

See discussions, stats, and author profiles for this publication at: <https://www.researchgate.net/publication/382447769>

Ontogeny and sexual dimorphism in the human hands through a 2D geometric morphometrics approach

Article in *American Journal of Biological Anthropology* · July 2024

DOI: 10.1002/ajpa.25001

CITATION

1

READS

90

3 authors:



[Verónica Fernández-Navarro](#)

Universidad de Cantabria

11 PUBLICATIONS 15 CITATIONS

[SEE PROFILE](#)



[Diego Garate](#)

Universidad de Cantabria

268 PUBLICATIONS 2,087 CITATIONS

[SEE PROFILE](#)



[Daniel García-Martínez](#)

Complutense University of Madrid

182 PUBLICATIONS 1,803 CITATIONS

[SEE PROFILE](#)

RESEARCH ARTICLE

Ontogeny and sexual dimorphism in the human hands through a 2D geometric morphometrics approach

Verónica Fernández-Navarro¹  | Diego Garate¹ | Daniel García Martínez^{2,3,4}

¹Instituto Internacional de Investigaciones Prehistóricas de Cantabria (IIIPC), Universidad de Cantabria, Gobierno de Cantabria, Santander, Spain

²Physical Anthropology Unit, Department of Biodiversity, Ecology, and Evolution, Faculty of Biological Sciences, Complutense University of Madrid, Madrid, Spain

³Centro Nacional de Investigación sobre la Evolución Humana (CENIEH), Burgos, Spain

⁴Laboratory of Forensic Anthropology, Centre for Functional Ecology, Department of Life Sciences, University of Coimbra, Calçada Martim de Freitas, Coimbra, Portugal

Correspondence

Verónica Fernández-Navarro, 1 Instituto Internacional de Investigaciones Prehistóricas de Cantabria (IIIPC), Universidad de Cantabria, Gobierno de Cantabria, 39005 Santander, Spain.

Email: veronica.fernandezn@unican.es; vericananana01@gmail.com

Funding information

"Concepción Arenal" 2020–21; Scientific virtual reality for the study and dissemination of the scenarios of artistic creation in Palaeolithic caves (RealCaveART), Grant/Award Number: PDC2022-133124-I00; MCIN/AEI/; European Union Next Generation EU/PRTR

Abstract

Objectives: This study aims to conduct a thorough characterization of hand morphology. Employing a 2D geometric morphometric approach, we scrutinize individual fingers and the palm, delineating the ontogenetic trajectories for each biological sex and investigating the alterations that take place at various stages of human development.

Materials and methods: A set of thirty-two 2D anatomical landmarks were assessed in a sex-balanced sample of human hands (F = 275, M = 250 males), spanning all stages of human development. Following Procrustes registration, the data on size and shape for individual fingers and the palm were examined for each biological sex and age group. Regression analysis was utilized to quantify ontogenetic trajectories for each biological sex.

Results: The findings suggest a gradual escalation in sexual dimorphism throughout human development, with statistically noteworthy distinctions becoming apparent in size starting at the age of 3, and in shape from the age of 7 onwards. Additionally, our analyses uncover a distinctive sigmoid pattern between sexes, indicating that biological male hands exhibit a sturdier build compared to biological female hands from early childhood onward.

Conclusions: In conclusion, this study enriches our insights into sexual dimorphism in human hands, stressing the importance of considering both size and shape across different ontogenetic stages. These findings not only expand our understanding of human biological variation but also lay the foundation for future interdisciplinary research in diverse scientific domains.

KEYWORDS

form variability, hands, morphometry, ontogeny, sexual dimorphism

1 | INTRODUCTION

Sexual dimorphism is a fundamental element of intraspecific biological diversity observed in both modern and fossil hominins. (Frayer & Wolpoff, 1985). In current human populations, it has been extensively

examined at craniofacial (Rosas & Bastir, 2002; Bastir et al., 2011) and postcranial levels (Bastir et al., 2014; García-Martínez et al., 2016, 2019; Karakostis et al., 2013, 2015; Rosas et al., 2015). Certain morphological changes might be attributed to allometry (shape differences explained by size variations), considering the general trend of

This is an open access article under the terms of the [Creative Commons Attribution-NonCommercial-NoDerivs](https://creativecommons.org/licenses/by-nc-nd/4.0/) License, which permits use and distribution in any medium, provided the original work is properly cited, the use is non-commercial and no modifications or adaptations are made.

© 2024 The Author(s). *American Journal of Biological Anthropology* published by Wiley Periodicals LLC.

biological males being larger than biological females (Agnihotri et al., 2005; Jowaheer & Agnihotri, 2011; Kanchan & Krishan, 2011).

Regarding the human hand, the meticulous morphological characterization, incorporating both shape and size, has been a focal point of interest across diverse realms within biological anthropology, notably in paleoanthropological studies (Berger et al., 2015; Karakostis et al., 2017, 2018; Kivell et al., 2011, 2015, 2022), functional anatomy and ergonomics (Bolstad et al., 2018; Karakostis et al., 2018; Mandahawi et al., 2008), archeological sciences applied to rock art (Groenen, 1988; Fernández-Navarro et al., 2022; Gunn, 2006; Snow, 2006, 2013), or even medicine or forensic sciences (Kulaksiz & Gözil, 2002; Standring et al., 2005).

In the case of sexual dimorphism in *Homo sapiens*, prior research has primarily focused on size variation between biological females and males. These studies utilized linear measurements as the principal parameters for hand characterization and sexual determination (Agnihotri et al., 2005; Kanchan & Krishan, 2011; Karakostis et al., 2019, Gupta et al., 2022). Employing conventional morphometry, these studies drew conclusions from maximum linear measurements and indices that account for various digital lengths, notably incorporating the “Manning Index.”

This index, initially proposed in the 19th century (Baker, 1888; Ecker, 1875) and subsequently generalized and adopted by Professor J.T. Manning (Manning et al., 1998), suggests that the 2D/4D ratio, indicating the length ratio of the index and ring fingers, exhibits sexual dimorphism due to variations in prenatal exposure to androgens. This results in a lower value of this ratio in biological males. This dimorphism is proposed to be observable as early as 2 years old (Ernsten et al., 2021, 2023; Manning, 2012; Manning et al., 1998) and forms the foundation of numerous studies focused on sexual dimorphism in hands. This approach has been employed in biological anthropology studies (Cooke, 2014; Hönekopp & Watson, 2010; Ibrahim et al., 2016) as well as in archeological sciences such as rock art hand representations (Chazine & Noury, 2006; Mackie, 2015; Rabazo-Rodríguez et al., 2017). These investigations have shown that adult biological males typically exhibit greater hand size compared with biological females, with a 5%–10% disparity in maximum hand length and a 10%–15% difference in maximum hand width (Aboul-Hagag et al., 2011; Agnihotri et al., 2005; Kanchan & Krishan, 2011; Králík et al., 2014; Mandahawi et al., 2008).

It is crucial to highlight that, apart from the 2D/4D digit index, sexual variation in size and shape has not been extensively explored in subadult populations (McIntyre et al., 2006; Ernsten et al., 2021, 2023). Additionally, the samples in the mentioned studies have primarily focused on very specific age groups, often limited to children or adults. These investigations fail to capture the changes in hand morphology throughout human development, that is, ontogeny. Therefore, while morphological differences related to biological sex have been recognized for specific static age groups, especially in the adult population, the comprehensive impact of human development has not been adequately addressed (see Kivell et al., 2013).

Lastly, a final challenge in examining the development of sexual dimorphism in the human hand concerns the methodological approach of classical studies. When the morphometric characterization of the hand depends solely on maximum linear dimensions, the shape of

the structure under analysis (i.e., the spatial configuration of the fingers and the palm) is not adequately captured (Mitteroecker & Gunz, 2009). Consequently, it has not been thoroughly explored whether there is a sex-related difference in the fingers and/or the palm during development and the potential morphological changes.

The goal of this study is to comprehensively investigate morphological changes throughout ontogeny in both sexes, employing a geometric morphometrics (GM) approach. GM enables the separate analysis of size and shape variables, allowing for the examination of individual elements of the hand and providing a visually intuitive representation of shape variation. Through this research, we aim to enhance understanding of sexual dimorphism in the hand at each stage of human life, also presenting, for the first time, morphological data on the actual growth of this extremity during ontogenetic development. As such, we will test the null hypothesis that individual fingers and the palm exhibit sexual dimorphism in both size and shape, with sexual dimorphism becoming more and more pronounced during hand development with age (H0).

2 | MATERIALS AND METHODS

2.1 | Materials

To explore differences in sexual dimorphism during ontogeny in hands, we gathered a diverse sample of scans through organized workshops in kindergartens, schools, and colleges. This experimental program involved various groups, categorized by age and biological sex, and focused on the European populations to determine the parameters for the morphometric study.

In total, the sample is sex-balanced, consisting of 546 individuals encompassing all age groups of human development (Female = 278, Male = 268) (Table 1). After capturing and anonymizing the scans in accordance with the Helsinki Declaration (Goodyear et al., 2007), we categorized individuals based on the classification proposed by Bogin and Smith (1996). Each participant provided information about their biological sex and age for subsequent classification.

This study addressed sexual dimorphism and ontogenetic development in human hands by collecting data from modern living humans. An intrinsic limitation of biometric data collection under these conditions is the difficulty in obtaining a high participation rate of children and infants. Consequently, we are aware of the scarcity of data in these age groups.

2.2 | Methods

2.2.1 | Sample acquisition: Hands

This experiment received approval from the Ethics Committee of Cantabria University (Cod. CE Tesis 03/2021) and adhered to all values and regulations for data protection and anonymity (Goodyear et al., 2007). It confirms that all steps of the experimental process were conducted following relevant guidelines and regulations.

TABLE 1 Age stages by Bogin and Smith (1996) and the individuals studied belonging to each of the groups.

Stage	Duration	Scanned hands (n)	Biological sex (M/F)
Infancy ^a	2–36 months	7	Female: 4 Male: 3
Childhood	3.0–6.9 years	76	Female: 37 Male: 39
Juvenile	Female: 7.0–10.9 Male: 7.0–12.9	117	Female: 42 Male: 75
Adolescence	Female: 11.0–17.9 Male: 13–20.9	199	Female: 114 Male: 85
Adulthood	Female: 18.0/20.0–45.9 Male: 21.0/25.0–55.9	119	Female: 66 Male: 53
Old age and senescence	Female: +46 Male: +56	28	Female: 15 Male: 13

^aExact age of the individuals: 365.M, 471.F, 472.F, 581.F—2 years old and 501.M,636-M—22 months old.

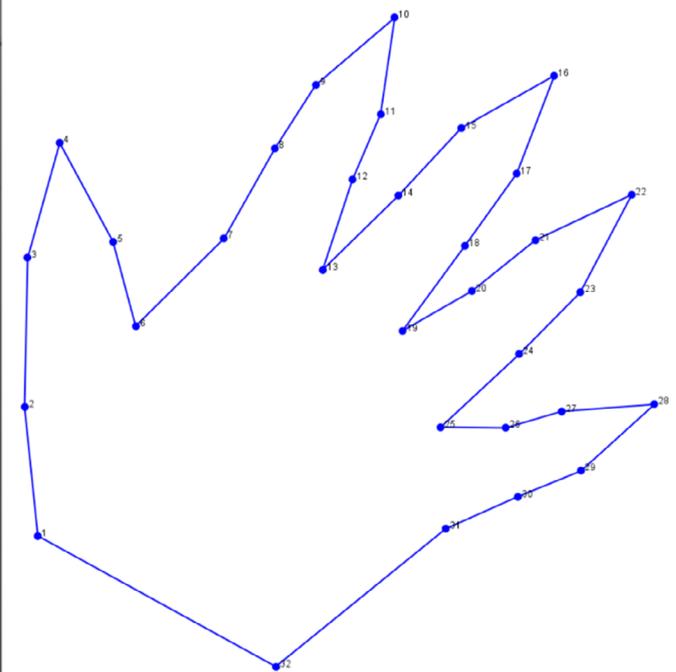
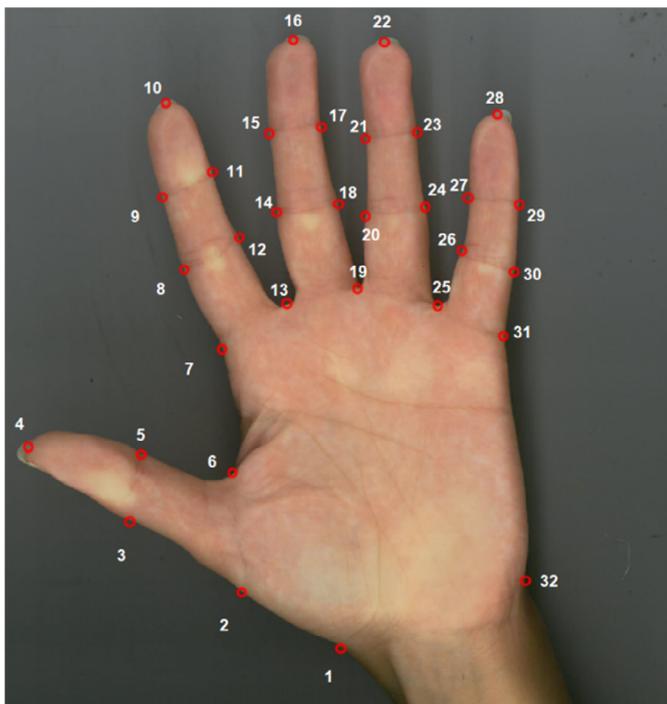


FIGURE 1 Landmarks system applied in the study.

Additionally, informed consent was obtained from all subjects and/or their legal guardian(s) for the collection, processing, and publication of the data. No personal information beyond what is strictly necessary for the study (biological sex and age) was collected.

The scans were obtained using a contact image scanner with an added scale, ensuring real and proportional measurements, concretely an Epson Workforce WF-C5790 scan, which provides a 1.200 ppp × 2.400 ppp image resolution. Participants were instructed to place their hand on the scanner in a relaxed posture (corresponding to position 2 in [Fernández Navarro et al., 2024]). They were guided on the force and position required to place their hand to homogenize the parameters as much as possible. To mitigate potential noise arising from laterality differences between left and right hands, only left hands were digitized and analyzed (Swami et al., 2015).

2.2.2 | Data collection: Landmark system

We utilized a template comprising 32 type I homologous 2D landmarks (Zelditch et al., 2012) for each hand, as illustrated in Figure 1. These landmarks were positioned on the primary anatomical reference points, providing a comprehensive representation of the hand's shape by capturing all the distinctive “markers” that precisely indicate the measurement locations (Table 2).

Each scan was imported into TPSdig2[®] (Rohlf, 2006) and the corresponding landmarks were applied to each hand scan. All GM software utilized in this study, tpsDig, tpsRelw, and MorphoJ (Klingenberg, 2011), is readily accessible on the SUNY Stony Brook Morphometrics website (<http://life.bio.sunysb.edu/morph/>). We opted for the 2D landmark system due to its capacity to demonstrate

TABLE 2 Corresponding landmark system formed by 32 conventional landmarks and their biological definition.

Landmark number	Landmark definition
1	Wrist and thumb junction point
2	Fold of the thumb joint on the medial side
3	Point of the distal palmar crease on the medial side
4	The central point of the fingertip (thumb f.)
5	Point of the distal palmar crease on the lateral side
6	The central point of the thumb joint corner
7	Digital-palmar crease on the medial side
8	The proximal digital crease of the index finger on the medial side
9	The distal digital crease of the index finger on the medial side
10	The central point of the fingertip (index f.)
11	The distal digital crease of the index finger on the lateral side
12	The proximal digital fold of the index finger on the lateral side
13	The central point of the second finger joint corner
14	The proximal digital crease of the middle finger on the medial side
15	The distal digital crease of the middle finger on the medial side
16	The central point of the fingertip (middle f.)
17	The distal digital crease of the middle finger on the lateral side
18	The proximal digital crease of the middle finger on the medial side
19	The central point of the third finger joint corner
20	The proximal digital crease of the ring finger on the medial side
21	The distal digital crease of the ring finger on the medial side
22	The central point of the fingertip (ring f.)
23	The distal digital crease of the ring finger on the lateral side
24	The proximal digital crease of the ring finger on the lateral side
25	The central point of the fourth finger joint corner
26	The proximal digital crease of the little finger on the medial side
27	The digital crease of the little finger on the medial side
28	The central point of the fingertip (little f.)
29	The digital crease of the little finger on the lateral side
30	The proximal digital crease of the little finger on the lateral side
31	Digital-palmar crease on the lateral side
32	Point of attachment between the little finger and the wrist

sufficiently strong differentiation, facilitating the testing of the hypotheses posited.

2.2.3 | Geometric morphometric statistical analysis

First, it is imperative to highlight that variation in finger positioning can obscure the assessment of real morphological differences between individuals when utilizing GM (Fernández Navarro et al., 2024). Given the impossibility of standardizing hand postures across various disciplines, such as archeological hand representations on rock walls, we have opted to analyze each element of the human hand separately: the palm, thumb (F1), index finger (F2), middle finger (F3), ring finger (F4), and little finger (F5). This approach enables a meticulous evaluation of each element and facilitates their integration into a comprehensive assessment of the entire hand. Thus, this methodology allows for potential future analysis of the data both individually and jointly.

The primary aim of this investigation was to meticulously delineate the morphology of the hand and its individual elements concerning both shape and size throughout the entire spectrum of human development, spanning from early infancy to old age. To achieve this objective, we utilized MorphoJ[®] software, a comprehensive program package for GM analysis (Klingenberg, 2011), along with the statistical software PAST[®] for data analysis (Hammer et al., 2001). Size and shape data were derived through generalized Procrustes analysis (GPA) of the landmark dataset (Mitteroecker et al., 2013; Zelditch et al., 2012). Following GPA, we isolated the landmarks corresponding to the individual elements of the hand, including fingers and palm, for further analysis. The size of the individual hand elements was quantified using centroid size, defined as the square root of the sum of squared distances of a set of landmarks from their centroid—the center of gravity (Mitteroecker & Gunz, 2009; O'Higgins, 2000; Zelditch et al., 2012).

We scrutinized the distribution of centroid size separately for each finger and the palm, conducting a mean size analysis for every ontogenetic stage, discerning disparities between biological males and females. Additionally, we investigated the ontogenetic trajectory of both sexes by plotting the centroid size distribution against the ontogenetic stages proposed by Bogin (1999). To delve into sexual dimorphism in shape, a mean shape analysis with a permutation test ($p = 1000$) was conducted by age group. This methodology, following the outlined approach by Bogin (1999), was applied to each individual element of the hand. The analysis facilitated the exploration of the average shape of each group and assessed significant differences between biological males and females through a nonparametric two-sample test. This test computed the average Procrustes distance difference between the two sexes (Zelditch et al., 2012).

Lastly, the potential difference in ontogenetic trajectories or trends by biological sex was approached by plotting the shape scores obtained through a multivariate regression analysis in MorphoJ (Klingenberg, 2011) against the age groups according to Bogin (1999).

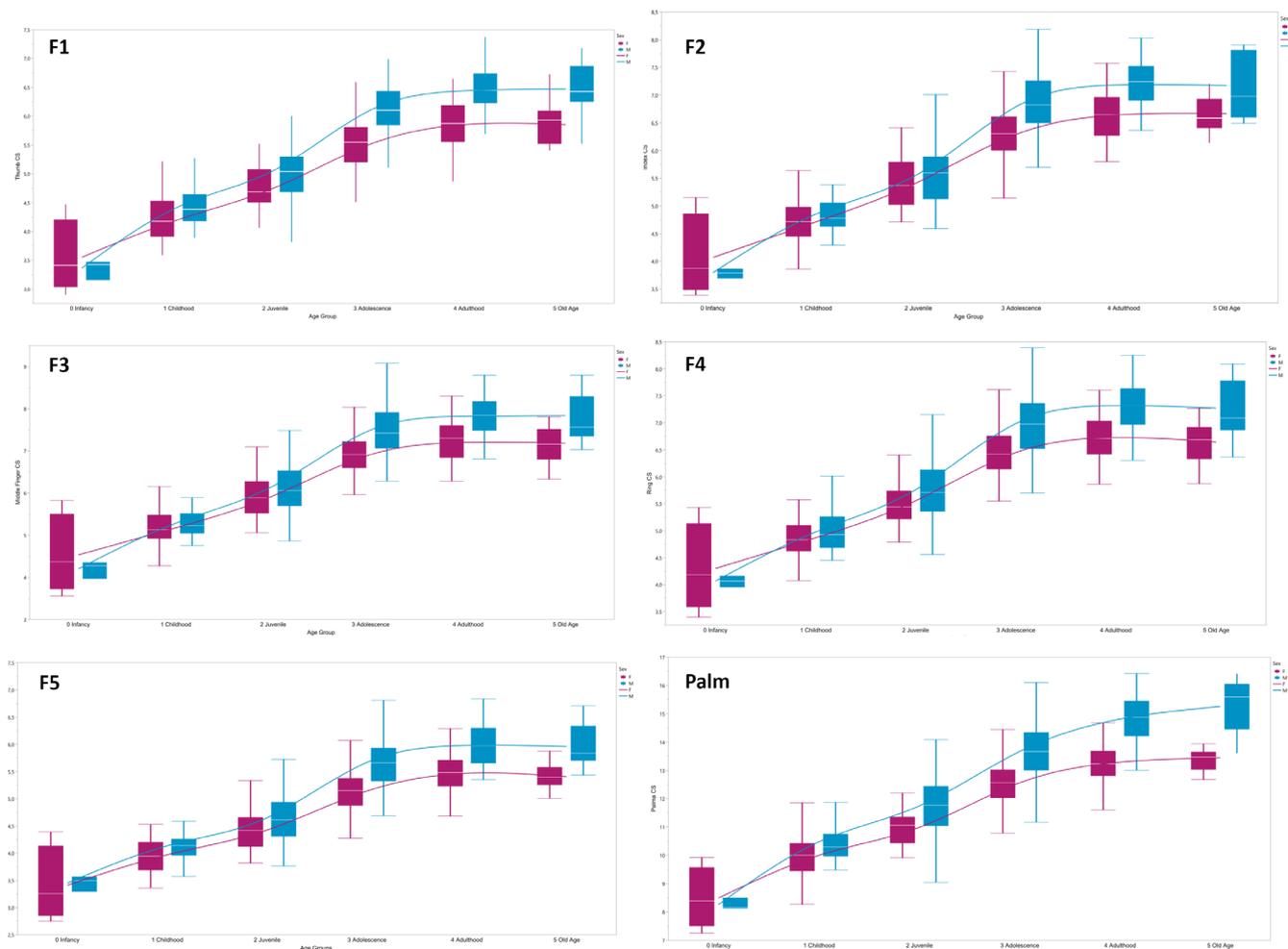


FIGURE 2 Thumb (F1), index (F2), middle finger (F3), ring finger (F4), little finger (F5), and palm growth. Boxplot of the growth trajectories of all hand components differentiated by sex, showing male (clear red) and female (clear blue) values from infancy (left) to old age (right).

This procedure was carried out for each finger and the palm individually. The graphical representation utilized JMP Pro 14[®] (Jones, 2011) employing a locally estimated scatterplot smoothing (LOESS) regression (Jacoby, 2000), enabling the exploration of ontogenetic trends within each biological sex.

GM data collection and analyses in this study were performed in tpsDig, tpsRelw, and MorphoJ, which are freely available at the SUNY Stony Brook Morphometrics website (<http://life.bio.sunysb.edu/morph/>). Statistical testing was undertaken in MorphoJ and Past (Hammer et al., 2001).

3 | RESULTS

3.1 | Size results

The size analysis was executed through a boxplot of the centroid size, computed for each age group stratified by biological sex, as illustrated in Figure 2 (detailed values provided in Tables S1–S3). This approach allows a visual exploration of ontogenetic trajectories for each biological sex across individual elements of the hand, encompassing fingers and the palm. The growth trend of each hand element is depicted

from childhood to old age, progressing from left to right. Both curves, representing biological males and females, exhibit a slightly divergent sigmoidal growth pattern characterized by a growth spurt between juveniles and adolescents, followed by a stabilization of size around adulthood. This consistent pattern is observable across every studied element, including fingers and the palm. Furthermore, it is worth noting that biological males consistently exhibit larger sizes than biological females in every age group and for every hand part examined, except for infants, where biological females surpass males in size in nearly all cases.

Considering these overarching differences, we performed statistical tests to assess the significance of distinctions between biological sexes in each part of the hand and age group. A Mann–Whitney test was employed, considering the nonparametric nature of the data, and the significance level was established at $p < 0.05$ (Table 3).

The Mann–Whitney test was utilized to evaluate the statistical differences in size between biological males and females. The findings reveal that all hand elements, including individual fingers and the palm, exhibit statistically significant sexual dimorphism in size from adolescence onwards (11 years for biological females and 13 years for biological males, following Bogin and Smith [1996]). Additionally, finger 1, finger 5, and the palm display statistically significant dimorphism in

		Infant	Child	Juvenile	Adolescent	Adult	Old age
F1	M	3.35	4.43*	5.07*	6.11*	6.44*	6.47*
	F	3.54	4.20*	4.76*	5.52*	5.86*	5.85*
F2	M	3.78	4.85	5.57	6.84*	7.18*	7.17*
	F	4.07	4.71	5.43	6.32*	6.65*	6.67*
F3	M	4.19	5.28	6.16	7.50*	7.82*	7.84*
	F	4.53	5.17	5.93	6.91*	7.21*	7.19*
F4	M	4.06	4.97	5.75	6.99*	7.32*	7.27*
	F	4.30	4.86	5.55	6.45*	6.72*	6.65*
F5	M	3.45	4.13*	4.65*	5.67*	5.98*	5.96*
	F	3.41	3.97*	4.42*	5.14*	5.47*	5.41*
Palm	M	8.26	10.47*	11.74*	13.67*	14.81*	15.26*
	F	8.49	10.00*	11.01*	12.57*	13.29*	13.45*

Note: Values marked with * are significantly different between males and females (p -value <0.05). Complete summary statistics are available in Tables S1 and S2.

TABLE 4 Average Procrustes distance between biological males and females at each age group and on each part of the hand.

	Infant	Child	Juvenile	Adolescent	Adult	Old age
F1	0.034	0.028	0.027	0.011	0.022	0.048
F2	0.066	0.015	0.023*	0.018*	0.021*	0.025
F3	0.068	0.011	0.017*	0.010*	0.018*	0.019
F4	0.052	0.019	0.021*	0.013*	0.017*	0.028
F5	0.033	0.018	0.025*	0.017*	0.022*	0.045*
Palm	0.043	0.019	0.018*	0.020*	0.027*	0.030

Note: Bold values marked with * are significantly different between biological males and females (p -value <0.05).

size even earlier, specifically from childhood (3 years old onwards). The overarching trend suggests that males consistently manifest larger sizes than females at every developmental stage except for infants.

3.2 | Shape results

Shape analysis was conducted on each group, and sexually dimorphic features on individual fingers and the palm were examined through a Procrustes distance analysis and a permutation test using MorphoJ software (Klingenberg, 2011), as detailed in Table 4.

Our findings reveal distinct general trends depending on the finger and age group. Specifically, the shape of the individual fingers and the palm lacks dimorphism in both infants and children. However, in juveniles, adolescents, and adults, the shape of the fingers and the palm demonstrates statistically significant sexual dimorphism, except for the thumb, which does not exhibit dimorphism at any age group. In old age, there is an overall absence of dimorphism in the individual fingers and the palm, with the exception of finger 4. For a visual representation of the average shape of each finger at every ontogenetic stage, please refer to Figure 3.

3.3 | Allometric changes in the human hand studied through their individual elements

We conducted a multivariate regression analysis of shape scores on centroid size (Tables S10–S12). Subsequently, we explored allometry by plotting the regression scores against the age group (Figure 4). Essentially, we observe closely parallel trajectories between biological males and females, reflecting a sigmoidal growth pattern. The overarching trend indicates that fingers undergo a process of becoming slenderer throughout ontogeny until adolescence or adulthood, after which they tend to become slightly stockier, characterized by being shorter and wider until old age. Notably, the palm deviates from the strict sigmoidal growth observed in other parts, consistently becoming slenderer with the effects of ontogeny, extending into old age. While this general developmental trend is shared by both biological sexes, biological females consistently exhibit more positive scores overall than males at every finger and palm, spanning nearly every ontogenetic stage. These more positive regression scores align with slender fingers and palms, maintaining a consistent pattern across each part and developmental stage, implying a potential dimorphic feature.

TABLE 3 The average centroid size for biological males and females for each hand part is presented below.

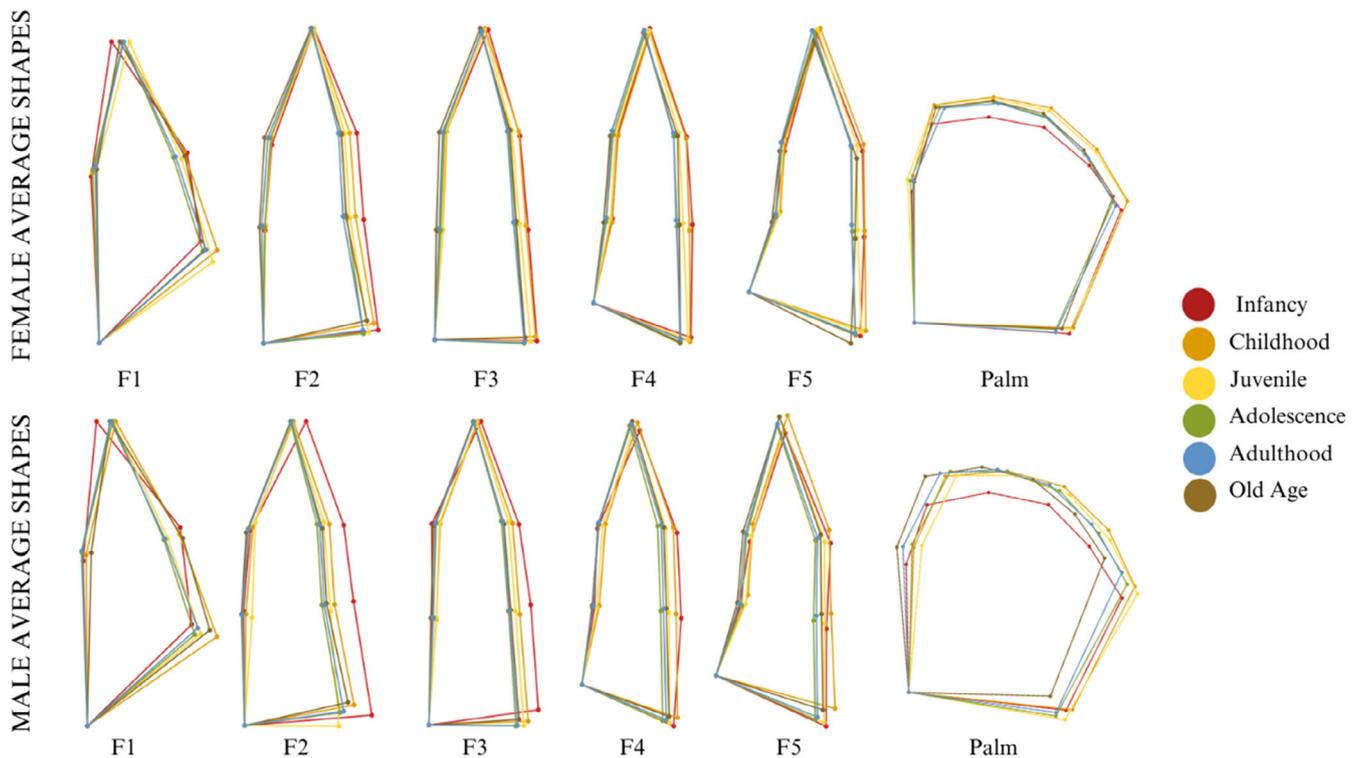


FIGURE 3 Average shape of each age group and hand parts divided by sex. Thumb (F1), index (F2), middle finger (F3), ring finger (F4), little finger (F5), and palm.

4 | DISCUSSION AND CONCLUSION

The comprehensive morphological analysis presented in this study offers profound insights into the nuanced aspects of sexual dimorphism across diverse ontogenetic stages. By integrating size and shape parameters through GM, we advance our understanding of the intricate developmental trajectories and distinctive features characterizing biological male and female hands. Traditionally, research has predominantly focused on size variation, utilizing linear measurements as principal parameters for hand characterization and sexual determination (Agnihotri et al., 2005; Gupta et al., 2022; Kanchan & Krishan, 2011; Napier, 1993).

Our findings affirm the observed sexual dimorphism in hand size, with biological males consistently exhibiting larger hands than biological females from childhood onwards, aligning with previous studies primarily focused on linear measures (Agnihotri et al., 2005; Mandahawi et al., 2008; Kanchan & Rastogi, 2009; Jowaheer & Agnihotri, 2011; Kanchan & Krishan, 2011; Ibrahim et al., 2016) or GM (Králík et al., 2014; Nelson et al., 2017). Notably, differences identified from adolescence onwards, supported by Mann–Whitney tests, underscore size as a robust indicator of sexual dimorphism. Early emergence of dimorphism in elements such as finger 1, finger 5, and the palm from childhood suggest a pivotal role for size differences in sexual dimorphism even in early development. In this sense, we find important to align these results with the previously mentioned Manning Index, which relates fingers 2 and 4, which do not show a significant difference in size until adolescence.

Additionally, the efficacy of the palm has been discussed in the scientific literature, indicating that it is the most appropriate element for the evaluation of sex through human hands (Kanchan & Rastogi, 2009; Sanfilippo et al., 2013), especially since it is not as exposed to changes in hand posture as are the fingers (Nelson et al., 2017). In our results we observed an early sexual dimorphism in the palm, at the same time as the thumb and the little finger. In form, all the elements of the hand except the thumb seem to show sexual dimorphism from youth onwards, without observing a particularly precocious behavior in the palm.

Remarkably, the examination of shape unveils a more nuanced pattern of sexual dimorphism. While certain age groups, particularly juveniles, adolescents, and adults, exhibit significant dimorphism in shape, and others, like infants and children, do not (see Medialdea et al., 2019). This underscores the importance of considering both size and shape for a comprehensive understanding of sexual dimorphism (see Nelson et al., 2017). The exception of the thumb from shape dimorphism suggests potential functional or adaptive differences in this digit (see Karakostis et al., 2021).

The identified sigmoidal growth pattern through ontogenetic trajectories indicates shared developmental trends in both biological sexes (see Kleisner et al., 2021). Divergence in size and shape during adolescence is particularly noteworthy, signifying critical morphological changes associated with sexual maturation. The consistent trend of becoming slightly stockier in adulthood implies a convergence in hand morphology post-growth spurt.

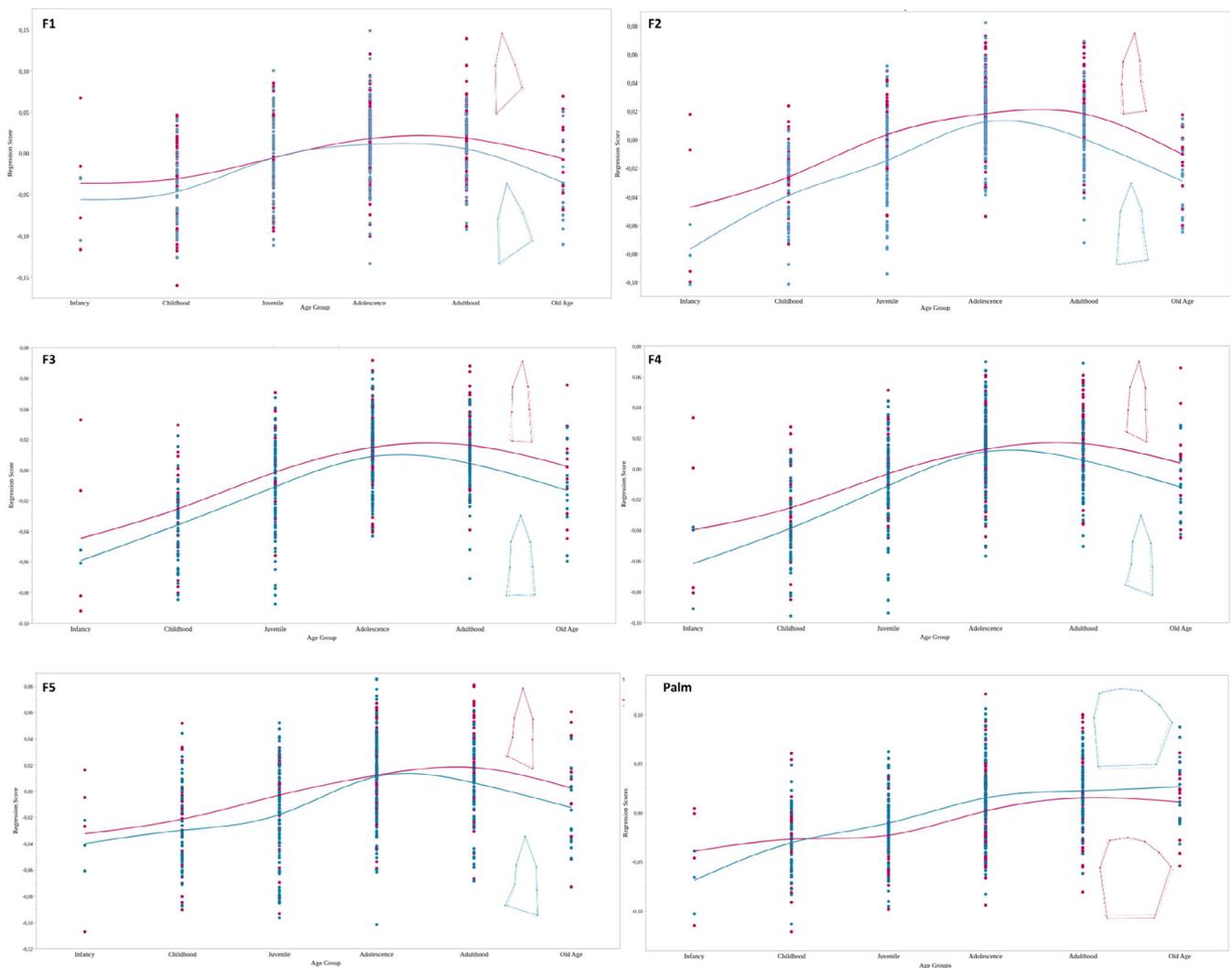


FIGURE 4 Thumb (F1), index (F2), middle finger (F3), ring finger (F4), little finger (F5), and palm LOESS (Locally estimated scatterplot smoothing) regression of multivariate regression score on age group (from infancy (left) to old age (right) and 2D warps illustrating the regression score variation.

Multivariate regression analysis and subsequent examination of allometric changes reveal intriguing patterns. Parallel trajectories between biological males and females underscore shared ontogenetic processes, with both biological sexes experiencing slenderization of fingers and palm. Indeed, the level of fat in the hands of infants is significantly higher compared with adults as it serves several essential functions such as protection, thermal regulation, or energy reserve (Kremer & Gilsanz, 2016; Rokoff et al., 2019). As individuals age, from infancy through adulthood fingers tend to adopt a stockier shape, characterized by being shorter and wider. Aging can lead to changes in bone and ligaments density and structure. Thus, the bones and tendons of the hands can undergo changes that might contribute to a wider appearance. Additionally, the physical stress accumulated over so many years becomes evident through the widening of the elements of the hand, which can also be influenced by fluid retention (Gregson, 2010; Loeser, 2010). Common age-related diseases, such as arthritis, atrophy, hypertension, and osteoarthritis, further contribute

to these morphological changes (Loeser, 2010; Walston, 2023; Zhang & Jordan, 2010). Lastly, the consistently more positive scores in biological females, associated with slender fingers and palms, prompt further exploration into potential functional or evolutionary implications (Touraille & Gouyon, 2008).

In conclusion, the use of GM proves to be a powerful methodological advancement, enabling a detailed analysis of shape and size independently. Incorporating ontogenetic stages provides a dynamic perspective on sexual dimorphism, significantly contributing to our understanding of how hand morphology evolves across the lifespan. The study's implications span various fields, including forensic anthropology, archaeology, and paleoanthropology, where precise morphological characterization is crucial for accurate interpretations. In fact, the results obtained in this paper constitute the comparative frame of reference for a work focused on the bioanthropological characterization to assess the biological sex and age of Upper Paleolithic artists through blown and printed hand representations. (see Fernández-

Navarro et al., 2022). Lastly, future research should re-evaluate whether/how their results reflect in the underlying bone morphology (Kivell et al., 2013; Karakostis et al., 2017, 2013, 2015).

AUTHOR CONTRIBUTIONS

Verónica Fernández-Navarro: Conceptualization (equal); formal analysis (equal); investigation (equal); methodology (equal); resources (equal); writing – original draft (equal). **Diego Garate:** Formal analysis (equal); funding acquisition (equal); investigation (equal); project administration (equal); supervision (equal); validation (equal); visualization (equal); writing – review and editing (equal). **Daniel García Martínez:** Conceptualization (equal); data curation (equal); formal analysis (equal); investigation (equal); methodology (equal); supervision (equal); validation (equal); writing – original draft (equal); writing – review and editing (equal).

ACKNOWLEDGMENTS

The authors would like to express their gratitude to Universidad Complutense de Madrid. Thanks to the Department of Biodiversity, Ecology, and Evolution for offering their facilities and tools for the final achievement of this study. This research was supported by a “Concepción Arenal” 2020–21 pre-doctoral scholarship at the University of Cantabria. The present study has been conducted as part of the research project “Scientific virtual reality for the study and dissemination of the scenarios of artistic creation in Palaeolithic caves (RealCaveART)” (PDC2022-133124-I00), PI: Diego Garate, funded by MCIN/AEI/10.13039/501100011033 and the European Union Next Generation EU/PRTR.

CONFLICT OF INTEREST STATEMENT

The authors declare conflicts of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available on request from the corresponding author. The data are not publicly available due to privacy or ethical restrictions.

ORCID

Verónica Fernández-Navarro  <https://orcid.org/0000-0003-3591-1835>

REFERENCES

- Aboul-Hagag, K. E., Mohamed, S. A., Hilal, M. A., & Mohamed, E. A. (2011). Determination of sex from hand dimensions and index/ring finger length ratio in Upper Egyptians. *Egyptian Journal of Forensic Sciences*, 1(2), 80–86.
- Agnihotri, A. K., Purwar, B., Jeebun, N., & Agnihotri, S. (2005). Determination of sex by hand dimensions. *The Internet Journal of Forensic Science*, 1(2), 1–3.
- Baker, F. (1888). Anthropological notes on the human hand. *American Anthropologist*, 1(1), 51–76.
- Bastir, M., Godoy, P., & Rosas, A. (2011). Common features of sexual dimorphism in the cranial airways of different human populations. *American Journal of Physical Anthropology*, 146(3), 414–422. doi:10.1002/ajpa.21596
- Bastir, M., Higuero, A., Ríos, L., & Martínez, D. G. (2014). Three-dimensional analysis of sexual dimorphism in human thoracic vertebrae: Implications for the respiratory system and spine morphology. *American Journal of Physical Anthropology*, 155(4), 513–521. <https://doi.org/10.1002/ajpa.22604>
- Berger, L. R., Hawks, J., de Ruiter, D. J., Churchill, S. E., Schmid, P., Deleuzene, L. K., Kivell, T. L., Garvin, H. M., Williams, S. A., DeSilva, J. M., Skinner, M. M., Musiba, C. M., Cameron, N., Holliday, T. W., Harcourt-Smith, W., Ackermann, R. R., Bastir, M., Bogin, B., Bolter, D., ... Zipfel, B. (2015). *Homo naledi*, a new species of the genus *Homo* from the Dinaledi Chamber, South Africa. *eLife*, 4, 1–35. <https://doi.org/10.7554/eLife.09560>
- Bogin, B. (1999). *Patterns of human growth* (2nd ed.). Cambridge University press.
- Bogin, B., & Smith, B. H. (1996). Evolution of the human life cycle. *American Journal of Human Biology*, 8(6), 703–716. [https://doi.org/10.1002/\(SICI\)1520-6300\(1996\)8:6<703::AID-AJHB2>3.0.CO;2-U](https://doi.org/10.1002/(SICI)1520-6300(1996)8:6<703::AID-AJHB2>3.0.CO;2-U)
- Bolstad, G., Benum, B., & Rokne, A. (2001). Anthropometry of Norwegian light industry and office workers. *Applied Ergonomics*, 32(3), 239–246.
- Chazine, J.-M., & Noury, A. (2006). Sexual determination of hand stencils on the Main panel of the Gua Masri li cave (East-Kalimantan/Borneo-Indonesia). *International Newsletter on Rock Art-INORA*, 44, 21–27.
- Cooke, A. (2014). Hands on research: The application of the 2D:4D ratio to Children's hand stencils.
- Ecker, A. (1875). *Einige Bemerkungen über einen schwankenden Charakter in der Hand des Menschen*. Verlag nicht ermittelbar.
- Ernsten, L., Körner, L. M., Heil, M., Richards, G., & Schaal, N. K. (2021). Investigating the reliability and sex differences of digit lengths, ratios, and hand measures in infants. *Scientific Reports*, 11(1), 10998.
- Ernsten, L., Körner, L. M., Schaper, M. L., Lawrenz, J., Richards, G., Heil, M., & Schaal, N. K. (2023). The association of prenatal amniotic sex hormones and digit ratio (2D:4D) in children aged 5 to 70 months: A longitudinal study. *PLoS ONE*, 18(3), e0282253.
- Fernández Navarro, V., Godinho, R. M., García Martínez, D., & Garate Maidagan, D. (2024). Exploring the utility of geometric morphometrics to analyse prehistoric hand stencils. *Scientific Reports*, 14(1), 6336. <https://doi.org/10.1038/s41598-024-56889-3>
- Fernández-Navarro, V., Camarós, E., & Garate, D. (2022). Visualizing childhood in Upper Palaeolithic societies: Experimental and archaeological approach to artists' age estimation through cave art hand stencils. *Journal of Archaeological Science*, 140(105), 574. <https://doi.org/10.1016/j.jas.2022.105574>
- Frazer, D., & Wolpoff, M. (1985). Sexual dimorphism. *Annual Reviews in Anthropology*, 14, 429–473.
- García-Martínez, D., Bastir, M., Torres-Tamayo, N., O'Higgins, P., Torres-Sánchez, I., García-Río, F., & Heuzé, Y. (2019). Three-dimensional analysis of sexual dimorphism in ribcage kinematics of modern humans. *American Journal of Physical Anthropology*, 169(2), 348–355. <https://doi.org/10.1002/ajpa.23829>
- García-Martínez, D., Torres-Tamayo, N., Torres-Sánchez, I., García-Río, F., & Bastir, M. (2016). Morphological and functional implications of sexual dimorphism in the human skeletal thorax. *American Journal of Physical Anthropology*, 161(3), 467–477. <https://doi.org/10.1002/ajpa.23051>
- Goodyear, M. D. E., Krleza-Jeric, K., & Lemmens, T. (2007). The Declaration of Helsinki. *BMJ*, 335(7621), 624–625. <https://doi.org/10.1136/bmj.39339.610000.BE>
- Gregson, C. L. (2010). Bone and joint aging. In H. Fillit, K. Rockwood, & J. Young (Eds.), *Brocklehurst's textbook of geriatric medicine and gerontology* (8th ed.). Elsevier.
- Groenen, M. (1988). Les représentations de mains négatives dans les grottes de Gargas et de Tibiran (Hautes-Pyrénées). Approche méthodologique. *Bulletin de La Société Royale Belge d'Anthropologie et de Préhistoire*.

- Gunn, R. G. (2006). Hand sizes in rock art: Interpreting the measurements of hand stencils and prints. *Rock Art Research: The Journal of the Australian Rock Art Research Association (AURA)*, 23(1), 97–112.
- Gupta, M., Srikrishna, G., Klein, S. L., & Bishai, W. R. (2022). Genetic and hormonal mechanisms underlying sex-specific immune responses in tuberculosis. *Trends in Immunology*, 43(8), 640–656. <https://doi.org/10.1016/j.it.2022.06.004>
- Hammer, Ø., Harper, D. A. T., & Ryan, P. D. (2001). PAST: Paleontological statistics software package for education and data analysis. *Palaeontologia Electronica*, 4(1), 1–9.
- Hönekopp, J., & Watson, S. (2010). Meta-analysis of digit ratio 2D: 4D shows greater sex difference in the right hand. *American Journal of Human Biology*, 22(5), 619–630.
- Ibrahim, M. A., Khalifa, A. M., Hagras, A. M., & Alwakid, N. I. (2016). Sex determination from hand dimensions and index/ring finger length ratio in north Saudi population: Medico-legal view. *Egyptian Journal of Forensic Sciences*, 6(4), 435–444.
- Jacoby, W. G. (2000). Loess. *Electoral Studies*, 19(4), 577–613. [https://doi.org/10.1016/S0261-3794\(99\)00028-1](https://doi.org/10.1016/S0261-3794(99)00028-1)
- Jones, S. (2011). JMP® Pro 14.0.0.
- Jowaheer, V., & Agnihotri, A. K. (2011). Sex identification on the basis of hand and foot measurements in Indo-Mauritian population—a model based approach. *Journal of Forensic and Legal Medicine*, 18(4), 173–176. <https://doi.org/10.1016/j.jflm.2011.02.007>
- Kanchan, T., & Krishan, K. (2011). Anthropometry of hand in sex determination of dismembered remains—a review of literature. *Journal of Forensic and Legal Medicine*, 18(1), 14–17.
- Kanchan, T., & Rastogi, P. (2009). Sex determination from hand dimensions of north and south Indians. *Journal of Forensic Sciences*, 54(3), 546–550. <https://doi.org/10.1111/j.1556-4029.2009.01018.x>
- Karakostis, F. A., Zorba, E., & Moraitis, K. (2013, 1–12). Sexual dimorphism of proximal hand phalanges. *International Journal of Osteoarchaeology*, 25(5), 733–742. <https://doi.org/10.1002/oa.2340>
- Karakostis, F. A., Haeufle, D., Anastopoulou, I., Moraitis, K., Hotz, G., Tourloukis, V., & Harvati, K. (2021). Biomechanics of the human thumb and the evolution of dexterity. *Current Biology*, 31(6), 1317–1325.e8. <https://doi.org/10.1016/j.cub.2020.12.041>
- Karakostis, F. A., Hotz, G., Tourloukis, V., & Harvati, K. (2018). Evidence for precision grasping in Neandertal daily activities. *Science Advances*, 4(9), eaat2369.
- Karakostis, F. A., Jeffery, N., & Harvati, K. (2019). Experimental proof that multivariate patterns among muscle attachments (entheses) can reflect repetitive muscle use. *Scientific Reports*, 9(1), 1–9.
- Karakostis, F. A., Lorenzo, C., & Moraitis, K. (2017). Morphometric variation and ray allocation of human proximal hand phalanges. *Anthropologischer Anzeiger*, 74(4), 269–281. <https://doi.org/10.1127/anthranz/2017/0715>
- Karakostis, F. A., Zorba, E., & Moraitis, K. (2015). Sex determination using proximal hand phalanges. *Papers on Anthropology*, 24(2), 37–56.
- Kivell, T. L., Baraki, N., Lockwood, V., Williams-Hatala, E. M., & Wood, B. A. (2022). Form, function and evolution of the human hand. *American Journal of Biological Anthropology*, 181, 6–57.
- Kivell, T. L., Deane, A. S., Tocheri, M. W., Orr, C. M., Schmid, P., Hawks, J., Berger, L. R., & Churchill, S. E. (2015). The hand of *Homo naledi*. *Nature communications*, 6, 8431. <https://doi.org/10.1038/ncomms9431>
- Kivell, T. L., Guimont, I., & Wall, C. E. (2013). Sex-related shape dimorphism in the human radiocarpal and midcarpal joints. *The Anatomical Record*, 296(1), 19–30. <https://doi.org/10.1002/ar.22609>
- Kivell, T. L., Kibii, J. M., Churchill, S. E., Schmid, P., & Berger, L. R. (2011). Australopithecus sediba hand demonstrates mosaic evolution of locomotor and manipulative abilities. *Science*, 333(6048), 1411–1417.
- Kleisner, K., Tureček, P., Roberts, S. C., Havlíček, J., Valentova, J. V., Akoko, R. M., Leongómez, J. D., Apostol, S., Varella, M. A. C., & Saribay, S. A. (2021). How and why patterns of sexual dimorphism in human faces vary across the world. *Scientific Reports*, 11(1), 5978. <https://doi.org/10.1038/s41598-021-85402-3>
- Klingenberg, C. P. (2011). MorphoJ: An integrated software package for geometric morphometrics. *Molecular Ecology Resources*, 11, 353–357.
- Králik, M., Katina, S., & Urbanová, P. (2014). Distal part of the human hand: Study of form variability and sexual dimorphism using geometric morphometrics. *Anthropologia Integra*, 5(2), 7–25.
- Kremer, R., & Gilsanz, V. (2016). Fat and bone: An odd couple. *Frontiers in Endocrinology*, 6, 1–12. <https://doi.org/10.3389/fendo.2015.00190>
- Kulaksiz, G., & Gözil, R. (2002). The effect of hand preference on hand anthropometric measurements in healthy individuals. *Annals of Anatomy-Anatomischer Anzeiger*, 184(3), 257–265.
- Loeser, R. F. (2010). Age-related changes in the musculoskeletal system and the development of osteoarthritis. *Clinics in Geriatric Medicine*, 26(3), 371–386. <https://doi.org/10.1016/j.cger.2010.03.002>
- Mackie, M. E. (2015). Estimating age and sex: Paleodemographic identification using rock art hand sprays, an application in Johnson County, Wyoming. *Journal of Archaeological Science: Reports*, 3, 333–341.
- Mandahawi, N., Imrhan, S., Al-Shobaki, S., & Sarder, B. (2008). Hand anthropometry survey for the Jordanian population. *International Journal of Industrial Ergonomics*, 38(11–12), 966–976.
- Manning, J. T. (2012). Sex differences and age changes in digit ratios: Implications for the use of digit ratios in medicine and biology. In *Handbook of anthropometry: Physical measures of human form in health and disease* (pp. 841–851). Springer.
- Manning, J. T., Scutt, D., Wilson, J., & Lewis-Jones, D. I. (1998). The ratio of 2nd to 4th digit length: A predictor of sperm numbers and concentrations of testosterone, luteinizing hormone and oestrogen. *Human Reproduction (Oxford, England)*, 13(11), 3000–3004.
- McIntyre, M. H., Cohn, B. A., & Ellison, P. T. (2006). Sex dimorphism in digital formulae of children. *American Journal of Physical Anthropology: The Official Publication of the American Association of Physical Anthropologists*, 129(1), 143–150.
- Medialdea, L., Bazaco, C., D'Angelo del Campo, M. D., Sierra-Martínez, C., González-José, R., Vargas, A., & Marrodán, M. D. (2019). Describing the children's body shape by means of geometric morphometric techniques. *American Journal of Physical Anthropology*, 168(4), 651–664. <https://doi.org/10.1002/ajpa.23779>
- Mitteroecker, P., & Gunz, P. (2009). Advances in geometric morphometrics. *Evolutionary Biology*, 36(2), 235–247. <https://doi.org/10.1007/s11692-009-9055-x>
- Mitteroecker, P., Gunz, P., Windhager, S., & Schaefer, K. (2013). A brief review of shape, form, and allometry in geometric morphometrics, with applications to human facial morphology. *Hystrix the Italian Journal of Mammalogy*, 24(1). <https://doi.org/10.4404/hystrix-24.1-6369>
- Napier, J. (1993). *Hands*. Princeton University Press.
- Nelson, E., Hall, J., Randolph-Quinney, P., & Sinclair, A. (2017). Beyond size: The potential of a geometric morphometric analysis of shape and form for the assessment of sex in hand stencils in rock art. *Journal of Archaeological Science*, 78, 202–213. <https://doi.org/10.1016/j.jas.2016.11.001>
- O'Higgins, P. (2000). The study of morphological variation in the hominid fossil record: biology, landmarks and geometry. *Journal of Anatomy*, 197(1), 103–120. <https://doi.org/10.1046/j.1469-7580.2000.19710103.x>
- Rabazo-Rodríguez, A. M., Modesto-Mata, M., Bermejo, L., & García-Díez, M. (2017). New data on the sexual dimorphism of the hand stencils in El Castillo cave (Cantabria, Spain). *Journal of Archaeological Science: Reports*, 14, 374–381.
- Rohlf, F. J. (2006). *tpsDig, Digitize Landmarks and Outlines, Version 2.05*. Department of Ecology and Evolution, State University of New York.
- Rokoff, L. B., Rifas-Shiman, S. L., Switkowski, K. M., Young, J. G., Rosen, C. J., Oken, E., & Fleisch, A. F. (2019). Body composition and

- bone mineral density in childhood. *Bone*, 121, 9–15. <https://doi.org/10.1016/j.bone.2018.12.009>
- Rosas, A., & Bastir, M. (2002). Thin-plate spline analysis of allometry and sexual dimorphism in the human craniofacial complex. *American Journal of Physical Anthropology*, 117(3), 236–245. <https://doi.org/10.1002/ajpa.10023>
- Rosas, A., Pérez-Criado, L., Bastir, M., Estalrich, A., Huguet, R., García-Tabernero, A., Pastor, J. F., & Rasilla, M. d. I. (2015). A geometric morphometrics comparative analysis of Neandertal humeri (epiphyses-fused) from the El Sidrón cave site (Asturias, Spain). *Journal of Human Evolution*, 82, 51–66. <https://doi.org/10.1016/j.jhevol.2015.02.018>
- Sanfilippo, P. G., Hewitt, A. W., Mountain, J. A., & Mackey, D. A. (2013). A geometric morphometric assessment of hand shape and comparison to the 2D:4D digit ratio as a marker of sexual dimorphism. *Twin Research and Human Genetics*, 16(2), 590–600. <https://doi.org/10.1017/thg.2013.5>
- Snow, D. R. (2006). Sexual dimorphism in Upper Palaeolithic hand stencils. *Antiquity*, 80(308), 390–404.
- Snow, D. R. (2013). Sexual dimorphism in European Upper Paleolithic cave art. *American Antiquity*, 78(4), 746–761.
- Standring, S., Ellis, H., Healy, J., Johnson, D., Williams, A., Collins, P., & Wigley, C. (2005). Gray's anatomy: The anatomical basis of clinical practice. *American Journal of Neuroradiology*, 26(10), 2703.
- Swami, S., Kumar, T., & Sharma, D. (2015). Correlation of handedness with hand anthropometric measurements in Haryanvi brahmins. *Journal of the Anatomical Society of India*, 64, S24–S30. <https://doi.org/10.1016/j.jasi.2015.04.011>
- Touraille, P., & Gouyon, P.-H. (2008). Why are women smaller than men? When anthropology meets evolutionary biology. *Nature Precedings*. <https://doi.org/10.1038/npre.2008.1832.1>
- Walston, J. (2023). Common clinical sequelae of aging. In L. Goldman & A. Schafer (Eds.), *Goldman-Cecil medicine* (26th ed., pp. 120–124). Elsevier.
- Zelditch, M. L., Swiderski, D. L., & Sheets, H. D. (2012). Theory of shape. *Geometric Morphometrics for Biologists*, 75–102. <https://doi.org/10.1016/b978-0-12-386903-6.00004-6>
- Zhang, Y., & Jordan, J. M. (2010). Epidemiology of osteoarthritis. *Clinics in Geriatric Medicine*, 26(3), 355–369. <https://doi.org/10.1016/j.cger.2010.03.001>

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Fernández-Navarro, V., Garate, D., & Martínez, D. G. (2024). Ontogeny and sexual dimorphism in the human hands through a 2D geometric morphometrics approach. *American Journal of Biological Anthropology*, e25001. <https://doi.org/10.1002/ajpa.25001>