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RESEARCH ARTICLE

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Occupational manual activity is reflected on the patterns among hand entheses

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Abstract

Objectives: In anthropological sciences, entheses are widely utilized as occupational stress markers. However, the reaction of entheseal surfaces to mechanical loading is not well understood. Furthermore, previous studies on entheses relied on the individuals' occupation-at-death. Past research by one of us has identified two patterns among hand entheses, proposing that they reflect two synergistic muscle groups. Here, we investigate the association between these patterns and habitual manual activity using an extensively documented skeletal sample and a three-dimensional system of quantification.

Materials and Methods: The hand bones utilized belong to 45 individuals from mid-19th century Basel. These were male adults (18 to 48 years old) who were not directly related, showed no manual pathological conditions, and whose occupational activities during their lifetime were clearly documented and could be evaluated according to historical sources. The patterns of entheses were explored using principal component analysis on both raw and size-adjusted variables. The influence of age-at-death, body mass, and bone length was assessed through correlation tests.

Results: The analysis showed that the previously proposed patterns of entheses are present in our sample. Individuals with the same or comparable occupations presented similar entheseal patterns. These results were not considerably affected by entheseal overall size, age-at-death, body mass, or bone length.

Discussion: Individuals involved in intense manual labor during their lifetime presented a distinctive pattern of hand entheses, consistent with the application of high grip force. By contrast, individuals with less strenuous and/or highly mechanized occupations showed an entheseal pattern related to the thumb intrinsic muscles.

KEYWORDS
3D quantification, musculoskeletal stress, Spitalfriedhof Saint Johann collection

1 | INTRODUCTION

Although habitual physical activity is recognized as an important factor affecting the skeleton (Scherf, Harvati, & Hublin, 2013; Scherf, Wahl, Hublin, & Harvati, 2015; Wolff, 1892), its influence is still poorly understood. In anthropology, entheses, the areas where ligaments, muscles, or tendons attach to bone, are widely considered as musculoskeletal stress markers when reconstructing the activity profiles of past populations (Foster, Buckley, & Tayles, 2012). As the hand performs a vital role in everyday human activities (Marzke et al., 1998), it has been the subject of intense study when trying to reconstruct the behavior of fossil hominins and past human populations (e.g., Almecija, Moya-Sola, & Alba, 2010; Niewoehner, 2001). In an osteological context, hand

Abbreviations: ABP, abductor pollicis; ADM, abductor digiti minimi; ADP, adductor pollicis; DI1, first dorsal interosseus; ECU, extensor carpi ulnaris; EPB, extensor pollicis brevis; FDM, flexor digiti minimi; FPB, flexor pollicis brevis; FPL, flexor pollicis longus; OP, opponens pollicis; PI1, first palmar interosseus.

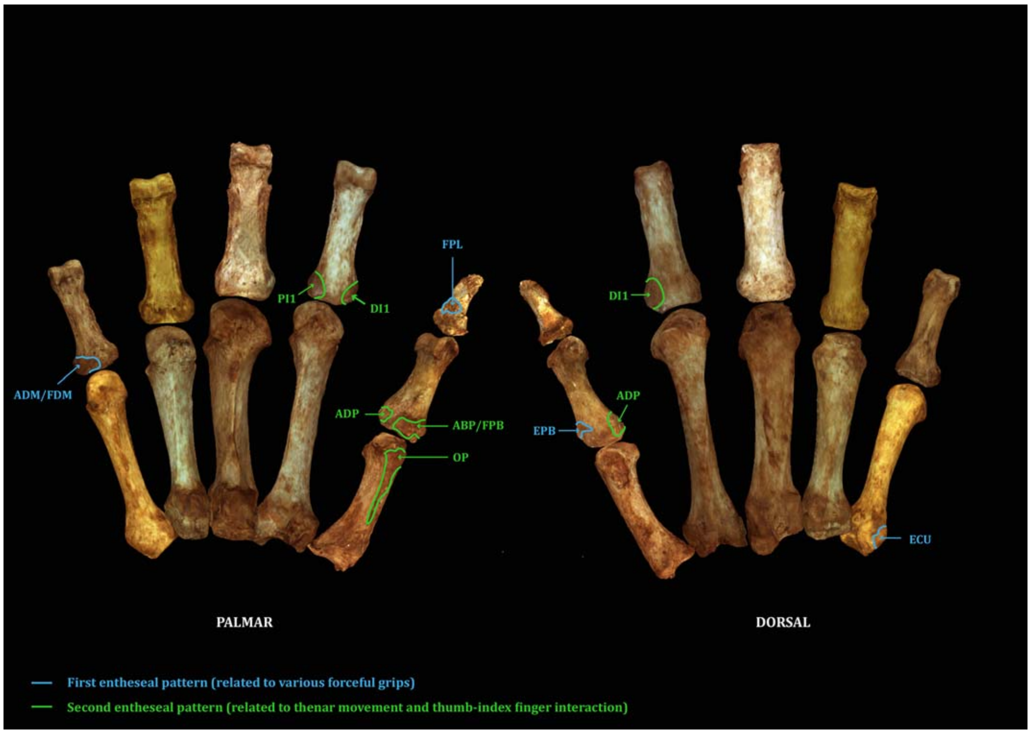

FIGURE 1 The nine entheseal surfaces of the two synergistic muscle groups described in previous research (Karakostis and Lorenzo, 2016). Each color (green or blue) represents one of the two observed entheseal patterns. For purposes of better demonstration, all five metacarpals and proximal phalanges are included in the figure. In two cases, the same enthesis corresponds to two different muscles ("ABP/FPB" and "ADM/FDM")

entheses are the sole direct sources of information about hand musculature. Identifying a strong association between habitual manual behavior and hand entheses, therefore, could provide the foundation for reconstructing occupational and habitual activity patterns based on human skeletal remains, thus enabling a greater understanding of the evolution of human manipulative capabilities.

Past work by one of us on entheseal 3D areas (Karakostis and Lorenzo, 2016) found two morphometric patterns among hand entheseal surfaces and suggested that they reflect two synergistic groups of muscles (Figure 1): one group typically contracts during hand movements associated with sustained high grip force, while the second one cooperates for positioning the thumb relative to the palm and fingers (Table 1) (Clarkson, 2000; Goislard de Monsabert, Rossi, Berton, & Bigouroux, 2012; Karakostis and Lorenzo, 2016; Maier and Hepp-Reymond, 1995; Marzke et al., 1998). However, the exact factors affecting entheseal form are highly controversial. Several recent studies

TABLE 1 The muscles related to the analyzed entheses and their function

Muscles	Primary function	Insertion site analyzed
Abductor pollicis	Abducts the thumb	Radial base of the first proximal phalanx
Flexor pollicis brevis	Flexes the first metacarpophalangeal joint	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 second finger towards the 3rd finger	Ulnar base of the second proximal phalanx
Opponens pollicis	Abducts, rotates, and flexes the thumb	Radial diaphysis of the first metacarpal
Extensor carpi ulnaris	Extends the wrist, adducts hand	Ulnar base of the fifth metacarpal
Flexor pollicis longus	Flexes the first distal phalanx	Palmar diaphysis of the first distal phalanx
Extensor pollicis brevis	Extends the thumb	Dorsal base of the first proximal phalanx
Abductor digiti minimi	Abducts the fifth finger	Ulnar base of the fifth proximal phalanx
Flexor digiti minimi	Flexes the fifth finger	Ulnar base of the fifth proximal phalanx

have questioned the relationship between muscle recruitment and entheseal form, concluding that occupational stress may not in fact be reflected on the morphology of entheseal surfaces (Djukic et al., 2015; Rabey et al., 2015; Williams-Hatala, Hatala, Hiles, & Rabey, 2016; Zumwalt, 2006). By contrast, others focused instead on the statistical relationships among different entheseal patterns, proposing that these patterns (rather than the entheseal forms themselves) could provide important information on physical activity (Karakostis and Lorenzo, 2016; Milella, Alves Cardoso, Assis, Lopreno, & Speith, 2015).

Previous research on the utility of entheses as occupational stress markers relied on the specimens' occupation-at-death (e.g., Alves Cardoso and Henderson, 2010; Alves Cardoso and Henderson, 2012; Lopreno, Alves Cardoso, Assis, Milella, & Speith, 2013). However, it has been demonstrated that information on specimens' occupation-at-death cannot provide an adequate basis for associating entheseal surfaces with physical activity (Alves Cardoso and Henderson, 2012). Indeed, assessing the relationship between bone entheses and occupation would require a sample which is documented for the activities of individuals over the last years before death. For this purpose, this study will investigate the factors influencing the morphometric patterns of hand entheses based on a skeletal sample which is extensively documented for the occupational activities of specimens during their active working life (Hotz & Steinke, 2012). The entheseal areas of these individuals will be analyzed using a precise three-dimensional (3D) system of quantification of entheseal surface area from high resolution surface scans (Karakostis and Lorenzo, 2016).

Subsequently, the results will be discussed on the basis of detailed historical sources and studies, which outline the manual activities of the occupations represented in our sample. Based on the previous hypothesis of two synergistic muscle groups (Karakostis and Lorenzo, 2016), we predict a distinctive pattern of hand entheses for individuals who systematically applied sustained high grip force during their lifetime. By contrast, we expect individuals involved in substantially less strenuous manual activities to present a pattern which reflects recruitment of the intrinsic thumb muscles.

2 | MATERIALS AND METHODS

2.1 | Sampling strategy

Our sample comprises part of the anthropological collection "Spitalfriedhof Saint Johann," housed at the Natural History Museum of Basel (Switzerland). This material was selected because of its unusually extensive documentation, which provides information not only about the sex and exact biological age, but also about the socioeconomic status, medical profile, and detailed occupational activities of each specimen during their active working life in Basel (Hotz & Steinke, 2012). Information on each individual's occupation is available in the town archives of the city of Basel and it derives from multiple legal institutions of the city (i.e., the Police, the Spitalfriedhof St. Johann Hospital, and the town's city hall) (Hotz & Steinke, 2012). Table 2 lists the occupations represented in our sample, accompanied by citations of historical sources describing their daily activity patterns in mid-19th century European cities.

A total of 45 individuals, who lived in Basel between 1804 and 1865, were analyzed. They originated from the wider region around the city and the vast majority worked in Basel only after 1840. Based on their income and social status, they all belonged to the middle or low socioeconomic classes (Hotz & Steinke, 2012; Lorenceau, 2001). The individuals analyzed were selected on the basis of six criteria, including state of preservation, pathology, sex, age, relatedness, and availability of detailed occupational information. All specimens selected preserved their hand bones intact and without pathological or taphonomic alterations (Villotte et al., 2010). Their medical documentation also did not report pathological conditions related to their hands. Sex and old biological age are also considered to be important factors of entheseal variation (Foster et al., 2012): it has been reported that after around the age of 50, entheseal surfaces are subject to extensive age-related changes (Myszka and Piontek, 2013). For this reason, our sample comprised only male adult individuals between 18 and 48 years of age. We further assessed the effect of age on our results statistically (see below). It should be mentioned that, in 19th century Basel, males of the middle or low socioeconomic classes usually started working at the age of 14 (Wadington, 1890). Thus, the duration of the individuals' active working life is directly related to their biological age. Moreover, in order to avoid the potential bias of genetic relatedness among individuals of the sample, we used its extensive documentation to verify that none of the selected specimens belonged to the same immediate family (c.f., Acknowledgements).

The selection of hand entheseal surfaces analyzed was based on the previous results establishing the association between manual muscle synergies and entheseal patterns (Karakostis and Lorenzo, 2016). The nine entheseal surfaces contributing to these two patterns are depicted in Figure 1. They are located on the surfaces of six hand elements, including the three thumb bones (first metacarpal, proximal phalanx, and distal phalanx), the index proximal phalanx, and two bones of the fifth hand ray (fifth metacarpal and fifth proximal phalanx). In two cases, the same entheseal area is associated with two muscles (*abductor pollicis/flexor pollicis brevis*, and *abductor digiti minimi/flexor digiti minimi*). In this study, only right hand bones were used, in order to control for the potential effects of bilateral asymmetry on entheseal patterns. A total of 270 bones were analyzed, comprising 405 entheseal surfaces.

2.2 | 3D scanning and measurement

High resolution 3D models of the bones were developed using a Breuckmann SmartScan structured-light scanner (Breuckmann Inc., Baden, Germany) with 125 FOV, an automatic turntable, as well as the accompanying Optocat software package (Breuckmann Inc.). Measurement accuracy was 9 μm. Full triangulation was selected. For each bone, scans were taken from 20 different angles along an arc of 360°. Subsequently all scans were aligned and merged into one 3D model. This was extracted as a single "ply" file and imported into the software

TABLE 2 Professions of individuals with citations of historical literature reporting their manual physical activities in mid-19th century European cities (c.f., in the Discussion)

Occupations involving sustained high-grip force		Less strenuous and/or mechanized occupations	
Occupations	Number	Occupations	Number
Bricklayer (Benjamin, 1827; Yeats, 1872; Anonymous, 1908)	5	**Baker** (Webster, 1845; Rochelle, 2001)	1
Butcher (Hennicke, 1866)	2	**Bookbinder** (Zaehnsdorf, 1880)	1
Carpenter (Yeats, 1872; Anonymous, 1908; Winpenny, 1990)	6	**Butler** (Beeton, 1861)	1
Day laborer (Anonymous, 1908; Mergnac and Bertrand, 2004)	1	**Doorman** (Bonnin and DeVillanova, 2006)	1
Mill builder (Benjamin, 1827)	1	**Coachman** (McShane and Tarr, 2007)	1
Saddler (Robertson, 1850; Beatie, 1981)	1	**Joiner** (Yeats, 1872; Anonymous, 1908; Shivers, 1990)	3
Stonemason (Yeats, 1872; Anonymous, 1908)	5	**Locksmith** (Yeats, 1872; Roper, 1976)	1
Tinsmith (Hall & Carpenter, 1866; Demer, 1978; Winpenny, 1990)	1	**Missionary** (Schlatterer, 1916)	1
Wood-cutter (Yeats, 1872; Anonymous, 1908; Winpenny, 1990)	1	**Painter** (Kugler and Head, 1854)	1
		Rope-maker (Chapman, 1857)	1
		Shoemaker (Phillips, 1817; Mergnac and Bertrand, 2004)	4
		Silk dyer (Hurst, 1892)	1
		Tailor (Urquhart, 1881; Mergnac and Bertrand, 2004)	5

"Meshlab version 1.3.3" (CNR-INC, Rome, Italy), in order to isolate the entheseal surface areas investigated.

The methodology followed for delineating the exact borders of hand entheseal surfaces is described elsewhere (Karakostis and Lorenzo, 2016). In that previous work by one of us (F.A.K.), the method applied presented statistically non-significant intra- and inter-observer error (maximum mean error was 0.60%). Briefly, the borders of entheseal areas were delineated on the surface models according to elevation, coloration, and surface complexity. Subsequently, the delimited entheseal areas were isolated from the rest of the bone surface and measured in square millimeters, using the Meshlab software package's tools. All measurements were collected by the same observer (F.A.K.). Throughout the quantification of entheseal surface areas, F.A.K. had no access to the occupational profile of the individuals selected.

2.3 | Statistical analyses

All analyses were conducted in the IBM SPSS software package (IBM Inc., Armonk, NY; version 24 for Windows). For identifying morphometric patterns among hand entheseal surfaces, a principal component analysis (PCA) was performed using all 45 individuals and the surface areas of the nine entheses as variables. A correlation matrix was selected because the nine variables had different scales (Field, 2013). The number of principal components (PCs) plotted was determined based on both the scree-plot technique and the Kaiser criterion (Jackson, 1991).

Given that the assignment of different occupations to wider occupational categories is considered to be often influenced by each researcher's perspective (Lopreno et al., 2013), our statistical analyses were not based on any *a priori* categorization of professions (Tabachnick and Fidell, 2001). Nevertheless, for the purpose of highlighting our results, individuals with the same occupation were highlighted in the resulting plots using different colors.

Previous research has reported strong correlation between entheseal 3D size and body size (Nolte and Wilczak, 2013). To evaluate whether the overall entheseal size of individuals influenced the observed patterns of entheses, a second PCA was conducted using size-adjusted variables. These variables were calculated by dividing each raw measurement by the geometric mean of all nine entheseal measurements for each individual. Then, the outcome was log-transformed on the basis of natural logarithms (e.g., Almecija et al., 2010).

Furthermore, a series of correlation tests were used for assessing the relationship between the observed entheseal patterns and age-at-death, body weight, as well as the maximum lengths of the six right hand bones utilized. All these three factors are previously reported to

TABLE 3 Eigenvalues and factor loadings of the two principal component analyses

Variables utilized	Principal component	Eigenvalue	% of variance	Factor loadings[a]								
				OP	ABP/FPB	ADP	EPB	FPL	DI1	PI1	ADM/FDM	ECU
Raw measurements	**PC 1**	4.78	53.02	0.70	0.87	0.62	0.63	0.71	0.73	0.82	0.75	0.69
	PC 2	1.15	12.74	**−0.39**	**−0.37**	**−0.48**	**0.48**	**0.14**	**−0.18**	**0.04**	**0.35**	**0.47**
	Total		65.76									
Size-adjusted variables	**PC 1**	2.75	30.57	**−0.56**	**−0.82**	**−0.54**	**0.62**	**0.23**	**−0.42**	**−0.29**	**0.53**	**0.71**
	PC 2	1.69	18.76	0.27	−0.05	0.42	−0.16	0.81	−0.73	−0.34	−0.34	0.03
	PC 3	1.24	13.75	−0.54	0.07	0.47	0.59	−0.08	0.19	−0.36	−0.40	−0.22
	Total		63.08									

[a]The factor loadings in bold are those of the principal components associated with the two investigated entheseal patterns.

affect the form of entheseal surfaces (Foster et al., 2012; Karakostis and Lorenzo, 2016; Nolte and Wilczak, 2013). Body mass was estimated using the femoral head anteroposterior breadth of individuals as a proxy and the equation presented by Grine, Jungers, Tobias, & Pearson (1995) (Arsuaga et al., 2012; Auerbach and Ruff, 2004). For reducing possible laterality biases, the measurements were taken on both anatomical sides and averaged (Auerbach and Ruff, 2004). The six right bone lengths and the femoral head diameters were measured by the first author (F.A.K.) in millimeters using an 8-in. digital sliding caliper (ABSOLUTE Digimatic Caliper, Mitutoyo, IL) with a calibration of 0.01 mm. Subsequently, all these measurements were repeated by the same author for twenty-five individuals and the intra-observer error was evaluated using paired *t* tests (Field, 2013). The resulting *p* values (over 0.05) indicated that all measurements were repeatable. The association between these variables and the PCs of both PCAs (the one on raw measurements and the one on size-adjusted variables) was tested using the Pearson's correlation coefficient (*r*) with an alpha level of 0.05. Significant *r* values between 0.40 and 0.60 demonstrate moderate positive association, whereas *r* values of 0.60 or above indicate strong positive correlation (Campbell, 2006). Considering that multiple correlation tests were conducted, the Holm-Bonferroni sequential correction test was utilized for reducing the probability of performing a type 1 error (Holm, 1979).

As far as statistical assumptions are concerned, the sampling adequacy of the dataset was verified using the Kaiser-Meyer-Olkin test. The outcome was 0.81 ("meritorious") (Field, 2013). Multivariate normality of the variables was assessed using the Doornik and Hansen test (Doornik and Hansen, 2008). The presence of significant outliers was diagnosed using modified Z-scores, while multivariate outliers were detected using Mahalanobis squared distances (Field, 2013; Iglewicz and Hoaglin, 1993). The linear relationship between variables was assessed using bivariate scatterplots and a Bartlett's test of sphericity was run to evaluate whether variables are suitable for data reduction (Field, 2013). Based on the results of the statistical procedures mentioned above, all assumptions of PCA and Pearson's correlation test were met (Field, 2013; Tabachnick and Fidell, 2001).

3 | RESULTS

3.1 | Patterns between hand entheses

A total of two PCs were plotted, which together accounted for the 65.76% of variance in the sample (Table 3). The first principal component (53.02% of the sample's variance) reflected overall entheseal surface size variation, given that all its factor loadings were positive. The loadings were also comparable among variables, suggesting that all nine entheseal surfaces had a similar contribution to metric variation across individuals. The second principal component (12.74% of the sample's variance) represented variation in the proportions among entheseal measurements. Positive values on this component were related to individuals with proportionally larger entheseal surfaces of the *abductor digiti minimi/flexor digiti minimi*, *flexor pollicis longus*, *extensor pollicis brevis*, and *extensor carpi ulnaris*. The latter two entheses had the highest factor loadings. Negative scores on the component represented individuals with relatively larger entheses of the thumb intrinsic muscles (i.e., *opponens pollicis*, *abductor pollicis/flexor pollicis brevis*, *adductor pollicis*) and the first dorsal *interosseus*. The three entheseal surfaces of the thenar muscles had similar factor loadings (Table 3).

As demonstrated in the plot of Figure 2, the vast majority of individuals with the same occupation were located in the same side of PC2 (positive or negative), thus sharing a similar pattern between their hand entheseal surfaces. To highlight this observation, the workers of each occupation were colored distinctively in the PCA plot (Figure 2). On PC2, the most striking similarity among individuals with the same work was observed for the groups of carpenters (PC scores ranged between −0.1 and 0.6), shoemakers (ranged between −1.3 and 0.2), and joiners (ranged between −0.8 and 0.2). The ranges of PC scores were greater for bricklayers (−0.1 to 2.30) and tailors (−0.2 to −2.4). It should be mentioned that most overlapping occupations seem to be of comparable nature (c.f., in the Discussion). For instance, bricklayers, carpenters, and stonemasons were all heavy construction manual workers (Alves Cardoso and Henderson, 2012; Winpenny, 1990; Yeats, 1872), while the wood-cutter (specialized carpenter) was within the range of

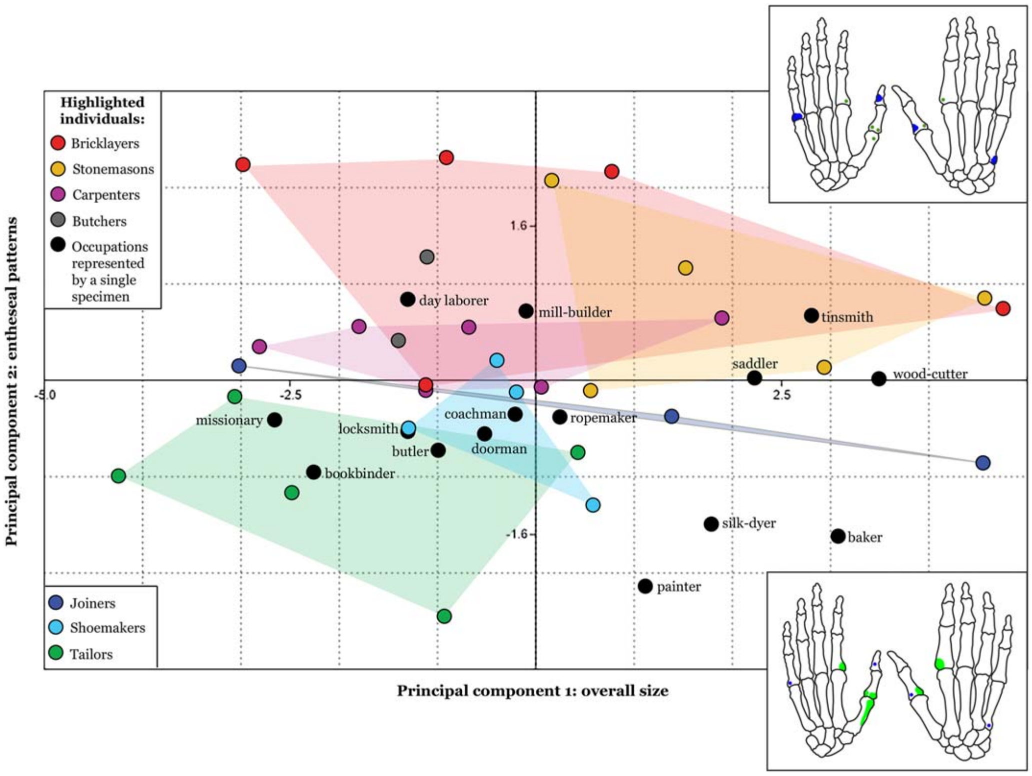

FIGURE 2 Scatter plot of the principal component analysis on raw entheseal 3D measurements without *a priori* group categorization. Individuals with the same occupation were highlighted. The two side figures demonstrate which entheseal areas are proportionally larger in individuals with higher scores on the second principal component (entheses in blue) and individuals with lower ones (entheses in green). Individuals with lower scores on the second principal component present proportionally larger entheses of the four thumb intrinsic muscles and the first dorsal *interosseus* (green areas in the side figures). By contrast, individuals with higher scores on this component show relatively larger entheses of the muscles *abductor digiti minimi/flexor digiti minimi*, *flexor pollicis longus*, *extensor pollicis brevis*, and *extensor carpi ulnaris* (blue areas in the side figures)

carpenters and the mill-builder (specialized builder) overlapped with the bricklayers (Figure 2).

3.2 | The effect of entheseal size, age, body weight, and bone length

A second PCA was carried out using size-adjusted variables, in order to estimate the influence of overall entheseal size on the results. The three first PCs represented the 63.08% of the total sample's variance. The two morphological tendencies identified in the PCA of raw measurements (PC2) were also observed in the PCA of size-adjusted variables (Table 3). In the latter, these patterns were associated with PC1, which represented the 30.57% of the total sample's variance. The factor loadings of this component were all substantially higher than those of PC2 in the first PCA, emphasizing the occurrence of the two proposed morphological trends among hand entheses (Karakostis and Lorenzo, 2016). Nevertheless, the factor loading of the enthesis of the first palmar *interosseus*, which was almost zero on PC2 of the previous PCA, appears here (on PC1 of the second PCA) to be marginally negative (Table 3). Overall, the mean difference in specimen PC scores between PC2 of the first PCA and PC1 of the second PCA was 0.24. As demonstrated in the plot of Figure 3, this slight change does not reduce the similarity observed among specimens with the same or relevant occupation.

The factor loadings of the remaining two components (PC2 and PC3) did not reflect the two entheseal patterns investigated here (Table 3). Furthermore, they showed no association with the occupational profile of individuals, which is the focus of this study. Particularly, variation in PC2 (18.76%) is mainly related to the proportion between the entheses of *flexor pollicis longus* and the first dorsal *interosseus*, while the score of specimens on PC3 (13.74%) is mainly regulated by the proportion between the enthesis of *opponens pollicis* and those of *adductor pollicis* and *extensor pollicis brevis*.

The correlation tests showed that there is a significant positive association between the scores of PC1 of the PCA on raw measurements and the values of biological age (Table 4), estimated body weight (Table 5), and the six bone lengths (Table 6). This PC represents overall size variation in the sample (Table 3). The strength of this correlation was moderate for biological age but considerably stronger for both body weight and bone lengths. By contrast, the values of all these variables did not significantly coincide with the scores of all remaining PCs of both PCAs (p value > 0.05). These included the two PCs whose factor loadings reflected the two hypothesized patterns of hand entheses (i.e., PC2 of the first PCA and PC1 of the second PCA).

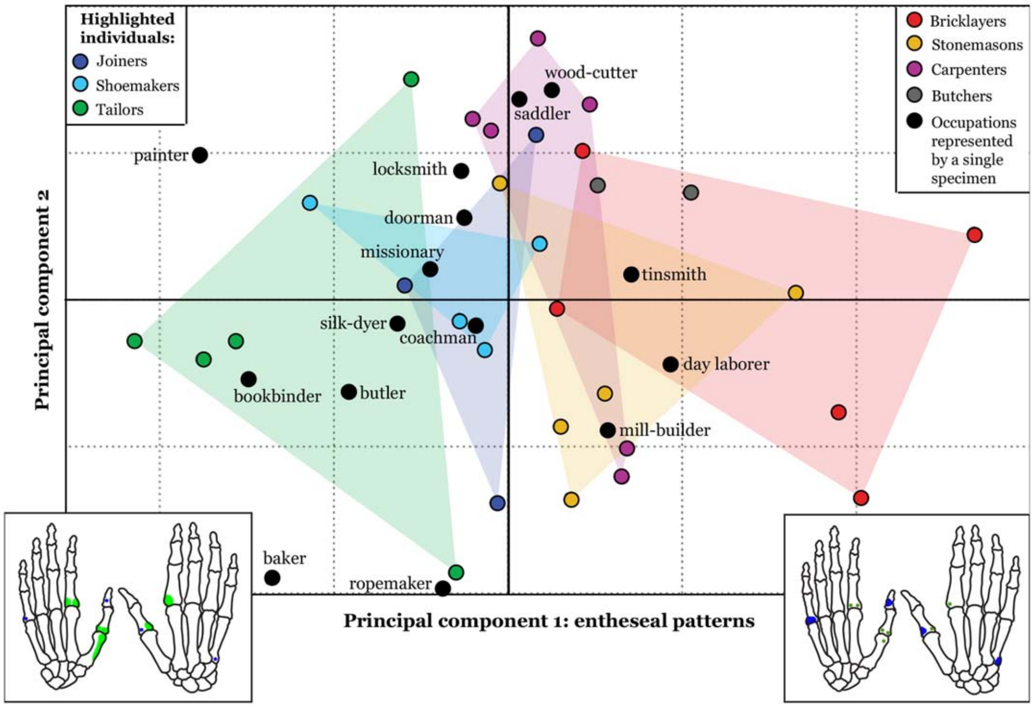

FIGURE 3 Scatter plot of the principal component analysis on size-adjusted 3D entheseal measurements without *a priori* group categorization. Individuals with the same occupation were highlighted. The two side figures demonstrate which entheseal areas are proportionally larger in individuals with higher scores on the first principal component (entheses in blue) and individuals with lower ones (entheses in green). Individuals with lower scores on the first principal component present proportionally larger entheses of the four thumb intrinsic muscles, the first dorsal *interosseus*, and the first palmar *interosseus* (green entheses in the side figures). By contrast, individuals with higher scores on this component show relatively larger entheses of the muscles *abductor digiti minimi*/*flexor digiti minimi*, *flexor pollicis longus*, *extensor pollicis brevis*, and *extensor carpi ulnaris* (blue entheses in the side figures)

4 | DISCUSSION

The historical literature provides a plethora of evidence surrounding the physical requirements of the occupations represented in our sample (Table 2). This information allows us to identify the occupations which required systematic application of sustained high grip force, within the historical context of our sample. Since the beginning of the 19th century, Basel was considered as the most industrialized city of Switzerland and a mass producer of its own mechanical equipment, which had already replaced intense manual force in multiple urban occupations (Berend & Berend, 2013; Connor, 2007; Mergnac and Bertrand, 2004). By the mid-19th century, this revolutionary change of working conditions in European cities is reported for multiple crafts, including bakers (Rochelle, 2001; Webster, 1845), locksmiths (Roper, 1976; Yeats, 1872), ropemakers (Chapman, 1857), shoemakers

TABLE 4 Correlations between biological age and the principal components of each principal component analysis (PCA) performed

Analysis	Principal components[a]	Biological age	
		p value[b]	*r* value
PCA on raw size	1st (overall size)	0.01	0.47
	2nd	**0.79**	**0.04**
PCA on size-adjusted variables	**1st**	**0.71**	**−0.05**
	2nd	0.73	0.05
	3rd	0.18	0.20

[a]The two principal components in bold are those associated with the investigated patterns between hand entheses (Karakostis and Lorenzo, 2016).
[b]Only the adjusted p-values are reported (Holm, 1979).

TABLE 5 Correlations between body weight and the principal components of each principal component analysis (PCA) performed

Analysis	Principal components[a]	Body weight[b]	
		p value[c]	*r* value
PCA on raw size	1st (overall size)	<0.01	0.57
	2nd	**0.32**	**0.16**
PCA on size-adjusted variables	**1st**	**0.81**	**0.04**
	2nd	0.61	0.08
	3rd	0.31	0.15

[a]The two principal components in bold are those associated with the investigated patterns between hand entheses (Karakostis and Lorenzo, 2016).
[b]Body weight was estimated using the femoral head anteroposterior breadth, based on the equation presented in Grine et al (1995).
[c]Only the adjusted *p* values are reported (Holm, 1979).

TABLE 6 Significant correlations between the principal components and the six bone maximum lengths

Bone length	1st Principal Component of the analysis on raw measurements[a]	
	p value[b]	*r* value
First metacarpal	<0.01	0.62
Fifth metacarpal	<0.01	0.60
First proximal phalanx	<0.01	0.68
Second proximal phalanx	<0.01	0.61
Fifth proximal phalanx	<0.01	0.62
First distal phalanx	<0.01	0.58

[a]This principal component represents overall entheseal size.
[b]Only the adjusted p-values are reported (Holm, 1979).

(Mergnac and Bertrand, 2004; Phillips, 1817), silk-dyers (Hurst, 1892), tailors (Mergnac and Bertrand, 2004; Urquhart, 1881), and joiners (Anonymous, 1908; Shivers, 1990; Yeats, 1872). By contrast, the historical sources clearly describe certain urban occupations as highly demanding handcrafts within the industrialized environment of the mid-19th century, underlining the strenuous and repetitive use of manual strength for performing a variety of tasks (Winpenny, 1990; Wrigley, 1972). This was the case -among others- for urban butchers (Hennicke, 1866), carpenters (Anonymous, 1908; Winpenny, 1990; Yeats, 1872), bricklayers (Anonymous, 1908; Benjamin, 1827; Yeats, 1872), saddlers (Beatie, 1981; Robertson, 1850), stonemasons (Anonymous, 1908; Yeats, 1872), tinsmiths (Demer, 1978; Hall & Carpenter, 1886; Winpenny, 1990), as well as unspecialized day laborers (Anonymous, 1908; Mergnac and Bertrand, 2004).

Based on these historical sources (Table 2), individuals can be divided into workers involved in highly demanding manual activities and individuals with less strenuous and/or highly mechanized manual tasks. When the individuals of each occupational group are colored differently in our PCA plot on raw measurements (Figure 4), this categorization provides a rather clear separation between the two groups of workers, with highly demanding occupations presenting distinctively higher positive scores on PC2. This difference between the two categories is also evident in Table 7, which contains the descriptive statistics with respect to each occupational category defined. The four entheseal areas associated with high grip force (Figure 1) have a larger mean size in individuals involved in demanding manual labor, while the mean size of the thenar muscles' entheses is larger in individuals with less strenuous professions (Table 3). It is worth mentioning that the vast majority of occupations represented in our sample were categorized similarly in previous works on entheseal change, which separated individuals based on the intensity of their physical activities (e.g., Alves Cardoso and Henderson, 2012; Villotte et al., 2010). Previous research on entheseal change has recommended that different occupational categories should present comparable mean age-at-death (Alves Cardoso

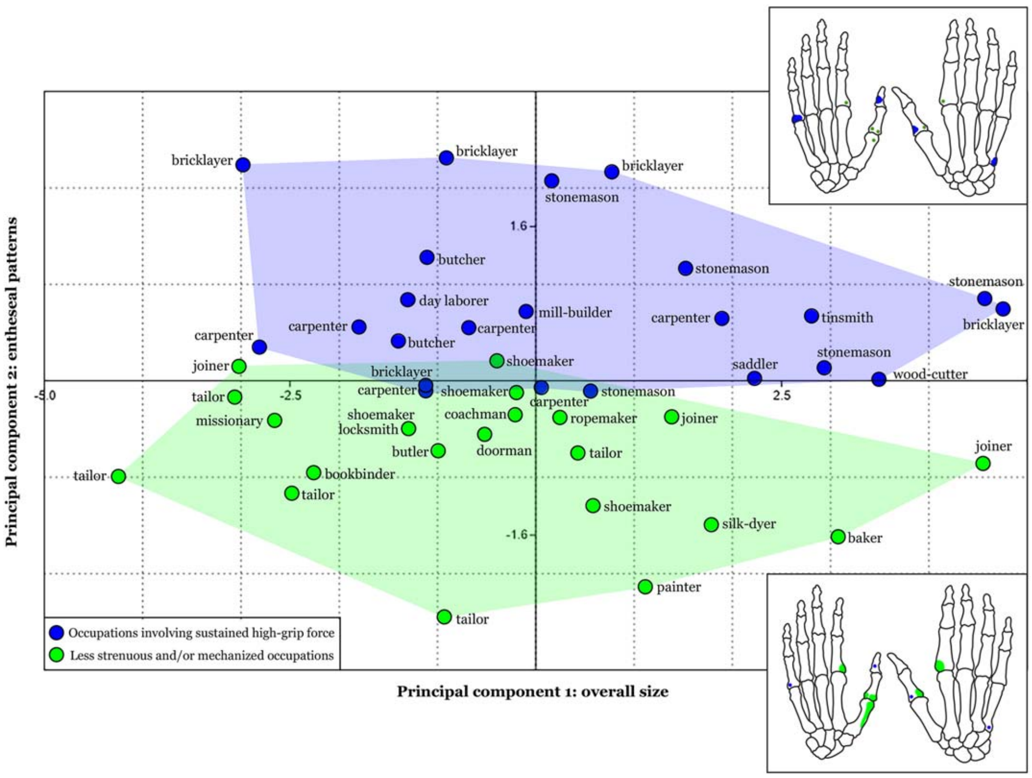

FIGURE 4 Scatter plot of the principal component analysis on raw entheseal 3D measurements without *a priori* group categorization. Occupations were classified (colored) based on the intensity of their manual activities, according to historical sources (c.f., Table 2). The two side figures demonstrate which entheseal areas are proportionally larger in individuals with higher scores on the second principal component (entheses in blue) and individuals with lower ones (entheses in green) (c.f., in the legend of Figure 2)

TABLE 7 Descriptive statistics for entheseal measurements (in square millimeters) and age at death (in years)

		Occupations involving sustained high-grip force				Less strenuous and/or mechanized occupations			
Bone	Measurements[a]	Range	Mean	Standard error of the mean	Standard deviation	Range	Mean	Standard error of the mean	Standard deviation
First proximal phalanx	ABP/FPB	82.67	82.02	4.74	22.72	92.92	86.34	5.04	23.65
	ADP	64.29	69.37	3.91	18.74	64.12	73.26	3.99	18.70
	EPB	55.93	67.24	3.45	16.56	59.90	44.56	2.93	13.74
Second proximal phalanx	DI1	113.44	121.97	6.34	30.38	117.28	120.07	6.21	29.14
	PI1	125.59	92.40	6.44	30.91	95.03	84.26	5.29	24.81
Fifth proximal phalanx	ADM/FDM	70.75	84.05	3.88	18.59	89.07	69.68	4.08	19.12
First metacarpal	OP	63.74	66.18	3.31	15.87	61.33	73.30	4.14	19.41
Fifth metacarpal	ECU	127.79	133.76	6.30	30.19	131.39	100.10	7.08	33.19
First distal phalanx	FPL	57.64	51.61	3.39	16.24	51.22	43.49	3.07	14.38
Age at death		30	28.91	1.79	8.57	26	27.14	1.57	7.37

[a]ABP/FPB: abductor pollicis/flexor pollicis brevis (common insertion area for both muscles); ADP: adductor pollicis; EPB: extensor pollicis brevis; DI1: first dorsal interosseus; PI1: first palmar interosseus; ADM/FDM: abductor digiti minimi/flexor digiti minimi (common insertion area for both muscles); OP: opponens pollicis; ECU: extensor carpi ulnaris; FPL: flexor pollicis longus.

and Henderson, 2012). As demonstrated in Table 7, mean age is very similar between the two categories of occupations defined here.

The purpose of this study was to assess the relationship between habitual manual activity and patterns of hand entheses, while controlling for as many confounding factors as possible in an anthropological sample (Foster et al., 2012). Our results verify the occurrence of the two previously described morphometric patterns of hand entheses (Karakostis and Lorenzo, 2016) in our sample, showing that these are not associated with interpopulation variation, sex, age (between 18 and 48 years), body mass, hand bone length, pathology, or close relatedness. In humans, the raw size of entheseal 3D areas has been reported to strongly correlate with body size (Nolte and Wilczak, 2013) as well as bone length (Karakostis and Lorenzo, 2016). This indicates that the size of entheseal areas, like any other bone part (Rauch, 2005), is highly dependent on the size of individuals. This is also supported by our results, which showed that the overall size of entheses is significantly associated with body weight and hand bone lengths (Tables 5 and 6). Furthermore, overall entheseal size was moderately correlated with age-at-death (Table 4). Previous research has also reported a significant effect of age on entheseal change (e.g., Foster et al., 2012; Milella, Belcastro, Zollikofer, & Mariotti, 2012) and 3D size (Nolte and Wilczak, 2013), probably due to age-related degenerative processes in combination with lifelong accumulation of mechanical stress. In our analysis, when the effect of overall entheseal size was removed, the two observed entheseal patterns accounted for almost one third of the sample's total variance (Table 3). On this basis, overall size and age-at-death could hardly be the regulating factors of the two observed entheseal patterns. This can be also supported by Figures 2 and 4 (PCA on raw measurements), where multiple individuals with extensive size differences (scores on PC1) presented almost the same entheseal pattern (scores on PC2).

The two entheseal patterns reported here (Table 3) are almost identical to the ones described in the previous research which proposed that they reflect two synergistic muscle groups (Figure 1), based on a sample from medieval Burgos in Spain (Karakostis and Lorenzo, 2016). This similarity suggests that different populations can potentially present comparable patterns of hand entheses. It should be mentioned that this previous study utilized both male and female individuals (Karakostis and Lorenzo, 2016).

Previous research has questioned the impact of physical activity on human entheseal size and shape (Djukic et al., 2015; Rabey et al., 2015; Williams-Hatala et al., 2016; Zumwalt, 2006). However, the results of these past studies may be strongly influenced by their methodological choices. Two of these (Djukic et al., 2015; Rabey et al., 2015) did not include a 3D analysis of entheseal surface areas, which could provide complete information on their form. Moreover, other works (Rabey et al., 2015; Zumwalt, 2006) utilized experimental models involving non-primate animals, even though it is not known whether the mechanisms of entheseal change differ between humans and other mammals. Another study (Williams-Hatala et al., 2016) found no correlation between the size of the entheseal areas of *opponens pollicis* and *opponens digiti minimi* and specific dimensions of the corresponding muscles. However, the specimens used in that work were of advanced age (an average of 77.9 ± 12 years). The mechanisms of entheseal change are highly influenced by old age (Myszka and Piontek, 2013), while muscle dimensions substantially decrease after the age of 50 (Doherty, 2001; Deschenes, 2004).

In this study, the observed differences among specimens with the same occupation could be due to numerous other variables affecting human behavior and bone morphology (Maier and Hepp-Reymond, 1995; Marzke et al., 1998), including inter-individual genetic variability, nutrition, hormone levels, or even individual hand preference (Foster et al., 2012; Rauch, 2005). In spite of the multiple and complex factors at play, our approach was able to identify a functional signal in the patterns between hand entheses. On this basis, future research on occupational stress markers would substantially benefit from the compilation and study of skeletal samples which are documented for the active working life of individuals over a considerable period of time before death. Although the sample size used in this study is larger than in the majority of previous works on 3D models of entheseal surface areas (Noldner and Edgar, 2013; Williams-Hatala et al., 2016; Zumwalt, 2005; Zumwalt, 2006)—with the exception of one study which focused on a single entheseal surface (Nolte and Wilczak, 2013) and our previous work on a medieval non-documented sample (Karakostis and Lorenzo, 2016)—future work on increased sample sizes will also help to further establish the functional signal observed here. The conclusions of our work suggest that habitual manual activity has an observable effect on the morphometric patterns among hand entheses. On this basis, future application of our quantitative 3D approach to the analysis of entheseal patterns in the human fossil record could further our understanding of the evolution of tool making behavior and subsistence strategies among hominins. In bioarchaeology, the analysis of hand bone entheses could become an essential tool for reconstructing the manual activities, division of labor, and social structure of past populations.

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