Digit ratios predict polygyny in early apes, *Ardipithecus*, Neanderthals and early modern humans but not in *Australopithecus*

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Social behaviour of fossil hominoid species is notoriously difficult to predict owing to difficulties in estimating body size dimorphism from fragmentary remains and, in hominins, low canine size dimorphism. Recent studies have shown that the second-to-fourth digit ratio (2D : 4D), a putative biomarker for prenatal androgen effects (PAEs), covaries with intra-sexual competition and social systems across haplorhines; non-pair-bonded polygynous taxa have significantly lower 2D : 4D ratios (high PAE) than pair-bonded monogamous species. Here, we use proximal phalanx ratios of extant and fossil specimens to reconstruct the social systems of extinct hominoids. *Pierolapithecus catalaunicus*, *Hispanopithecus laietanus* and *Ardipithecus ramidus* have ratios consistent with polygynous extant species, whereas the ratio of *Australopithecus afarensis* is consistent with monogamous extant species. The early anatomically modern human Qafzeh 9 and Neanderthals have lower digit ratios than most contemporary human populations, indicating increased androgenization and possibly higher incidence of polygyny. Although speculative owing to small sample sizes, these results suggest that digit ratios represent a supplementary approach for elucidating the social systems of fossil hominins.

Keywords: pair-bonded; polygyny; prenatal androgens; hominin; social system;
second-to-fourth digit length ratio

1. INTRODUCTION

Predicting social systems of extinct primates and hominins is crucial for understanding human palaeobiology. Sexual dimorphism in canine and skeletal features is the main method used to predict social behaviour in extinct primates [1,2]. In species where males compete strongly for females, reproductive skew manifests as sexual dimorphism in canine and body size; where intra-sexual competition is reduced, such as with social monogamy, dimorphism in these characters is reduced. Although this model provides a rule of thumb for most extant primates [3], it is more problematic to apply to extinct primates, including hominins. Firstly, canine dimorphism is reduced in hominids compared with other primates [4,5]. Secondly, estimates of skeletal size dimorphism from small and often spatially and temporally dispersed fragmentary fossils are prone to error [6]. Furthermore, evidence suggests that sexual dimorphism in extinct primates may exceed levels in extant species [7]; this

indicates either a broader range of social systems in extinct species or potential systematic biases in estimating dimorphism.

The controversy resulting from inferences based on dimorphism in postcranial remains is exemplified by predictions of social systems for *Australopithecus afarensis*, which range from monogamous [4,8] to highly promiscuous [2,6]. The debate has been reviewed in detail in a series of publications [4,6,9–11] and hinges on a number of methodological issues that could significantly impact the estimated levels of dimorphism (reviewed in [6]).

The story is not much clearer for other early hominins. Most recently, evidence has been put forward for low canine and body dimorphism in *Ardipithecus ramidus*, leading to the proposal that human-like pair-bonded (PB) characteristics evolved early and, therefore, could be a cardinal trait of the hominin lineage [12]. However, based on facial dimorphism and maturation rates, a gorilla-like harem social system has been proposed for the later *Paranthropus robustus* [2], which appears to have differed from that of *Australopithecus africanus* [2]. Marked levels of sexual dimorphism may also have characterized some populations of *Homo erectus* [13] and *Homo heidelbergensis* [14]; dimorphism only approaches

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Table 1. Comparative sample of 2PP : 4PP ratios. PB, pair-bonded; NPB, non-pair-bonded; INT, between PB and NPB. For provenance of museum samples, see electronic supplementary material.

extant species	social system	male			female			Cohen's <i>d</i>	species		
		<i>n</i>	2PP : 4PP	s.d.	<i>n</i>	2PP : 4PP	s.d.		<i>n</i>	2PP : 4PP	s.d.
<i>Homo sapiens</i>	INT/PB	177	0.956	0.02	143	0.957	0.02	−0.06	320	0.957	0.03
<i>Pan troglodytes</i>	NPB	38	0.901	0.03	62	0.903	0.03	−0.06	100	0.902	0.03
<i>Gorilla gorilla</i>	NPB	62	0.918	0.03	50	0.920	0.02	−0.08	112	0.919	0.03
<i>Pongo pygmaeus</i>	NPB	15	0.901	0.02	31	0.911	0.02	−0.49	46	0.908	0.02
<i>Hylobates lar</i>	PB	26	1.009	0.01	20	1.009	0.01	−0.02	46	1.009	0.01

human-like levels in *Homo floresiensis* [15] and *Homo neanderthalensis* [16]. Inferring social systems in stem hominins and hominoids is complicated by the fragmentary nature of Middle Miocene fossils [17].

Given the difficulties associated with conventional methods of estimating social systems in fossils, employing alternative markers of sexual selection should be a key focus of research. The second-to-fourth digit ratio (2D : 4D) is a proposed marker for prenatal sex hormones [18,19], with lower ratios associated with higher prenatal androgen effects (PAEs). In humans, 2D : 4D is sexually dimorphic such that, within a population, digit ratios are generally lower in males than in females [18,19]. These relationships are supported by evidence of lower 2D : 4D ratios in humans with disorders linked to high PAE, such as autistic spectrum conditions [20], congenital adrenal hyperplasia (reviewed in [21]), polycystic ovary syndrome ([22], but see [23]) and higher 2D : 4D ratios in genetic males with androgen insensitivity syndrome [24].

In humans, low 2D : 4D is associated with dominance-related behaviours in both sexes (reviewed in [25]). Population differences in 2D : 4D have been linked to marriage systems, with polygynous populations expressing lower 2D : 4D ratios compared with more monogamous groups [19]. In non-human primates, 2D : 4D is higher in PB monogamous species than in promiscuous and more competitive species [26]. Lower 2D : 4D ratios in chimpanzees (*Pan troglodytes*) compared with bonobos (*Pan paniscus*) are consistent with differences in their social behaviour [27]. It has been proposed that low PAE may be important in potentiating behaviours linked to pair-bonding such as paternal care and provisioning in haplorrhines [26].

As the lengths of the underlying skeletal components of the digits (phalanges) are related to overlying soft-tissue finger length [18], the potential exists to use digit bone ratios to investigate social behaviour in extinct primate species. The proximal phalanges (PP) are the most likely of the phalangeal bones to fossilize (because they are the largest) and can be assigned to the correct digit with confidence [28,29]. Here, we investigate relationships between species-level manual PP ratios and social systems in extant hominoids, and then use fossil bone ratios to predict the social systems of extinct hominoids.

2. MATERIAL AND METHODS

(a) Extant sample

Samples of extant ape species (contemporary humans and non-human hominoids) were taken from museum collections

(scanned bones) and data on contemporary humans were supplemented with archaeological material (table 1). All specimens were of known sex, in good condition with no visible skeletal pathologies. Metacarpals, proximal and intermediate phalanges were present in most specimens (see electronic supplementary material).

Bones from museum specimens were assigned their anatomical positions by C.R. as follows. If available, the articulated side of the skeleton was used to assign identity on the disarticulated side. Alternatively, the first, third and fifth proximal phalanges were identified based on size differences [29]. The 2PP and 4PP were then assigned in relation to the other three using the following criteria: (i) increased robusticity and presence of a bony flange on the proximal radial aspect of 2PP in humans and some African apes [29,30]; (ii) asymmetric head of the second compared with the fourth metacarpal, causing a bony lip on the ventral–radial aspect of the proximal end of 2PP for *Pongo*, African apes and humans [28,29]; and (iii) larger surface area of the second compared with fourth metacarpophalangeal joints (p. 218 in [29]).

For scanning, bones were placed ventrally in anatomical position on a flatbed scanner (Microtek i320 ScanMaker) and imaged in TIF format at 300 dpi [31]. Maximum length of the 2PP and 4PP was obtained (E.N.) by magnifying the image, placing the digital ruler on the most distal point on the PP and then measuring to the most proximal point on the PP in pixels using TPSDIG2 [32]. Each bone was measured twice and the mean values of bones provided the length value. Assignment of the scanned phalanges was also checked (as far as was possible on a two-dimensional image) by E.N., using the same morphological criteria as above.

Length measurements for adult human phalanges were also obtained from archaeological specimens (electronic supplementary material, table S1). Bones exhibiting pathologies were excluded from the analysis, as were those that could not be confidently assigned using the morphological criteria cited above. Phalanges were also rejected if the total number of hand bones (for the individual) was low, as this is known to lead to uncertainty in phalangeal assignment [33]. Sexing and ageing the burials were undertaken using standard osteological techniques (i.e. pelvic morphology and epiphyseal fusion). Additionally, if material could not be sexed, it was omitted from the dataset. Maximum length of hand bones was obtained using callipers (Powerfix; resolution 0.01 mm) by taking the straight distance from the middle point of the surface of the base to the topmost point of the head (L. A. Cashmore 2009, unpublished PhD thesis). Intra-observer error for these data was shown to be within acceptable limits (L. A. Cashmore 2009, unpublished PhD thesis).

Based on the anatomical features used to assign the proximal phalanges (outlined above), in the human sample (museum and archaeological collections combined) 2PP was shorter than 4PP in 97.7 per cent of males and in 97.9 per cent of females. This pattern (2PP < 4PP) is consistent with phalangeal formulae in other great apes [29].

(b) Extinct sample (fossil data)

Digital scans were taken of one anatomically modern human (AMH) and four *H. neanderthalensis* fossils archived at Washington University in Saint Louis (permission to use the data was granted by Erik Trinkaus): AMH: Qafzeh 9 (right hand); Neanderthals: Kebara 2 (left hand), Shanidar 4 (right hand), La Ferrassie I (left hand), Le Regourdou (both hands). For the Le Regourdou fossils, the mean lengths of 2PP and 4PP from both hands were used to obtain a single value for the individual. Fossil phalanges were assigned, scanned (C.R.) and measured (E.N.) using the same methods as for the extant human sample. All scanned fossils were measured 10 times (E.N.) and remeasured three months later to assess intra-observer error (see electronic supplementary material). Correct assignment of the scanned phalanges was also checked, as far as was possible on a two-dimensional image, by E.N. using the same morphological criteria above.

Data were also taken from the literature: *Au. afarensis* A.L. 333 ($n = 1$) [34,35]; *Ar. ramidus* ARA-VP6/500 ($n = 1$) [36]; *Hispanopithecus laietanus* IPS18800 ($n = 1$) [37]; *Pierolapithecus catalaunicus* IPS21350 ($n = 1$) [38]; *H. neanderthalensis* Spy II [39]. Note that among these specimens only the *Ardipithecus* hand fossils were found associated *in situ*. For the remaining fossils (except Spy II), we used the phalangeal identification proposed in their respective descriptions. For the Spy Neanderthal, measurements were taken from a published photographic image [39] (see supplementary electronic material).

We rejected those fossils for which length looked like it had been altered significantly owing to breakage or other post-depositional effects (e.g. the left 4PP in Qafzeh 9), and those in which the morphology of the bone looked to be abnormal (e.g. the proximal end of the right 4PP in Kebara 2). However, we retained fossils that may have been broken but whose length appeared minimally affected (e.g. 2PP; ARA-VP-6/500-043 of *Ardipithecus*, stated as having a length measurement of 43 mm $\pm$ 0.3) [36].

We tested for measurement error within the scanned bone samples and looked for distortion in 2PP : 4PP that may have been caused by the imaging process (see electronic supplementary material). Measurement error within samples was found to be minimal, and comparisons of ratios derived from scanned measurements and direct measurements (of the same set of bones) did not significantly differ ($t = -1.91$, $p = 0.07$, d.f. = 24). For results of measurement error, see electronic supplementary material.

(c) Ratio calculations

We calculated 2PP : 4PP for each individual (extant and extinct) by dividing the length of 2PP by the length of 4PP. In cases in which bones were available for the two hands, mean values of left and right 2PP : 4PP were used to prevent pseudo-replication. A mean value 2PP : 4PP and standard deviation for each extant species were calculated (table 1). We tested for skew in the 2PP : 4PP data using the Kolmogorov–Smirnov tests; 2PP : 4PP was normally

distributed over the whole sample (species means: 0.28, $p = 0.2$, d.f. = 5; individuals: 0.03, $p = 0.19$, d.f. = 535). However, when individuals within species were analysed separately, *Gorilla* data were skewed (0.11, $p < 0.01$, d.f. = 112), so 2PP : 4PP data for all the individuals in all the samples were log-transformed.

(d) Social system

The social system of extant species was defined by classifying each taxon as either PB monogamy, which included species in which males usually mate with only one female, or non-pair-bonded (NPB) polygyny, which included species in which males usually mate with more than one female [3]. As contemporary humans do not fit strictly into a PB category (i.e. pair-bonds within a multi-male, multi-female social system) [40], separate analyses were performed with contemporary humans classified as PB and as intermediate (i.e. something other than PB or NPB).

(e) Other variables

We used data on extant ape 2D : 4D ratios and associations with social systems as a comparative sample [26,41]. As substrate use is associated with variation in hand morphology [42], we included categories of substrate in the analysis [1] as a means of controlling for possible functional effects on digit ratios. We also included measures of species body weights [43] to ensure 2D : 4D was not being unduly influenced by size. Body dimorphism estimates were calculated by dividing male body weight by female body weight. Kolmogorov–Smirnov tests indicated skew in body weight and body dimorphism data ($p < 0.001$); skewed data were log-transformed.

(f) Analysis

We used *t*-tests to estimate differences between male and female species mean 2PP : 4PP. Cohen's *d* was used to assess the size effect between male and female species mean ratios within species. A negative *d* value indicates lower male 2PP : 4PP compared with females. Linear regression was used to compare species mean 2PP : 4PP with species mean 2D : 4D. This regression equation also allowed us to estimate 2PP : 4PP from 2D : 4D for a Zulu population [44].

To control for phylogenetic effects, associations between extant species digit ratios (2PP : 4PP and 2D : 4D) and social systems were analysed using phylogenetic generalized least squares (PGLS) analysis with an optimized lambda (using the Ape package in R) [26]. In all PGLS analyses with social systems, we checked to see whether digit ratios correlated with body weight or substrate; these variables were removed from the model if not significant.

For comparisons between extant and extinct taxa, we employed a Monte Carlo resampling method (see electronic supplementary material). The routine derives a distribution of population 2PP : 4PP means in extant species based on the means of 10 000 subsamples of *n* individuals (where *n* = number of individuals in the fossil sample) drawn randomly, with replacement, from each extant taxon in order to derive 5 and 95 per cent confidence levels for each species. We then calculated the probability of sampling an individual in each extant species with a 2PP : 4PP ratio equal to the 2PP : 4PP of the individual fossil. For the Neanderthal sample, the results were based on the percentage probability of sampling five individuals within the

Figure 1. (a) Histogram of the frequencies of 2PP:4PP in the modern human sample (white arrow; Qafzeh 9) with Neanderthal fossils superimposed as black arrows: 1, Spy; 2, Le Regourdou; 3, Kebara; 4, La Ferrassie; 5, Shanidar. (b) Contemporary humans (10 000 resampled means) with Neanderthal mean 2PP:4PP (black arrow). Monte Carlo analysis gives a 0.19 per cent probability of drawing a sample of five modern humans with a mean 2PP:4PP ratio as low as the observed Neanderthal mean.

extant samples with the same 2PP:4PP ratios as the five Neanderthal fossils.

Discriminant function analysis (DFA) was used to predict the social systems of extinct taxa based upon extant hominoid 2PP:4PP and their known social systems. As sample sizes for fossil species were very small (all but one represented by a single individual), we performed a DFA on the 2PP:4PP ratios of individuals (rather than mean for species values). As contemporary humans show some flexibility in social systems (i.e. broadly PB [40]), we ran the DFA three times; once with humans assigned as PB, again with them assigned as intermediate and, lastly, they were omitted from the analysis (see electronic supplementary material). We also performed a step-wise DFA with both species mean 2PP:4PP and species mean body size dimorphism (logged values) as dependent variables, and social system as the grouping variable.

3. RESULTS

(a) Sex differences in 2PP:4PP in extant species

Consistent with the proposed relationships between digit ratios and PAE, within species males had lower 2PP:4PP ratios than females, reflected in negative Cohen's *d* based on mean ratios (table 1), although sex differences in 2PP:4PP were not significant ($p > 0.1$) when individuals within species were compared (see electronic supplementary material).

(b) Relationships between 2PP:4PP and 2D:4D, and correlations with social systems

We regressed hominoid species mean 2PP:4PP on to species mean 2D:4D ratios [26,41] and found the ratios to be highly correlated, despite 2PP:4PP being substantially lower than 2D:4D (with humans: $R^2 =$

0.967, $F_{1,4} = 86.79$, $p < 0.01$; without humans: $R^2 = 0.961$, $F_{1,3} = 49.23$, $p = 0.02$).

We classified extant hominoid species as PB (*Hylobates*) or NPB (*Pan*, *Pongo*, *Gorilla*). 2PP:4PP was significantly lower in NPB than in PB species both when humans were classified as PB (PGLS: $F_{1,3} = 11.55$, $p = 0.04$, $\lambda = 1$) and when they were removed from the analysis (PGLS: $F_{1,2} = 49.78$, $p = 0.02$, $\lambda = 0$). These results are consistent with 2D:4D for the same species (with humans, PGLS: $F_{1,3} = 9.48$, $p = 0.05$, $\lambda = 1$; without humans, PGLS: $F_{1,5} = 20.85$, $p < 0.01$, $\lambda = 0$) [26]. Correlations between digit ratios and body weight and substrate were not significant in PGLS analyses ($p > 0.1$).

(c) Comparisons in 2PP:4PP between extinct and extant hominids

Contemporary human mean 2PP:4PP was 0.957, s.d. = 0.02 ($n = 320$; CL = 0.92–0.95), while Neanderthal 2PP:4PP mean was 0.928, s.d. = 0.03 (CL = 0.89–0.96). The Monte Carlo resampling analysis shows that only 19 out of 10 000 resampled means in *Homo sapiens* are as low or lower than the Neanderthal mean (figure 1b). In other words, there is an approximately 0.2 per cent probability of drawing a sample of five modern humans with a mean 2PP:4PP ratio as low as the observed Neanderthal mean (table 2). The early AMH Qafzeh 9 is within range of contemporary human 2PP:4PP ratios (table 2), but falls at the lower end of the range (figure 1a). The Qafzeh 9 2PP:4PP (0.935) is similar to (polygynous) Zulu 2PP:4PP (0.939), estimated by inputting 2D:4D values (0.95 ± 0.040) [44] into the hominoid regression equation.

Table 2. Percentage probabilities of sampling a 2PP : 4PP ratio from the extant species (10 000 iterations) that is as extreme as the observed fossil 2PP : 4PP ratios. Neanderthal probabilities are based upon resampling five individuals (see §2 for resampling procedures). WR, within range (i.e. between the 5 and 95% confidence levels (CL) for the extant population distribution).

extant species	<i>Homo sapiens</i>	<i>Hylobates lar</i>	<i>Pan troglodytes</i>	<i>Gorilla gorilla</i>	<i>Pongo pygmaeus</i>
2PP : 4PP (<i>n</i>)	0.957 (320)	1.009 (46)	0.909 (100)	0.919 (112)	0.908 (46)
5–95% CL	0.923–0.995	0.992–1.028	0.858–0.947	0.873–0.949	0.878–0.940
fossils (<i>n</i>)	2PP : 4PP	probability estimates			
Qafzeh (1)	0.935	WR	0%	WR	WR
Neanderthals (5)	0.928	0.19%	0%	1.59%	WR
<i>Australopithecus</i> (1)	0.979	WR	0%	0%	0.95%
<i>Ardipithecus</i> (1)	0.899	0.14%	0%	WR	WR
<i>Hispanopithecus</i> (1)	0.848	0	0%	4.31%	0%
<i>Pierolapithecus</i> (1)	0.908	0.39%	0%	WR	WR

Table 3. Discriminant function analysis: predicting the social system of fossil hominids. PB, Pair-bonded; NPB, non-pair-bonded; INT, between PB and NPB. Extant 2PP : 4PP sample = *H. sapiens*, *P. troglodytes*, *Gorilla gorilla*, *Pongo pygmaeus*, *Hylobates lar*. Substrate and body weight $p > 0.05$.

species	fossil	predicted social system		
		humans as PB	humans as intermediate	humans removed
anatomically modern human	Qafzeh	PB	INT	NPB
Neanderthal	Shanidar 4	PB	INT	PB
Neanderthal	Kebara 2	PB	INT	NPB
Neanderthal	La Ferrassie	PB	INT	NPB
Neanderthal	Le Regourdou	NPB	NPB	NPB
Neanderthal	Spy II	NPB	NPB	NPB
<i>Australopithecus</i>	A.L. 333	PB	INT	PB
<i>Ardipithecus</i>	ARA-VP	NPB	NPB	NPB
<i>Hispanopithecus</i>	IPS18800	NPB	NPB	NPB
<i>Pierolapithecus</i>	IPS21350	NPB	NPB	NPB
Wilks's $\lambda_{(d.f.)}$ (p)		0.52 _{1,622} ($p < 0.001$)	0.40 _{2,621} ($p < 0.001$)	0.32 _{1,302} ($p < 0.001$)
eigenvalue (canonical correlation)		0.93 (0.70)	1.54 (0.78)	2.15 (0.82)
% of original cases correctly classified		82	75	99

Table 2 shows the probabilities (based on 10 000 iterations) of sampling observed fossil 2PP : 4PP values from each extant species. *Australopithecus* is within range of human 2PP : 4PP, but falls outside the confidence interval of all other extant hominoids. In contrast, the Miocene apes and *Ardipithecus* have 2D : 4D ratios that fall below the 5 per cent confidence level for modern humans, but within the range of 2D : 4D ratios for African apes and *Pongo*.

(d) Predictions of social system for extinct hominids

Predicted social systems for Miocene apes and *Ardipithecus* were NPB and were stable across all DFAs (table 3 and figure 2). Predicted social systems for *Australopithecus*, the early modern human and Neanderthals with the highest 2PP : 4PP ratios (Shanidar 4, Kebara 2, Le Ferrassie I) mirror the designated social system of contemporary humans (PB or intermediate), while the Neanderthals with the lowest 2PP : 4PP ratios (Le Regourdou and Spy II) were classed as NPB in all analyses (table 3 and figure 1a).

With humans removed from the analysis, 99 per cent of original cases are classified correctly and all fossil

specimens except the Shanidar 4 Neanderthal and *Australopithecus* are classified as NPB (table 3). Comparisons between extant apes and Miocene and Pliocene hominids show *Australopithecus* to be positioned between PB monogamous gibbons and NPB apes, while *Ardipithecus*, *Pierolapithecus* and *Hispanopithecus* are all within the range of NPB great apes (figure 2).

For contemporary humans, the percentage of original cases classified as correct in DFA was 56 per cent when classed as PB and 42 per cent when classed as intermediate. Thus, contemporary human 2PP : 4PP appears to sit in between NPB apes and the PB gibbons (figure 2). In NPB extant apes, it was 98 per cent for chimpanzees, 98 per cent for gorillas, 100 per cent for orang-utans and 100 per cent for PB gibbons.

In addition, we also ran a step-wise DFA on extant species with species mean 2PP : 4PP and species mean (logged) body size dimorphism as predictors of social systems. 2PP : 4PP was retained in the final model while body size dimorphism was dropped when humans were assigned as PB (2PP : 4PP: Wilks's $\lambda = 0.17$, $p = 0.03$, d.f. = 1; body dimorphism: Wilks's $\lambda = 0.54$, $p = 0.21$, d.f. = 1) and when humans were assigned as intermediate

Figure 2. Histogram of variation in extant hominoid 2PP:4PP with Miocene and Pliocene fossils transposed. Miocene apes and *Ar. ramidus* are classified as non-pair-bonded (NPB), while *Australopithecus* is classified as having a social system that is pair-bonded (PB) monogamous or intermediate (i.e. between pair-bonded and non-pair-bonded). Frequencies of individuals within species are scaled to the same dimensions; for sample sizes, see table 1).

(2PP:4PP: Wilks's $\lambda = 0.018$, $p = 0.02$, d.f. = 2; body dimorphism: Wilks's $\lambda = 0.54$, $p = 0.54$, d.f. = 2). These results suggest that 2PP:4PP is a better predictor of the social system in extant hominoids than body size dimorphism.

4. DISCUSSION

The relationship between social system and digit ratio across extant haplorrhines suggests that 2D:4D reflects links between prenatal androgen effects (PAEs) and sexually selected social behaviours [26,27]. We have used this hypothesis to predict social systems of extinct hominids from digit ratios calculated from fossil remains. DFAs using 2PP:4PP of Middle and Late Miocene apes (*Pierolapithecus* and *Hispanopithecus*) predict they lived within promiscuous social systems, but that this pattern began to vary in Pliocene hominins. The predicted social system of *Ardipithecus* was non-pair-bonded (NPB) polygyny and differed from that of *Australopithecus*, predicted to be pair-bonded (PB) monogamy (table 3 and figure 2). During the Middle and Late Pleistocene, social systems of *Homo* sp. may have been more promiscuous than those evident in most contemporary human populations (figure 1).

Our inferred social system for *Au. afarensis* tentatively supports the claim by Lovejoy [8] and Reno et al. [4] that this species may have been monogamous (contra [6,9,11]). However, our inference for *Au. afarensis* is

potentially biased by taphonomic factors. There remains a possibility that phalangeal bones from more than one individual are included in the A.L. 333 assemblage [34], and hence in the hand reconstructed by Alba et al. [35]. Similarly, *Hispanopithecus* and *Pierolapithecus* hand remains were found disassociated, although their identity may be more secure based on additional taphonomic and morphological consideration [37,38]. *Ardipithecus ramidus* fossil hand bones were found associated *in situ*, and our analysis of the phalanges conflicts with Lovejoy's recent claim, based on canine and body dimorphism, that *Ar. ramidus* was PB [12].

The 2PP:4PP ratio of the early AMH Qafzeh 9 (approx. 90 Kyr ago) was lower than mean values for most contemporary human populations and in this respect was similar to the mean value for the Neanderthal sample (approx. 73–36 Kyr ago; figure 1). The 2PP:4PP of Qafzeh 9 is close to published digit ratios from a polygynous Zulu sample [44,45]. These similarities suggest that both *H. neanderthalensis* and early AMH may have lived within a (facultative?) polygynous social structure and may have expressed higher levels of male–male competition than most contemporary human populations. However, variance in Neanderthal digit ratios (figure 1) might indicate that these Middle and Late Pleistocene hominins, like contemporary humans, exhibited some flexibility in their social systems and mating behaviour across populations.

Pair-bonding, in a broad sense, is universal among humans [40], but it is not known when the transition

from a promiscuous mating system to a stable bonded one occurred. The persistence of marked levels of skeletal dimorphism in *Homo* until the Middle Pleistocene (e.g. [14]), combined with genetic evidence indicating that male population size (ancestral to people today) was low compared with females' until the spread of agriculture [46], implies that human-like pair-bonding was not common until late in human evolution. The fact that human 2PP:4PP ratios fall between those of PB and NPB apes (figure 2) also suggests that human pair-bonding differs from that of other socially monogamous primates (in this case gibbons). Unlike PB monogamous gibbons, humans live within a multi-male–multi-female social system [40]; the potential therefore remains for variation in levels of male–male competition. Maintaining this potential may be adaptive during range expansion across ecologically diverse environments.

Relationships between individuals' whole finger lengths relative to the lengths of the proximal phalanges are not known. However, the fact that species 2PP:4PP and 2D:4D are very closely related, and that they both significantly correlate with hominoid social systems, suggests that 2PP:4PP also reflects a species-level androgenic response. This is supported by our findings that 2PP:4PP ratios show sex differences in the expected direction (table 1) and is in line with a recent meta-analysis in humans showing similarities in sex differences between X-ray-derived 2D:4D and 2D:4D based on finger lengths taken from the skin surface [21]. Measurement methodologies do impact digit ratios, and there is accumulating evidence to show that imaging the hand using scanners or photocopiers distorts the soft tissue of the digits, which lowers digit ratios and increases sex differences [21,47]. Our data were not influenced by distortional factors because bones do not distort when imaged and the 2D:4D ratios used in our regression analysis are based on measurements taken directly from the skin surface [26,41].

Based on associations between digit bone ratios and social systems, the evidence suggests that the social systems of Neanderthals and early AMH may have been similar and characterized by a more competitive social system than is evident in most contemporary human populations. This is in line with increasing evidence showing developmental similarities between Neanderthals and early AMH [48]. A promiscuous social system is indicated for the Miocene apes *H. laietanus* and *P. catalaunicus*. Owing to problems with sampling of the data, our results are unable to resolve questions surrounding the social system of *Au. afarensis*, although evidence from *Ar. ramidus*, which is more securely assigned to an individual, suggests that the social system of this early hominin was promiscuous. Although sample sizes for fossil digits are small, this evidence suggests that, as more postcranial fossils become available, digit ratios could augment current methods of estimating social systems for fossil primates and our understanding of human social evolution.

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