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Reconstructing the ancestral phenotypes of great apes and humans (Homininae) using subspecies-level phylogenies

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Owing to their close affinity, the African great apes are of interest in the study of human evolution. Although numerous researchers have described the ancestors we share with these species with reference to extant great apes, few have done so with phylogenetic comparative methods. One obstacle to the application of these techniques is the within-species phenotypic variation found in this group. Here, we leverage this variation, modelling common ancestors using ancestral state reconstructions (ASRs) with reference to subspecies-level trait data. A subspecies-level phylogeny of the African great apes and humans was estimated from full-genome mitochondrial DNA sequences and used to implement ASRs for 14 continuous traits known to vary between great ape subspecies. Although the inclusion of within-species phenotypic variation increased the phylogenetic signal for our traits and improved the performance of our ASRs, whether this was done through the inclusion of subspecies phylogeny or through the use of existing methods made little difference. Our ASRs corroborate previous findings that the last common ancestor of humans, chimpanzees and bonobos was a chimp-like animal, but also suggest that the last common ancestor of humans, chimpanzees, bonobos and gorillas was an animal unlike any extant African great ape.

ADDITIONAL KEYWORDS: African apes – ancestral state reconstruction – apes – Bayesian – comparative biology – Homininae – human evolution – last common ancestor – phenotypic variation – phylogenetics.

INTRODUCTION

Since the time of Darwin and Huxley, the relationship between humans and apes has been a source of both controversy and information about human evolution. Molecular techniques have since clarified these phylogenetic relationships, opening up new avenues of research. In particular, phylogenetic techniques allow the reconstruction of ancestral states; for example, the nature of the last common ancestor (LCA) of humans and chimpanzees. However, these techniques are sensitive to the domains of data selected, the amount of within- and between-taxon variation and the pattern of evolution across the branches. Here, we reconstruct hominin ancestral states across several domains and explore the influence of subspecies patterning among the apes.

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THE HOMININAE

Humans, the four species of African great apes [chimpanzees (*Pan troglodytes*), bonobos (*Pan paniscus*) and the eastern and western gorillas (*Gorilla gorilla* and *Gorilla beringei*)] and their extinct relatives compose a monophyletic clade usually referred to as the subfamily Homininae. Many studies have compared these species in order to make inferences about the evolutionary history of humans, with a considerable effort being dedicated to describing the last common ancestor of chimpanzees, bonobos and humans ($LCA_{H\text{-}P}$). Typically, this has involved referential modelling, i.e. treating an extant ape as analogous to the $LCA_{H\text{-}P}$ for at least some traits of interest. Chimpanzees tend to be the preferred candidate (Pilbeam & Lieberman, 2017), but bonobos have also been put forward (Parish *et al.*, 2006), and others have argued that the fossil species, such as *Ardipithecus ramidus*, point to a more generalized ape, unlike any modern species (Lovejoy, 2009; Lovejoy *et al.*, 2009a,b; White *et al.*, 2009, 2015). Some studies used a more formal phylogenetic method,

but did not use ancestral state reconstructions (ASRs) (Wrangham, 1987; Foley & Lee, 1989).

ASRs are a class of phylogenetic comparative methods that use the trait data and phylogeny for a set for taxa to estimate the state of a trait in the LCA of those taxa. ASRs are routinely applied to published phylogenies to test macroevolutionary hypotheses (for recent examples, see Limeri & Morehouse, 2016; Pereira *et al.*, 2017; Audino *et al.*, 2019; De Meester *et al.*, 2019), but only a handful of studies have applied these to the Homininae (Duda & Zrzavý, 2013; Herlyn, 2016; Schroeder & von Cramon-Taubadel, 2017). For example, Herlyn (2016) used maximum parsimony to infer ancestral states for the primates, including the Homininae, based on published species-level trait data whereas Duda & Zrzavý (2013)undertook a species-level reconstruction of 65 discrete character traits for all extant apes, using both maximum likelihood and maximum parsimony techniques.

One obstacle to the use of ASRs with the Homininae is the considerable amount of within-species phenotypic variation. For example, between populations chimpanzees are known to vary in mean body size for both male and female individuals (Smith & Jungers, 1997; Grabowski *et al.*, 2018), group size (Furuichi, 2009) and tool use (McGrew, 2010a). Phenotypic variation is particularly well documented for cultural behaviour in the Homininae, with different research sites reporting different suites of putatively cultural tools and behaviours in chimpanzees (Whiten *et al.*, 1999; Sanz & Morgan, 2007; Langergraber *et al.*, 2011), bonobos (Hohmann & Fruth, 2003) and, most recently, gorillas (Robbins *et al.*, 2016). If we were simply to take the species mean of these traits, we would: (1) sacrifice information about the variation in a population; and (2) risk attributing to a species a trait value that is not represented in any living population.

However, there are ways in which these challenges can be overcome. Firstly, ASR methods now exist that can incorporate phenotypic variation into their analysis, allowing researchers to assign multiple trait values to a single tip (Pagel *et al.*, 2004; Felsenstein, 2008; Bruggeman *et al.*, 2009; Goolsby *et al.*, 2017). Secondly, much of the phenotypic variation reported among the Homininae is found between the genetically and geographically distinct subspecies of both gorillas and chimpanzees. Therefore, it is plausible that the problem of phenotypic variation can be overcome by: (1) using ASR techniques that explicitly account for it; and (2) treating subspecies rather than species as the operational taxonomic unit. In fact, a few such studies already exist (McGrew, 2010b; Schroeder & von Cramon-Taubadel, 2017). We would expect the inclusion of subspecies to improve the performance of most ASRs, because an increase in taxon sampling is known to reduce the uncertainty of ancestral state estimates (Alisbury & Kim, 2001).Thus, we propose that the application of phylogenetic comparative methods to the Homininae might be improved by the inclusion of subspecies-level trait data and a subspecies phylogeny.

A topology for Homininae subspecies

Although once a topic of debate, the topology of the Homininae is now well understood (Goodman, 1963; Sarich & Wilson, 1967; Wilson & Sarich, 1969; Sibley & Ahlquist, 1987; Lebedev *et al.*, 2000; Stone *et al.*, 2002; Salem *et al.*, 2003; Becquet *et al.*, 2007; Thalmann *et al.*, 2007; Caswell *et al.*, 2008; Gonder *et al.*, 2011). In particular, molecular studies have untangled the relationships among the four purported subspecies of chimpanzees [western (*Pan troglodytes verus*), central (*Pan troglodytes troglodytes*), eastern (*Pan troglodytes schweinfurthii*) and the Nigeria–Cameroon chimpanzee (*Pan troglodytes ellioti*) (Goldberg & Ruvolo, 1997; Gonder *et al.*, 2006, 2011; Oates *et al.*, 2009; Hey, 2010; Wegmann & Excoffier, 2010; Bjork *et al.*, 2011; Prado-Martinez *et al.*, 2013)] and the four subspecies of gorilla [the western lowland and cross-river varieties (*Gorilla gorilla gorilla* and *Gorilla gorilla diehli*) and the eastern lowland and mountain varieties (*Gorilla beringei graueri* and *Gorilla beringei beringei*) (Anthony *et al.*, 2007; Prado-Martinez *et al.*, 2013; Das *et al.*, 2014)]. Although estimates of the split time for the Homininae phylogeny are still being debated (Hobolth *et al.*, 2011; Prüfer *et al.*, 2012; Langergraber *et al.*, 2012; Scally & Durbin, 2012; Moorjani *et al.*, 2016a, b; Besenbacher *et al.*, 2019), we now have a well-resolved subspecies-level topology with which to implement phylogenetic comparative methods (Fig. 1).

In this study, we use subspecies-level trait data to implement an ASR of the Homininae. We do this with a view to: (1) determining whether the inclusion of subspecies helps to account for within-species phenotypic variation; and (2) describing the traits of the Last Common Ancestor of humans, chipmanzees and bonobos ($LCA_{H\text{-}P}$) and the Last Common Ancestor of gorillas, humans, chimpanzees and bonobos ($LCA_{G\text{-}HP}$), using several continuous traits relating to morphology, life history, sociality, behaviour and ranging.

MATERIAL AND METHODS

Collation of trait data

Subspecies-level trait data were used to reconstruct the ancestral trait values of the Homininae LCAs. Data were collated for 14 different continuous traits from 22 different studies published between 1999 and

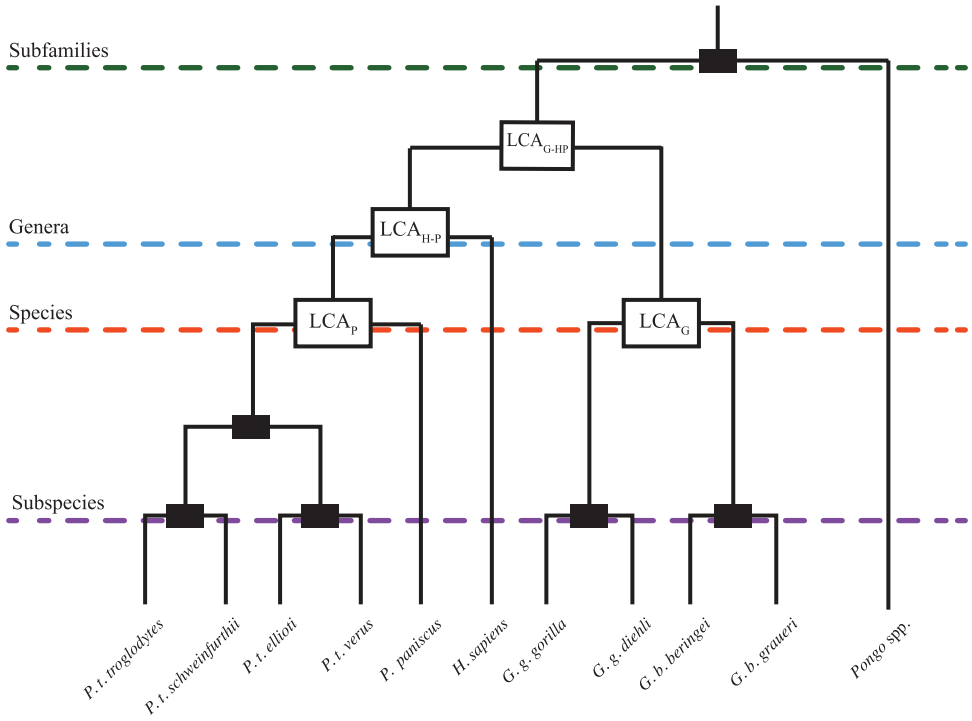

Figure 1. A subspecies-level topology of the Homininae with an orangutan outgroup (*Pongo*). Each of the last common ancestors (LCAs) is identified by a white box placed at the relevant node. These include the last common ancestor of the Homininae (LCA_{G-HP}), of humans, chimpanzees and bonobos (LCA_{H-P}), of chimpanzees and bonobos (LCA_{P}) and of eastern and western gorillas (LCA_{G}). The smaller black boxes indicate the locations of common ancestors that are not discussed explicitly in the present study. The coloured dashed lines define the points at which all lineages of a specified taxonomic level have been established. Thus, by the green line, all subfamilies are established as independent lineages, by the blue line all genera, by the red line all species, and by the purple line all subspecies. The lengths of the branches are for illustrative purposes and do not reflect any measure of evolutionary distance.

2016. A description of each of these traits is provided in Table 1, and Table 2 summarises the observations collected for each trait, indicating whether data were missing for any taxa and the study from which it were sourced.

Homo sapiens is a member of the Homininae, and thus it is important that this species is included in our analyses. However, collection of trait data for humans presents a particular challenge compared with other hominids. Although gorillas, chimpanzees and bonobos all exhibit some phenotypic and cultural variation between populations, this pales in comparison to the variation found within and between contemporary human societies (Foley & Lahr, 2011). Rather than attempting to capture this variation, we opted to use a single, small-scale human society to represent all traits. The Hadza of Tanzania were selected not because they represented the ancestral human state, but because they occur in areas close to those in which extinct hominins lived (Lahr & Foley, 2016). Given their lifestyle and locality, we might expect that the Hazda operate under similar environmental constraints (Marlowe, 2010), providing at least some limits to the difference in scale between contemporary humans and the *H. sapiens* lineage that we attempted to reconstruct. Unless otherwise noted, these data were sourced from Marlowe (2005, 2010).

Collection of cultural trait data

Of the data collected, putatively cultural traits were included as reported in chimpanzees (Whiten *et al.*, 1999, 2001; Sanz & Morgan, 2007), bonobos (Hohmann & Fruth, 2003), gorillas (Robbins *et al.*, 2016) and orangutans (van Schaik *et al.*, 2003). To define a behavioural trait as cultural, these studies all used the criteria first developed by Whiten *et al.* (1999); behaviours that were present in some communities but absent from others, without an obvious ecological explanation, were defined as cultural. This resulted in a dataset of 98 putatively cultural behaviours taken from 24 separate study sites. In order to summarise these data as a continuous variable, we used two different metrics, calculating both for all 24 sites. The first metric, hereafter referred to as the cultural count, was simply the number of cultural behaviours

Table 1. Definitions of all the traits reconstructed in this study; where appropriate, these definitions have been sourced from the relevant literature

Cultural traits: behavioural traits that have been proposed as putatively cultural because they vary between research sites and meet other criteria (Whiten *et al.*, 1999).	**Infant mortality:** the percentage of infants who die in their first year of life.
Body size: the average mass of both male and female adults (in kilograms).	**Interbirth interval:** the average number of months between births for female individuals.
Effective population size (N_e): the size of an idealized population that would give rise to the rates of inbreeding and changes in gene frequencies observed in the population of interest (Wang *et al.*, 2016).	**Gestation length:** the average number of days between fertilization and birth.
Census population size: the estimated number of wild individuals.	**Age at weaning:** the average age (in days) of juven iles when they cease to suckle from their mothers.
Day journey distance: the average distance (in kilometres) that individuals travel per day.	**Age at first reproduction:** the average age (in years) at which individuals begin their first reproduction.
Home range: the total area (in square kilometres) in which a group moves and lives. Typically contains all necessary resources.	**Community size:** the average number of individuals in temporally stable groups. For chimpanzees, bonobos and humans, this differs from party size (Lehmann & Boesch, 2004).
	Party size: the average number of individuals in temporary subgroups, typically associated with fission–fusion societies, such as those of chimpanzees (Lehmann & Boesch, 2004).

expressed at each of the study sites. The second metric was a modification of Shannon's H (Shannon, 1948) designed to measure the the cultural diversity of each research site. To make Shannon's H suitable for the cultural data, we treated each research site as equivalent to a community, each trait as a species and the frequency scores of those traits (absent, present, habitual or customary) as their abundances. Given that the different cultural traits are not comparable between all studies, Shannon's H was calculated across all sites within each genus using the R package vegan v.2.5-2 (Oksanen *et al.*, 2019). We also noted that because these cultural surveys have not been applied to human populations, we could not measure cultural diversity for *H. sapiens*, and thus data were missing for this taxon.

Estimation of the subspecies-level phylogeny

In order to implement a subspecies-level phylogenetic estimate for the Homininae, we took full-genome mitochondrial DNA (mtDNA) sequence data from the Great Ape Genome Project (Prado-Martinez *et al.*, 2013), randomly selecting one sequence for each Homininae species and subspecies, except for *G. b. beringei*, for which there was no sequence available. We also selected a full-genome mtDNA sequence for the Sumatran orangutan (*Pongo abelii*) to act as the outgroup in our phylogenetic analyses. Sequence identification and accession numbers can be viewed in the Supporting Information Appendix S1, Table S1.1.

Sequences were aligned using MUSCLE (Edgar, 2004), executed via the sequence-management software Geneious (Kearse *et al.*, 2012). The final alignment was 15 495 base pairs long. To account for within-genome rate variation, the alignment was partitioned into non-coding and the first, second and third codon positions of coding regions. PartitionFinder2 (Guindon *et al.*, 2010; Lanfear et al., 2012, 2016) was used to select substitution models for each of the four partitions (full details are given in Supporting Information, "Appendix S1, Table S1.2").

Phylogenetic inference was implemented under a Bayesian framework, using BEAST v.2.4.8 (Bouckaert *et al.*, 2014). To deal with between-lineage rate variation, we used the log-normal uncorrelated relaxed clock model (Drummond *et al.*, 2006). The clock model was calibrated by the divergence date of the human and chimpanzee–bonobo lineages; the prior for the calibration took the form of a log-normal distribution, with a lower hard bound of 6 Myr, a mean of 7 Myr and no upper bound. These parameters encompass the range of estimates of the split time reported in two recent studies (Moorjani *et al.*, 2016a; Besenbacher *et al.*, 2019). The Markov chain Monte Carlo was set

Table 2. The trait observations for Homininae taxa, including the source references

Trait	*Hs*	*Ptv*	*Ptt*	*Pte*	*Pts*	*Pp*	*Ggg*	*Ggd*	*Gbb*	*Gbg*	*Poa*
Cultural surveys	+[1*]	++++[2,3]	++[2,4,5]	–	++++++[2,3]	+[6]	+++[7]	–	++[7]	–	++[8]†
Body size male (kg)	+[1]	+[9]	+[9]	–	+[9]	+[9]	+[9]	–	+[9]	+[9]	+[9]
Body size female (kg)	+[1]	+[9]	+[9]	–	+[9]	+[9]	+[9]	–	+[9]	+[9]	+[9]
Effective population size	+[10]	+[10]	+[10]	+[10]	+[10]	+[10]	+[10]	+[10]	–	+[10]	+[10]
Census population size	+[11]	+[12]	+[12]	+[12]	+[12]	+[12]	+[12]	+[12]	+[12]	+[12]	+[12]
Day journey distance (km^2)	+[11]	++[14]	–	–	++[14]	++[14]	+[14]	–	+[14]	–	+[14]
Home range (km^2)	+[11]	++[14]	–	–	++[14]	++[14]	+[14]	–	+[14]	–	+[14]
Infant mortality at 1 year (%)	+[1]	+[13]	–	–	+[13]	+[13]	+[13]	–	+[13]	+[13]	+[13]
Interbirth Interval (months)	+[1]	++[15]	–	–	+++[15]	++[15,17]	+[7]	–	+[15]	+[4]	+[16]
Gestation length (days)	+[18]	+[13]	–	–	++[13]	+[13]	++[13]	–	++[13]	++[13]	++[13]‡
Age at weaning (days)	+[1]	+[13]	–	–	+++[13]	+[13]	+[13]	–	+[13]	+[13]	+[13]‡
Age at first reproduction (years)	+[1]	++[13]	–	–	+++[13]	+[13]	–	–	+[13]	–	+[13]
Party size	+[1]§	++[19]	+[19]	–	+++++[19]	++[20]	+[21]¶	–	–	–	+[22]¶
Community size	+[1]‖	++[19]	+[29]	–	++++[29]	++[20]	+[21]¶	–	–	–	+[22]¶

The rows represent each of the traits included in the study, and the columns represent the 11 taxa included in the phylogenetic analysis: *Homo sapiens* (*Hs*), *Pan troglodytes verus* (*Ptv*), *Pan troglodytes troglodytes* (*Ptt*), *Pan troglodytes ellioti* (*Pte*), *Pan troglodytes schweinfurthii* (*Pts*), *Pan paniscus* (*Pp*), *Gorilla gorilla gorilla* (*Ggg*), *Gorilla gorilla diehli* (*Ggd*), *Gorilla beringei beringei* (*Gbb*), *Gorilla beringei graueri* (*Gbg*) and *Pongo abelii* (*Poa*). A '+' sign indicates that data were available for the taxa, and a number of '+' signs indicates the number of sites from which observations were taken, whereas a '–' sign indicates that no data were available for this taxon.

Reference citations are as follows: [1]Marlowe (2010); [2]Whiten *et al.* (1999); [3]Langergraber *et al.* (2011); [4]Whiten *et al.* (2001); [5]Sanz & Morgan (2007); [6]Hohmann & Fruth (2003); [7]Robbins *et al.* (2016); [8]van Schaik *et al.* (2003); [9]Smith & Jungers (1997); [10]Prado-Martinez *et al.* (2013); [11]Marlowe (2005); [12]IUCN Red List Assessments (Robbins *et al.*, 2008; Bergl *et al.*, 2016; Fruth *et al.*, 2016; Humle *et al.*, 2016; Maisels *et al.*, 2016a, b; Oates *et al.*, 2016; Plumptre *et al.*, 2016; Singleton *et al.*, 2017); [13]Reichard & Barelli (2008); [14]Dunbar (2000); [15]Boesch & Boesch-Achermann (2000); [16]Shumaker *et al.* (2008); [17]De Lathouwers & van Elsacker (2005); [18]Jukic *et al.* (2013); [19]Wrangham (2000); [20]Furuichi (2009); [21]Parnell (2002); [22]van Schaik (1999).

*No cultural survey was available for *H. sapiens*. Hadza tool kit size was used as a proxy.

†Survey data were also collected for four *Pongo pygmaeus* sites.

‡No data were available for *Pongo abelii*; therefore, *Pongo pygmaeus* was used instead.

§The mean size of female Hadza foraging parties was used (5.31).

¶The distinction between communities and parties is not meaningful for gorillas and orangutans; therefore, the same value was used in both traits.

‖The mean Hadza camp size was used (30.4).

to 50 million generations, with trees sampled every 50 000 generations. The first 20% of these samples were discarded as burn-in. We extracted the maximum clade credibility (MCC) tree from our final posterior distribution of 801 trees (Fig. 2) and attached a tip for *G. b. beringei* halfway along the terminal branch of its sister subspecies, *G. b. graueri*.

Ancestral state reconstructions

Before any ASRs were conducted, all trait data were transformed using the natural logarithm in order to be expressed on a ratio scale, ensuring that the model would be reconstructing relative changes in trait values rather than absolute changes. ASRs were implemented within a maximum likelihood framework, using the statistical language and environment R (R Development Core Team, 2018) and the package Phylopars (Bruggeman *et al.*, 2009; Goolsby *et al.*, 2017). Phylopars allows for ASRs even when data are missing for some tips, using stochastic mapping procedures to assign a value to a tip based on its phylogenetic position and the overall distribution of trait values. This is preferable to simply pruning tips where data are missing and compounding the effects of incomplete taxon sampling (for discussion, see Pybus & Harvey, 2000; Rosenberg & Kumar, 2001; Wiens & Tiu, 2012). Moreover, Phylopars can

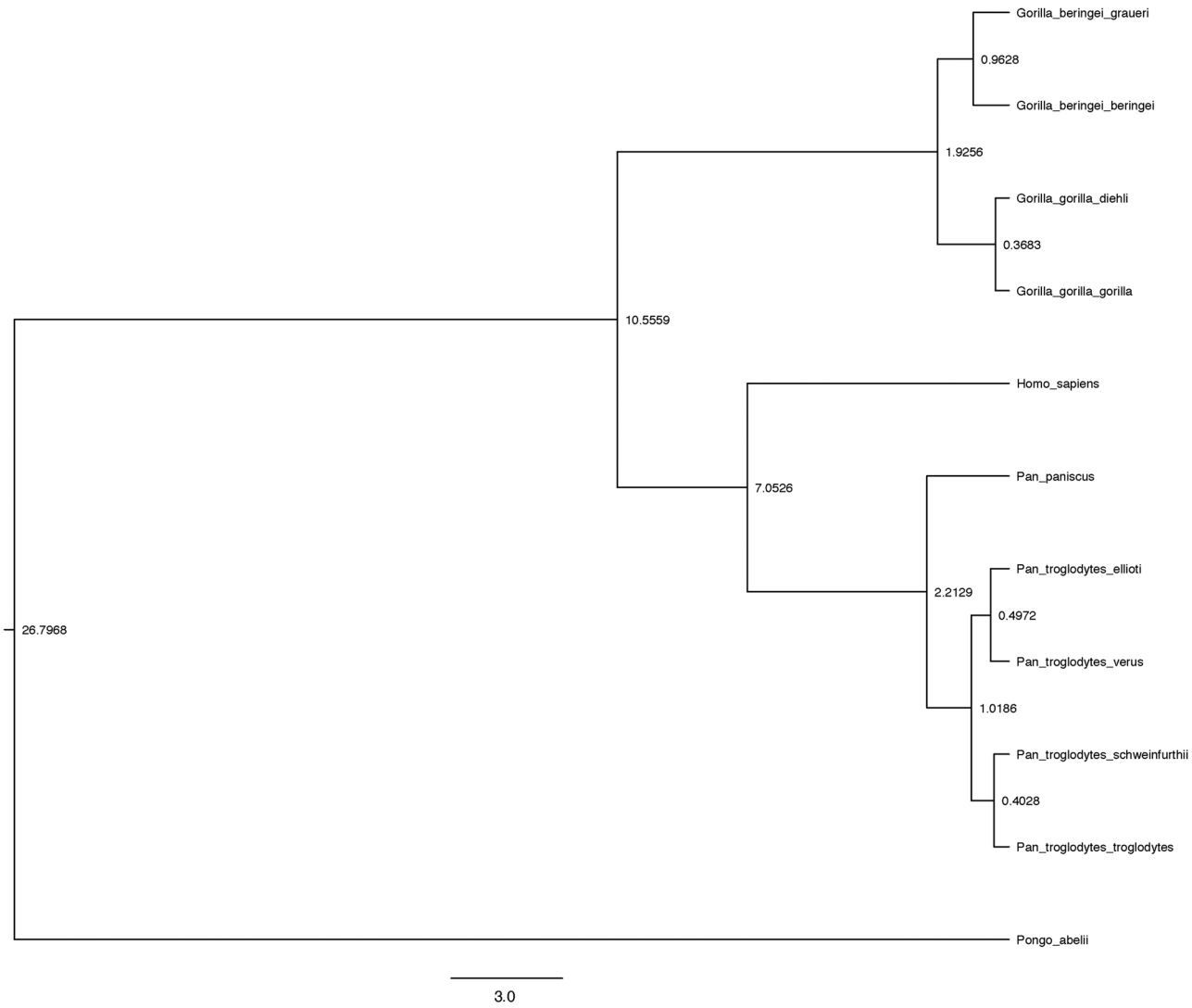

Figure 2. Maximum clade credibility tree extracted from the posterior sample of 801 trees. Estimated divergence times are given for each of the nodes in millions of years ago. A full mitochondrial DNA genome was not available for *Gorilla beringei beringei*; therefore, its tip was fixed halfway along the *Gorilla beringei graueri* tip, thus the divergence date given for the *G. beringei* has not been derived using the molecular clock model and should be interpreted with caution.

handle multiple observations of the same trait for a given tip by assuming autocorrelation between those observations, thus allowing for within-subspecies variation to be included in the analyses.

Ancestral state reconstructions were implemented under three different evolutionary models: Brownian motion (BM); Ornstein–Uhlenbeck (OU); and early burst (EB). The best-fitting model was selected using the Akaike information criterion (AIC). From this best-fitting model, we then extracted ancestral state values and 95% confidence intervals (CI) at each node in the phylogeny and for each trait. Scripts for all analyses can be accessed via Appendix S2.

Phylogenetic signal and significance testing

As part of the ASR procedure for each trait, we estimated Pagel's λ (1994), using Phylopars. Pagel's λ estimates phylogenetic signal, i.e. the tendency for related taxa to express similar traits, by comparing the correlation of traits among taxa with the correlation expected under Brownian motion (λ = 1, correlation exactly as expected under a Brownian evolutionary model; and λ = 0, no correlation). To determine whether the estimated phylogenetic signal was statistically meaningful, we used a log-likelihood ratio test, comparing the likelihood of the MCC tree with that of a null or star phylogeny (i.e. λ = 0).

We also took an alternative measure of phylogenetic signal, Blomberg's *K* (2003). Like Pagel's λ, Blomberg's *K* describes the phylogenetic signal of a trait compared with the signal expected under a Brownian motion model of character evolution. Unlike λ, *K* is capable of distinguishing cases where the phylogenetic signal is greater than expected under Brownian motion (*K* < 1, signal lower than expected; *K* = 1, signal exactly as expected; and *K* > 1, signal higher than expected). Unfortunately, Blomberg's *K* could not be calculated using Phylopars, and thus where there were multiple or missing observations for a tip, we used the imputed mean trait values that were calculated by Phylopars to measure λ. The function phylosig from the R package phytools (Revell, 2012) was used to measure Blomberg's *K* for each of our traits, and we tested whether *K* was significant using the randomisation test described by Blomberg *et al.* (2003), hereafter referred to as Blomberg's test.

We note that Münkemüller *et al.* (2012) demonstrated that both tests have limited power and are susceptible to false positives when estimated for small trees (< 20 tips). Additionally, although λ and *K* both measure phylogenetic signal, they do so differently [λ using maximum likelihood to find the parameter value that best explains the data and *K* comparing the amount of observed variance with that expected under Brownian motion (Kamilar & Cooper, 2013)] and, as such, can often produce inconsistent results (Münkemüller *et al.*, 2012). Therefore, given the phylogeny used in the present study has 11 tips, we believe it is prudent only to treat traits as phylogenetically significant when both tests returned *P*-values ≤ 0.05.

In addition to the two measures of phylogenetic signal, we also applied Pagel's δ transformation to each of the traits (Pagel, 1999a,b). Pagel's δ is sensitive to variation in the rate of evolution over time (δ < 1, the overall rate of evolution has slowed towards the tips; δ = 1, rate is constant across the tree; and δ > 1, the rate has accelerated towards the tips).

Comparison of subspecies- and species-level analyses

To assess the effect of subspecies-level trait data on phylogenetic signal, we first created a species-level version of our MCC tree. We then calculated λ and *K* on this species-level tree, but only for the traits that were found to be phylogenetically significant. We also applied the best-fitting model, determined by the subspecies analysis, to the species tree and extracted the median variance in the ancestral state estimates for every node shared between the two trees.

To assign trait values for these tests, we used two different approaches. Firstly, for each species' tip we drew a trait value at random from its descendent subspecies; thus, to assign male body size to *P. troglodytes*, we randomly selected a value from all of the body sizes reported for the four subspecies. We repeated this process 100 times for each of the traits. Secondly, we simply treated all subspecies data as multiple observations for the relevant species. Thus, to assign male body sizes to *P. troglodytes*, we used all of the observations reported for the four subspecies of chimpanzee.

RESULTS

Phylogenetic signal for species vs. subspecies trees

For 13 of the 15 traits, λ was > 0.9, suggesting that the MCC subspecies tree was a strong predictor of the distribution of the traits. Although λ was high in a majority of cases, the log-likelihood ratio tests found that phylogeny was a significant predictor of trait distribution for only four of the reconstructed traits: male body size ($\chi 2 = 10.75$, d.f. = 1, $P \leq 0.01$) and female body size ($\chi 2 = 5.92$, d.f. = 1, $P \leq 0.01$), community size ($\chi 2 = 5.94$, d.f. = 1, $P \leq 0.01$) and gestation length ($\chi 2 = 4.64$, d.f. = 1, $P = 0.03$).

For eight of the 15 traits, *K* was greater than one, again suggesting that there was high phylogenetic signal for several of the collated traits. Blomberg's test

also found this signal to be significant for all traits except census size, effective population size and infant mortality (for *P*-values, see Supporting Information, Appendix S3, Table S3.1). All of the traits that were found to be significant by the log-likelihood ratio tests were also found to be significant by Bloomberg's test. Thus, we treat only these traits (male and female body size, community size and gestation length) as phylogenetically significant.

Neither cultural index was found to be phylogenetically significant, although the signal was high for cultural count ($\lambda = 0.99$; $K = 2$). To explore whether our decision to use the Hadza toolkit as a proxy for cultural count in *H. sapiens* was affecting our analysis (42 tools, twice as large as any other site included in the study), we reran the ASR omitting the Hadza toolkit. Phylogenetic signal ($\lambda = 0.63$; $K = 0.3$) was lower when the Hadza toolkit was omitted and remained insignificant ($\chi 2 = 0.09$; d.f. = 1; $P = 0.76$). For a brief discussion of the phylogenetic signal and reconstruction of the cultural indices, see the Supporting Information (Appendix S4).

Model choice was relatively consistent between traits. For the vast majority of traits (12 of 15), BM was found to be the best-fitting model, with the lowest AIC value. Census size and effective population size were best explained by an OU model of evolution, and community size was the only trait in which an EB model was selected.

For three of the phylogenetically significant traits, δ was found to be greater than one (male body size, $\delta > 2.99$; female body size, $\delta > 2.99$; gestation length, $\delta = 1.4$), whereas community size was found to lower than one ($\delta = 0.14$). In fact, for male and female body size δ exceeded the maximum value of the parameter space (2.99). Figure 3 shows the δ-transformed trees for each of the four significant traits plotted against the MCC tree.

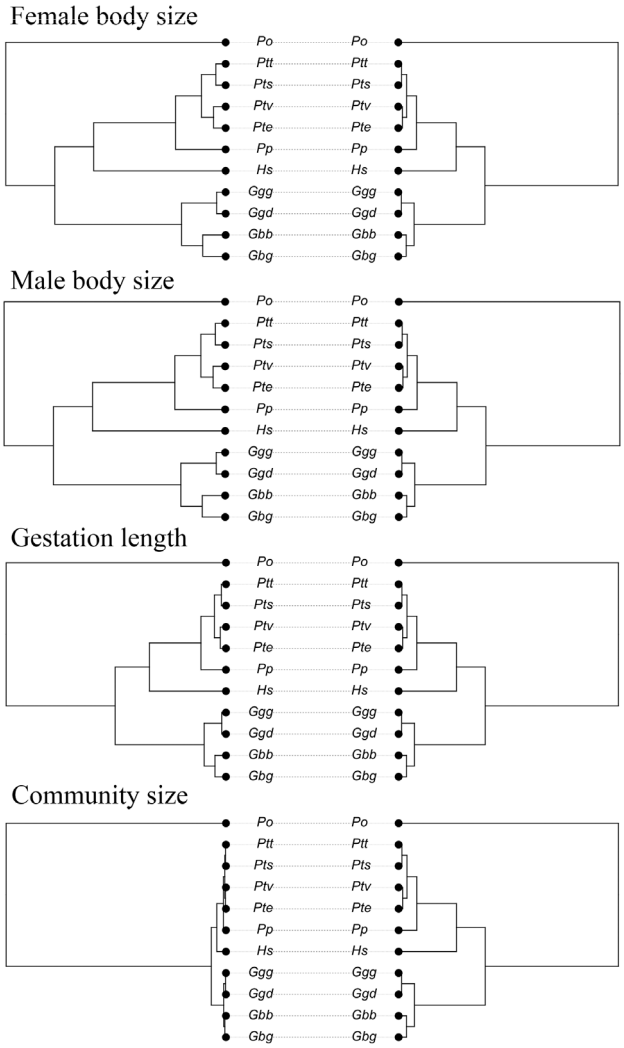

Figure 3. The maximum clade credibility tree transformed by the δ of each trait (left) compared with the original maximum clade credibility tree (right) for the 11 taxa: *Homo sapiens* (*Hs*), *Pan troglodytes verus* (*Ptv*), *Pan troglodytes troglodytes* (*Ptt*), *Pan troglodytes ellioti* (*Pte*), *Pan troglodytes schweinfurthii* (*Pts*), *Pan paniscus* (*Pp*), *Gorilla gorilla gorilla* (*Ggg*), *Gorilla gorilla diehli* (*Ggd*), *Gorilla beringei beringei* (*Gbb*), *Gorilla beringei graueri* (*Gbg*) and *Pongo abelii* (*Poa*). Branch lengths on the transformed trees are now relative to the amount of evolutionary change that occurred along each branch. Here, we can see that for body size and gestation length, much of the evolution in the traits has occurred on the shallower branches of the tree. In contrast, community size shows that the deeper branches are most evolutionarily significant, because the average community size of the outgroup, *Pongo abelii*, is considerably smaller than any value reported for the Homininae.

Comparison of subspecies- with species-level analyses

The median value of the permuted species-level λ was considerably lower than the median estimates for the subspecies tree for all traits except community size, whereas the median value of the permuted species-level K was lower for everything other than female body size (Table 3). Likewise, the subspecies-level estimate of K was higher than the median value of the species-level estimates for all traits except female body size.

The λ values for the species-level analysis, where all observations were included, were roughly equivalent to those reported in the subspecies analysis, except for gestation length, which was considerably lower ($\lambda_{sub} > 0.99$; $\lambda_{species} < 0.01$). In contrast, the K values were much more variable between the two tests, finding similar levels of phylogenetic signal for male body size ($K_{sub} = 0.91$; $K_{species} = 0.95$), but a higher signal on

Table 3. Comparison of phylogenetic signal of subspecies and species-level trait data for the traits where λ and *K* were found to be significant

Trait	λ_{sub}	$\lambda_{species}$	$\lambda_{permute}$ (25th–75th percentile)	Number of significant runs	K_{sub}	$K_{species}$	$K_{permute}$ (25th–75th percentile)	Number of significant runs
Male body size	0.97	> 0.99	0.17 (< 0.01–0.79)	4	0.91	0.95	0.29 (0.18–0.49)	9
Female body size	0.91	> 0.99	0.82 (< 0.01–> 0.99)	9	0.41	1.04	0.47 (0.29–0.67)	17
Gestation length	> 0.99	< 0.01	< 0.01 (< 0.01–0.74)	0	1.8	0.51	0.3 (0.24–0.5)	0
Community size	> 0.99	> 0.99	> 0.99 (> 0.99–> 0.99)	13	4.7	1.34	1.46 (1.24–1.68)	96

The table includes the λ and *K* values when calculated using the subspecies tree (λ_{sub} and K_{sub}), the species tree with all observations ($\lambda_{species}$ and $K_{species}$), the median λ and *K* values of the permuted species-level analyses ($\lambda_{permute}$ and $K_{permute}$) and the 25th and 75th quantiles, and the number of runs where the *P*-value was found to be < 0.05.

the species-level tree for female body size (K_{sub} = 0.41; $K_{species}$ = 1.04) and much lower signal for both gestation length (K_{sub} = 1.8; $K_{species}$ = 0.51) and community size (K_{sub} = 4.7; $K_{species}$ = 1.34).

Figure 4 compares the variance of the reconstructed ancestral estimates in both the subspecies- and species-level analyses, for each of the four phylogenetically significant traits. Here, we can see that for the $LCA_{G\text{-}HP}$, LCA of the gorillas (LCA_G), $LCA_{H\text{-}P}$, LCA of bonobos and chimpanzees (LCA_P) and the root of the phylogeny the variance of the subspecies was lower overall than the variance of the permutated species analyses. However, we also see that the variances of the subspecies-level analysis and species-level analysis where all observations were included are roughly equivalent to one another.

Ancestral state estimates

The results of the analysis suggest that the body size of the $LCA_{G\text{-}HP}$ for both males (82.13 kg; 95% CI = 43.03–156.78 kg) and females (51.71 kg; 95% CI = 27.92–95.78 kg) was roughly intermediate to those found in modern African great apes, and larger than any extant chimpanzee. Thereafter, the trends diverge (Fig. 5), with the male and female body sizes of the gorilla lineage increasing by 8.92 and 2.72 kg/Myr, respectively, until the LCA of *Gorilla* (LCA_G). In contrast, between the $LCA_{G\text{-}HP}$ and the $LCA_{H\text{-}P}$ the human–chimpanzee–bonobo lineage declined in male and female body size by 5.44 and 1.69 kg/Myr, respectively. Body sizes estimated for the $LCA_{H\text{-}P}$ were 63.07 kg (95% CI = 36.86–107.94 kg) for male individuals and 45.79 kg (95% CI = 27.44–76.42 kg) for female individuals. Although the value for females reported here falls at the upper end of the body sizes reported in *Pan* (33.2–45.8 kg), the ancestral size for males is larger than all the values reported in *Pan* (42.7–59.7 kg) and even the value reported for *Homo* (53.03 kg).

The reconstruction also found that the body sizes of bonobos and the chimpanzee subspecies are highly derived from those of the LCA_P, which had a male body size of 49.33 kg (95% CI = 35.97–67.65 k) and a female body size of 38.40 kg (95% CI = 28.42–51.89 kg). In particular, the sister subspecies *P. t. troglodytes* and *P. t. schweinfurthii* appear to have diverged rapidly in body sizes for both sexes since their split. This is consistent with the very high δ values reported for both body sizes (> 2.99), which suggest that much of the evolution of this trait occurred on the shallowest branches of the phylogeny.

Gestation length is highly clustered by genus, with very little change arising among species and subspecies. The reconstruction suggests that the $LCA_{G\text{-}HP}$ had a gestation length of 255.21 days (95%

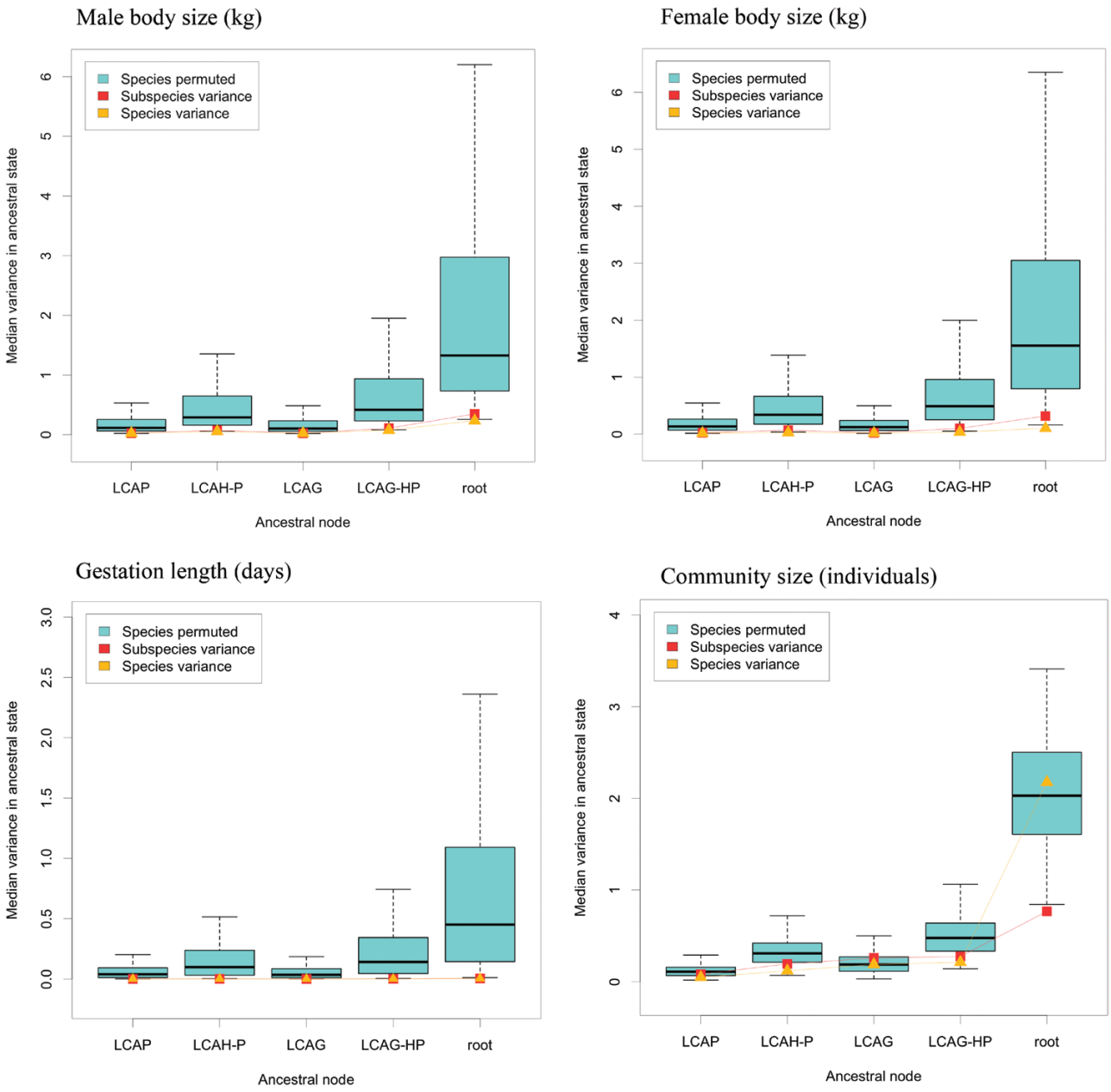

Figure 4. Log_{10}-transformed median variance for the permuted species-level analysis (blue boxplots), the species-level analysis with all observations (yellow lines and points), and the subspecies-level analysis (red lines and points). Here, we can see that although both the total data species analysis and the subspecies analysis generally outperform the permuted analyses, neither appears to be consistently better than the other.

CI = 235.73–276.3 days), intermediate to those found in modern hominids. Thereafter, the gestation length increased in the *Gorilla* lineage (1.66 days/Myr), whereas that in the *Homo* and *Pan* lineage declined until the $LCA_{H\text{-}P}$ (1.4 days/Myr). The gestation length in the *Pan* lineage continued to decline (2.75 days/Myr), whereas that in the *Homo* lineage increased (2.51 days/Myr), suggesting that the longer gestation periods of gorillas and humans evolved convergently.

According to the best-fitting model, the majority of change in community size occurred among the deeper branches of the phylogeny. This was also reflected in the comparatively low δ value calculated for this trait and the fact that this was the only trait where the EB model was preferred over BM. Although the *Gorilla* lineage community size declined after the $LCA_{G\text{-}HP}$ (0.71 individuals/Myr), the community size in *Homo* and *Pan* lineages generally increased towards the

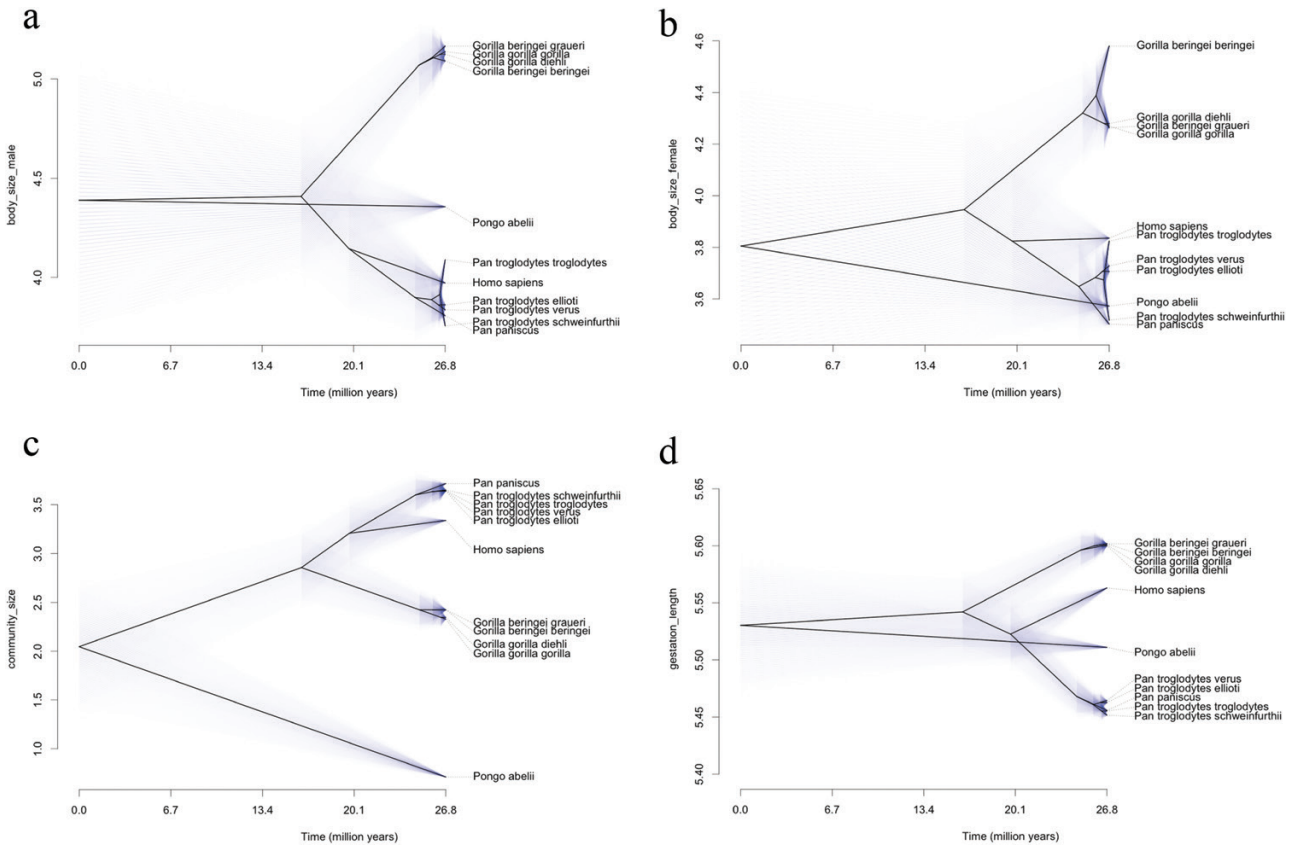

Figure 5. Density phenograms for Ln-transformed traits including male body size (A), female body size (B), community size (C) and gestation length (D). The blue shading indicates the 95% confidence intervals of the probability densities.

$LCA_{H\text{-}P}$ (2.11 individuals/Myr). This suggests that the large group sizes of *Pan* and *Homo* might have evolved convergently. Although the group size recorded for *H. sapiens* is slightly less than those reported for *Pan*, it is worth noting that we use the average Hadza camp site size and that there is considerable variation in this trait for the Hadza, with some camps exceeding 150 individuals (Marlowe, 2010).

DISCUSSION

PHYLOGENETIC SIGNAL AND TAXONOMIC RESOLUTION

We have shown that although phylogenetic signal, measured both λ and *K*, may be high for many traits, it is significant only for body size, community size and gestation length. Our analyses demonstrate that incorporation of subspecies-level trait data, or at least data on phenotypic variation, increased phylogenetic signal and reduced uncertainty in ancestral state estimates. However, it did not matter whether this phenotypic variation was analysed using a subspecies-level phylogeny or a method that assumes autocorrelation between multiple within-species observations.

These results should be interpreted cautiously. Phylogenetic signal is a measure of patterning. It can only tell us whether the distribution of traits among a group of related taxa conforms or departs from the distribution expected under Brownian motion. Simulation studies have shown that different evolutionary scenarios, with very different dynamics (e.g. neutral vs. selection), can produce similar measures of phylogenetic signal (Hansen *et al.*, 2008; Revell *et al.*, 2008). We also note that simply because the phylogenetic signal of a trait was found to be non-significant by the criteria of the present study, it does not prove that this trait has no phylogenetic signal. The power of both tests are limited when trees are small (Münkemüller *et al.*, 2012), such that if our analyses were expanded to a larger sample of primates, we might find that other traits were phylogenetically significant. In fact, Kamilar & Cooper (2013) reported significant phylogenetic signal across primates for four of the traits that we report as non-significant in the present study (age at weaning, home range,

infant mortality and interbirth interval), in addition to gestation length and body size. Nonetheless, phylogenetic signal is useful insofar as it allows us to limit our interpretation of our ASRs to those traits where phylogeny was shown to be a significant predictor of their current distribution.

Phylogenetic signal can also be used to interrogate the performance of our subspecies-level analysis compared with our species-level analyses. Although the phylogenetic signal was generally higher on the subspecies-level analysis compared with the permuted species-level analyses (the exception being community size, where estimates remained high on both levels), the results of the total data species analysis were essentially the same as those for the subspecies analysis. This was also true of the variance in ancestral state estimates for each of the phylogenetically significant traits.

This suggests that although the inclusion of subspecies-level trait data improved the performance of our ASRs, the inclusion of a subspecies phylogeny made little difference. This is surprising, because we expected the phylogenetic signal to be higher on the subspecies tree given that: (1) subspecies are similar and are separated by only shallow branches, thus conforming to the expectations of Brownian motion; and (2) increased taxon sampling has been shown to reduce the amount of variance in ancestral state estimates (Alisbury & Kim, 2001). Phylopars handles within-species phenotypic variation by modelling a layer of variability, assuming autocorrelation between observations reported for a single tip; in our case, a single species (Felsenstein, 2008; Bruggeman *et al.*, 2009). If these estimates of autocorrelation correct for structured differences among subspecies, it might mean that they are very similar functionally to a subspecies-level analysis. Regardless, our results illustrate the importance of including and modelling within-species phenotypic variation in ASRs.

Ancestral state estimates

The reconstruction implemented in the present study estimates that the body size of the $LCA_{G\text{-}HP}$ was broadly intermediate to those of modern African great apes, and the body size of the $LCA_{H\text{-}P}$ fell somewhere around the upper limit of those reported in modern *Pan* lineages. These results are seemingly contrary to the findings of several other studies, both theoretical and empirical, suggesting that the body sizes of the $LCA_{G\text{-}HP}$ and $LCA_{H\text{-}P}$ were equivalent to modern chimpanzees (Pilbeam, 1996; Richmond & Strait, 2000; Grabowski & Jungers, 2017; Pilbeam & Lieberman, 2017).

Intriguingly, our estimates for the body size of the $LCA_{H\text{-}P}$ are similar to estimates for the body size of some of the oldest known fossil hominin species. Grabowski (2018) used the scaling relationships between body mass and osteological traits in chimpanzees to estimate an average body size of 45 kg for the hominin genus *Orrorin* and a range of 41.9–59.3 kg for the genus *Ardipithecus*. Although our estimate for male body size is greater than either reported by Grabowski (2018), the ASR also predicts that male body size declined rapidly over the *Homo* lineage, meaning that our estimate might, in fact, be on track to reach that of the two archaic hominins. The $LCA_{H\text{-}P}$ female body size, however, which falls comfortably within the estimates of Grabowski (2018), declines at a much slower rate of only 0.28 kg/Myr.

We have to be cautious when interpreting these ancestral state estimates, because they represent a hypothetical value derived from a necessarily simplistic model of trait evolution. A BM model, given enough evolutionary time, will tend to produce ancestral values that are the intermediate to those found in the sampled taxa. If the large size of male gorillas was driven by strong positive selection, this rate might not be captured in a reconstruction, leading to overestimated ancestral values. Nonetheless, what these results do show is that even under a deliberately simplistic model, we predict some evolutionary change across the branch connecting the $LCA_{G\text{-}HP}$ to the $LCA_{H\text{-}P}$.

We should also look to deeper evolutionary history to interpret these findings. Although the estimates for body size of the $LCA_{G\text{-}HP}$ are similar to those reported in extant Ponginae (Smith & Jungers, 1997), like *H. sapiens*, the Sumatran, Bornean (*Pongo pygmaeus*) and Tapanuli (*Pongo tapanuliensis*) orangutans are relics of a once diverse lineage. Ponginae fossil species show considerable variation in body size and include the largest known hominoid, *Gigantopithecus blacki* (Zhang & Harrison, 2017). Additionally, one of the most frequently commented on features of the hominid fossil record is the striking variation in the sizes of these fossil species (Pilbeam & Gould, 1974; Jungers & Susman, 1984; Jungers *et al.*, 2016; Pilbeam & Lieberman, 2017; Grabowski *et al.*, 2018), and body size is known to be labile in primates more generally (Smith & Jungers, 1997; Grabowski *et al.*, 2018). If changes in body size are prolific among the Ponginae and the hominins, we might expect that they should also be frequent in the deeper history of the Homininae. Future ASRs of body size in the Homininae could be improved by including data for fossil hominins (Finarelli & Flynn, 2006), but this would require reliable estimates of both the body size of the species (Grabowski *et al.*, 2015) and their place on the phylogeny.

The results of this analysis suggest that both the *Gorilla* and the *Homo* lineages have experienced a convergent increase in the length of gestation, whereas that of *Pan* has steadily declined. This pattern is broadly consistent with those found in female

body size, and thus some of the change in gestation length might be a consequence of allometry. Kamilar & Cooper (2013), who found a strong phylogenetic signal for gestation length across 213 primate species, also suggested that this was a likely consequence of a correlation between life history and body mass. To measure the evolutionary correlation among these traits explicitly, an additional ASR would need to be implemented that modelled the evolution of both traits simultaneously. In *Homo*, selection for larger infant brain size might also have played a role in lengthening gestation (Cunnane & Crawford, 2003).

It is worth noting that although gestation periods are clearly delineated between genera in our dataset, other studies have reported considerable variation in this trait among some Homininae species. For example, Jukic *et al.* (2013) reported that the range of gestation length in healthy human births is 37 days (247–284 days), encompassing most of the range of our dataset, and Roof *et al.* (2005) reported that the mean gestation period of captive chimpanzees was 217.3 days (N = 272 female chimpanzees), ~11 days shorter than those reported in our dataset. If all species of Homininae showed high phenotypic plasticity for gestation period, then it would be difficult to determine how much of the interspecific differences in this trait are plastic responses to these species living in different environments.

Community size was particularly interesting, because it was the only phylogenetically significant trait for which BM was not the best-fitting model. Instead, the EB (Harmon *et al.*, 2010) was favoured. The EB describes an evolutionary scenario where a period of rapid trait evolution is followed by a slowdown or stasis. The ASR itself estimates that the community size of the $LCA_{G\text{-}HP}$ was approximately intermediate to that of extant African great apes. Thereafter, the trait diverges, with the gorilla lineage rapidly evolving smaller community sizes, whereas the community size of the chimpanzee–bonobo–human lineage increases. This trend for larger communities continues convergently for both the chimpanzee–bonobo and human lineages after they diverge at the $LCA_{H\text{-}P}$.

As with body size, it is worthwhile considering an alternative scenario that could produce similar ancestral estimates to those reported here. In this scenario, the community size of the $LCA_{G\text{-}HP}$ is that of gorillas, or near enough, and after divergence the community size of the gorilla lineage remains relatively unchanged, whereas the chimpanzee–bonobo–human lineage is subject to strong directional selection for larger communities. The EB model, which is an extended BM model where the magnitude of dispersion decreases through time (Harmon *et al.*, 2010), would not distinguish this scenario from one in which the $LCA_{G\text{-}HP}$ is intermediate to the extant African great apes.

Conclusion

The aims of the present study were to reconstruct the ancestral states of the Homininae for a variety of continuous traits known to vary among subspecies and to assess the performance of subspecies-level ASRs. To do this, we collated published data on traits from different domains that were known to vary among subspecies and reconstructed the hominoid evolutionary history using Bayesian phylogenetic inference techniques. The inclusion of phenotypic variation at the levels of species and subspecies led, in general, to a higher phylogenetic signal and lower uncertainty for our ancestral state estimates. However, it is not clear whether inclusion of a subspecies phylogeny is preferable to using techniques that model autocorrelation among within-species observations. Our best models estimate that for the phylogenetically significant traits, the $LCA_{H\text{-}P}$ was broadly similar to a chimpanzee, whereas the $LCA_{G\text{-}HP}$ exhibited some important differences, including larger body sizes, a longer gestation period and smaller communities. Future research should focus on inclusion of fossil evidence in ASRs, because this adds additional evidence regarding the evolution of morphology and even behavioural traits (Lister, 2014) and can reduce uncertainty in ancestral state estimates (Finarelli & Flynn, 2006). However, this would require reliable phylogenetic hypotheses regarding the relationship of extant species to extinct ones. Phylogenetic techniques that integrate both molecular and morphological data to reconstruct the evolutionary history of living and fossil lineages [so-called 'total evidence phylogenies' (Ronquist *et al.*, 2012, 2016; Wood *et al.*, 2013)] represent a promising avenue.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Appendix S1. Phylogenetic reconstruction using BEAST.
Appendix S2. Analyses scripts.
Appendix S3. λ, *K* and δ values and test statistics.
Appendix S4. Reconstruction of cultural traits.
Table S1.1. Individual names and identification numbers for each of the mitochondrial DNA sequences sourced from the Great Ape Genome Project.
Table S1.2. Best-fitting partition scheme according to PartitionFinder 2.
Table S3.1 For each of the reconstructed traits, we present the λ value, the χ2 and *P*-values of the log-likelihood ratio test, the *K* value, the *P*-value of Blomberg's test, and the δ value.