

RESEARCH ARTICLE

Evolutionary selection and morphological integration in the hand of modern humans

Mikel Arlegi¹  | Carlos Lorenzo^{2,3} 

¹McDonald Institute for Archaeological Research, University of Cambridge, Cambridge, UK

²Departament d'Història i Història de l'Art, Universitat Rovira i Virgili, Tarragona, Spain

³Institut Català de Paleoecologia Humana i Evolució Social (IPHES-CERCA), Tarragona, Spain

Correspondence

Mikel Arlegi, McDonald Institute for Archaeological Research, University of Cambridge, CB2 3ER, UK.
Email: mikelarlegui@hotmail.com

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Abstract

Objectives: To enhance our understanding of the evolutionary dynamics of the modern human hand by analyzing the degree of integration and ability to respond to selection pressures of each phalanx and metacarpal bone.

Materials and Methods: The sample comprised 96 adult individuals, both female and male, from Euro-American, Afro-American, and European populations. We collected 10 linear measurements from the 19 metacarpals and proximal, middle, and distal phalanges that constitute the five digits of the hand. Using these data, we constructed variance/covariance matrices to quantify the degree of integration and assess the hand ability to respond to selective pressures.

Results: Distal phalanges are the most evolvable and flexible elements, while being the least integrated and constrained. The thumb is similarly integrated as the second and third rays, while medial rays (fourth and fifth digits) are more integrated. However, the thumb presents different integration and response to selection patterns. No significant relationship was found between functionality and the indices of selection and integration. Finally, the correlation between hand and foot indices yielded significant results for conditional evolvability and flexibility.

Discussion: The findings suggest different evolutionary trajectories for the metacarpal and distal phalanx in the modern human thumb, likely reflecting varying functional and developmental pressures. The first metacarpal, characterized by high flexibility and low evolvability, appears to have reached a stable, optimal morphology, under stabilizing selection. In contrast, the distal phalanx seems to have undergone directional evolution, suggesting specialization for a specific function. Comparisons between hands and feet suggest that these structures evolve differently under directional selection but similarly under stabilizing selection.

KEYWORDS

adaptation, constraints, evolvability, flexibility, hands

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1 | INTRODUCTION

Complex skeletal structures represent a vast source of evolutionary information, particularly when they contain homologous elements (Gould, 1986). However, comprehending the obscure evolutionary processes that shapes these morphologies can be challenging (Arlegi et al., 2020; Galis, 1999; Rolian, 2009; Young & Hallgrímsson, 2005). The morphology of the modern human hand suggests a nonlinear evolutionary model (Almécija et al., 2015; Kivell et al., 2023). Modern human hands are distinct from those of apes due to their relatively long thumbs compared to fingers (e.g., Almécija et al., 2015; Almécija & Alba, 2014; Marzke & Wullstein, 1996; Napier, 1993; Napier & Napier, 1967; Smith & Jungers, 1997), a feature shared with other cercopithecoid primates (Straus, 1942), and Late Miocene apes (Moyà-Solà et al., 1999; Moyà-Solà et al., 2005). The intrinsic proportions of the human hand have been extensively perceived as a functional advantage for manipulation behaviors, facilitating pad-to-pad opposition, precision grip and control (Almécija et al., 2010; Almécija et al., 2015; Bardo et al., 2018; Dunmore et al., 2020a, Bardo, et al., 2020; Feix et al., 2015; Hu et al., 2018; Marzke, 1997; Napier, 1956, 1960; Susman, 1979).

Several theories have been proposed to explain these proportions, including (i) retention of the primitive anthropoid (plesiomorphic) hand proportion pattern (Almécija et al., 2014); (ii) evolution in response to lithic (or other materials) manipulation behaviors (Hamrick et al., 1998); (iii) relaxation of selection pressures for forelimb locomotion due to bipedalism in favor of selection for manipulation (Alba et al., 2003); and (iv) morphological adaptations for bipedalism in the foot due to pleiotropic effects (Rolian et al., 2010). Aside from the first theory, the others suggest that the relaxation of selection pressures for bipedal locomotion had an important factor in the evolution of the hands. Thus, the evolutionary process of the human hand can be partially understood as both an exaptation and an adaptation for manipulation. Features related to arboreal locomotion, such as long and curved fingers, evolved into short and straight metacarpals and non-pollical digits, resulting in a relatively long and robust thumb (Almécija et al., 2015; Kivell et al., 2023; Lovejoy et al., 2009; Richmond, 1998; Susman, 1979; Tocheri et al., 2008; Ward, 2002). This skeletal morphology is accompanied by an enlarged thenar muscular complex, which enhances the hand unique rotation, stabilization, and grasping abilities (Bardo et al., 2018; Bucchi et al., 2020; Diogo et al., 2012; Karakostis et al., 2019; Tocheri, 2007; Tocheri et al., 2008). This is facilitated by the reorientation of the carpal-metacarpal articulation, providing compressive loading from the thumb to the palm (Kivell, 2015, 2016; Lewis, 1989; Tocheri, 2007; Tocheri et al., 2003).

These features confer biomechanical advantage for manual dexterity, offering evolutionary advantage for bipedal hominins (Dunmore et al., 2023; Kivell et al., 2023). However, reconstructing the evolutionary history of these traits is challenging due to scarce fossil records (Richmond et al., 2016; Trinkaus, 2016) and the mosaic nature of hand evolution, where derived traits appear in early hominins and primitive traits persist in modern *Homo* species (Hamrick, 2012; Kivell

et al., 2011; Richmond et al., 2016; Rolian, 2016). For example, *Orrorin tugenensis* dated to approximately 6 Ma, exhibits a curved climbing primate-like proximal phalanx along with a human-like distal thumb phalanx with likely precision grip abilities (Almécija et al., 2010; Gommery & Senut, 2006; Senut, 2020; Senut et al., 2001). Later, *Ardipithecus ramidus* (ca. 4.4 Ma), shows robust thumbs and short metacarpals while retaining long fingers suitable for arboreal locomotion (Lovejoy et al., 2009; Prang et al., 2021). *Australopithecus* species display large variability in hand proportions and morphology, often estimated from unassociated and fragmentary fossil remains (e.g., Alemseged et al., 2006; Bush et al., 1982; Drapeau et al., 2005; Marzke, 1983; Ward et al., 2001). The best-preserved hand fossils, such as those from *Australopithecus prometheus* “little foot” individual (3.41–3.61 Ma [Granger et al., 2022]), show a mix of modern human-like and primitive features (Clarke, 1999; Clarke, 2013; Kivell et al., 2015). Similarly, other fossils isolated from various specimens of Sterkfontein (thought to be *Australopithecus africanus* (*Au. africanus*) or *Australopithecus* sp.), showed considerable variation, modern human-like hand proportions, and relatively curved phalanges (Napier, 1959; Pickering et al., 2018). In *Australopithecus afarensis* (3.85–2.95 Ma), hand proportions range from human-like (Rolian & Gordon, 2013) to gorilla-like (Almécija & Alba, 2014), with adaptations for locomotor grasping (Bush et al., 1982; Susman et al., 1984). The presence of muscular insertion in the palmar surface of the distal phalanx of the thumb suggests the necessary presence of the *flexor pollicis longus*, which is essential for activities that require gripping with the hand (Almécija et al., 2010). *Australopithecus Sediba* (1.98 Ma) also presents a mosaic of primitive and derived features (Dunmore et al., 2020b; Kivell et al., 2011, 2018, with a long thumb suitable for manipulation and gracile metacarpals that are similar to those of orangutans, and slightly curved proximal and middle phalanges (Dunmore et al., 2020b, Skinner, et al., 2020).

Previous research interpreted this pattern of curved phalanges as consistent with locomotor grasping in an arboreal context while suggesting that the long thumb is associated with human-like manipulation behaviors (Kivell et al., 2011). Other authors (Karakostis et al., 2021), however, contend that *Australopithecus* would not have been capable of modern human-like levels of manual dexterity, based on virtual modeling of soft tissue and bone anatomy of the thumb (but see Bardo et al., 2018). According to this view, although the earliest potential artifacts in the archaeological record dated to 3.3 Ma (Harmand et al., 2015), the fully human-like manipulative ability would not have emerged until the emergence of the genus *Homo* approximately 2 Ma (or Swartkrans specimens attributed to *Paranthropus*), thanks to a robust thumb morphology combined with a strong *opponens pollicis* muscle (Karakostis et al., 2021). Fossils from various *Homo* species, such as *Homo habilis*, *Homo antecessor*, Sima del Elefante, Sima de los Huesos (the last three from Atapuerca sites, Spain), and Neandertals, show relative modern human-like hands (Domínguez-Rodrigo et al., 2015; Lordkipanidze et al., 2007; Lorenzo et al., 1999, 2015; Ward et al., 2014, but see Bardo et al., 2020). However, mosaic evolution is evident in later *Homo* species like *Homo naledi* (Bowland et al., 2021; Kivell et al., 2015) and *Homo floresiensis*

(Larson et al., 2009). The diversity of hand morphologies observed in hominins indicates multiple evolutionary pathways for tool-related behaviors (Kivell, 2021). Therefore, the evolutionary history of hominin hand morphology is complex and cannot be reconstructed based solely on chronology.

In this study, we aim to understand the interplay between morphological integration, responses to selection, and functionality in the evolution of the modern human hand. Morphological integration, the correlation between traits due to genetic, developmental, and functional factors, influences the direction of evolutionary change (Cheverud, 1982, 1996; Klingenberg, 2008; Olson & Miller, 1958). Strong integration can promote response to selection along the path of least resistance (Schluter, 1996) but may also constrain evolvability in the direction of selection (Arlegi et al., 2020; Gómez-Robles & Polly, 2012; Goswami et al., 2014; Marroig et al., 2009; Rolian et al., 2010; Rolian, 2020). The response to selection approach, developed by Hansen and Houle (2008), quantifies how traits respond to selection. Applying these methods to the modern human hand, and the incorporation of functional data, can provide insights into how the hand has evolved and diversified over time, thereby revealing information regarding the role of function. Previous research on morphological integration and evolvability in primates and mammalian limbs suggest that functional factors related to locomotion influence limb integration and coevolution (Goswami et al., 2014; Rolian et al., 2010; Young & Hallgrímsson, 2005; Young et al., 2010). In this study, we test two hypotheses: (i) bones involved in stone tool manipulation, especially the thumb, will exhibit higher integration due to functional selection (Cheverud, 1996; Goswami & Polly, 2010), and (ii) hand integration and evolvability will be similar to those of the foot (Arlegi et al., 2023), reflecting shared developmental patterns (Hall, 2012; Hendrikse et al., 2007) and genetic influences (Fromental-Ramain et al., 1996; Hamrick, 2012; Reno et al., 2008; Zakany & Duboule, 2007).

2 | MATERIALS AND METHODS

2.1 | Sample and data

To investigate the integration and responses to selection in the *Homo sapiens* hand, we examined the 19 metacarpal and phalangeal bones of 96 adult female and male Euro-American, Afro-American, and European individuals from the Hamann-Todd Osteological Collection (Cleveland Museum of Natural History, USA). We collected 10 homologous linear measurements, following Musgrave (1977) and Trinkaus (1983), on each bone using a caliper (Table S1). Only specimens with all the 19 hand bones preserved were included. Carpals were excluded due to the difficulty of obtaining accurate and reproducible homologous measurements. Specimens with pathological findings were also excluded. To ensure our sample size was adequate for statistical analyses, we assessed its reliability and accuracy based on Grabowski and Porto's (2017) proposal. Our tests confirmed that a sample size of 96 individuals was suitable and accurate (accuracy <0.05, 95% confidence) for these analyses.

2.2 | Methodological procedure

We calculated the magnitudes of integration and various indices of selection following the same procedure used in the companion work (Arlegi et al., 2023), using the variance/covariance (V/CV) matrices, normalized to the mean of each trait (Hansen & Houle, 2008). Sources of variation associated with sexual dimorphism and population were removed by adjusting the datasets through permutational multivariate analysis of variance (ANOVA) relative, and constructing each V/CV matrix using the residuals obtained. Specifically, we employed the integration coefficient of variation of the eigenvalues (ICV; Shirai & Marroig, 2010), and four indices of evolutionary responses: evolvability, conditional evolvability, flexibility, and constraints (Hansen & Houle, 2008; Marroig et al., 2009). All the analyses were performed using basic functions of R v.4.3.3 (R Core Team, 2024) and the package *evolqg* v.0.3–4 (Melo et al., 2015).

After calculating the magnitudes of the integration and responses to selection, we performed three series of correlations. First, we correlated integration with the four evolutionary indices to test whether integration acts as a constraint on selection. Second, we correlated integration, evolvability, conditional evolvability, flexibility, and constraint with values representing the pressure exerted by each hand bone during four different Lower Paleolithic stone tool production behaviors. This analysis was aimed at testing the potential selective role of stone tool production in hand evolution. Hand pressure data during stone knapping were sourced from Key et al. (2019), though data for metacarpals and the fourth and fifth middle phalanges were not available (Table S2). Finally, we correlated the values obtained for each metacarpal and phalanx across all the indices in this study with those derived from the foot in our previous work (Arlegi et al., 2023).

3 | RESULTS

3.1 | Magnitudes of integration

The magnitudes of integration are summarized in Table 1 and illustrated in Figure 1. Among the anatomical modules (i.e., metacarpal, proximal phalanx, middle phalanx, and distal phalanx), the distal phalanx exhibited the lowest values of integration (ICV = 1.316), whereas the middle phalanx showed the highest (ICV = 1.746). This pattern indicates a proximal–distal trend where the magnitudes of integration increase from the metacarpals to the middle phalanges and then decrease sharply at the distal phalanges (Table 2). When analyzed by digit, on average, the second ray had the lowest integration values (ICV = 1.507), while the fourth digit had the highest (ICV = 1.653). This demonstrates an increasing trend of integration from the lateral to medial positions, with the first three rays showing similar relatively low values, which peak in the fourth and fifth rays. The least integrated bones of the entire hand were the second and third distal phalanges (ICV = 1.216 and 1.202, respectively), while the most integrated were the fourth and fifth middle phalanges (ICV = 1.823 and 1.847, respectively).

TABLE 1 Magnitudes of integration and indices of selection from each metacarpal and phalanx hand bone.

	n	ICV		Evolvability		Cond. Evol.		Flexibility		Constraints	
		Value	SE	Value	SE	Value	SE	Value	SE	Value	SE
Mc.I	96	1.463	0.004	0.464	<0.001	0.099	<0.001	0.662	0.004	0.741	0.009
Mc.II	96	1.452	0.004	0.648	<0.001	0.091	<0.001	0.637	0.003	0.710	0.009
Mc.III	96	1.531	0.004	0.482	<0.001	0.123	<0.001	0.658	0.004	0.775	0.008
Mc.IV	96	1.650	0.004	0.779	<0.001	0.104	<0.001	0.594	0.003	0.761	0.008
Mc.V	96	1.578	0.004	0.568	<0.001	0.106	<0.001	0.636	0.004	0.788	0.008
Ph.P.I	96	1.670	0.004	0.417	<0.001	0.109	<0.001	0.616	0.004	0.792	0.008
Ph.P.II	96	1.685	0.004	0.363	<0.001	0.079	<0.001	0.621	0.004	0.799	0.008
Ph.P.III	96	1.714	0.004	0.356	<0.001	0.060	<0.001	0.610	0.004	0.798	0.008
Ph.P.IV	96	1.769	0.004	0.399	<0.001	0.060	<0.001	0.600	0.004	0.813	0.008
Ph.P.V	96	1.766	0.004	0.456	<0.001	0.071	<0.001	0.592	0.003	0.825	0.009
Ph.M.II	96	1.673	0.004	0.448	<0.001	0.084	<0.001	0.610	0.004	0.790	0.009
Ph.M.III	96	1.642	0.004	0.443	<0.001	0.079	<0.001	0.606	0.004	0.803	0.008
Ph.M.IV	96	1.823	0.004	0.521	<0.001	0.086	<0.001	0.576	0.004	0.836	0.007
Ph.M.V	96	1.847	0.004	0.623	<0.001	0.108	<0.001	0.557	0.003	0.822	0.007
Ph.D. I	96	1.416	0.004	0.627	<0.001	0.140	<0.001	0.666	0.003	0.735	0.009
Ph.D.II	96	1.216	0.003	0.598	<0.001	0.128	<0.001	0.715	0.003	0.692	0.009
Ph.D.III	96	1.202	0.003	0.620	<0.001	0.193	<0.001	0.722	0.003	0.694	0.009
Ph.D.IV	96	1.371	0.004	0.670	<0.001	0.158	<0.001	0.674	0.003	0.744	0.008
Ph.D.V	96	1.377	0.004	0.719	<0.001	0.175	<0.001	0.685	0.003	0.730	0.008

Abbreviations: Cond. Evol., conditional evolvability; ICV, integration coefficient of variation of the eigenvalues; Mc., metacarpal; Ph.M., middle phalanx; Ph. P., proximal phalanx; Ph.D., distal phalanx.

3.2 | Responses to selection

The results for the four indices of responses to selection are presented in Tables 1 and 2. A detailed explanation for each index is provided below.

3.2.1 | Evolvability

Figure 2 illustrates the results of evolvability, which measures the ability of a structure to evolve in the direction of selection. Among the modules, there is an increasing trend of evolvability from proximal to distal phalanges, with metacarpals showing the second highest values. By digits, there is a progression from lateral to medial positions, where the first three rays display similar values, followed by an increase in the fourth and fifth rays. The most evolvable elements of the hand were the fourth and fifth distal phalanges (mean = 0.670 and 0.719, respectively), while the least were the second and third proximal phalanges (mean = 0.363 and 0.356, respectively).

3.2.2 | Conditional evolvability

Among modules, conditional evolvability follows a similar pattern to evolvability, decreasing from metacarpals to proximal phalanges, then increasing towards the distal positions. By digit, the highest values

were found in the first and fifth digits (mean = 0.116 and 0.115, respectively), closely followed by the third (0.114). At the bone level, the third and fifth distal phalanges had the highest values (mean = 0.193 and 0.175, respectively), whereas the third and fourth proximal phalanges had the lowest (both mean = 0.060).

3.2.3 | Flexibility

At the anatomical modules level, flexibility showed a decreasing trend from metacarpals to middle phalanges, with a notable peak in the distal phalanges, which were the most flexible elements. By digit, the fourth and fifth rays exhibited lower flexibility compared with the others, which had similar values. By bone, the second and third distal phalanges were the most flexible elements (mean = 0.715 and 0.722, respectively), while the fourth and fifth middle phalanges were the least flexible (mean = 0.571 and 0.557, respectively).

3.2.4 | Constraints

Among the anatomical modules, distal phalanges were notably the least constrained elements, and middle phalanges were the most constrained. By digit, medial rays (fourth and fifth) were the most constrained, while lateral rays (first and second) were the least. By bone, the fourth and fifth middle phalanges were the most constrained

bones of the entire hand, whereas the second and third distal phalanges were the least constrained elements.

3.3 | Correlations

3.3.1 | Among indices

The correlation tests between integration and the values obtained from the responses to selection indices showed a significant negative

correlation with evolvability and flexibility and a significant positive correlation with constraints (Figure 3).

3.3.2 | With function

The results of the correlation between integration, the different indices of selection, and the values related to functionality of the hand bones during four technologically distinct Lower Paleolithic stone tool production behaviors showed non-significant results across all tests (Table 3).



FIGURE 1 Overall magnitudes of integration of each hand bone in modern humans. Note the proximal–distal trend, with integration increasing from metacarpals to middle phalanges and then decreasing at the distal phalanges, as well as the increase from lateral to medial digits. The thumb deviates from this pattern, showing relatively low integration in the metacarpal and the highest in the distal phalanx.



FIGURE 2 Evolvability in the modern human hand. Note two trends: evolvability increases from proximal to distal phalanges, with metacarpals showing high values, and there is a lateral to medial progression, where the first three rays have similar evolvability, which then increases in the fourth and fifth rays.

TABLE 2 Indices of integration and responses of selection by anatomical module and digit.

	ICV	Evolvability × 100	Cond. Evol. × 100	Flexibility	Constraints
Anatomical modules					
Metacarpals	1.535	0.588	0.105	0.637	0.755
Proximal phalanx	1.721	0.398	0.076	0.608	0.805
Middle phalanx	1.746	0.509	0.089	0.587	0.813
Distal phalanx	1.316	0.647	0.159	0.692	0.719
Digits					
First digit	1.516	0.503	0.116	0.648	0.756
Second digit	1.507	0.514	0.095	0.646	0.748
Third digit	1.522	0.475	0.114	0.649	0.767
Fourth digit	1.653	0.592	0.102	0.611	0.789
Fifth digit	1.642	0.591	0.115	0.617	0.791

Abbreviations: Cond. Evol., conditional evolvability; ICV, integration coefficient of variation of the eigenvalues.

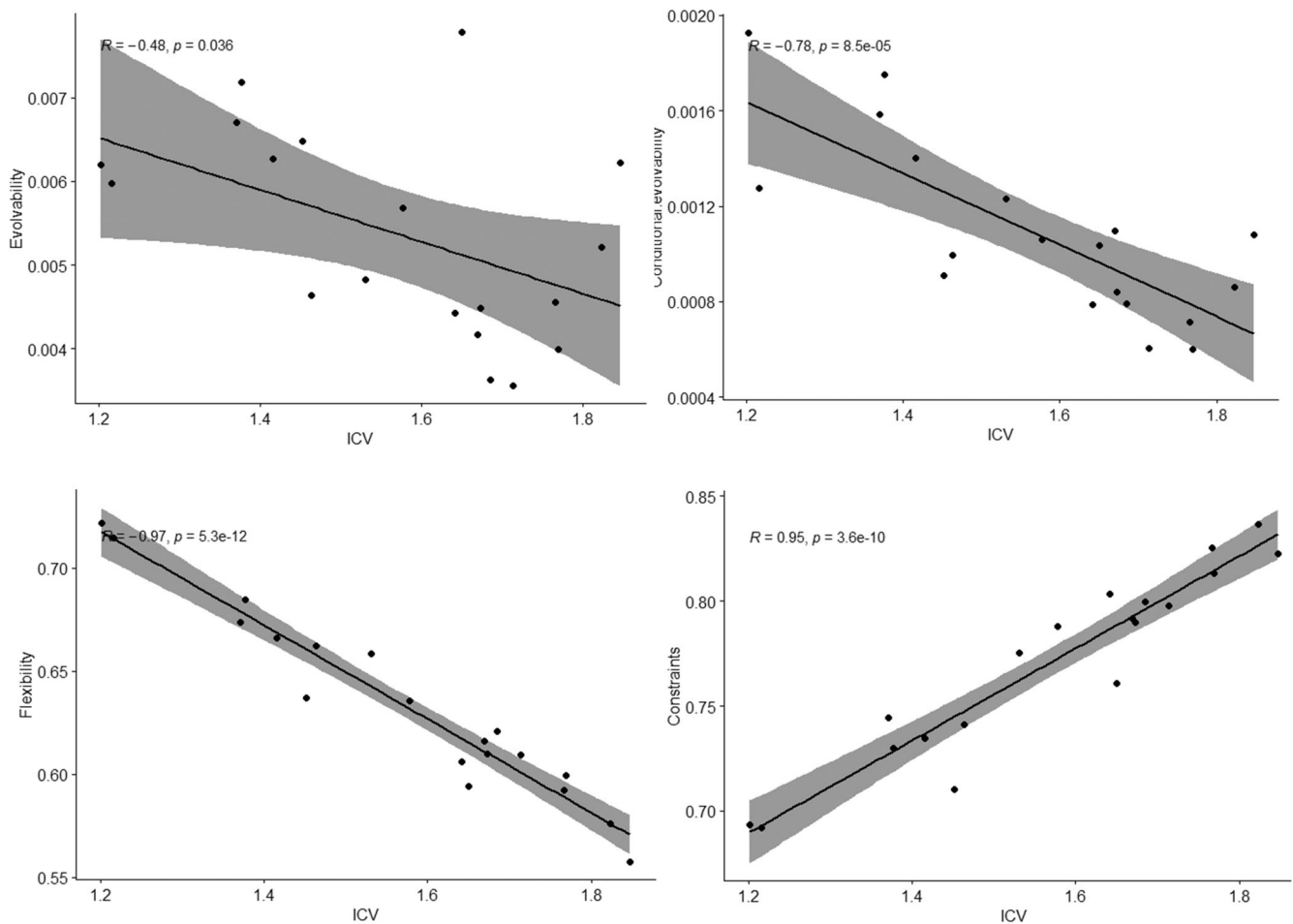


FIGURE 3 Scatterplots showing the correlation between integration and different indices of response to selection in the entire modern human hand. Significant negative correlations were found between integration and both evolvability and flexibility, while a significant positive correlation was observed between integration and constraints. ICV, integration coefficient of variation of the eigenvalues.

TABLE 3 Correlation between integration and evolvability, and the functionality of the hand during four technologically distinct Lower Paleolithic stone tool production behaviors.

	Oldowan	Early AH	Late AH	Plat. Prepar.
Integration	-0.136; $p = 0.673$	-0.400; $p = 0.197$	-0.479; $p = 0.115$	-0.422; $p = 0.171$
Evolvability	0.133; $p = 0.680$	0.349; $p = 0.267$	0.448; $p = 0.144$	0.378; $p = 0.226$

Abbreviations: AH, early Acheulean handaxe; LAH, late Acheulean handaxe; Plat. Prepar., platform preparation.

TABLE 4 Correlation between hands and feet integration and selection indices.

Integration	Evolvability	Cond. Evol.	Flexibility	Constraints
0.345; $p = 0.148$	0.325; $p = 0.174$	0.721 ; $p = <0.001$	0.473 ; $p = 0.041$	-0.101; $p = 0.679$

Note: Significant values are indicated in bold.

Abbreviation: Cond. Evol., conditional evolvability.

3.3.3 | With the foot

The correlation analysis between the indices obtained in this study and those from the foot revealed a positive correlation for all indices between both autopods, except for constraints, which exhibited a

negative correlation. Statistically significant results were found only for conditional evolvability ($r = 0.721$) and flexibility ($r = 0.473$; see Table 4 and Figure 4).

In summary, these findings indicate that distal phalanges are the most evolvable and flexible elements, while being the least integrated

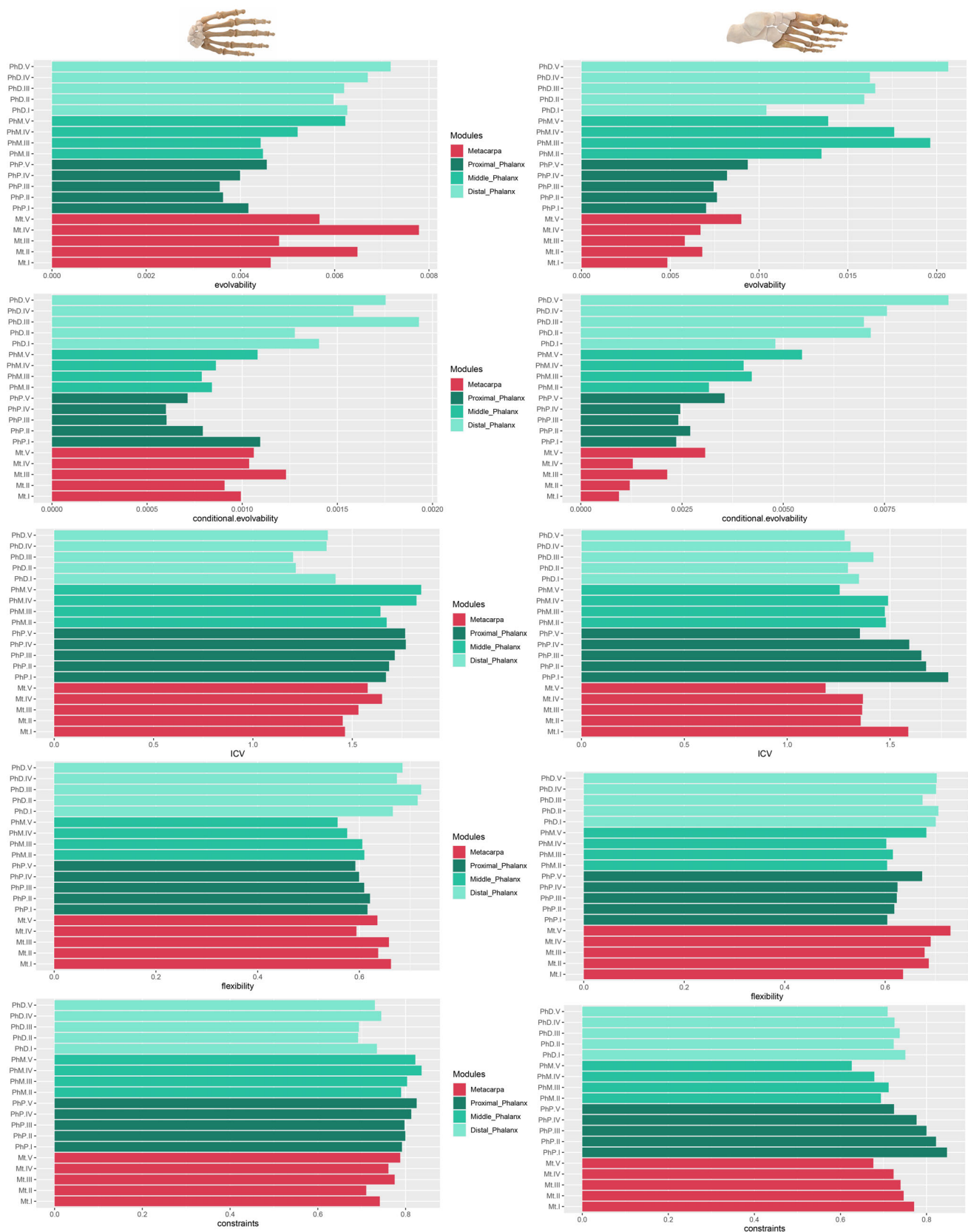


FIGURE 4 Values of integration and response to selection in the hand and foot indices. Data for the foot were obtained from Arlegi et al., 2023. Positive correlations were found for all indices except constraints, which showed a negative correlation. Statistically significant results were observed for conditional evolvability and flexibility (Table 4).

and constrained. Medial rays (fourth and fifth digits) are more integrated, evolvable, and constrained but less flexible than their counterparts. Integration is positively correlated with constraints and negatively correlated with evolvability, conditional evolvability, and flexibility. No significant relationship was found between functionality and the indices of selection and integration. Significant correlations between hand and foot indices were observed only for conditional evolvability and flexibility. Finally, the correlation between hand and foot indices only yielded significant results for conditional evolvability and flexibility.

4 | DISCUSSION

The human hand is a highly complex structure that has been the focus of extensive research in human evolution. Its mosaic nature—where different aspects of the hand evolved at varying times and rates—alongside gaps in the fossil record, complicates tracing the evolution of its unique combination of traits. This study aims to deepen our understanding of the evolutionary dynamics of the modern human hand by analyzing the degree of integration and the ability to respond to selection pressures in each phalanx and metacarpal bone. We test two hypotheses: (a) functional pressures lead to higher levels of integration, expecting the thumb to show the greatest integration; (b) The hands and feet share similar genetic and developmental mechanisms, predicting comparable integration and evolvability patterns in both autopods (Arlegi et al., 2023). Overall, the results do not fully support the first hypothesis. The thumb's average integration was similar to digits IV–V. However, the distal phalanx of the thumb exhibited the highest integration in this module, coinciding with the greatest pressure levels during Lower Paleolithic stone tool production behaviors. The second hypothesis is partially supported, highlighting hands and feet similar proximal–distal patterns with increased evolvability and flexibility, along with reduced integration and constraint. In contrast, in the medial–lateral pattern, the autopods show parallel increases in evolvability from the first to the fifth digit, but with opposite integration directions.

4.1 | First hypothesis

The first hypothesis suggested that the thumb, essential for hand manipulation, would exhibit the highest levels of integration. The connection between morphological integration and functionality is elucidated as a response to strong selective pressures, indicating the necessity for structures to be integrated to preserve their functional roles (Arlegi et al., 2020; Gómez-Robles & Polly, 2012; Riedl, 1978; Wagner, 1984). Therefore, elements with strong integration are highly variable and linked to evolutionary scenarios marked by high functional pressures. Contrary to our prediction, these results do not support this hypothesis. However, when examining individual bones, the thumb distinguished itself with a unique proximal–distal integration pattern within the hand. The first metacarpal had the second-lowest

integration level, the lowest evolvability, and the highest flexibility among the digits. Conversely, the first distal phalanx showed the highest integration and lowest flexibility, suggesting distinct selection pressures and evolutionary pathways for these skeletal components.

Low integration in the first metacarpal could imply lower variability or, conversely, a lesser need for structural correlations to maintain functionality, suggesting a more stable or less variable structure compared with the other digits. Theoretically, low integration is associated with stabilizing selection, where many eigenvalues are linked to similar variance amounts in any direction of phenotypic space (Steppan et al., 2002). This could allow the first metacarpal to revert to an optimal morphology from various deviations, enhancing morphological flexibility over time. Our findings show a low evolvability and high flexibility for the first metacarpal, suggesting stabilizing selection or canalization. This mechanism could maintain a stable first metacarpal morphology over time, due to the ease of restoring the optimal morphology in any direction of the morphospace. The hominin fossil record shows diverse shapes and sizes for the first metacarpal bone, with no clear linear evolutionary direction (Bowland et al., 2021). An effective thumb opposition emerged around 2 million years ago, coinciding with the appearance of the genus *Homo*. However, stone tool production is not exclusive to *Homo*, as tool use evidence suggests dates back to 3.3 Ma and is associated with *Au. Afarensis* (Harmand et al., 2015). This indicates that different hominins could perform stone tool behaviors, finding multiple morphological solutions for similar functional challenges. The high flexibility of the first metacarpal may explain its ability to adapt to selection over time. Nonetheless, the low evolvability linked to stabilizing selection does not match the hominins panoply of morphologies. A plausible explanation is that the observed limited evolvability in the first metacarpal is unique of *Homo sapiens*, suggesting it has reached an optimal local fitness with its current morphology.

In contrast, the high integration in the first distal phalanx may be associated with greater morphological variability. Maintaining strong structural correlations and specific functionalities could have driven the evolution towards higher integration in this phalanx, indicating a scenario of directional evolution in response to strong selective pressures. The fossil record shows the first distal phalanx in hominins has been relatively human-like since the late Miocene (Gomery & Senut, 2006). However, detailed anatomical examination reveals distinct features in the first distal phalanx of modern humans compared to fossil hominins, including pronounced *flexor pollicis longus* insertion, the presence of an unguis fossa, and dissymmetric unguis spines, particularly the prominent ulnar spine. Comparative analysis shows *Orrorin* with a more human-like morphology than later species such as *Au. Africanus*, *Paranthropus robustus*, and *Homo habilis* (OH 7), and Neanderthals, indicating that fossil hominins lack distinctly human functional features (Almécija et al., 2010; Shrewsbury et al., 2003). These findings suggest that the first distal phalanx morphology did not remain constant but may have initially been enhanced by selection for manipulative capabilities, followed by stone tool making adaptations, and ultimately specializing in precision grip with pad-to-pad contact within the genus *Homo*.

These distinct evolutionary trajectories observed within the thumb, specifically between the metacarpal and the first phalanx, may respond to distinct functional and developmental pressures acting on each bone. From a functional perspective, the first metacarpal might have achieved a stable, optimal functional state with the capacity for flexibility, while the distal phalanx could have undergone directional evolution for specialized functions, limiting its flexibility but enhancing its adaptation to more specific demands. It is plausible that the first metacarpal reached an early optimum for pad-to-pad opposition with the fingers, while ongoing functional demands continued to shape the distal phalanx for enhanced control and manipulation of small objects. While we did not find a significant correlation between integration and pressure magnitudes across the entire hand during Lower Paleolithic stone tool production behaviors, the first distal phalanx displayed the highest integration and experienced the greatest functional pressures in stone tool production. The development of the thumb occurs relatively independently and later than the other digits, conferring the first metacarpal and phalanges higher variability (Hamrick, 2012; Reno et al., 2008). Functional pressures in some vertebrate groups can lead to phalanges reduction or disappearance (Reno et al., 2013; Tague, 2002), but the first metacarpal remains morphologically unaltered. This phenomenon is associated with the non-expression of *Hoxd11* and *Hoxd12* genes (Vargas & Fallon, 2005; Wagner & Vargas, 2008). This absence of genetic influence results in a unique case of an independent module within the hand from a developmental perspective, establishing a more stable scenario for the first metacarpal irrespective of selection acting on the first two phalanges (Reno et al., 2007; Reno et al., 2008). Developmental patterning genes such as *Hoxc13*, *BAMBI*, and *Msx1* and *Msx2* transcription factors are exclusively expressed in the first distal phalanx (Casanova & Sanz-Ezquerro, 2007). This unique expression pattern suggests changes in the first distal phalanx may occur independently of other digits, which function as a more correlated module (Mori et al., 2000). The late development of the distal phalanx (Reno et al., 2008), contributes to a greater degree of variation compared with other digits, which may show closer developmental integration (Hamrick, 2012). This aligns with previous research indicating modern humans differ from other taxa primarily in the distal phalanx, not the metacarpal, associated with the *Hoxd* gene expression domains (Reno et al., 2008).

4.2 | Second hypothesis

The second hypothesis proposed similar selection and integration patterns in the hands and feet along the proximal–distal and lateral–medial axes. The results partially support this hypothesis, revealing greater similarity in the proximal–distal dimension, with an increasing trend in flexibility and evolvability along this axis, where the distal phalanges are the most evolvable, flexible, and less integrated elements. Distal phalanges, along with preaxial (digit I) and postaxial (digits II–V) units, form one of the three developmental domains (Hamrick, 2012). Unlike the first digit, they develop last in the

proximal–distal patterning sequence, rendering them the most variable bones of the autopods (Hamrick, 2012). High variability may have been advantageous for adapting to specific functional demands involving fine manipulation and precision grip, requiring high adaptability and flexibility for diverse morphologies and evolutionary trajectories in response to shifting selection pressures. These findings, as previously proposed (Arlegi et al., 2023), suggest that the developmental process, unfolding in the proximal–distal direction in both feet and hands, strongly influences evolvability and, to a lesser extent, integration. The lack of significant correlation in integration and constraints may result from different functional selections on each autopod, focused on the first digit for locomotor pressures in the foot, and more evenly distributed in the hand for manipulation activities.

In contrast, differences emerge in the lateral–medial dimension between hands and feet in integration, flexibility, and constraint trends. However, there is a relatively similar trend in the evolvability index, especially for conditional evolvability when considering the constraint factor. This suggests that constraints influence evolvability, as evidenced by the increased similarity in trends observed in both autopods when considering constraints in proximal–distal and medial–lateral directions. Surprisingly, hands and feet differ in the integration patterns, especially in the medial–lateral direction. This is counterintuitive since they follow the same developmental patterning, with the greater functional and biomechanical stress on the first digit. However, no significant correlation exists between selection and integration indices with manual pressure during stone tool production, indicating that, at least using this approach, stone tool production may not be as crucial for hand evolution as bipedalism is for feet. Differences in integration patterns may respond to parcellation through functional demands, as genetic integration is the primitive property of serially homologous structures (Cheverud, 1996; Young & Hallgrímsson, 2005). Functional selection in the feet, particularly in the first digit, is likely stronger than in the hand, where a relatively consistent proportion between the thumb and non-pollex digits has been favored. Previous research shows that selection for increased hallux length and toe reduction for bipedalism produced a parallel, correlated reduction in fingers, enhancing opposability and potentially facilitating tool use (Rolian et al., 2010). Other studies also suggested that this covariation is stronger in the first digit than in the postaxial (II–V) ones (Rolian, 2009; van Heteren et al., 2022).

Both autopods show similar magnitudes for all the indices, except for higher evolvability in the feet, suggesting greater evolvability capacity in the feet than hands. These results align with previous studies highlighting the stability of human hand morphology compared with greater variability observed in other primates (Almécija et al., 2015), emphasizing stronger selection on the foot, leading to parallel phenotypic changes in the hand (Rolian et al., 2010). Interestingly, correlation results between both autopods reveal a highly significant correlation in conditional evolvability, but not in overall evolvability. Evolvability represents the ability of a set of traits to evolve in response to selection, regardless of covariation, while conditional evolvability considers response magnitude limited to the direction of selection by stabilizing forces (Hansen & Houle, 2008; Marroig

et al., 2009). This means that the ability of their traits to evolve in response to selection may differ, yet this difference might not be apparent when considering the specific stabilizing selection constraints. Speculation arises concerning the constraints influencing the analogous evolvability patterns in hands and feet under a stabilizing selection scenario. Given their divergence in functional factors (see above), it seems plausible that pleiotropic effects stemming from a shared developmental bauplan contribute to shared stabilizing selection (Cheverud, 1996; Hansen, 2003; Lande, 1980). In other words, hand and foot evolve differently under a scenario of directional selection, but similarly under stabilizing selection, possibly driven by pleiotropic effects. However, for a more nuanced understanding of the distinct selection pressures and evolutionary trajectories shaping hands and feet, direct comparison of evolvability patterns within each homologous autopod element is necessary.

This study is limited by its exclusive focus on morphological integration and selection responses in *Homo sapiens*, which aids in identifying variability and trends across individual skeletal elements. Although our findings provide insights into selection processes when compared with fossil records, a comprehensive macroevolutionary understanding needs analyzing these indices in phylogenetically related species to discern primitive patterns. Consequently, further research involving other great apes is essential to test these macroevolutionary hypotheses.

5 | CONCLUSIONS

The findings of this study reveal that the thumb exhibits similar levels of integration to the second and third rays on average, while the fourth and fifth rays showed higher integration. However, a distinct pattern emerges within the thumb itself, indicating different evolutionary trajectories for the metacarpal and distal phalanx. This divergence likely reflects varying functional and developmental pressures on these elements. The first metacarpal, characterized by high flexibility and low evolvability, appears to have reached a stable, optimal morphology, facilitating pad-to-pad opposition with the fingers under stabilizing selection. In contrast, the distal phalanx seems to have undergone directional evolution, suggesting specialization for a specific function, which limits its flexibility but enhanced its adaptation to more precise demands. The unique development of the thumb, associated with the *Hoxd11* and *Hoxd12* genes, along with the specific expression pattern in the first distal phalanx, likely provided the necessary variation to respond to diverse selection pressures.

Despite the lack of a significant overall correlation between selection and integration indices and manual pressure during stone tool production, the first distal phalanx exhibited the highest degree of integration and experienced the greatest functional pressures during tool use. This finding suggests that functional selection may have acted specifically on critical manipulative elements of the hand. When comparing the hands and feet, a greater similarity is observed in the proximo-distal axis than in the medio-lateral axis, especially in terms

of evolvability rather than integration. These results can be attributed to the strong influence of the proximo-distal developmental pattern shared by both autopods on evolvability. Additionally, differences in the functional pressures—manipulation in the hand versus bipedal locomotion in the foot—result in weaker integration in the hand. Interestingly, a highly significant correlation in conditional evolvability was found between the hands and feet, whereas no such correlation was observed in overall evolvability. This suggests that hands and feet evolve differently under a scenario of directional selection but similarly under stabilizing selection, the latter likely driven by pleiotropic effects. Consistent with previous studies, we observed higher evolvability in the feet compared with the hands, indicating the foot is subject to stronger selection pressures. However, whether these pressures result in parallel phenotypic changes in the hand, as previously proposed, remains an open question in this study. Further research is needed to explore these dynamics in more detail, particularly in terms of the evolutionary pathways that have shaped hands and foot current morphologies.

AUTHOR CONTRIBUTIONS

Mikel Arlegi: Conceptualization (lead); formal analysis (lead); funding acquisition (equal); investigation (lead); methodology (lead); project administration (equal); resources (equal); software (lead); supervision (equal); validation (lead); visualization (lead); writing – original draft (lead). **Carlos Lorenzo:** Conceptualization (supporting); data curation (lead); formal analysis (supporting); funding acquisition (equal); investigation (supporting); methodology (supporting); project administration (equal); resources (equal); software (supporting); supervision (supporting); validation (supporting); visualization (supporting); writing – original draft (supporting).

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

ORCID

Mikel Arlegi  <https://orcid.org/0000-0001-5665-9275>

Carlos Lorenzo  <https://orcid.org/0000-0001-5706-293X>

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