

Special Issue: The Apidima Legacy Collections: New Analyses and Interpretations

Exploring the Habitual Manual Activities of a Possible Upper Paleolithic Individual from Greece (“Apidima 3”)

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ABSTRACT

The timing and conditions of early human dispersals into Europe remain fundamental questions in paleoanthropology, with Southeast Europe playing a pivotal role as both a dispersal corridor and a potential glacial refugium. However, compared to other regions of Europe, human skeletal evidence from the Paleolithic of the South Balkans remains scarce. One of the very few proposed burials from this time period is the skeleton recovered at Apidima Cave C (Mani Peninsula, southern Greece) during excavations conducted by the Museum of Anthropology of the School of Medicine, University of Athens, in the 1980s. These remains, designated as 'Apidima 3,' were preliminarily attributed to a young biological female from the Upper Paleolithic, despite the insecure context and unknown temporal attribution. Since the original brief description of the skeleton, no further anthropological analysis has been conducted. Recently, a direct U-series date of the skeleton produced a minimum age in the Terminal Pleistocene, while a comprehensive analysis of the lithic assemblage recovered from Cave C confirmed its Aurignacian character. Here, we attempt to shed light on aspects of Apidima 3's living conditions through a reconstruction of this individual's habitual manual activities. We employ an analysis of its well-preserved hand bones using the experimentally supported "Validated Entheses-based Reconstruction of Activity" (V.E.R.A. 1.0) method. Our comparative samples include a diverse range of adequately preserved prehistoric hand skeletal remains, along with a reference basis of modern skeletons with extensively documented long-term occupational records. The findings revealed a distinctive pattern of thumb muscle use in Apidima 3, characterized by proportionally enlarged attachment sites associated with thumb extension and—to a lesser degree—opposition. This pattern, broadly consistent with power-grasping tendencies, closely resembles that observed in documented long-term manual laborers, as well as in certain Upper Paleolithic males in our sample. Notably, Apidima 3 appears to be the only Paleolithic female in our small sample exhibiting this specific trend. Overall, our findings contribute to a growing understanding of the high variability and adaptability of manual behaviors among prehistoric populations, and they encourage further interdisciplinary research on the valuable human skeletal remains from the Apidima cave complex.

INTRODUCTION

Investigating the timing and driving factors of early human dispersals into Europe constitutes a major research focus of European paleoanthropology. In this regard, the potential importance of South-East Europe is evident, as this region forms a natural crossroads between continents, acting as a major dispersal route into Europe (from Africa and the Near East) as well as a potential refugium during the glacial times (e.g., Harvati 2022; Harvati and Reyes-Centeno 2022; Harvati et al. 2009; Mihailovic et al. 2022; Roditi et al. 2024; Roksandic 2016; Roksandic et al. 2022; Tourloukis and Harvati 2018; Tsakanikou et al. 2021). The unique value of this region for elucidating early human dispersals has been recently demonstrated by the discovery of the earliest modern human presence outside Africa in the cave complex of Apidima, which is located on the western coast of the Mani Peninsula, in southern Greece (Delson 2019; Harvati et al. 2019).

In contrast to several other European regions, the currently known anthropological evidence from the Paleolithic of the South Balkans is relatively scarce. This is true especially for the Upper Paleolithic, with only few human remains potentially attributed to this period (e.g., Elefanti and Marshall 2018; Mompheratou and Pitsios 1995; see also Harvati et al. 2009 and references therein). One relatively well-preserved potential Upper Paleolithic burial was discovered in the Apidima complex (Pitsios 1985), unearthed during excavations by the Museum of Anthropology, University of Athens, in Cave C (about 19masl). According to a preliminary assessment of the skeleton and the artifacts re-

covered in Cave C at the time (Aurignacian-like lithics; perforated shells interpreted as potential beads), the Apidima 3 burial was attributed to a young female, possibly dating to around 30 ka—although no radiometric dates were obtained at the time (e.g., Darlas 1995; Harvati et al. 2009; Lirintzis and Maniatis 1995; Mompheratou and Pitsios 1995; Pitsios 1999). Recently, the chronology of the remains was investigated using Uranium-series dating, which indicated a Terminal Pleistocene minimum age (Harvati et al. 2021), a date possibly compatible with an Upper Paleolithic cultural affiliation. In parallel, our team's recent comprehensive re-analysis of the Apidima legacy collections corroborated the original anthropological assessments of female biological sex for Apidima 3 (Naumann et al. 2026 [this issue]), as well as an Aurignacian, and potentially Protoaurignacian, attribution of the lithic assemblage from Cave C (Lombar-do et al. 2026 [this issue]). The latter observation may provide some additional support for a potentially early Upper Paleolithic age for Apidima 3. Nevertheless, due to the lack of proper documentation during excavation, the association between the skeleton and the cultural assemblage, and thus an early Upper Paleolithic chronology for the human remains, cannot be confirmed (see Harvati et al. 2026 [this issue]).

Regardless of its exact chronology, a Paleolithic age for Apidima 3 renders it a unique finding in the region of South Balkans and one of the few well-preserved Upper Paleolithic skeletons in Europe. Here, we aim to investigate its habitual manual activities through a morphological analysis of its relatively well-preserved hand skeleton. We

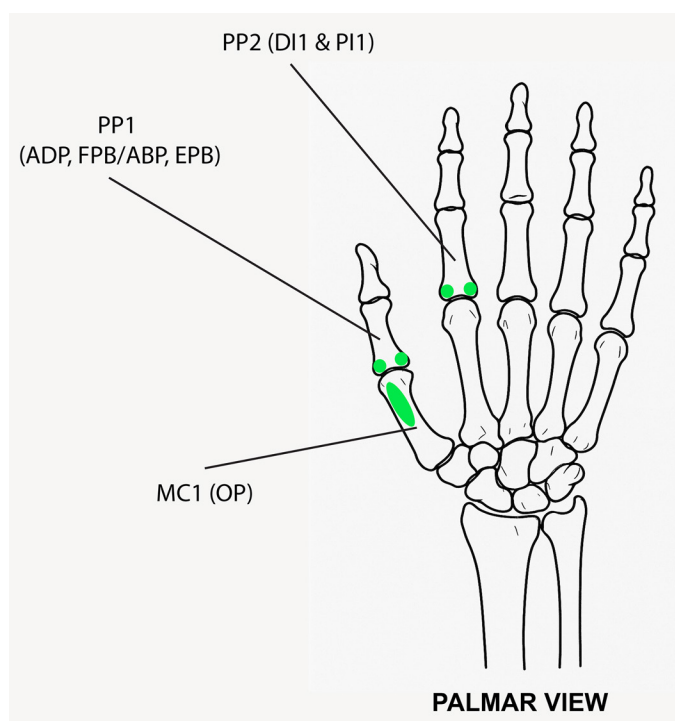


Figure 1. Schematic representation of the three hand bones analyzed in this study: the first metacarpal (MC1), proximal phalanx (PP1), and second proximal phalanx (PP2). The associated entheses (highlighted in green) are labeled next to each bone, corresponding to the following muscles: opponens pollicis (OP), abductor pollicis brevis / adductor pollicis brevis (ABD/ADP), adductor pollicis (ADP), extensor pollicis brevis (EPB), first palmar interosseus (PI1), and first dorsal interosseus (DI1). The EPB entheses is not depicted as it is located on the dorsal-proximal side of PP1.

rely on an experimentally validated approach developed by the lead author (FAK; Karakostis and Lorenzo 2016), which was recently named the “Validated Entheses-based Reconstruction of Activity” 1.0 (V.E.R.A. 1.0) method (see literature reviews by Buikstra 2024; Karakostis 2022; Karakostis and Harvati 2021). This approach focuses on the morphology of the three-dimensional (3D) bone structures where muscles or ligaments attach (“entheses”). Our comparative materials consist of a diverse series of Late Pleistocene – Holocene individuals and a recent reference sample with extensively documented occupational activities (Hotz and Steinke 2012; Karakostis and Hotz 2022; Karakostis et al. 2017a).

MATERIALS AND METHODS

THE APIDIMA 3 HAND SKELETON AND COMPARATIVE SAMPLES

The Apidima 3 skeleton consists of several well-preserved remains from the mandibular and post-cranial skeleton, including several hand bones (Mompheratou and Pitsios 1995; Naumann et al. 2026 [this issue]). For the purposes

of this study, the anatomical allocation of all hand skeletal elements was conducted anew by one of us (FAK), given that several identifications in the original publication (Mompheratou and Pitsios 1995) were not consistent with standard protocols for positioning and siding hand skeletal remains (e.g., see Karakostis et al. 2017b; Varas and Thompson 2011; White and Folkens 2005). In total, the identified hand bone remains associated with the Apidima 3 skeleton include a left capitate (wrist), three left metacarpals (rays 1, 3, and 4), one right metacarpal (ray 2), three left proximal phalanges (rays 2–4), one partial right proximal phalanx (ray 1), two intermediate phalanges (right ray 2 and left ray 3), and two left distal phalanges (possibly rays 2 and 3). Most of these hand bones are excellently preserved, without traces of weathering (except for the hard sediment still attached to parts of their surfaces). Nevertheless, the first proximal phalanx is only represented by its intact base (preserving all three enthesal areas), while metacarpals 2 and 4 are missing their heads, and the distal part of the thumb metacarpal is slightly damaged medially and dorsally (also see figures in Results). It should be noted that other hand bone remains were also found in Cave C, but their original labeling suggests that they may not be contextually associated with the Apidima 3 individual (Mompheratou and Pitsios 1995). Of the preserved hand bones, three (the right first metacarpal, the left first proximal phalanx, and the left second proximal phalanx) were selected for analysis, as they exhibit well-preserved entheses of key functional relevance and are represented in comparable condition across our reference samples (Figures 1 and 2).

The comparative samples of our study include a diverse series of seven well-preserved Late Pleistocene – Holocene hand skeletons (3 biological females and 4 biological males) from Eurasia, Asia Minor, and South America (Table 1; Karakostis et al. 2018; 2020). Notably, for the first time, this comparative sample also includes the hand skeletal remains of individual ‘Feature 15-03’ from the high-altitude site Cuncaicha of the Peruvian Andes (Francken et al. 2018; Rademaker et al. 2014; 2018). In addition, following previous applications of our approach (e.g., Karakostis et al. 2018; 2020; 2021), we compare these individuals with a reference sample of recent individuals with an exceptional level of occupational documentation. The latter originate from the anthropological collection “Basel-Spitalfriedhof” (Basel, Switzerland), which is dated to the mid-19th century. The archived information on this collection’s individuals is extremely valuable for anthropological comparisons, as it includes occupational documentation for a considerable amount of time before death, exact position at work (hierarchy), and hiring organization/institution (Hotz and Steinke 2012; Karakostis and Hotz 2022; Karakostis et al. 2017).

ENTHESEAL SELECTION AND MEASUREMENT (V.E.R.A. 1.0)

For the purposes of this study, we focused on a total of six muscle attachment sites, located in the first metacar-

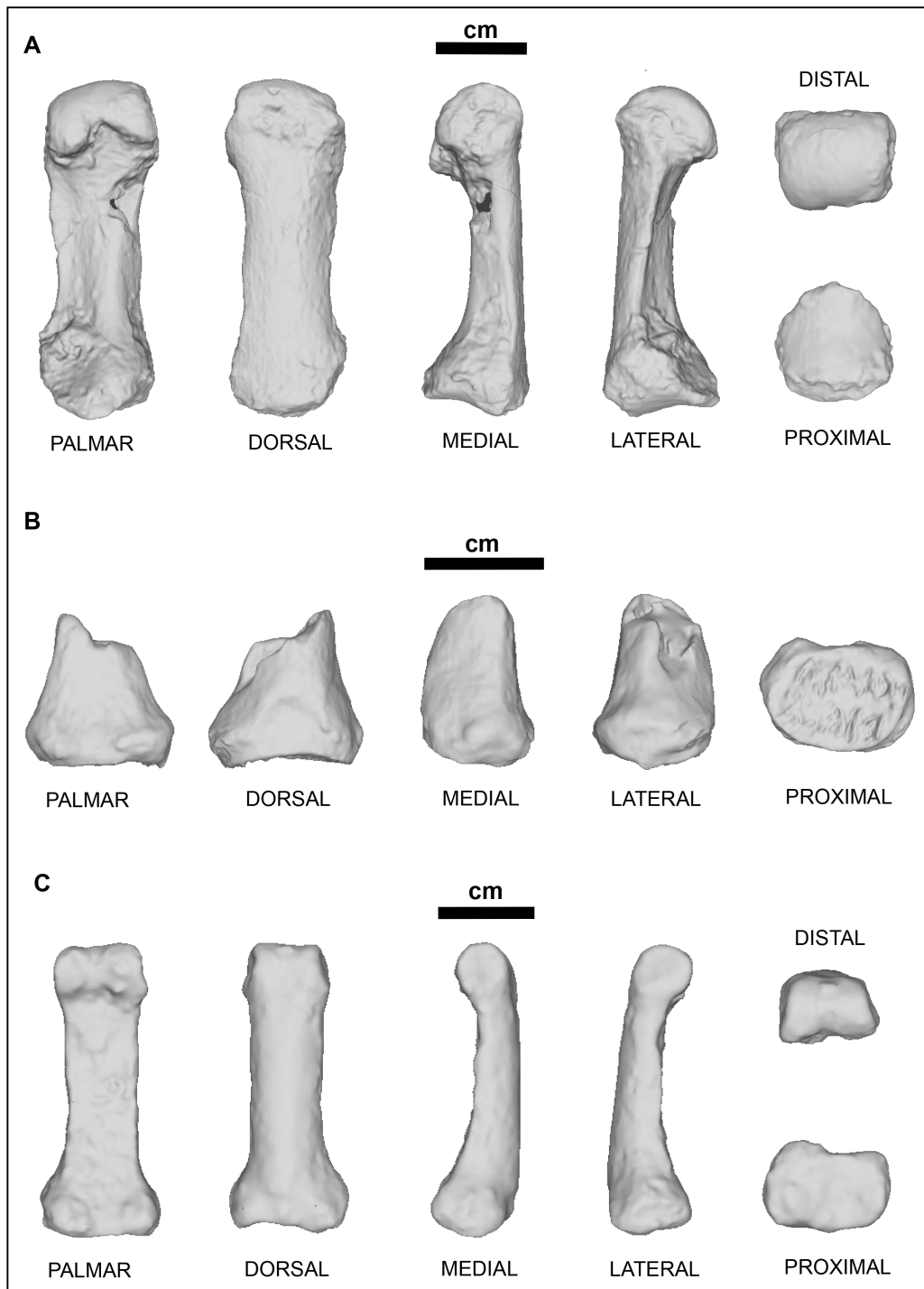


Figure 2. Aspects of the 3D surface models of the three hand bones of *Apidima 3* analyzed in this study, including the first metacarpal (A), first proximal phalanx (B), and second proximal phalanx (C).

pal, first proximal phalanx, and second proximal phalanx. These were the enthesal areas of muscles *opponens pollicis* (OP), *abductor pollicis brevis / adductor pollicis brevis* (ABD/ADP), *adductor pollicis* (ADP), *extensor pollicis brevis* (EPB), first palmar *interosseus* (PI1), and first dorsal *interosseus* (DI1) (e.g., Karakostis and Lorenzo 2016; see Figure 1). These specific entheses were selected due to their central

functional importance for human stone tool use (e.g., Dunmore et al. 2022; Eteson et al. 2024; Key et al. 2020; Maki and Trinkaus 2011; Marzke 1997; Marzke et al. 1998) and based on our previous research on reconstructing manual activities, which highlighted their contribution to accurate activity reconstruction in individuals with extensive occupational documentation (e.g., Karakostis et al. 2017a). In

TABLE 1. BASIC CHARACTERISTICS OF THE COMPARATIVE SAMPLES USED IN THIS STUDY
(Francken et al. 2018; Karakostis et al. 2018; 2020).

Group	Specimen(s)	Biological Sex	Location	Date BP
Prehistoric hunter-gatherers	Apidima 3	Female	Europe	Minimum age: Terminal Pleistocene
	Individual 15-06	Female	Peruvian Andes (Cuncaicha)	8536–8384 (95% calibrated age)
	Individual 15-03	Male	Peruvian Andes (Cuncaicha)	4349–4019 (95% calibrated age)
	Abri Pataud (Layer 2, “P1”)	Female	Europe	28,000–26,000
	Qafzeh 9	Female	Near East	130,000–100,000 / 92,000 ka
	Arene Candide 2	Male	Europe	11,800–10,900
	Ohalo 2	Male	Near East	around 19,000
	Nazlet Khater 2	Male	North Africa	44,000–32,000
Documented reference sample	Basel-Spitalfriedhof Collection (45 individuals)	Males	Europe	mid-19th century

the latter study, applying the V.E.R.A. protocols on these entheses identified distinct variation between documented heavy manual laborers and precision laborers. Unfortunately, other hand entheses of high importance (e.g., those of the fifth ray; Karakostis and Hotz, 2022; Kunze et al. 2024) were not preserved in the Apidima 3 skeleton.

The three bones selected for analysis were 3D-scanned using an Artec Space Spider structured-light scanner (Artec Inc., Luxembourg), which can provide 3D surface models with a measuring accuracy of up to 50 microns. Subsequently, using the detailed V.E.R.A. 1.0 protocols developed by one of us (FAK; Karakostis 2022, 2025a and references therein; Karakostis and Harvati 2021; Karakostis and Lorenzo 2016), the six enthesal areas were delineated and measured in square mm. In brief, the exact borders of the enthesal areas on the bone surface are identified based on three criteria (elevation, irregularity, and coloration) and the step-by-step application of specific 3D imaging filters, in the open-access software Meshlab (CNC Inc., Rome). Subsequently, the selected enthesal areas are virtually separated from the rest of the bone and measured in square mm. The measuring precision of this method has been previously extensively confirmed using intra- and inter-observer repeatability tests (Bousquie et al. 2022; Castro et al. 2021; Ieng et al. 2024; Karakostis and Lorenzo 2016; Karakostis et al. 2018; Kunze et al. 2022; 2024).

STATISTICAL ANALYSIS (V.E.R.A. PROTOCOLS)

All obtained measurements were size adjusted using the geometric mean approach, following our approach’s standard procedures (e.g., Karakostis et al. 2017a; 2018). The latter process involves calculating each individual’s geometric mean (based on the six entheses) and then dividing each enthesal area (square mm) by that geometric mean (per individual). This process has shown to decouple the association of enthesal measurements with body size proxies, bone length, and biological age (e.g., Karakostis and Hotz, 2022; Karakostis and Lorenzo 2016; Karakostis et al. 2017a; 2018).

Subsequently, following the standard V.E.R.A. 1.0 statistical protocols (Karakostis 2022), we ran two principal component analyses (PCAs) on the size-adjusted measurements of all documented individuals, the seven prehistoric skeletons, and Apidima 3. PCA is an ordination method which is commonly used to explore patterns of variance in phenotypic data (e.g., Harvati 2009; Harvati et al. 2019; Liang et al. 2023; Mitteröcker 2021; Schillaci and Gunz 2013). It has been used across all applications of our approach (Karakostis and Harvati 2021; Karakostis and Lorenzo 2016), including several of the experimental studies on laboratory animals (Castro et al. 2021; Karakostis and Wallace 2023; Karakostis et al. 2019a; 2019b). In the latter, PCAs were able

TABLE 2. STATISTICS OF THE TWO PCAS CONDUCTED IN THIS STUDY.

Analyses	Eigenvalue	Variance explained (%)	Factor loadings					
			OP	EPB	ABP/FPB	ADP	DI1	PI1
Six entheses								
PC1	1.89	31.45	0.70	-0.77	0.72	0.37	-0.17	-0.35
PC2	1.31	21.75	-0.12	-0.48	0.31	-0.52	0.57	0.61
Total		53.20						
Three entheses								
PC1	1.97	65.58		-0.99	0.66	0.74		
PC2	1.00	33.22		0.00	0.75	-0.66		
Total		98.80						

to identify multivariate associations among entheses that reflected habitual muscle synergy groups. For both PCAs, we relied on a correlation matrix and confirmed that basic statistical recommendations are met (i.e., no extreme outliers and at least five individuals per variable used) (Field 2013). The number of PCs plotted was decided based on the standard scree-plot approach (Field 2013).

The first PCA focused on all six entheses mentioned above. Given that the three selected elements were not preserved in both anatomical sides (the first proximal phalanx is right and the other two bones are left), we combined the measurements from both sides of Apidima 3 for the first analysis, following previous applications of our approach on fossil hominin hand skeletons (see supplementary information in Karakostis et al. 2018) as well as bioarchaeological contexts (e.g., Karakostis et al. 2021). The same process was applied for the other seven prehistoric skeletons, in which the right-side enthesis was preferred, when available. When, however, the right side was absent or not well-preserved, it was replaced by the left-side enthesis. In the recent documented sample from Basel, the right side was preferred across individuals because it was consistently more well-preserved. In previous research on fossil hominins as well as bioarchaeological contexts, we confirmed that this procedure did not have a substantial effect on the resulting patterns (Karakostis et al. 2018; 2021).

Nevertheless, in order to account for this inescapable bias as much as possible, we also ran a second PCA on the three entheses of the right thumb's proximal phalanx (i.e., the same bone from the same anatomical side for all individuals). Thanks to the biomechanical importance of the muscles associated with these three entheses, these have been previously shown to independently reveal satisfying

differences between individuals of distinct occupational trends (e.g., Karakostis et al. 2018; 2021).

RESULTS

Figure 3 (top) presents the results of the first PCA on six entheses after size-adjustment (PC1 and PC2, together representing a total of 53.2% of the sample's variance; Table 2). On PC1 (31.5%), in agreement with our previous research (e.g., Karakostis et al. 2017a; 2018), there is clear differentiation between documented heavy manual laborers (shown in blue) and precision workers (shown in green). The latter show proportionally large thenar entheses associated with variable thumb movement and opposition (OP, ABP/FPB, and ADP), whereas heavy manual laborers exhibit a relatively larger area for the thumb's extensor at the metacarpo-phalangeal joint (EPB). On PC2 (21.8%), occupational trends overlap. Regarding prehistoric foragers, mirroring the results of our previous research (Karakostis et al. 2018), two Upper Paleolithic modern humans (Nazlet Khater 2 and Ohalo 2) plot very close to the heavy manual laborers, one shows a relatively intermediate pattern (Abri Pataud 2-P1), and the remaining four present a distinctive precision-grasping pattern. On PC2 (21.8%), occupational trends largely overlap.

Interestingly, Apidima 3 is the only presumed female prehistoric individual that plots distinctively with heavy manual laborers. In fact, when focusing on the three thumb entheses of the right side (see Figure 3, bottom), the power-grasping tendency of Apidima 3 becomes highly distinctive. This seems to be due to the fact that Apidima 3's enthesal pattern is mainly driven by a proportionally exceptionally large EPB enthesis, combined with a comparatively well-expressed OP attachment site (Figure 4, top). Given that the

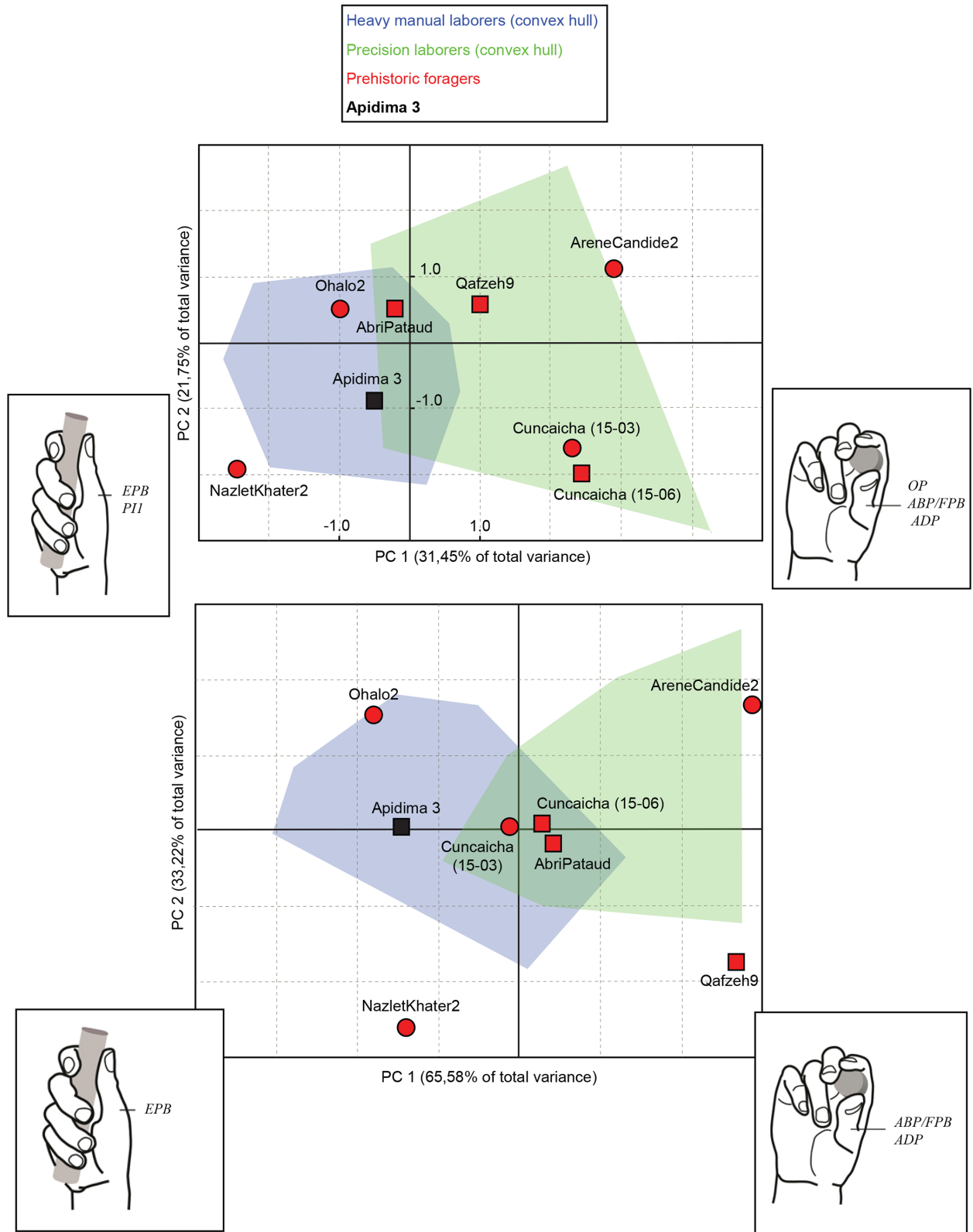


Figure 3. Plots of the two PCAs conducted in this study, using either six (top) or three (bottom) size-adjusted enthesal measurements. The side figures illustrate the enthesal patterns associated with negative (left) and positive (right) scores of PC1 (only variables with loadings of 0.30 or above are included; see Table 2). More information on the individuals labeled is provided in Table 1. For reasons of visual clarity, the reference samples (two occupational trends) are represented by convex hulls. Their enthesal patterns have been extensively studied and illustrated in several previous studies (e.g., Karakostis 2025a; Karakostis and Hotz 2022; Karakostis et al. 2017a; 2018; 2020; 2021; Kunze et al. 2022; 2024).

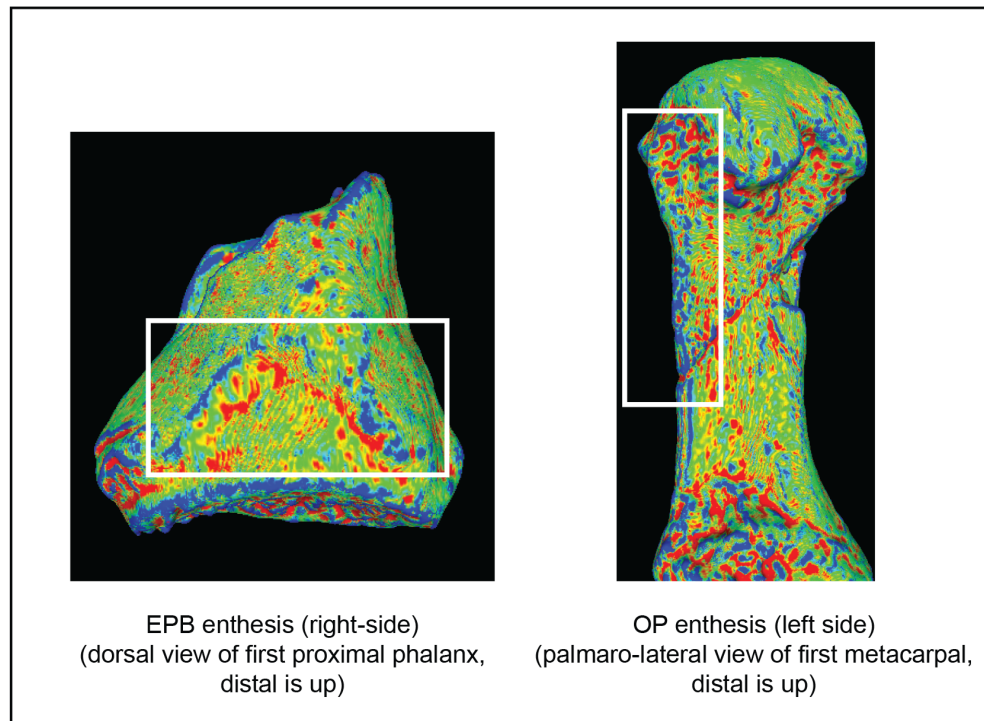
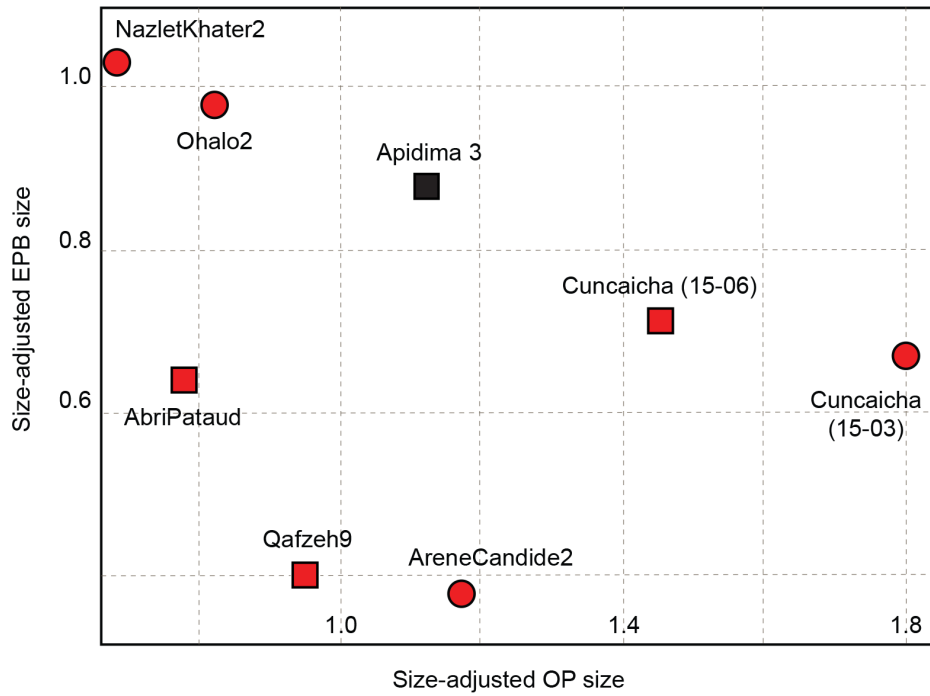


Figure 4. Top: Bivariate plot of the size-adjusted values of OP against those of EPB in prehistoric individuals of our sample, highlighting the tendency of Apidima 3 to show a pattern that combines relatively large EPB with moderately sized OP muscle attachment sites. More information on the individuals labeled is provided in Table 1. Bottom: Aspects of Apidima C's EPB and OP entheses (roughly indicated by white rectangles). Specimens are magnified for visualization purposes (scale not respected). For clearer visualization of the areas, the filter "Discrete Curvatures" has been activated in the software Meshlab, following the standard V.E.R.A. 1.0 protocols developed by the lead author (Karakostis 2023; Karakostis and Harvati 2021; Karakostis and Lorenzo 2016).

factor loadings of these two entheses are opposite on PC1 (see Table 2), the position of Apidima 3 in the first analysis (including all six entheses) is closer to the center of the plot, albeit still clearly within the convex hulls of documented heavy manual workers (see Figure 3, top). In the second PCA (which does not include OP), the proportionally large EPB enthesis of Apidima 3 leads it to plot even more distinctively with heavy manual laborers. It should be noted that, as shown in the bivariate plot of Figure 4 (top), this enthesal pattern combining relatively large EPB with moderately sized OP entheses was not found in most prehistoric foragers of our small, yet diverse, sample.

DISCUSSION

Our analyses highlight the presence of a distinctive enthesal pattern in the hand skeleton of Apidima 3, apparently reflecting relatively increased thumb extension at the metacarpophalangeal joint through recruitment of the EPB muscle (see Figure 3, top and bottom). This pattern is exclusively shared with the documented heavy manual laborers of our reference sample as well as two male Upper Paleolithic individuals (Ohalo II and Nazlet Khater 2). In contrast, in the first PCA (see Figure 3, top), four other prehistoric specimens show a clear precision-grasping enthesal pattern, which is especially evident in the two Holocene individuals from the high-altitude Peruvian Andes (Cuncaicha). Nevertheless, this trend is greatly reduced in the second PCA (see Figure 3, bottom) for specimen 15-06 and almost disappears for 15-03, clearly due to the removal of the OP enthesis, which is remarkably large in these two individuals (see Figure 4, top; also see Karakostis et al. 2020). This is not the case for specimens Qafzeh 9 and Arene Candide 2, which persistently plot with long-term precision workers in both PCAs, in line with Karakostis et al. (2018a). In this comparative framework, Apidima 3 appears to be the only presumed female individual in our prehistoric sample to present such a distinctive “power-grasping” tendency in its hand skeletal remains (see Figure 3).

Interestingly, Apidima 3’s proportionally large EPB area appears to coincide with a moderately sized insertion site for the OP muscle (see Figure 4, top), which is associated with flexion and abduction at the thumb’s carpometacarpal joint during opposition (Maki and Trinkaus 2011). The relatively sizeable OP enthesis contributes to Apidima 3’s somewhat intermediate PC1 position in the first PCA (see Figure 3, top). This combination appears to be relatively uncommon among the hand skeletons of our small prehistoric sample, where both individuals with proportionally large EPBs did not exhibit a similarly sizeable OP (see Figure 4, top). This diversity may reflect the occupational variability proposed for modern human groups during the Upper Paleolithic (e.g., French 2024; Seuru et al. 2024; Stiner and Kuhn 2009; Villotte et al. 2010).

A comparatively frequent co-activation of muscles EPB and OP could potentially be associated with the manipulation of relatively large objects, such as sizeable stones. Such grips would be facilitated by the performance of a “cupping motion” (via slight opposition of the thumb at its car-

pometacarpal joint) combined with extension of the thumb at its metacarpophalangeal joint (via contraction of EPB), in order to increase the thumb’s capacity to resist against a larger portion of the object’s surface. These hand movements would be conceptually useful for various Paleolithic manual tasks, such as, for example, using a sizeable hammerstone for stone tool knapping, transporting various resources (e.g., raw stone materials or portions of animal carcasses), or forcefully manipulating an elongated stone tool using the thumb (e.g., for food processing).

There are several margins of improvement for this pilot study, which constitutes one of the first anthropological analyses of “Apidima 3” following its initial description (Mompferatou and Pitsios 1995). The insights provided here can be corroborated and/or enriched by additional analyses of other morphological aspects of Apidima 3, such as enthesal patterns in other anatomical regions (e.g., the shoulder girdle or the lower limbs), and long bone cross-sectional robusticity (Buikstra 2024; Profico et al. 2020; Shaw and Stock 2009). Lastly, the proposed evidence of increased biomechanical stress in Apidima 3 could be further investigated by applying the newly developed semi-automated V.E.R.A. 2.0 method (Karakostis 2025a; b), which specifically targets direct signs of cumulative muscle-related stress on enthesal surfaces. Future work applying this approach to key attachment sites across the skeleton would allow for a more holistic reconstruction of the individual’s living conditions and interaction with their environment.

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DATA AVAILABILITY STATEMENT

All data generated and analyzed during this study will be made openly available in the Zenodo repository upon acceptance of the manuscript.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

AUTHOR CONTRIBUTIONS

FAK: Conceptualization, Formal analysis, Investigation, Methodology, Project administration, Supervision, Visualization, Data curation, Writing – Original Draft; **GH:** Resources, Writing – Review & Editing; **KR:** Data Curation, Resources; Writing – Review & Editing; **VGG:** Resources, Writing - Review & Editing; **KE:** Resources, Writing - Review & Editing; **KH:** Conceptualization, Resources, Project administration, Supervision, Funding acquisition, Writing - Review & Editing.



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Special Issue: The Apidima Legacy Collections: New Analyses and Interpretations

Supplement 1 to Exploring the Habitual Manual Activities of a Possible Upper Paleolithic Individual from Greece (“Apidima 3”)

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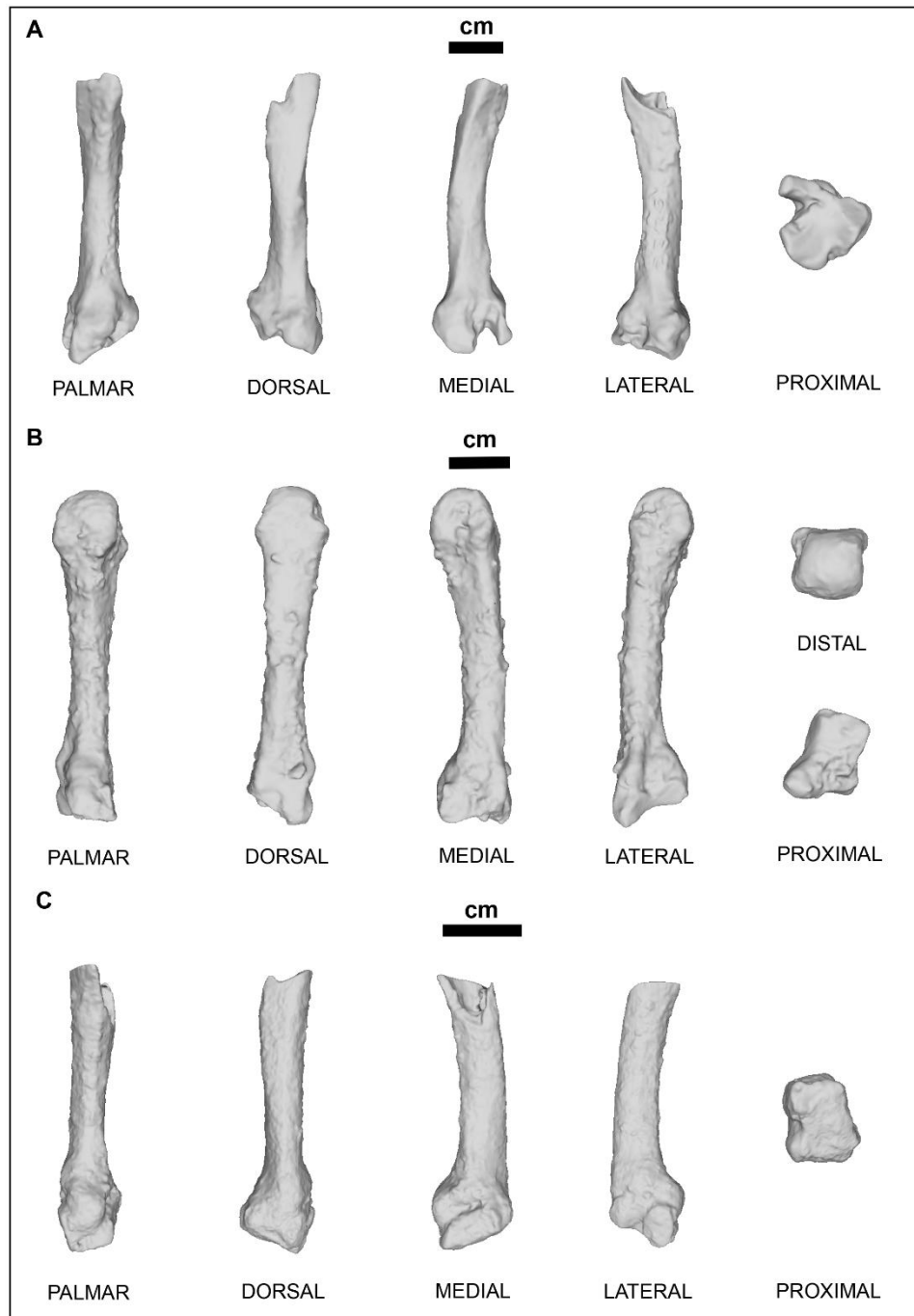
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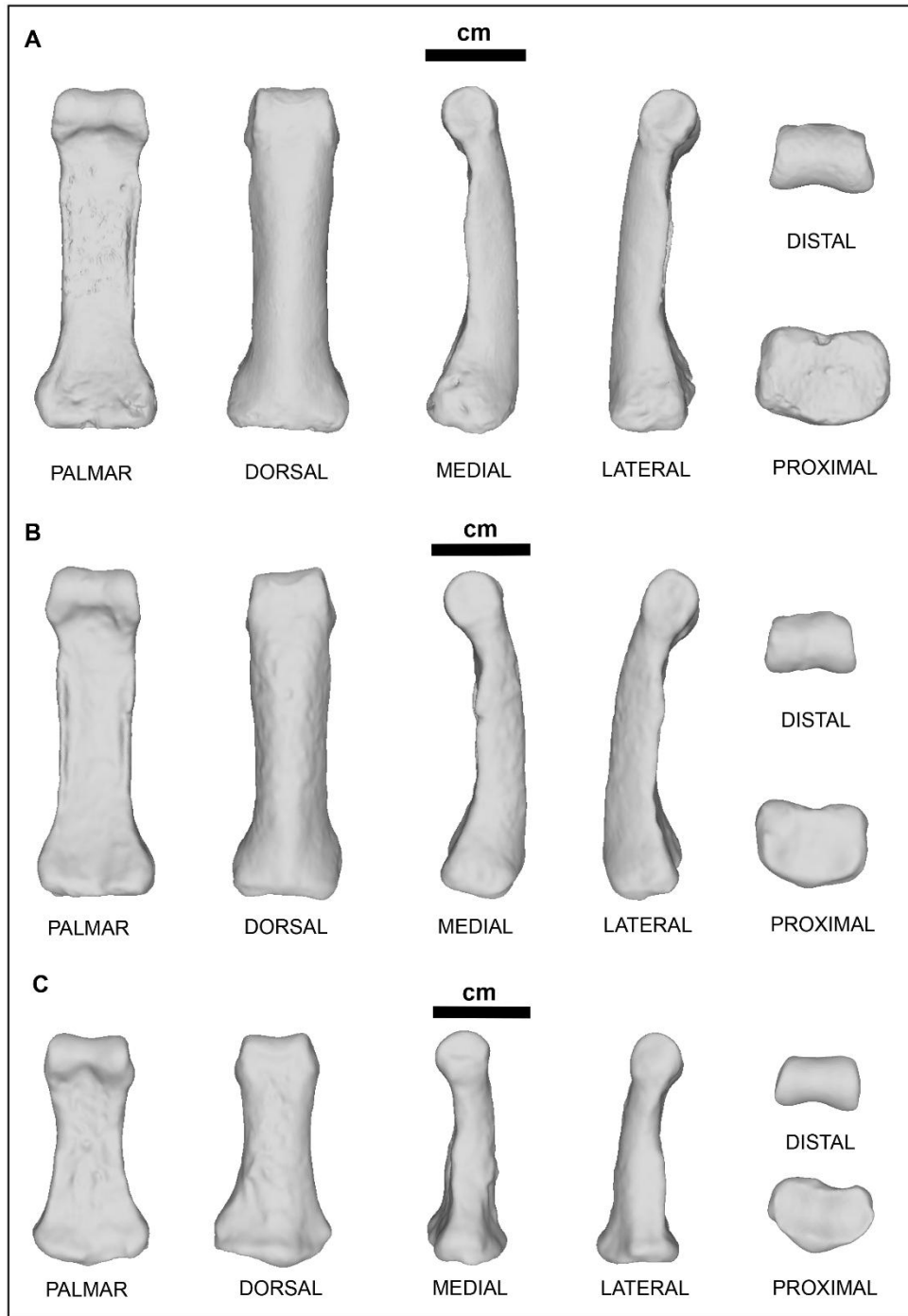
SUPPLEMENT 1

This supplement contains: Supplementary Figures 1–3.

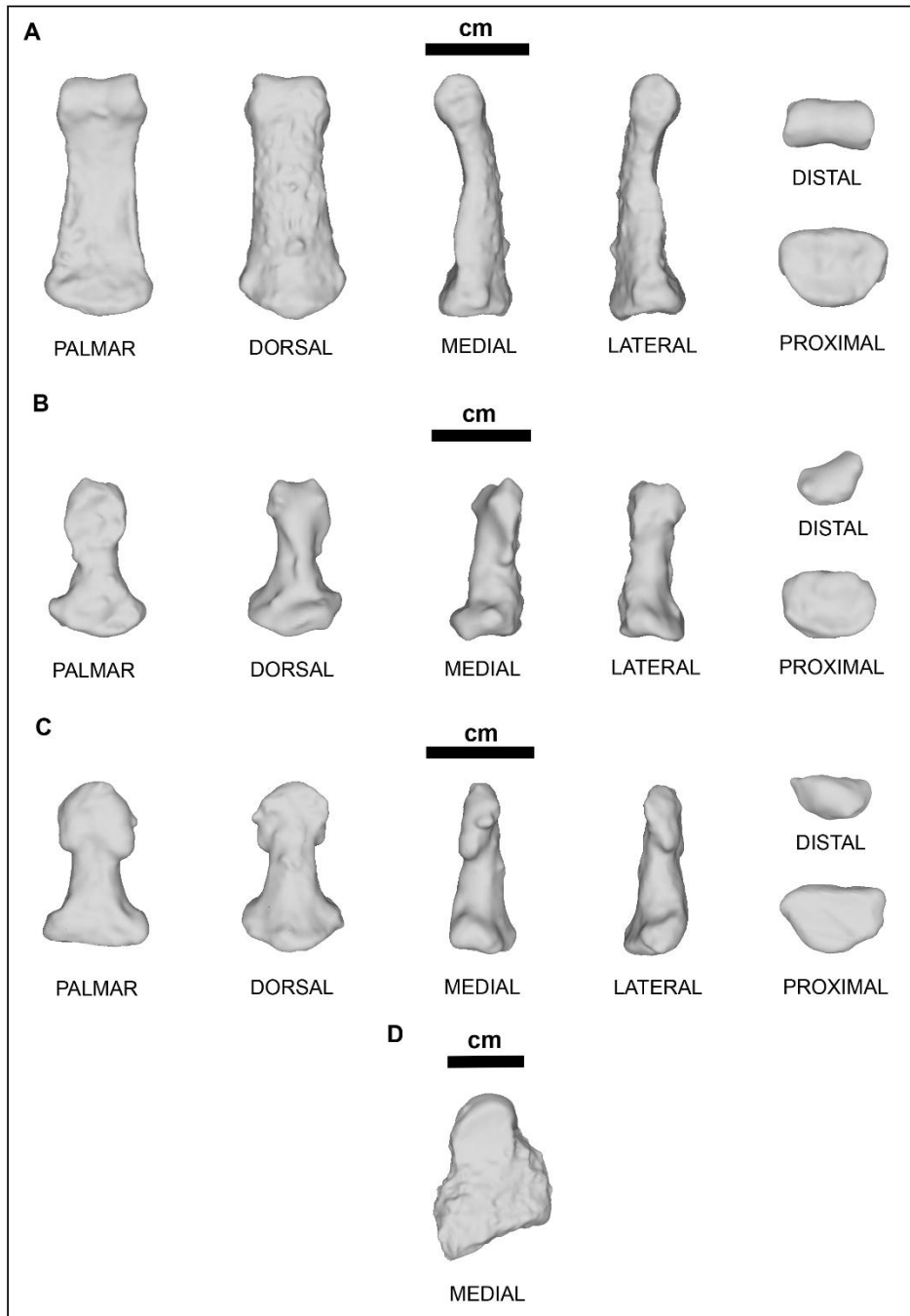
Supplementary Figures



Supplementary Figure 1. Aspects of three-dimensional surface models of three hand bones of Apidima 3, comprising the second right metacarpal (A), third left metacarpal (B), and fourth left metacarpal (C), shown from various perspectives (distal end oriented upward in the palmar, dorsal, medial, and lateral aspects). In the proximal views, the palmar side is oriented upward; in the distal views, the dorsal side is oriented upward. The second and fourth metacarpals are missing their distal ends, and the proximal end of the second metacarpal is damaged. Extensive hard sediment adheres to the bone surfaces.



Supplementary Figure 2. Aspects of three-dimensional surface models of three hand bones of Apidima 3, comprising the left third proximal phalanx (A), left fourth proximal phalanx (B), and left second intermediate phalanx (C), shown from various perspectives (distal end oriented upward in the palmar, dorsal, medial, and lateral aspects). In the proximal views, the palmar side is oriented upward; in the distal views, the dorsal side is oriented upward.



Supplementary Figure 3. Aspects of three-dimensional surface models of four hand bones of Apidima 3, comprising the left third intermediate phalanx (A), second right distal phalanx (B), third left distal phalanx (C), and the left capitate (D), shown from various perspectives (distal end oriented upward in the palmar, dorsal, medial, and lateral aspects). In the proximal views, the palmar side is oriented upward; in the distal views, the dorsal side is oriented upward. The capitate is extensively covered by hard sediment across most of its surface; therefore, only the medial diagnostic view is shown. The anatomical allocation of the distal phalanges remains tentative, as no additional distal phalanges were recovered from the individual.