Neandertals from all modern human samples (the latter broadly overlapping) along PC2 and PC3 (18 and 15% of total sample variance, respectively) (Fig. 1B). Neandertals showed high PC2 scores, reflecting proportionally larger enthesal surface areas for the opponens pollicis (opposes the thumb), adductor pollicis (adducts the thumb), and flexor pollicis longus (flexes the thumb) muscles compared to all remaining enthesal measurements (see Table 1 and table S3). Their high PC3 scores correspond to proportionally larger entheses for muscles recruited during the performance of tool-related precision grips involving the fifth finger muscles (Table 1 and table S3) (6), including, additionally, extensor carpi ulnaris, which provides stability to the wrist's ulnar side by extending it while adducting the hand (cf., Table 1) (16). Although the latter muscle's enthesal area also contributes to the power grip pattern illustrated in Fig. 1A, in the Neandertal pattern of PC3 (Fig. 1B) there is no considerable contribution of certain thumb entheses (flexor pollicis longus and extensor pollicis brevis), whose attaching muscles are fundamental for performing power grips (for simultaneous extension of the thumb's proximal phalanx and flexion of its distal one) (6) (see also cited literature in Table 1).



**Fig. 2. PCA (three thumb entheses) without a priori group categorization, PC1 versus PC2.** The bottom figures describe the muscle entheses with high factor loadings on PC1 (see Statistical analysis in Materials and Methods).



## Results of the DFAs

The DFA results were consistent with those of the PCA. We classified all Neandertal specimens with habitual precision workers with a posterior probability of 98% or higher (Table 2). We classified the six early modern human specimens in both categories, with probability values close to 95% or higher, with the exception of Abri Pataud 1, classified with the power grip group with a probability of 68% in the three entheses analysis (Table 2). This specimen also had an intermediate PC1 score in the corresponding PCA (Fig. 2). Overall, original and cross-validation classification for the documented specimens showed a mean accuracy of approximately 95% for both DFAs (Table 2 and table S4).

## DISCUSSION

### Habitual precision grasping in Neandertals

Previous research has concluded that even though Neandertals were anatomically capable of performing precision grips (3, 7, 8), their habitual manual activities were mainly based on transverse power grasping (1, 2, 7). Our results challenge this interpretation by providing morphological evidence that their habitual behavior primarily involved precise manual tasks. This evidence involves their hand enthesal multivariate patterns, which directly reflect muscle combinations recruited for precision grasping (cf., Table 1 and Figs. 1 and 2) (5, 6, 8, 21, 22, 32–34). Moreover, Neandertals differed from both early and recent modern humans investigated here in their apparent more frequent use of two precision grip varieties (Fig. 1B),

reflecting the performance of thumb movement toward the rest of the hand (PC2) in combination with the use of precision grasping (PC3) thought to be related with lithic tool use (6).

In contrast to Neandertals, who consistently fell with the precision grip category in all analyses, early modern humans were variably grouped with either precision or power grip samples. Although our samples are very small, these results are consistent with the hypothesized intensification of division of labor among early modern human groups (15). Our results are also consistent with previous interpretations of individual specimens. Nazlet Khater 2, classified with the power grip category, was previously associated with strenuous physical activities (that is, mining) based on its robust postcranial morphology and vertebral lesions (35). Furthermore, the cultural contexts of Ohalo 2, Dolni Vestonice, and Arene Candide are indicative of communities with high occupational variability (36–38).

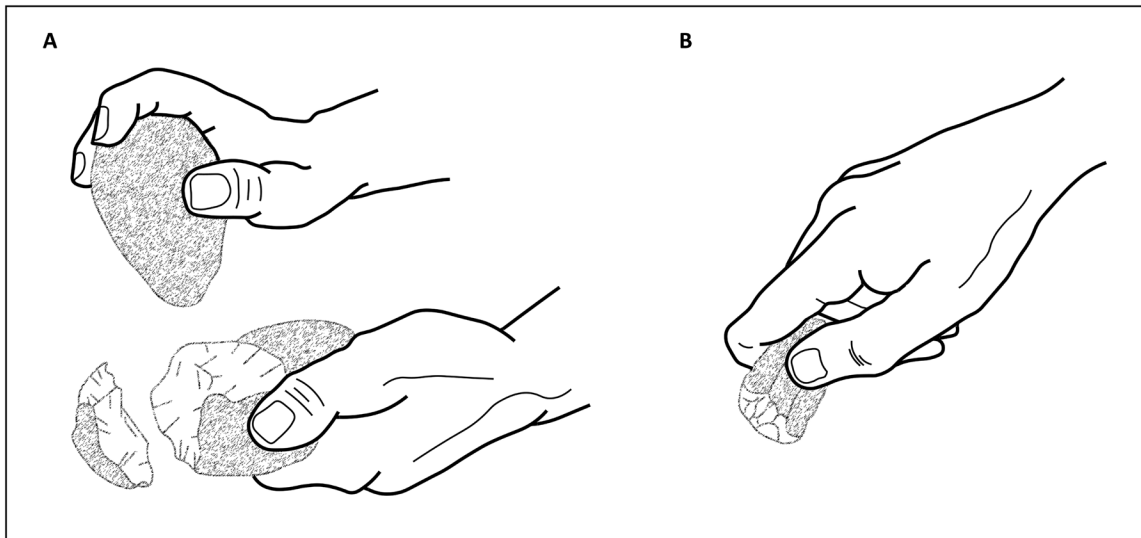
Previous research has described several anatomical differences between Neandertals and modern humans, which may have provided the latter with a biomechanical advantage for precision grasping (3, 7). Nevertheless, Neandertals were still fully capable of performing precision grips relying on the thumb and the index finger (3), with a recent kinematic study suggesting that Neandertal hands may have been slightly more dexterous (that is, higher “workspace values”) than some recent modern humans for manipulating very small objects using thumb-index precision grasping (8). Even if modern human hand anatomy is slightly better adapted for precision grasping, this in itself does not negate habitual precise manipulation by Neandertals, especially in light of the growing body of archeological evidence suggesting otherwise (10–12). In this framework, our study provides novel insight into the habitual activity patterns of Neandertals (rather than the biomechanical properties of their hand anatomy) based on a comparative sample documented for the individuals’ occupational activities in life.

## CONCLUSIONS

Our findings establish a clear link between the biological and cultural remains of Neandertals and challenge the common portrayal of Neandertal manual behavior as relying on power and rarely performing tasks requiring precision (1, 2, 7). The habitual performance of precision grasping evidenced here is consistent with the sophisticated cultural behavior increasingly documented for this group [for example, (10–12, 39)]. It also fits well with the production and/or use of flake-based industries (5, 23, 40), which comprise the primary cultural context of Neandertals (14) and include flakes so small that their function has puzzled archeologists (13). These production activities (knapping) and use (for example, for cutting, defleshing, and disarticulating animal carcasses) require the systematic performance of forceful precision grips relying mainly on the thumb and the index finger (5, 33), such as those found by our results, during which the thumb forcefully secures the tool against the fingers and/or the palm, while the index finger opposes its cutting edge (for example, Fig. 3) (33). Our study provides the first direct anatomical evidence to support the archeological indications that Neandertals habitually performed delicate manipulation of objects and substances and produced and used small-sized tools in activities that necessitated a certain (high) level of precision, challenging the long-held ideas about the complexity of their behavior.

**Table 2. Mean accuracy rates and posterior probability values of the two discriminant function analyses.**

DFA		First (nine entheses data set)	Second (three entheses data set)
Accuracy (original/cross-validated)		95.6%/93.3%	95.6%/95.6%
<b>Predicted group/posterior probability values</b>			
Neandertals	Kebara 2	Precision grip/>0.99	Precision grip/>0.99
	La Ferrassie 1	Precision grip/>0.99	Precision grip/>0.99
	La Ferrassie 2	Precision grip/>0.99	Precision grip/>0.99
	Shanidar 3	—	Precision grip/>0.98
	Shanidar 4	Precision grip/>0.99	Precision grip/0.99
	Tabun 1	—	Precision grip/>0.99
	Early modern humans	Abri Pataud 1	—
Arene Candide 2		Precision grip/>0.98	Precision grip/>0.99
Dolni Vestonice 14		—	Precision grip/>0.99
Nazlet Khater 2		Power grip/0.98	Power grip/0.89
Ohalo 2		Power grip/0.93	Power grip/0.99
Qafzeh 9		Precision grip/>0.99	Precision grip/>0.99



**Fig. 3. Two examples of precision grasping involving mainly the thumb and the index finger during the production and use of lithic flakes.** Here, these hand movements are represented by high values on PC1 of the PCA using nine entheses (Fig. 1A).

## MATERIALS AND METHODS

### Biomechanical significance of entheses

Entheses comprise the only skeletal markers directly associated with the musculotendinous system (16). Their morphology has been found to influence the biomechanical efficiency of the attaching muscles by regulating their moment arm [for example, (4, 17)], while enthesal variation in 3D size among different species strongly correlates with muscle force levels [for example, (18)]. Previous research has reported a statistically significant correlation between human aggregate muscle markers and cross-sectional robusticity (widely considered as a good proxy of biomechanical stress) [for example, (19)]. Furthermore, a multivariate analysis of enthesal scores found a significant variation across different occupational classes (20), while the multivariate patterns among hand enthesal 3D surface areas were reported to reflect fundamental manual muscle synergies (21, 22) as well as the nature of lifelong occupational activities (22). In an evolutionary context, past studies have used particular aspects of enthesal morphology as indicators of manipulative dexterity and/or behaviors in fossil hominins [for example, (4, 7, 17, 23)].

Nevertheless, past research on entheses was plagued by several methodological issues, including low measurement precision (24) and the rare application of advanced statistical methods [see (20–22)]. Several recent studies have questioned the functional significance of entheses, relying on either anatomical or experimental data (25–28). In particular, Williams-Hatala *et al.* (27) investigated the association between hand morphology and muscle measurements related with biomechanical stress, reporting no linear correlation in a sample of human cadavers. A series of experimental works on various nonprimate species (25, 26, 28) compared the entheses of two independent groups of individuals, following relatively short experimental sessions (that is, a few months). These studies found no statistically significant difference between the exercised and control groups. However, several important limitations of these works must be kept in mind.

First, even though longitudinal experimental work on humans has found that physical activity appears to have a substantial effect on the distribution of bone mineral density across different skeletal areas but less so on the raw amount of bone mineral density per individual [for example, (29, 41, 42)], the recent research mentioned above (25–28) did not perform multivariate analyses among different muscle attachments. Instead, it focused on comparing the same enthesal form across individuals (or groups of individuals). Furthermore, the morphology of enthesal surface areas was known to be strongly correlated with factors other than physical activity, which have not always been taken into account: For example, a recent study questioning the relationship between physical activity and entheses by assessing the linear association between muscle architecture and hand enthesal form (27) relied on old individuals (mean age,  $77.9 \pm 12$  years), despite the widely demonstrated effects of advanced age on muscle dimensions, enthesal form, the capacity for bone remodeling, and the levels of activity expected (19, 22, 29, 30). The same study (27) also did not take into consideration that muscle and bone do not react identically to stress: Muscle changes are already observable within 2 months of systematic physical exercise [for example, (43)], whereas a significant increase in the levels of bone formation—as well as an average human bone remodeling period—requires much longer periods of time [for example, (29, 41)].

Similarly, although previous research based on biochemical markers has shown that a significant increase in the levels of human bone formation may not be observed for over 1 year of highly intense and systematic exercise (29, 41), no previous anthropological studies used samples with documented activities over several years before death. Rather, they typically relied on occupation at death, which is known to provide inadequate information on habitual, long-term activities [see (31)]. Moreover, past experimental work on the entheses of various nonprimates involved training sessions lasting less than 13 weeks (25, 26, 28) with 1 hour (25) or 30 min (28) of daily activity, even though the exact threshold of biomechanical

strain required to form a significant amount of new bone is not yet defined (25) and could vary greatly across taxa. These experimental studies also did not analyze enthesal morphology in the same individuals before and after a particular training session (25, 26, 28). By contrast, they used two independent groups of specimens (“control group” and “exercised group”), which were directly compared through bivariate statistical analyses for each enthesis separately. However, given the relatively short training periods and the numerous factors affecting interindividual variability in entheses (19, 22, 31), the slight enthesal changes gradually leading to multivariate patterns were likely not detectable through direct probability comparisons between different individual groups. Furthermore, while one of these experimental studies found a significant effect of exercise on certain bone cortical and trabecular measurements but not on enthesal bone surfaces (28), the authors did not address several additional factors influencing their interpretations, including the verified capacity of enthesal surfaces for new bone formation in association with changes in the immediately adjacent trabecular structures (44), the very high correlations reported by past research between external and internal bone robusticity measures (45), and the fact that their measuring techniques (28) have rarely been applied—or tested—in enthesal research.

Taking the above into consideration, our approach relies on a precise technique for 3D quantification of hand enthesal surfaces in combination with multivariate statistical analysis (21, 22). This methodology can reveal multivariate patterns of hand entheses with functional significance (21, 22). Its application on a sample with thoroughly documented long-term habitual activities has shown that enthesal patterns reflect the general nature of life-long manual activities (power grasping versus precision grasping behaviors) (22).

### Experimental design: Materials

The reference sample of this study comprises part of the Basel-Spitalfriedhof collection, housed at the Natural History Museum of Basel. It consists of 45 individuals documented in detail for their biological, medical, genealogical, socioeconomic, and long-term occupational profiles. A recent study on the same reference sample (22) found a close association between occupational activities and multivariate patterns of hand entheses. The occupational documentation archived in the Public Record Office of Basel-Stadt includes longitudinal information on the individuals’ occupational activities, hiring company or institution, changes during life, as well as their position at work (22, 46–48). To our knowledge, this level of documentation is unique among reference samples in biological anthropology. To control for factors responsible for enthesal variation (31, 49), criteria for sample selection included excellent state of preservation, male sex (for avoiding the effects of sexual dimorphism), an age range between 18 and 48, no reported medical pathologies (based on medical records) involving or affecting the hands, no direct relatedness among individuals, same wider geographical origin, similar socioeconomic status (middle or low socioeconomic classes), and extensively detailed occupational information (22, 46–48). It should also be mentioned that the hand enthesal patterns of this reference sample were not associated with biological age (18 to 48 years), body size, or hand bone length (22). Previous research on entheses relied on specimens’ occupation at death, which is shown to be an inadequate basis for inferring physical activity using human skeletal remains (31).

Besides its unique documentation, there are certain essential advantages in using a reference sample from this specific historical context (early industrial period in Basel). The occupational activities of most individuals with low socioeconomic status were highly intense and systematic throughout their lifetime. In particular, most of these individuals in Basel started working at 14 years of age, spending the vast majority of their daily hours on specific manual tasks (50). The numerous historical sources for this period and urban area offer detailed descriptions of the manual techniques instructed and performed in each specialized labor [for example, see references in (22)]. Based on them, there were profound differences between the manual grips performed by our sample’s heavy manual workers (systematic sustained power grasping) and the ones carried out by the urban precision workers (systematic coordinated actions of the thumb and the index finger) (Table 1). In this framework, the exceptional documentation of our sample (22, 46–48), which captures the full variability between these two occupational tendencies (22), makes it an appropriate reference basis for assessing the nature of habitual grasping performance (power or precision) in unidentified individuals. More information on the two occupational tendencies in our sample is provided below, in “Statistical analysis.”

All fossil specimens that could be included in the multivariate analyses of this study are listed in table S1, while the enthesal measurements are presented in Table 1 and table S2. The approach of this study required hand bone sets that are as complete as possible, given that the presence of multiple hand entheses for each individual is necessary for the multivariate analyses. Furthermore, the hand entheses of each individual set must be safely associated with each other (when different bones are used), which is frequently not the case in Paleolithic contexts. All enthesal surfaces showing taphonomic or pathological damage were excluded from this study. Moreover, all selected specimens corresponded to adult individuals with fully fused and developed hand bones. In total, the number of both adequately preserved and available fossil individuals involved six Neandertals and six early modern humans (table S1). Multiple other individual hand bone sets were also available for this research (for example, specimens from Amud, La Chapelle-aux-Saints, Shanidar, Spy, Regourdou, Abri Pataud, Arene Candide, Dolni Vestonice, Pavlov, Qafzeh, Skhul, and other contexts) but had to be excluded from the analyses because some of their most essential hand entheses either were not preserved, were pathological, damaged, or unavailable. To include all 12 eligible and well-preserved fossil individuals (table S1) in this research, two analyses were performed on the basis of different numbers of entheses (table S3; see also below, in Statistical analysis).

### Experimental design: Selection of hand entheses

The nine hand enthesal surface areas selected for the analysis (Table 1 and table S2) were those contributing significantly to the two multivariate patterns of entheses reflecting power or precision grasping, based on the results of two previous studies on two distinct modern human population groups (21, 22). One of these (22) focused on the same reference sample as this study (and the same enthesal measurements), while the other used a medieval sample from Burgos in Spain (21). In each of these two population groups, these particular muscle groups provided considerable variation across individuals. It should be mentioned that previous research suggested that the combination of a proportionally large enthesal area for opponens pollicis and a well-developed crest in Neandertal fifth

metacarpals' midshaft diaphysis (not analyzed in this study) could indicate the forceful performance of various power or precision grips involving the thumb and the little finger (7). This assumption is based on the fact that this relatively short crest lies within the much wider area of attachment for the muscle *opponens digiti minimi* (which draws the fifth metacarpal into opposition with the thumb) (16). However, as also noted in the same previous research (7), this crest is much subtler (or nearly absent) in some Neandertal individuals whose *opponens pollicis* entheses remains proportionally massive (for example, Amud or La Chapelle-aux-Saints). At the same time, it was not traceable in the majority of either early or recent modern humans (7, 21). Only 27% of our reference sample presented this bone elevation, including only 26% of the individuals associated with habitual power grasping. Furthermore, as Niewoehner (7) also observed, this structure was not compatible for comparative analysis, as its form and position are usually not homologous even within each human species (21). Finally, it is worth noting that the fifth proximal phalanges of most Neandertals present a relatively similar bone projection at an equivalent point of their midshaft diaphysis, even though this bone area in modern humans does not comprise a muscle attachment site (16). This raises the possibility that the narrow crest observed in the midshaft diaphysis of fifth metacarpals may also not be associated with a muscle and/or its contraction. For the above reasons, this feature could not be possibly included in our comparative morphological analysis.

### Experimental design: 3D scanning and raw measurements

The hand bones of the reference sample were 3D-scanned using a Breuckmann SmartSCAN structured light scanner (Breuckmann Inc.) with 125 fields of view, which provides a measurement accuracy of 9  $\mu\text{m}$ , as described by Karakostis *et al.* (21, 22). Full triangulation was selected, and each bone was scanned from 20 different angles along an arc of 360°. These were aligned and merged into one 3D model, which was imported into the software package "MeshLab version 1.3.3" (CNR Inc.) for defining and measuring the enthesal surfaces. The digital method for delineating the exact borders of entheses is described in detail elsewhere (21). In this procedure, the main criteria used for identifying the limits of enthesal areas on the bone surfaces were elevation, surface complexity, and coloration (when available). Finally, the separated enthesal surface was quantified in square millimeters. As demonstrated in previous research (21), this method for delineating and measuring enthesal 3D areas is precise, presenting nonsignificant intra- and interobserver error (maximum mean error was 0.60%).

Most fossil specimens were scanned and measured in the same manner, using high-resolution structured light scanners with a measurement accuracy of 9  $\mu\text{m}$ . However, some fossil models could only be developed using other scanning methods. In particular, the hand bones of three specimens (Tabun, Shanidar 3, and Shanidar 4) were scanned using 3D laser scanning (with an accuracy of approximately 125  $\mu\text{m}$ ), while microcomputed tomography (with an accuracy of approximately 50  $\mu\text{m}$ ) was used for scanning the hand bones of Nazlet Khater 2 (see Acknowledgments). To evaluate whether including the latter two scanning methods produced intermethod measurement error, an intraobserver intermethod repeatability analysis was performed 2 months after the initial measurement of the data. The tests were performed on two randomly selected entheses (*opponens pollicis* and *abductor digiti minimi/flexor digiti minimi*) of eight randomly selected individuals for the structured light

scanner versus laser scanner comparison and a further eight randomly selected individuals for the structured light scanner versus computer tomography comparison. Subsequently, intermethod error was statistically tested using paired *t* tests, which found no significant difference ( $P > 0.05$ ) across the three scanning techniques. In particular, the *P* values ranged between 0.19 and 0.27.

### Statistical analysis

All variables used in this study were size-adjusted to control for the potential effects of overall size on the multivariate relationships among hand entheses. Including the effects of size in our analyses would not provide new information, given that it is an already known fact that most Neandertal hand entheses are typically larger than those of modern humans (7). The size-adjusted variables were computed by dividing each enthesal 3D measurement (in square millimeters) by the geometric mean of all enthesal measurements for the same individual (17). Overall, two statistical methods were applied for identifying multivariate enthesal patterns in the sample, involving PCA and DFA. The statistical analyses of this study were performed using the IBM SPSS software package (IBM Inc., version 24 for Windows).

Initially, a series of PCAs were performed using the nine size-adjusted surface measurements of entheses as variables, without any a priori group categorization in the sample. Given that some of the size-adjusted variables presented different scales, a correlation matrix was preferred. A total of four PCAs were carried out in this study. For all analyses, the statistical assumptions for PCA were met, including the absence of multivariate outliers, factorability, sample size, and linearity (51). The first two analyses were performed on entheses from the same anatomical side (either left or right) of each specimen in the data set, the third PCA was applied on a mixed-sides data set, and the fourth PCA was based on three entheses (for maximizing sample size). Following standard methodological practice (51), the interpretations of this study relied mainly on factor loadings of 0.30 or above (table S3).

In the first two PCAs (figs. S1 to S3), the side used in both analyses for the fossil specimens was the one preserving the most hand entheses (either the left or the right ones). This assessment was rather straightforward, given that the hand bone entheses of most fossil specimens were much better preserved in only one of their two anatomical sides (the left or the right). For the reference sample, the right hand bones were used in the first PCA (figs. S1 and S2), and the left ones were used in the second PCA (fig. S3). The purpose of repeating this process for each side was to investigate whether the anatomical side of the reference material affects the multivariate patterns of the fossil specimens. In addition, for the purpose of increasing the sample size for the fossil sample, one entheses (*adductor pollicis*) was omitted in the first PCA (right anatomical side of the reference sample). The second PCA included 20 individuals of the reference sample whose left hand bones were adequately preserved. To maintain this sample size for the reference sample, two entheses had to be removed (*adductor pollicis* and *flexor pollicis longus*) from this analysis. Therefore, the first two PCAs of this study (figs. S1 to S3) were based on different anatomical sides as well as different numbers of entheses used. Nevertheless, their main results were in agreement with those of the mixed-sides analysis, which was based on more fossil individuals and all nine entheses.

Because of the incompleteness of the fossil record, directly comparing hand enthesal patterns between each specimen's left and



right side, and therefore assessing asymmetry possibly resulting from handedness, was not possible. However, both left and right hand entheses of the documented individuals of the comparative sample provided very similar results (figs. S1 to S3), indicating that the general nature of manual behavior (sustained high grip force or precision grasping) did not substantially differ between the two sides of each recent modern human individual. Furthermore, even though our fossil samples were small, both the left and the right hand bone sets of different Neandertal individuals showed a very similar enthesal pattern (Fig. 2 and figs. S1 to S3). This was also the case for the second PCA (on three thumb entheses of the same anatomical side) involving three left (La Ferrassie 1, Shanidar 4, and Tabun) and three right (Kebara 2, La Ferrassie 2, and Shanidar 3) Neandertal specimens (Fig. 2). Concerning early modern humans, individual hand bone sets from the same anatomical side presented different enthesal patterns (Fig. 2 and figs. S1 to S3). In the PCA on three entheses from the same anatomical side (Fig. 2), three early modern human specimens were represented by their right side (Abri Pataud 1, Dolni Vestonice 14, and Qafzeh 9) and another three individuals by their left side (Arene Candide 2, Nazlet Khater 2, and Ohalo 2). We therefore consider that handedness likely has no major influence on the enthesal patterns described in our analysis.

To increase the number of complete fossil individuals in the sample, the third PCA combined the left and right hand bones in each fossil specimen using the right anatomical side of the reference sample (that is, the best preserved). This allowed for all nine enthesal measurements to be represented in the analysis. The main results of this mixed-sides analysis (Fig. 1A) were in agreement with the observations of the PCAs on hand bone sets from the same anatomical side (Fig. 2 and figs. S1 to S3). In particular, in all four analyses, the Neandertal group presented consistent enthesal patterns on PC1, overlapping exclusively with documented long-term precision workers. The early modern human individuals also showed similar patterns in all PCAs performed. Furthermore, despite some entheses being omitted in the first analyses, the factor loading patterns of PC2 and PC3 (table S3) involved the same entheses between the first PCA (right side of the reference sample) and the third PCA (mixed-sides PCA). In the second PCA (left side of the reference sample), PC2 differed from the other two PCAs because the important enthesis of flexor pollicis longus could not be included (because of incompleteness of the left anatomical side in the reference specimens). Nevertheless, in this PCA, the factor loading pattern of PC2 (table S3) was relatively similar to the one of PC3 from the other two PCAs (right side analysis and mixed-sides analysis) (table S3). On the basis of this overall consistency among the three PCAs, the main text of this study focused on the results of the mixed-sides analysis (Fig. 1), as this provides the best possible balance between sample size and number of variables.

The fourth PCA was based on three entheses (corresponding to four muscles) from a single hand bone (either the left or the right thumb proximal phalanx), for the purpose of maximizing the size of the fossil sample. These were the common insertion point of abductor pollicis and flexor pollicis brevis, the attachment area of adductor pollicis, and the enthesis of extensor pollicis brevis (Fig. 2).

A total of two DFAs were performed using only the specimens from the documented reference collection, whose long-term occupational activities were thoroughly recorded (22, 46–48). For these group-based analyses, the individuals of the reference sample were classified on the basis of the categorization proposed for this sample

by Karakostis *et al.* (22). Following that publication, individuals were grouped on the basis of the systematic performance of either power or precision grasping throughout their active working life. This categorization relies on the extensive archived documentation for these individuals' life histories, which include different long-term occupations, exact job position, potential access to mechanical equipment (which is associated with specific power or precision grasping patterns), duration of each work in life, official medical profile, and socioeconomic characteristics (22, 46–48). In the first analysis, the first three PCs of the mixed-sides data set (nine entheses) were used as independent variables (representing the 64% of total sample variance). In the second analysis, the first component (PC1) of the three entheses data set was used as independent variable (representing the 72% of total sample variance). In both procedures, the number of PCs included in the DFA was based on the scree plot technique (51).

In both analyses, all assumptions of DFA were met (51). Given that the Box's M was high ( $P > 0.05$ ), the within-groups covariance matrix was used for developing the discriminant functions (51). For each of the two functions, the unstandardized coefficients, the constant, and the group centroids were computed (table S4). For the calculation of each reference specimen's discriminant score, the unstandardized coefficients and the constant were used. Then, the accuracy rate of the function was estimated for both the original sample and the cross-validated one (following a "leave-one-out classification" process) based on the individuals' discriminant scores and the sectioning point between the two group centroids (51). Subsequently, the developed discriminant functions (table S4) were used to calculate the predicted occupational group for each fossil specimen as well as the respective posterior probability for this assessment (Table 2).

## SUPPLEMENTARY MATERIALS

Supplementary material for this article is available at <http://advances.sciencemag.org/cgi/content/full/4/9/eaat2369/DC1>

Fig. S1. PCA using eight entheses from the same anatomical side of each fossil, either left (L) or right (R), and the right side of the reference specimens, PC1 versus PC2.

Fig. S2. PCA using eight entheses from the same anatomical side of each fossil, either left (L) or right (R), and the right side of the reference specimens, PC2 versus PC3.

Fig. S3. PCA using seven entheses from the same anatomical side of each fossil and the left side of the reference specimens, PC1 versus PC2.

Table S1. Individual hand bone sets comprising the fossil samples.

Table S2. Descriptive statistics for the size-adjusted enthesal surface area measurements of the fossil specimens.

Table S3. Eigenvalues and factor loadings of the four PCAs on size-adjusted enthesal surface measurements.

Table S4. Statistics of the two discriminant function analyses.

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