

**Adult *Homo naledi* hand skeleton  
points to life before birth**

Zachary COFRAN & Tracy L. KIVELL



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Dorsal view of the "Hand 1" skeleton of *Homo naledi*. Credits: photograph by Peter Schmid.

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# Adult *Homo naledi* hand skeleton points to life before birth

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## ABSTRACT

Morphology evolves through modifications to growth and development, yet inferences about ontogeny of extinct organisms are often limited by small and fragmentary fossil samples. The remarkable circumstances and preservation of *Homo naledi* Berger *et al.*, 2015 material from Rising Star Cave, South Africa allow unique insights into the prenatal period of growth and development. We focus here on what a nearly complete adult *H. naledi* hand skeleton can tell us about embryonic pattern formation. On the one hand, it has been proposed that the proportional lengths of phalanges within a digit are established by a reaction-diffusion mechanism that can be described mathematically by the “inhibitory cascade” model. On the other hand, the proportional lengths of the second and fourth digits are mediated by prenatal exposure to sex hormones, and may serve as a biomarker for social behavior. Viewed through the lens of development, the *H. naledi* hand suggests that a simple developmental shift could have facilitated the evolution of manual dexterity in early hominins. In addition, *H. naledi* presents the highest ratio of second to fourth digit of all known fossil hominins, which may reflect reduced aggression compared to other fossil *Homo* Linnaeus, 1758. The remarkable preservation of the *H. naledi* hand skeleton provides a unique view of life before birth.

## KEY WORDS

Hominin,  
ontogeny,  
development,  
phalanx,  
prenatal androgens.

## RÉSUMÉ

*Le squelette de la main adulte d'Homo naledi montre la vie avant la naissance.*

La morphologie évolue au fil des modifications de la croissance et du développement, mais les inférences sur l'ontogenèse d'organismes disparus sont souvent limitées par des échantillons fossiles petits et fragmentaires. Les circonstances remarquables et la préservation du matériel d'*Homo naledi* Berger *et al.*, 2015 provenant de Rising Star Cave, en Afrique du Sud, offrent un aperçu unique de la période prénatale de croissance et de développement. Nous nous concentrons ici sur ce qu'un squelette de main adulte presque complet d'*H. naledi* peut nous apprendre sur la formation de modèles embryonnaires. D'une part, il a été proposé que les longueurs proportionnelles des phalanges au sein d'un doigt soient établies par un mécanisme de réaction-diffusion qui peut être décrit mathématiquement par le modèle de la « cascade inhibitrice ». D'autre part, les longueurs proportionnelles des deuxième et quatrième doigts dépendent de l'exposition prénatale aux hormones sexuelles et peuvent servir de biomarqueur du comportement social. Considérée sous l'angle du développement, la main d'*H. naledi* suggère qu'un simple changement dans le développement aurait pu faciliter l'évolution de la dextérité manuelle chez les premiers hominidés. De plus, *H. naledi* présente le rapport le plus élevé entre le deuxième et le quatrième doigt de tous les hominines fossiles connus, ce qui peut refléter une agressivité réduite par rapport aux autres fossiles du genre *Homo* Linnaeus, 1758. La préservation remarquable du squelette de la main d'*H. naledi* offre une vision unique de la vie avant la naissance.

## MOTS CLÉS

Hominine, ontogenèse, développement, phalange, androgènes prénataux.

## INTRODUCTION

Morphology evolves through modifications to ontogenetic processes that tend to be phylogenetically conserved. Within a body or organ, shared developmental processes integrate structures such that they may not evolve completely independently of one another (Olson & Miller 1958; Gould & Lewontin 1979; Cheverud 1996). Understanding these developmental patterns can therefore provide insight into how and why species vary in morphology. Importantly, this “morphological integration” of structures, such as bones of the hand skeleton (Rolian 2014), means that developmental patterns can be inferred from adult remains. The goal of this study is to use an adult *Homo naledi* Berger *et al.*, 2015 hand skeleton, along with insights from developmental biology, to illuminate the evolution of finger bone lengths.

*Homo naledi* is a recently discovered, extinct hominin known from the Rising Star Cave system in the Cradle of Humankind, South Africa (Berger *et al.* 2015). One of the many remarkable aspects of the *H. naledi* assemblage is its immense volume, with over 2 000 fragmentary remains representing most of the skeleton and elements deriving from over a dozen individuals who ranged in age from young infants to old adults (Hawks *et al.* 2017; Bolter *et al.* 2018; Brophy *et al.* 2021). Although the morphology of *H. naledi* is in many ways similar to earlier hominins from over two million years ago, the fossils likely date to between 241–330 kya (Dirks *et al.* 2017; Robbins *et al.* 2021). *Homo naledi* was therefore a primitive species that was contemporaneous with early members of the modern *Homo sapiens* Linnaeus, 1758 and Neandertal lineages, among others (Hublin *et al.* 2017).

Because of the remarkable representation across the skeleton and lifespan, *H. naledi* provides a unique lens into ontogeny, or the patterns and processes of individual growth and development. Previous research in this fossil assemblage has

focused largely on single skeletal elements to infer growth during the postnatal period. For example, an ilium fragment, U.W. 102a-138, is clearly unfused at the acetabulum, and its size relative to adult remains is similar to that of humans in the juvenile state of development (Cofran *et al.* 2022). The ilium further suggests that the flaring ilium similar to 2-million-year-old australopiths was present early in development, yet its sacroiliac joint is larger and more similar to humans of a similar overall size. While this individual suggests interesting differences (morphology) and similarities (joint size) with human growth, it nevertheless represents a snapshot of the dynamic process of growth and development.

Inferring patterns of postnatal growth and development generally requires representation of multiple individuals at different, known stages of maturation or even chronological ages at death. In contrast, because many aspects of adult morphology are established prenatally (Weaver *et al.* 2016; Young *et al.* 2022), even remains from a single adult may provide a surprising window into developmental processes during the embryonic and fetal periods of life before birth. For example, the tetrapod limb is a well-coordinated proliferation of segments, well-illustrated by the primate autopod (i.e., hand and foot) containing five rays each of which is composed of 3–4 bones arranged end to end (Kivell *et al.* 2023). Primate hands are adapted for both diverse types of locomotion as well as enhanced manipulation relative to most other mammals. Compared with many other primates, such as lorises, spider monkeys or aye-ayes, the human hand can be described as surprisingly conservative/primitive in many aspects of its form but derived in its dexterous function (Kivell *et al.* 2023). This form-function combination is traditionally considered to be the result of shifting hand function away from locomotion towards primarily object manipulation throughout hominin evolution. Among several morphological features that distinguish the human hand from that of other apes, the intrinsic

hand proportions are considered a key adaptation to enhanced dexterity and particularly the use of forceful pad-to-pad precision grips (Marzke 1997; e.g. Alba *et al.* 2003; Feix *et al.* 2015; Kivell 2015). Whereas non-human apes have long fingers with a shorter thumb, humans have short fingers and a relatively long thumb (Napier 1960). These intrinsic hand proportions appear in the fossil hominin record by at least two million years ago (Kivell *et al.* 2011) and perhaps much earlier (Almécija *et al.* 2015).

Because robustly quantifying intrinsic hand proportions involves multiple associated elements from the same individual, reconstructing manual evolution is generally hampered by a lack of associated hand skeletons (Rolian & Gordon 2013). In the past 15 years, the fortuitous discoveries of *Australopithecus sediba* (Berger *et al.*, 2010) and *Homo naledi* (Berger *et al.* 2015) include partial skeletons of single individuals preserving relatively complete hands found in semi-articulation (Kivell *et al.* 2011, 2015). The adult “MH 2” *Au. sediba* individual, dating to just under 2 mya (Dirks *et al.* 2010; Pickering *et al.* 2011), preserves a right hand skeleton that is nearly complete and missing only the distal phalanges of rays 2-5 and three carpal bones (Kivell *et al.* 2011, 2018). Similarly, “Hand 1” of *H. naledi* contains all the hand and wrist bones except the pisiform from an adult individual (Kivell *et al.* 2015). These hand skeletons show human-like intrinsic hand proportions with a relatively long thumb (particularly in *Au. sediba*), and enthesal markings suggestive of tool-making and -using capabilities (particularly in *H. naledi*).

Relatively complete hand skeletons like those of *Au. sediba* and *H. naledi* allow for robust inferences about hand function and potential adaptation, as well as the developmental bases of the hominin autopod. Intrinsic hand proportions are established by mechanisms of pattern formation during embryonic development (Green & Sharpe 2015). Specifically, the mass of mesenchymal cells that will become the hand or foot (i.e., the autopod) differentiate proximodistally, forming first the carpus, then metacarpus followed by the phalanges (Stricker & Mundlos 2011; Rolian 2016). Each digital ray (e.g. the index finger) is initially represented by a single cartilage precursor that elongates and divides into separate digit segments (Hamrick 2001; Sanz-Ezquerro & Tickle 2003). This segmentation occurs due to concentrations of gene expression that repress cartilage formation and initiate joint cavitation (Hiscock *et al.* 2017). It is hypothesized that a reaction-diffusion mechanism involving the coordinated activation and inhibition of these genes (Turing 1952) specifies where these joint interzones will form (Stricker & Mundlos 2011; Kavanagh *et al.* 2013; Hiscock *et al.* 2017), which in turn determines the relative length of each phalanx in a ray (Young *et al.* 2015).

The evolutionary diversity in digit proportions likely reflects—and is even biased by—fundamental developmental patterns (Kavanagh *et al.* 2013). Kavanagh and colleagues (2007) theorized a mathematical model for the proportional size relationships between serially repeating structures, which they called the ‘inhibitory cascade’ (IC) model. While their analyses were based on mouse molars, the model has been applied to other skeletal elements including avian limb

digits (Young *et al.* 2015). Young and colleagues (2015) showed that the IC model makes specific predictions for a three-segment series (e.g. finger phalanges). First, the intermediate phalanx should be roughly 1/3 of the total series length. Second, the relationship between the proximal and distal phalanges (PP and DP, respectively) can be modeled by the line:  $DP = 0.667 \cdot 1 \cdot PP$ , where DP and PP lengths are proportional to the full series length. Analyzing the degree to which *Homo naledi* “Hand 1” and other hominin finger skeletons fit this developmental model can yield insights into how manual dexterity evolved (Fig. 1).

Another marker of embryonic development recorded in hand proportions is the ratio of the second to fourth digit lengths (Nelson & Shultz 2010; Nelson *et al.* 2011). In humans and many other mammals (e.g. baboons), the second and fourth manual digits tend to be more similar in length among females (i.e., a higher 2D:4D “digit ratio”) whereas males tend to have relatively longer fourth digits (i.e., a lower digit ratio). This digit ratio dimorphism has been argued to reflect exposure to sex hormones during embryonic and fetal development (Lutchmaya *et al.* 2004). On the one hand, experimental evidence in mice suggests that differing androgen/estrogen-receptor activity levels early during hand development influence cartilage cell morphology and proliferation, and therefore growth of the fourth digit (Zheng & Cohn 2011). On the other hand, a recent meta-analysis of dozens of 2D:4D studies in humans found much more limited support for a relationship between the digit ratio and various measures of prenatal testosterone exposure (Sorokowski & Kowal 2024). While this meta-analysis might seem to undermine the digit ratio as a biomarker, those reviewed studies examined testosterone only, while the experimental mouse evidence examined androgen and estrogen *receptors* and identified a narrow window of embryonic development when sexual dimorphism arises. Thus, even if the exact mechanisms influencing 2D:4D ratio in humans remain obscure, there is still compelling evidence that the ratio is established during embryonic development and influenced by sex hormones (Hönekopp *et al.* 2007).

Prenatal sex hormones are not only vital for development of the female and male phenotype in mammals (Thornton *et al.* 2009), but because they affect brain development, they are also associated with variation in behavior and sociality (Josephs *et al.* 2006, 2003; Trumble *et al.* 2015). Prenatal androgens play a key role in shaping an individual’s competitive behaviors (Josephs *et al.* 2003, 2006; Bodo & Rissman 2008) while prenatal estrogens play a role in enhancing cooperative and affiliative behaviors (Coleman *et al.* 2011; Trumble *et al.* 2015). Thus, variation in digit ratios can be used as a proxy not only for exposure to sex hormones during development, but also, as a consequence, for social behavior in extant and extinct taxa. For example, comparisons among non-human primates reveal lower average digit ratios among species with higher levels of male-male mating competition and agonistic aggression (McIntyre *et al.* 2009; Nelson & Shultz 2010; Howlett *et al.* 2015; Howlett 2019). Examining the more limited fossil evidence, Nelson and colleagues (2011) found that the digit ratio based solely on the second and fourth proximal



FIG. 1. — Dorsal view of the “Hand 1” skeleton of *Homo naledi* Berger *et al.*, 2015 illustrating the data used in this study; **blue highlights** the three phalanges of the second ray used for the Inhibitory Cascade analysis; **red highlights** the PP4 used for the 2P:4P analysis. Abbreviations: **DP**, distal phalanx; **IP**, intermediate phalanx; **PP**, proximal phalanx. Scale bar: 1 cm. Credits: photograph by Peter Schmid.

phalanges (“2P:4P ratio”) yields similar results as full-finger studies, and that extant humans have a lower 2P:4P ratio on average compared to Neandertals and other Pleistocene humans (Fig. 1). This finding has been used in support of the “Human Self-Domestication” hypothesis, that prosocial behavior and reduced aggression and reactivity were critical in our recent cognitive and social evolution (Hare 2017).

Here, we use these developmental models to infer potential developmental expressions and social behavior from adult hominin hand skeletons with emphasis on *H. naledi* (“Hand 1”). We first examine the relative segment lengths of the second ray in extant apes, humans, and fossil hominins, to test the degree to which they fit the IC model. We then compare the ratio of second and fourth proximal phalanges (2P:4P) across these taxa.

TABLE 1. — Fossil specimens analyzed in this study. Columns indicate whether the specimen was included in the Inhibitory Cascade and/or 2P:4P analyses. Fossils are listed in roughly chronological order from geologically oldest to most recent.

| Fossil ID          | Taxon   | Inhibitory Cascade | 2P:4P | Data source                                      |
|--------------------|---|--------------------|-------|--|
| IPS21350           | <i>Pierolapithecus catalunicus</i><br>Moyà-Solà, Köhler, Alba,<br>Casanovas-Vilar & Galindo, 2004       | –                  | ×     | Fossil (Sergio Almécija, personal communication) |
| IPS18800           | <i>Hispanopithecus laietanus</i> Comella &<br>Crusafont-Pairó, 1944                                     | ×                  | ×     | Fossil (Sergio Almécija, personal communication) |
| BA 140             | <i>Oropithecus bambolii</i> Gervais, 1872   | –                  | ×     | Fossil (Sergio Almécija, personal communication) |
| IGF 11778          | <i>Oropithecus bambolii</i>   | ×                  | –     | Fossil (Sergio Almécija, personal communication) |
| ARA-VP-6/500       | <i>Ardipithecus ramidus</i><br>(White, Suwa, & Asfaw, 1995)   | ×                  | ×     | Fossil (Kivell); Lovejoy <i>et al.</i> (2009)    |
| StW 573            | <i>Australopithecus africanus</i> Dart, 1925  | ×                  | ×     | Fossil (Kivell)                                  |
| MH 2               | <i>Australopithecus sediba</i> Berger,<br>de Ruiter, Churchill, Schmid,<br>Carlson, Dirks & Kibii, 2010 | –                  | ×     | Fossil (Kivell)                                  |
| naledi Hand 1      | <i>Homo naledi</i> Berger <i>et al.</i> , 2015  | ×                  | ×     | Fossil (Kivell)                                  |
| Kebara 2           | <i>Homo sapiens neanderthalensis</i><br>Kleinshmidt, 1922   | ×                  | ×     | Fossil (Kivell)                                  |
| Spy II             | <i>Homo sapiens neanderthalensis</i>  | –                  | ×     | Nelson <i>et al.</i> (2011)                      |
| Regourdou          | <i>Homo sapiens neanderthalensis</i>  | –                  | ×     | Nelson <i>et al.</i> (2011)                      |
| La Ferrassie I     | <i>Homo sapiens neanderthalensis</i>  | –                  | ×     | Nelson <i>et al.</i> (2011)                      |
| Shanidar 4         | <i>Homo sapiens neanderthalensis</i>  | –                  | ×     | Nelson <i>et al.</i> (2011)                      |
| Qafzeh 9           | <i>Homo sapiens</i> Linnaeus, 1758  | ×                  | ×     | Fossil (Kivell); Nelson <i>et al.</i> (2011)     |
| Ohalo II           | <i>Homo sapiens</i>   | ×                  | –     | Fossil (Kivell); Nelson <i>et al.</i> (2011)     |
| Dolni Věstonice 16 | <i>Homo sapiens</i>   | ×                  | ×     | Sládek <i>et al.</i> (2000)                      |

## MATERIAL AND METHODS

### SAMPLES

Raw data include the maximum lengths of the proximal, intermediate, and distal phalanges from articulated hand skeletons of hominoids including *Hyllobates lar* (Linnaeus, 1771) (N = 5), *Pongo pygmaeus* (Linnaeus, 1760) (N = 10), *Gorilla gorilla* (Savage, 1847) (N = 4), *Pan paniscus* Schwarz, 1929 (N = 5), *Pan troglodytes* (Blumenbach, 1775) (N = 9), and recent humans (N = 45). Human phalanges represent individuals of African and European ancestry. Data are drawn from the Supplemental Material of Feix *et al.* (2015), which includes both measurements and names of museum collections associated with each skeletal individual.

We only included fossils for which phalanges could be confidently associated to the second and fourth rays and their full lengths measured or reliably estimated (Table 1). Data come from direct observation (TLK and Sergio Almécija, personal communication) and published literature (Sládek *et al.* 2000; Almécija *et al.* 2007, 2009; Lovejoy *et al.* 2009; Feix *et al.* 2015; Kivell *et al.* 2023). *Australopithecus* R.A.Dart, 1925 specimen StW 573 was measured directly on fossils still embedded in breccia, so its data are tentative and must be interpreted cautiously. We do not include the composite hand of *Australopithecus afarensis* Johanson, White & Coppens, 1978 in this analysis because it includes elements from different individuals (Marzke 1983; Kivell *et al.* 2023).

### ANALYSES

We follow the approach of Young *et al.* (2015) to assess the degree to which taxa meet the predictions of the IC model, by examining proportional lengths of second ray phalanges.

We converted raw phalanx length to its proportional size by dividing each phalanx in the series by the sum of the proximal, intermediate, and distal phalanges for each individual. We used reduced major axis (RMA) regression of distal versus proximal phalanx relative length to examine the scaling relationship between these variables separately for humans, non-human hominoids, and non-human great apes, using the “lmodel2” package (Legendre 2018) in R version 4.1.2 (R Core Team 2021). We also plotted the proportional lengths of each segment individually, comparing humans, non-human hominoids, and fossil hominins; this allowed a visual appraisal of interspecific patterns, as well as a test of whether the intermediate phalanx is two-thirds of the series length as the IC model predicts.

We assessed the 2P:4P ratio among the fossil sample, comparing these ratios with the summary statistics for mixed-sex samples of humans and other apes published by Nelson and colleagues (2011). To help visualize these published patterns, we plotted each extant genus' mean  $\pm$  two standard deviations (i.e., 95% range). We do not test specific hypotheses about the 2P:4P ratio, but simply examine the fossils in light of extant ranges of variation.

## RESULTS

Phalanx proportional lengths show that humans and other apes generally follow the predicted IC patterns, but with some interesting deviations (Table 2 and Fig. 2). The IC model predicts  $DP = 0.667 \cdot 1 \cdot PP$  (Young *et al.* 2015). The model slope and intercept are within the 95% confidence intervals for RMA regression parameters for the modern human sample, but just outside the ape confidence intervals.

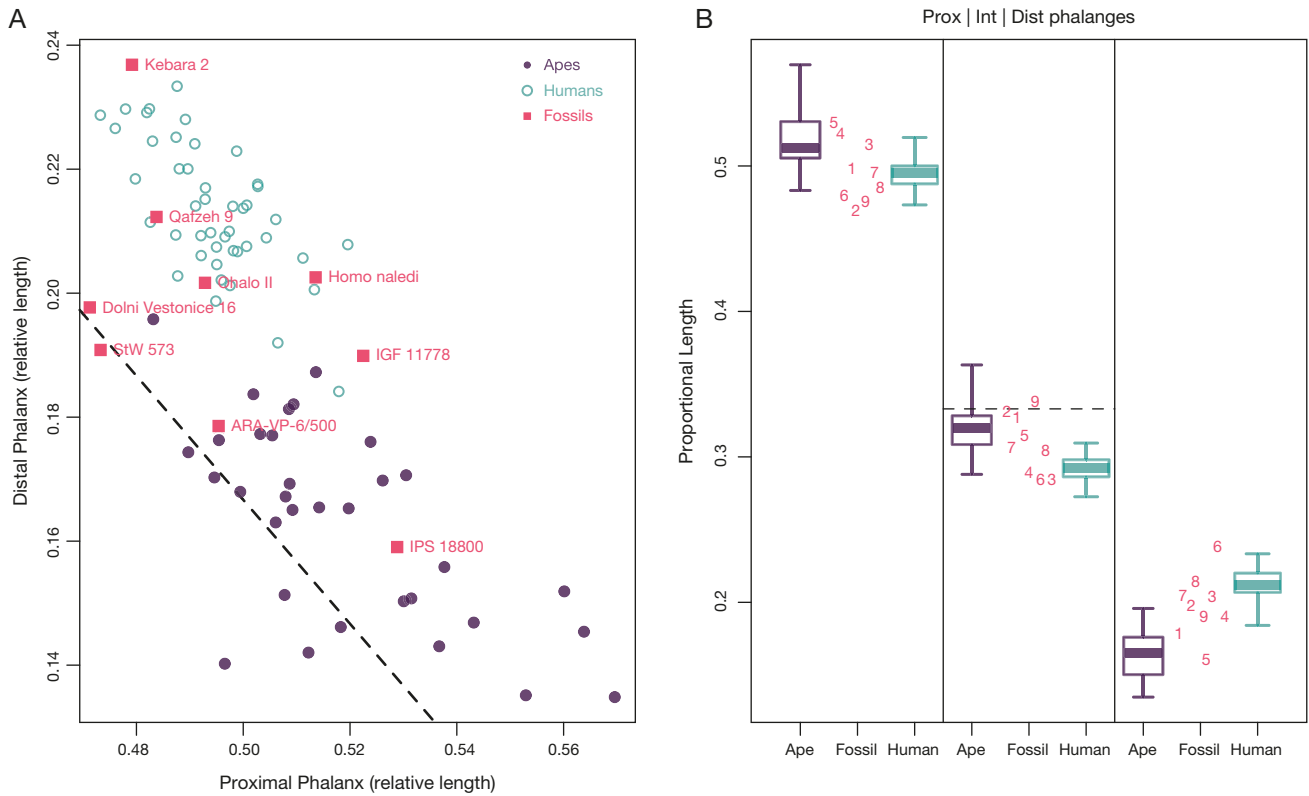


FIG. 2. — **A**, Distal/proximal intermediate phalanx proportional length among extant and extinct hominids. The **dashed line** depicts the IC model prediction; **B**, boxplot of proportional length of the proximal, intermediate, and distal phalanges, with colors matching the taxonomic groups in the left graph; fossil numbers: 1, ARA-VP-6/500; 2, Dolni Vestonice 16; 3, *Homo naledi* Berger *et al.*, 2015; 4, IGF 11778; 5, IPS 18800; 6, Kebara 2; 7, Ohalo II; 8, Qafzeh 9; 9, StW 573.

TABLE 2. — Results of the RMA regressions used to test the inhibitory cascade model of distal and proximal phalanx relative lengths. Model predictions are in the first row while subsequent rows provide regression results for specific samples. Hominoidea Gray, 1925 includes all apes except humans, and “Great Apes” excludes *Hylobates* Illiger, 1811 from Hominoidea.

| Group        | Slope | Slope (95%)  | Intercept | Intercept (95%) | R <sup>2</sup> | P (2-tailed) |
|--------------|-------|--------------|-----------|-----------------|----------------|--------------|
| IC model     | -1.00 | —            | 0.67      | —               | —              | —            |
| Homo sapiens | -1.03 | -1.29, -0.82 | 0.72      | 0.62, 0.85      | 0.46           | 3.46E-07     |
| Hominoidea   | -0.75 | -0.98, -0.57 | 0.55      | 0.46, 0.67      | 0.43           | 3.62E-05     |
| Great Apes   | -0.69 | -0.88, -0.54 | 0.52      | 0.45, 0.62      | 0.65           | 2.61E-07     |

This disparity may be due to the taxonomic heterogeneity of the “ape” sample and limited sample sizes. The fossil assemblage, including Miocene apes and Plio-Pleistocene hominins, bridges the gap between the extant ape and human distributions. Notably, all specimens attributed to genus *Homo* including *H. naledi* fall in or around the extant human range, with the exception Dolni Vestonice 16 from Late Pleistocene, who falls nearest StW 573 (*Australopithecus*) below the extant human distribution. In contrast, both the Middle Miocene ape *Hispanopithecus* Villalta & Crusafont Pairó, 1944 (IPS 18800) and Early Pliocene *Ar. ramidus* White, Suwa & Asfaw, 1995 (ARA-VP-6/500) fall within the extant ape range. The Late Miocene *Oreopithecus* Gervais, 1872 (IGF 11778) is intermediate between the ape and human extremes. StW 573 and Dolni Vestonice 16 fit the ape RMA model nearly perfectly, coincidentally almost identical to IC model predictions.

The IC model also predicts that as the second segment in the series, the intermediate phalanx should be about two-thirds of the entire series length (Fig. 2B). Nearly all individuals in the sample fall just shy of this prediction. Human intermediate phalanges are entirely below the model prediction (mean = 0.29, SD = 0.008), while the ape range (mean = 0.32, SD = 0.016) more closely approximates the prediction. The human range encompasses most of the smaller half of the ape distribution. The limited fossil sample shows little taxonomic patterning. As with the proximal and distal phalanges, both StW 573 and Dolni Vestonice deviate from other hominin fossils in closely matching the model predictions; these individuals’ relatively longer intermediate phalanges explain why they fall away from the human cluster in the graph of distal versus proximal phalanx length. *Hispanopithecus* is close to the ape average and just outside the human range. All other fossils fall within the human range overlapping the lower half of the ape distribution.



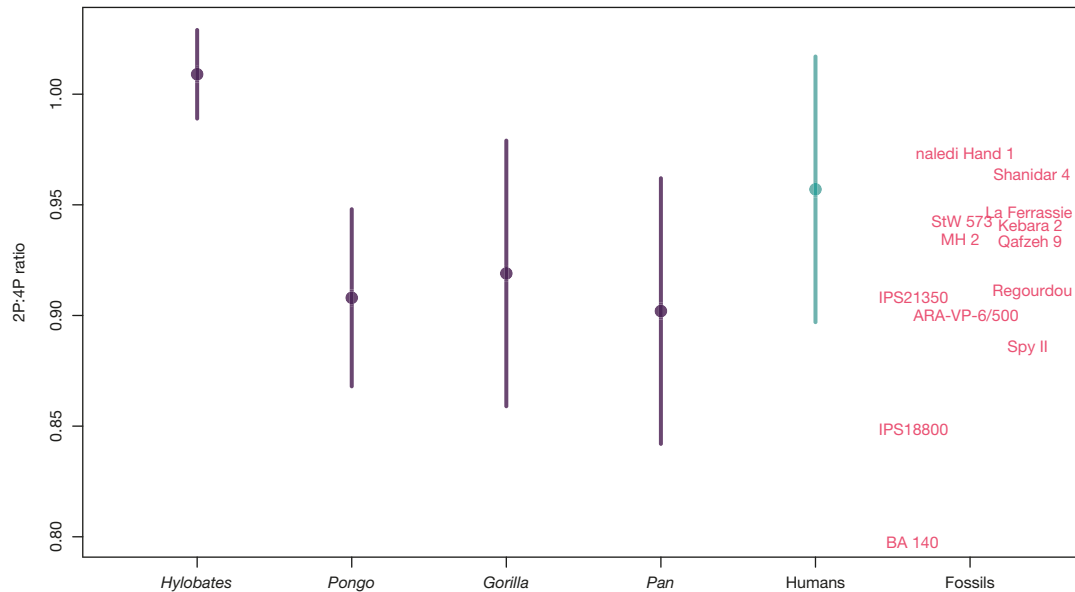


FIG. 3. — 2P:4P ratios for extant and extinct hominoids. **Solid circles and lines** represent species mean  $\pm$  2 standard deviations, respectively, as reported in Nelson *et al.* (2011). Fossil specimens are organized with Miocene apes on the left, Plio-Pleistocene hominins in the center, and Neandertals/early modern humans on the right.

The proportional length of each the proximal and intermediate phalanges individually does not show any clear taxonomic patterning. Proportional length of the distal phalanx, however, does seem to show a graded pattern between “ape” and human, whose distributions are more differentiated than for the proximal and intermediate phalanges. Fossils fit or bridge this ape-human trend with *Australopithecus* and older taxa falling in the upper half of the ape range and all *Homo* specimens being higher, falling within or beyond the modern human range.

In addition to examining intrinsic digit proportions, we also examined the ratio of the second and fourth proximal phalanges (2P:4P), which is also established during embryonic development. Figure 3 depicts the summary statistics for extant genera as reported by Nelson and colleagues (2011: table 1). The fossils as a whole span from beyond the low end of the great ape range to the lower half of the human range. The Miocene apes *Hispanopithecus* (IPS 18800) and *Oreopithecus* (BA 140) have lower ratios than almost all extant taxa reflecting an especially long PP4 relative to PP2. The remaining extinct taxa, from the Miocene *Pierolapithecus* (IPS 21350) to later Pleistocene humans and Neandertals, fall within the overlap between the upper end of extant apes and the lower half of the modern human range. While this intermediacy makes it difficult to infer social behavior for fossil specimens, none of them approaches the pair-bonded *Hylobates* Illiger, 1811 distribution. *Homo naledi* Hand 1 has the highest 2P:4P ratio of the entire fossil sample, joined only by the Shanidar 4 Neandertal above the extant human average.

## DISCUSSION

A developmental perspective elucidates the proximate mechanisms that led to major evolutionary changes in the hominin lineage. Advances in developmental biology over the past few

decades have shown that many species-specific morphologies that distinguish adults are established in the earliest stages of development. Adult remains can therefore provide evidence of ontogenetic patterns, with the caveat that relatively complete and reliably associated elements must be preserved for serially repeating structures. Although such conditions are rarely met in the fossil record, a fortuitous handful of specimens from the Middle Miocene to the present day helps establish the ancestral conditions out of which hominin finger proportions may have evolved.

Phalanx lengths support the hypothesis that intrinsic finger proportions reflect a general developmental mechanism, i.e., reaction-diffusion pattern formation, which can be mathematically described by the inhibitory cascade model. The present samples do not fit the model perfectly, however, perhaps best illustrated by the fact that most individuals’ intermediate phalanx is slightly shorter than the predicted one-third of the total series length. One explanation for this modest discrepancy is that adult morphology is the result of myriad developmental events (Hallgrímsson *et al.* 2009), such that it is possible that the model predictions hold perfectly in the earliest stages of development, but this pattern becomes obscured by subsequent growth processes. Proximal-distal phalanx curvature is probably not a confounding factor since the highly curved phalanges of *Pongo* Lacépède, 1799 and *Hylobates* (e.g. Wennemann *et al.* 2022) differ in intermediate phalanx proportional length, with *Pongo* encompassing the lower half and *Hylobates* bracketing the upper half of the entire non-human ape range in Figure 2 (not shown). Similarly, the proportionally shortest intermediate phalanges among the fossil sample are the highly curved phalanx *H. naledi* (Kivell *et al.* 2015) and straight phalanx of the Kebara 2 Neandertal.

An evolutionary interpretation of the IC model results based on the sample available in the current study is that the ancestral developmental pattern seen in living apes and *Hispanopithecus*

also characterized the earliest hominins (*Ardipithecus* White, Suwa & Asfaw, 1995 and *Australopithecus*). A relatively simple developmental shift occurred at some point in the evolution of genus *Homo*; given the uncertain phylogenetic position of *H. naledi* (Dembo *et al.* 2016), it is unclear whether this developmental pattern was established at the origin of the genus or later on. The somewhat “intermediate” positioning of *Oreopithecus* (IGF 11778; Fig. 2) could be interpreted as convergent evolution with the *Homo* condition, similar to what has been suggested for other hand proportions in this unusual Late Miocene ape (Moyà-Solà *et al.* 1999). The IC model therefore likely describes a developmental mechanism underlying the evolution of precision grip.

The 2P:4P results are based on data presented by Nelson and colleagues (2011), with the addition of *Oreopithecus*, South African *Australopithecus*, and *H. naledi*. These additional samples are largely consistent with Nelson and colleagues’ (2011) interpretation that prenatal androgen exposure decreased over time from hominin origins to the present day. Intriguingly, the *H. naledi* Hand 1 skeleton yields the highest ratio in the hominin fossil record. Alongside low levels of skeletal and dental size variation (Garvin *et al.* 2017), this uniquely high 2P:4P ratio could reflect lower levels of intraspecific aggression compared with the living great apes, and possibly even compared with other Middle Pleistocene hominins.

The high digit ratio of *H. naledi* is interesting in the context of the Human Self-Domestication hypothesis (Hare 2017; Sánchez-Villagra & van Schaik 2019; Benítez-Burraco *et al.* 2020). Proponents of this hypothesis posit that many morphological differences between recent *H. sapiens* and Middle-Late Pleistocene hominins mirror the “domestication syndrome” in other animals: anatomical byproducts of selection for reduced aggression (Trut *et al.* 2009; Hare *et al.* 2012; Wilkins *et al.* 2014). Along with higher digit ratios, smaller faces and brain sizes have also been argued to be part of the domestication syndrome (Cieri *et al.* 2014; Hare 2017). Craniodental characteristics support a close evolutionary relationship between *H. naledi* and later Middle Pleistocene *Homo* (Dembo *et al.* 2016; Schroeder *et al.* 2017). In this light, the small brain size and low degree of encephalization of *H. naledi* compared with other *Homo* taxa (Grabowski *et al.* 2016; Garvin *et al.* 2017; Hawks *et al.* 2017) could be interpreted as evidence for “self-domestication” in *H. naledi*. Along these lines, cranial lesions caused by blunt force trauma show a high frequency in fossil *Homo* crania, and have been interpreted by some researchers as evidence for pervasive interpersonal violence from the oldest *H. erectus* to the present day (Saladié *et al.* 2012; Estabrook & Frayer 2013; Sala *et al.* 2015; Margvelashvili *et al.* 2022). Such lesions have not been documented in any of the numerous *H. naledi* cranial remains representing several individuals, although the cranial remains of *H. naledi* include a “taphonomic divot” on the supraorbital torus of the DH3 cranium and another possible pathology of unknown etiology on another frontal fragment (Laird *et al.* 2017: 107). Thus, the low frequency or potential absence of healed cranial wounds in the Rising Star hominins could indicate lower levels of violence and aggression compared with other Pleistocene *Homo*.

Other evidence of more affiliative and less aggressive behaviors in *H. naledi* may come from the unusual taphonomic context of the remains in Rising Star Cave itself (Berger *et al.* 2015; Dirks *et al.* 2017). Of over 2000 fragmentary elements recovered from the Dinaledi Chamber, nearly all are *H. naledi* that come from around 20 individuals (Dirks *et al.* 2015; Bolter *et al.* 2018). At least one immature and one adult individual are known from the Lesedi Chamber of the cave system (Hawks *et al.* 2017), and isolated fragments of an infant cranium were recovered from a small fissure of another corridor (Brophy *et al.* 2021). No other South African cave site to date has yielded so many hominins and so little other fauna. This, and other evidence, has led some to argue that *H. naledi* engaged in human-like (i.e., cultural) mortuary practices (Dirks *et al.* 2015; Randolph-Quinney 2015; Berger *et al.* 2023), although others are highly skeptical (Val 2016; Martín-Torres *et al.* 2023). Regardless of how and why partial skeletons of several *H. naledi* individuals ended up deep within the dark and remote reaches of Rising Star Cave system, the abundance of remains could reasonably reflect group-affiliative behaviors in *H. naledi*. This interpretation of the taphonomic evidence is complemented by the behavioral implications of the high 2P:4P ratio of *H. naledi* Hand 1 skeleton. Future research on the unusual preservation and context of the *H. naledi* remains, in addition to the possibility of more associated hand skeletons will provide further insights into potential behavioral implications of its distinct digit ratios.

## CONCLUSION

The nearly complete adult hand skeleton of *H. naledi* provides insights into the developmental biology and social behavior of this extinct species. Proportional relationships among associated phalanges suggest, first, that a shift in embryonic development may have facilitated the evolution of precision grip in early hominins. Based on our fossil sample, this developmental shift may have occurred after the divergence of *Homo* from australopiths, but this does not necessarily preclude the dexterous hand use, and particularly tool use, in earlier hominins. Second, the ratio of second and fourth manual phalanges could reflect reduced aggressive and increased prosocial behaviors in *H. naledi* compared with other fossil *Homo*. These interpretations are based on a single *H. naledi* hand skeleton, and could potentially be supported or refuted by the discovery of new associations among *H. naledi* phalanges, or by development of randomization-based approaches to analyze commingled remains (cf. Rolian & Gordon 2013).

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