Phylogenetic rate shifts in feeding time during the evolution of Homo

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Edited by Richard G. Klein, Stanford University, Stanford, CA, and approved July 26, 2011 (received for review May 17, 2011)

Unique among animals, humans eat a diet rich in cooked and nonthermally processed food. The ancestors of modern humans who invented food processing (including cooking) gained critical advantages in survival and fitness through increased caloric intake. However, the time and manner in which food processing became biologically significant are uncertain. Here, we assess the inferred evolutionary consequences of food processing in the human lineage by applying a Bayesian phylogenetic outlier test to a comparative dataset of feeding time in humans and nonhuman primates. We find that modern humans spend an order of magnitude less time feeding than predicted by phylogeny and body mass (4.7% vs. predicted 48% of daily activity). This result suggests that a substantial evolutionary rate change in feeding time occurred along the human branch after the human–chimpanzee split. Along this same branch, Homo erectus shows a marked reduction in molar size that is followed by a gradual, although erratic, decline in H. sapiens. We show that reduction in molar size in early Homo (H. habilis and H. rudolfensis) is explicable by phylogeny and body size alone. By contrast, the change in molar size to H. erectus, H. neanderthalensis, and H. sapiens cannot be explained by the rate of craniodental and body size evolution. Together, our results indicate that the behaviorally driven adaptations of food processing (reduced feeding time and molar size) originated after the evolution of Homo but before or concurrent with the evolution of H. erectus, which was around 1.9 Mya.

Feeding time is dependent on the metabolic needs of the organism as well as on ingestion time, chewing time, and bolus formation. The occlusal surface area with which food is chewed also plays an important role in food processing and has long been used to infer shifts in feeding behavior in extinct hominins (11–14). The reduction of molar size during hominin evolution is thought to be associated with the advent of advanced food processing, because cooking softens food (15) and soft food puts less biomechanical demand on chewing teeth (16). Softer foods also adhere more quickly while being chewed and therefore, are swallowed after fewer chewing cycles (17).

Here, we investigate the amount of time spent feeding by humans compared with other primates, and we use a phylogenetic analysis to distinguish hominin species according to whether changes in molar size are explicable by the overall rate of craniodental evolution. This analysis allows us to test the hypothesis that a major shift in selection pressure involving food processing occurred in the human past. We, thus, use comparative phylogenetic methods to test an explicit phylogenetic prediction of the cooking hypothesis, namely that a significant phylogenetic rate change occurred in molar size and feeding time along the human lineage.

Results

We regressed feeding time on body mass for wild populations of nonhuman primates in a statistical model that accounted for the phylogenetic relationships among the primates using a Bayesian posterior distribution of trees (18). We found that time spent feeding increases with body mass in nonhuman primates [mean slope (β) = 0.24, σ = 0.06, with 95% of the variation in feeding time in nonhuman primates explained by variation in body mass (Fig. 1 A and B)]. Although the variance explained is relatively low, the model can still be used to predict feeding time in humans, with the lower R² producing a wider posterior probability distribution and thus, making it harder to detect an outlier (i.e., a conservative test).

The posterior distribution of the regression models was then used to predict the time spent feeding in modern humans by adding H. sapiens to the distribution of trees and supplying an estimate of human body mass as a predictor variable. The posterior predictive distribution (Fig. 1C) of time spent feeding shows that, based on the regression models and phylogenetic position, modern humans should spend roughly 48% of the day feeding. The actual value of 4.7% falls well outside the 99% credible interval (21–76%) and outside the entire posterior distribution (minimum = 13%), indicating that, compared with nonhuman primates, modern humans are clear evolutionary outliers for the amount of time spent feeding.

To better pinpoint when this shift in feeding time occurred, we applied phylogenetic prediction (19) to infer feeding time in...
extinct hominins by studying the biological significance of shifts in molar size based on a phylogenetic outlier test. Although evolutionary changes in tooth size have been well-studied in the fossil record (14, 20–22), advances in Bayesian phylogenetic methods have yet to be applied to compare empirical patterns with those patterns predicted by evolutionary modeling. More specifically, the rate of molar size evolution—in relation to the rate of other characters across hominins—is unknown. This distinction is important, because if the overall rate of craniodental evolution across primates can account for changes in molar size for specific hominins, then molar size evolved in pace with other craniodental characters. Consistent with this view, we find that, for nonhuman haplorhines (tarsiers, monkeys, and apes), time spent feeding is related to log_{10} molar size (μ = 51, 95% credible interval for the slope of 0.04–0.5, mean r^2 = 0.12, mean phylogenetic signal, λ = 0.68).

To analyze feeding time and molar size in extinct hominins, we included 14 extinct hominins into our dataset using standard craniodental data (23) and inferred phylogenetic trees with branch lengths in units of character change and branch lengths in time (Fig. 2 A and B). We found highly resolved trees that generally match the most parsimonious tree for the same data (23) but with stronger support for some groups. For the dated tree using molecular and morphological data, we find that the group Homo, which includes our most recent relatives, dates to 2.9 Mya. This age is slightly older than estimates based on the fossil record (roughly 2.3 Mya) (9), although the 95% credible interval on our estimate is 2.1–3.9 Mya. Given that first and last fossil occurrences are rare observations (the Siganor–Lippes effect) (24), our results predict that older Homo fossils may be discovered given a sufficiently adequate fossil record. We combined molecular and morphological data to create a phylogeny that included living primates and the extinct hominins. This distribution of trees showed high levels of support among extant primates, but Ardipithecus grouped with Pan in 62% of the trees (68% in the time trees) and the analysis provided slightly lower support near Homo, likely because of large amounts of missing data.

We investigated molar size and feeding time evolution over both the combined dataset (including the dated trees) and trees in which we grafted the posterior morphology trees for the fossil taxa, from Pan to Homo, onto the molecular and time trees of extinct nonhuman primates (Fig. S1). Analyses yielded similar results regardless of the trees that were used. In each case, our comparative analyses were integrated over 1,000 trees, thereby accounting for phylogenetic uncertainty (25), although sensitivity analyses showed that the phylogenetic ambiguities as well as the grouping of Ardipithecus with Pan do not affect our results or conclusions.

We used estimated body mass (based on postcrania and orbit data), the posterior distributions of the regression coefficients, and the distribution of trees to perform a phylogenetic outlier test for extinct hominins. We found that the association between molar size and body mass covaries strongly with the phylogenetic relatedness of different primate species (mean λ = 0.9). Molar size increases with body mass in non-Homo primates (mean slope, β = 0.62, σ = 0.04), with 77% of the variation in molar size explained by variation in body mass (Fig. 3 A and B). Using the posterior distributions of the regression coefficients, estimated body mass for fossil taxa, and distribution of trees, we performed a phylogenetic outlier test of molar size for members of the genus Homo. The posterior predictive distributions (Fig. 3 C–G) show that H. erectus, H. neanderthalensis, and H. sapiens have substantially smaller molars than predicted for a typical primate (actual molar size falls outside the 99% credible intervals for all three species). To represent the higher rate of evolution along these lineages, the branches in the clad containing H. erectus, H. neanderthalensis, and H. sapiens would need to be 50 times longer under a random walk (Brownian motion) model of evolutionary change. Thus, it is highly unlikely that the large changes in molar size would have occurred via the same processes that characterize the evolution of molar size in other primates.

To predict feeding time for H. erectus and H. neanderthalensis, we used the posterior regression models of feeding time and body mass but included feeding time data for H. sapiens. The posterior predictive distributions of feeding time in extinct hominins are, then, a function of correlated evolution between feeding time and body mass in nonhuman primates, estimated body mass of the extinct hominin, phylogenetic relatedness to Homo sapiens, and feeding time in H. sapiens. The posterior predictive distributions of feeding time suggest that H. erectus and H. neanderthalensis spent 61% and 7%, respectively, of their active day feeding (σ = 1.4 and 1.8), which is similar to modern humans (μ = 4.7%, σ = 2). The evolutionary decrease in feeding time is unlikely to have been caused solely by shifts to a carnivorous diet, because no tropical or subtropical people are known to subsist on a diet of more than 50% meat (26). Additionally, tool use associated with butchery originated by 2.6 Mya (27), and recent evidence suggests that tool-assisted carnivory in hominins may date to over 3.39 Mya, possibly the activity of Australopithecus (28).

Discussion

In this paper, we have taken advantage of phylogenetic methods to reevaluate existing hypotheses and promote the generation of hypotheses. As in many recent phylogenetically based studies,
our analysis made a critical distinction between observable differences (typological) and the evolution of those differences (transformational), with the latter type of question explicitly addressed by phylogenetic comparative methods (29). This type of comparative phylogenetic analysis allows quantitative testing of hypotheses about the evolution of traits, including brain size in hominins (30), body size in animals (31), and differences in promiscuity in birds (32). These studies have provided insights into evolution by analyzing traits for which observable variation had long been known.

Concerning the work presented here, the question is whether the overall rate of craniodental evolution across primates can explain the decrease in relative tooth size in hominins under a random walk (Brownian motion) model of character change. Our approach moves this question into a broader comparative framework and connects feeding time (a behavior) with the evolution of anatomical characters. If we had found that the evolutionary change in molar size of *Homo* was predicted from evolutionary rates across primates, we would have concluded that the transformation of tooth size in hominins was not associated with a specific new behavior. With our approach, however, we made the opposite finding; human feeding time and molar size are truly exceptional compared with other primates, and their oddity began around the start of the Pleistocene.

Changes in body size have important ramifications for feeding, because large animals generally have greater caloric requirements. Large-bodied animals can accommodate this need by ingesting larger food boluses, eating a greater number of food items at a time, and feeding more often throughout the day. Our results show that the amount of the day spent feeding scales with body size in primates, probably to compensate, in part, for the per chew food processing rate, which declines with increased body size (38, 39). The phylogenetic expectation is that human feeding time should be similar to the feeding time of great apes such as chimpanzees. The dramatic difference in feeding time between chimpanzees and humans contrasts sharply with our close phylogenetic distance and indicates that feeding time was substantially reduced on the lineage to modern humans.

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Fig. 2. Phylogenetic trees for great apes and extinct hominins along the human lineage. (A) This tree is inferred using morphological characters in a Bayesian framework, and it has branch lengths relative to the amount of evolutionary change in the characters. (B) A time-calibrated tree shows the same general relationships. Labels at nodes are posterior probability support (the fraction of times that the node appeared in the posterior distribution of trees) for *A* and *B*.
previous research has shown that some of the cross-species variation in feeding time is also explained by changes in the number of types of food items consumed. For example, our result that humans are evolutionary outliers for the small amount of time spent feeding could be explained by the inclusion of large amounts of meat in the human diet (42), except that feeding time was measured for modern humans whose diets were dominated by plant material. Furthermore, human tooth morphology is clearly not adapted for obligatory carnivory (42), and only extreme high-latitude populations are able to survive solely on animal foods (26). The best explanation for our result is that a shift in consumption (from raw unprocessed foods to soft cooked and nonthermally processed foods) originated somewhere along the line to modern H. sapiens after the human–chimpanzee split.

Early H. erectus (ergaster) lived in southern and eastern Africa from 1.9 to 1.5 Mya (43). Based on reconstructions indicating that it had small molars and a small gut volume, H. erectus has been hypothesized to have cooked its food (1). Our findings support this view by showing that, by the time that H. erectus evolved, the molars in our lineage were so small that changes in body mass cannot account for the change in molar size. Hence, they spent substantially less of their day engaging in feeding activities. Facilitative food processing, including cooking, likely originated, therefore, before the appearance of H. erectus, perhaps even in H. habilis or H. rudolfensis. Although distinct morphological correlates of feeding time are difficult to distinguish in these species, inference of feeding time based on body size and phylogenetic position suggests that H. habilis is within the human range (μ = 7.2%, σ = 2.3), whereas H. rudolfensis (μ = 9.5%, σ = 3.3) borders the human range. Outside of the genus Homo, we have no a priori reason to expect species to have had feeding times like modern humans. Our model predicts that Paranthropus spent an average of 43% (σ = 11.3%) of its day feeding, which is similar to the time that chimpanzees spend feeding (37%). Nevertheless, our phylogenetic analyses reveal that behavioral, physiological, and other nonfossilizing adaptations related to feeding and now necessary for long-term survival of modern humans evolved by the time of H. erectus and before our lineage left Africa.

Materials and Methods

We generated posterior distributions of phylogenetic trees (in units of character change and time) for extinct hominins based on 109 morphological characters from Strait and Grine (23) to assess how the Hominini tree compares with previous parsimony-based inferences. Next, we inferred trees for comparative analysis that included Loris and 12 species of lemurs (Strepsirrhini), 28 species of New World monkeys (Platyrrhini), and 33 species of Old World monkeys, gibbons, and apes (Catarrhini). The genetic data were obtained from the 10kTrees (version 1) website (http://10ktrees.fas.harvard.edu) (18) and the European Molecular Biology Laboratory Nucleotide Sequence Database for H. neanderthalensis. We used MrBayes v3.1.2 (44) to infer phylogenetic relationships separately for the morphological and molecular datasets. In both cases, four Markov chain Monte Carlo (MCMC) replicates were run for 20,000,000 generations, each with eight chains and a sampling frequency of 2,000. The average SD of split frequencies between replicates were run for 20,000,000 generations, each with eight chains and a sampling frequency of 2,000. The average SD of split frequencies between the MrBayes runs was less than 0.01, which indicates that the runs converged. We double-checked that the runs had reached a stationary phase by examining a time series plot for the log-likelihoods in Tracer (45).

We extracted body mass (mean of male and female) and percentage of the active day spent feeding from the literature (Table S1), being careful to distinguish feeding time from nonfeeding components of feeding, such as searching for food. For these data, adult mean values (both sexes) are reported. Feeding data for humans were obtained from the literature (Table S2). Feeding time data were logit-transformed—a standard practice for percentile data (46).

For the molar data, the occlusal surface area of the second lower molar was estimated by multiplying the buccolingual breadth by the mesiodistal length. Molar data were averaged for adult males and females. When available in the literature, we used an average of the trigonid (mesial portion of the molar)
and talonid (distal portion of the molar) buccolingual breadth. If no data were available from the lower second molar (mandibular), upper second molar (maxillary) measurements were used instead. Note that the dataset used to build the phylogeny contains characters derived from molar size (but not molar occlusal area), which is an acceptable procedure given that branch lengths are assumed to reflect rates of evolution in the character of interest.

We used this posterior distribution of trees and the program BayesTraits (47) to analyze time spent feeding (percentage of daily activity) relative to body mass and molar size relative to body mass. We generated posterior distributions of phylogenetic generalized least square regression models that account for the nonindependence among the characters created by common evolutionary descent (47). Because trees are sampled in proportion to their posterior probability, this approach accounts for the phylogenetic uncertainty (25) surrounding the evolutionary relationships of extinct hominins (9, 23, 48). The scaling parameter \( \lambda \) (phylogenetic signal) was sampled from the MCMC regression analysis, which produced posterior distributions of regression models (slopes, intercepts, and \( \lambda \)) (Tables 53 and 54).

We ran the analysis for 2,000,000 iterations, sampling every 200 iterations with a burn-in of 200,000. The rate deviation setting was adjusted so that acceptance values ranged between 0.2 and 0.4.

Based on the Bayesian phylogenetically informed prediction method developed in the work by Organ et al. (19), we developed a phylogenetic outlier test. This test (47) provides the posterior distribution of predictions for the dependent variable \( y \) in a new taxon given (i) its value for the independent variable \( x \), (ii) the posterior distribution of regression models derived from the initial analysis, and (iii) the phylogenetic tree. Predictive distributions that deviate strongly from the known value (i.e., outliers) provide evidence that the species has undergone a substantial amount of evolutionary change that cannot be accounted for by its phylogenetic position, branch lengths, and evolutionary change in the independent variable. The implication is that the trait has adaptive value for the species in ways not shared by its close relatives. This test may be used to evaluate hypotheses about evolutionary singularities, and we call it a phylogenetic outlier test.

Because log-log regressions estimate the geometric mean as opposed to the arithmetic mean, we performed a correction when antilogging the predictions by adding one-half the mean square error (mean square error = sum of squared errors/\( n – p – 1 \)) to the prediction before the back transformation (49, 50). More details about the methods and data used in this report are in SI Appendix.

ACKNOWLEDGMENTS. We thank the Departments of Human Evolutionary Biology and Organismic and Evolutionary Biology and the Museum of Comparative Zoology at Harvard University for providing support that enabled this research. We also appreciate help from M. Plavcan for access to his morphological dataset; C. Arnold and L. Matthews for compiling the genetic dataset and providing advice on its analysis; and C. Venditti and M. Fujita for discussions about phylogenetic inference. Discussions, advice, and comments from D. Strait, R. Carmody, D. Lieberman, J. J. Wiens, D. Pilbeam, C. Tiffon, C. Stetler, N. Kroupa, S. Hadley, and N. Hobbs helped improve this manuscript.
Outline of Materials and Methods

We generated posterior distributions of phylogenetic trees (in units of character change and time) for extinct hominins based on 109 morphological characters from Strait and Grine (2004). Next we inferred trees for comparative analysis that included *Loris* and 12 species of lemurs (Strepsirrhini), 28 species of New World monkeys (Platyrrhini), and 33 species of Old World monkeys, gibbons, and apes (Catarrhini). The genetic data were obtained from the 10kTrees (version 1) website (http://10ktrees.fas.harvard.edu/) (Arnold, Matthews et al. 2010) and from the EMBL Nucleotide Sequence Database for *H. neanderthalensis*. We inferred trees that included all taxa (extant and extinct) by combining morphological and molecular data, and by grafting the individual morphological and molecular trees together (see Supporting Materials). We used this posterior distribution of trees and the program BayesTraits (Pagel 1999) to analyse time spent feeding (percentage of daily activity) relative to body mass, and molar size relative to body mass. We tested whether a random walk or directional model of character evolution better fit the data and estimated phylogenetic signal (see Supporting Materials). Next, we generated posterior distributions of phylogenetic generalized least square (PGLS) regression models that account for the non-independence among the characters created by common evolutionary descent (Pagel 1999). Because trees are sampled in proportion to their posterior probability this approach accounts for phylogenetic uncertainty (Pagel and Lutzoni 2002) surrounding the evolutionary relationships of extinct hominins (Collard and Wood 2000; Strait and Grine 2004; Wood and Lonergan 2008). The regression models, the phylogenetic trees, and estimates of body mass were then used to generate distributions of phylogenetically-informed predictions for dependent variables involving
feeding time and molar size. Predictive distributions that deviate strongly from the known value (i.e., outliers) provide evidence that the species has undergone a substantial amount of evolutionary change that cannot be accounted for by the length of its phylogenetic position, branch lengths, and evolutionary change in the independent variable. The implication is that the trait has adaptive value for the species in ways not shared by its close relatives. This may be used to test hypotheses about evolutionary singularities, and we call it a phylogenetic outlier test.

**Phylogeny**

Genetic data for extant species and were obtained pre-aligned using MUSCLE (Edgar 2004) from the 10kTrees webpage v2 (http://10ktrees.fas.harvard.edu/) (Arnold, Matthews et al. 2010). We used their protocol, but will outline it briefly. Taxon sampling for our analysis included 12 species of strepsirrhines (including *Loris*), 29 species of platyrrhines, 47 species of catarrhines, and the Sunda Flying Lemur (*Galeopterus variegatus*) as an outgroup. Species were chosen based on the availability of trait data (see below). The genetic dataset consisted of the following genes: CYTB (Cytochrome B), COX1 (Cytochrome c oxidase subunit I), COX2 (Cytochrome c oxidase subunit II), ND1 (NADH dehydrogenase subunit 1, 12S ribosomal rRNA, 16S ribosomal rRNA, MC1R (melanocortin 1 receptor), CCR5 (chemokine (C-C motif) receptor 5), and SRY (Sex-determining Region Y) for a total of 5243 base pairs. The 10kTrees webpage and associated articles provide more details on the construction of the dataset and protocol. To these we added (and aligned by hand) the following genetic sequence data for *H. neanderthalensis* obtained from NCBI: cytochrome b, cytochrome c oxidase subunit I, cytochrome c oxidase subunit II, 12S ribosomal rRNA, 16S ribosomal rRNA, and NADH dehydrogenase subunit 1 (complete mitochondrion genome, NC_011137). The dataset was partitioned by gene, each of which used a GTR model with gamma-distributed rate variation across sites and a proportion of invariable sites (as determined by Mr. Modeltest (Nylander 2004)).
The morphological dataset consisted of 109 traditional characters obtained from Strait and Grine (2004) and ordered following those authors. Gamma-shaped rate variation was assigned to the morphological data. The morphological data was sequestered into a separate partition for the combined dataset analysis (see below).

To reduce the amount of uncertainty during tree inference, we constrained 27 nodes based on genomic Alu insertion events (Schmitz, Ohme et al. 2001; Salem, Ray et al. 2003; Roos, Schmitz et al. 2004; Ray and A. 2005; Ray, Xing et al. 2005; Xing, Wang et al. 2005; Xing, Witherspoon et al. 2007; Li, Han et al. 2009; Osterholz, Walter et al. 2009). Constraints applicable to extant taxa in the morphology dataset (see Mr. Bayes block below) were used in tree inference based on morphology.

We used MrBayes v3.1.2 (Huelsenbeck and Ronquist 2001) to infer phylogenetic relationships separately for the morphological dataset and for the molecular dataset. In both cases, four MCMC replicates were run for 20,000,000 generations, each with 8 chains and a sampling frequency of 2,000. The average standard deviation of split frequencies between the MrBayes runs was less than 0.01, which indicates that the runs converged. We double-checked that the runs had reached a stationary phase by examining a time-series plot for the log-likelihoods in Tracer (Rambaut and Drummond 2007).

**The Nexus File for the Mr. Bayes Morphology Tree**

```nexus
#NEXUS
begin data;
dimensions ntax=20 nchar=109;
format datatype=standard gap=- missing=?;
matrix
Colobus_guereza
000022100000?2122000120010000210010001000001001110000001000000010000001000121001200003000000100100000102101
Papio_anubis
000001100000?20020001011300002000013000000000001011110000000000000000000000000000000000000010010210001
Hylobates_lar
110131100000?312200012001000010000001001111111104200000000000000000000000000001100102000003000000100010300012101
Pongo_pygmaeus
21010210300003000000001000000000000000000000010113000011011111211100021000001000000001003000010002010110210010200
Gorilla_gorilla
2010201110002000000000110200200001000000012100002020111000320000000010220111010000000000100110110110102010
Pan_troglodytes
2011201120002100000010001000000000100000000010000002113000021101200000000000000000000000102021000000000001001121100000000
Sahelanthropus_tchad
????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????
Ardipithecus_ramidus
????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????
Australopithecus_an
????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????
```

3
BEGIN MRBAYES;
outgroup Colobus_guereza;
constraint constrain1 -1 = Pongo_pygmaeus Gorilla_gorilla Pan_troglodytes Homo_ergaster Homo_habilis Homo_rudolfensis Paranthropus_aethio Paranthropus_boisei Paranthropus_robustus Sahelanthropus_tchad Ardipithecus_ramidus Australopithecus_af Australopithecus_an Australopithecus_ga Kenyanthropus_platyops Praeanthropus_afaren Homo_sapiens;
constraint constrain2 -1 = Gorilla_gorilla Pan_troglodytes Homo_ergaster Homo_habilis Homo_rudolfensis Paranthropus_aethio Paranthropus_boisei Paranthropus_robustus Sahelanthropus_tchad Ardipithecus_ramidus Australopithecus_an Australopithecus_ga Kenyanthropus_platyops Praeanthropus_afaren Homo_sapiens;
constraint constrain3 -1 = Pan_troglodytes Homo_ergaster Homo_habilis Homo_rudolfensis Paranthropus_aethio Paranthropus_boisei Paranthropus_robustus Sahelanthropus_tchad Ardipithecus_ramidus Australopithecus_an Australopithecus_ga Kenyanthropus_platyops Praeanthropus_afaren Homo_sapiens;
constraint constrain4 -1 = Papio_anubis Colobus_guereza;
prset topology=constraints(constrain1, constrain2, constrain3, constrain4);
ctype ordered: 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25 26 27 28 30 31 32 33 34 35 36 37 38 39 40 41 42 43 44 45 46 47 48 49 50 51 52 53 54 55 56 58 59 60 61 62 63 64 65 66 67 68 70 71 72 73 74 75 76 77 78 79 80 82 83 84 85 86 88 89 90 91 92 93 94 95 96 97 98 99 100 101 102 104 105 106 107 108 109;
iset rates=gamma;
mcmc ngen=20000000 nchains=8 samplefreq=2000 printfreq=5000000 temp=0.1;
sump burnin=2500;
sfmt burnin=2500;
END;

Time Calibrated Phylogeny

Time calibrated phylogenies were inferred using BEAST v1.5.4 (Drummond and Rambaut 2007) for the morphological dataset and for the molecular dataset. We used settings in BEAST similar to those detailed above for Mr.Bayes, including a relaxed, uncorrelated log normal clock (standard deviation uniform prior from 0 to infinity). BEAST does not implement ordered standard characters by default.

We dummy-coded each morphological (standard) character into binary strings 5 characters long that
were equivalent to ordered characters. For example, the character state “1” can be decomposed to “10000”, “2” can be decomposed to “11000”. A standard time-reversible binary model was used in BEAST for this partition. We verified that trees inferred with these dummy-coded characters were equivalent to trees inferred using the original dataset in PAUP and MrBayes, both of which implement ordered standard characters by default.

Because fossils can rarely be assumed to be members of the ancestral lineage of a clade (in which case an exponential prior may be more appropriate), normally distributed date priors were used. Fossil calibrations were obtained from the Date-a-Clade website (Benton and Donoghue 2007): *Galeopterus*/root (mean = 66 Mya, with sd = 1); Strepsirrhini/Haplorrhini split (mean = 60 Mya with sd = 3); Catarrhini (mean Mya = 29 with sd = 3); Cercopithecoida (mean Mya = 20 with sd = 3); and Hominini (mean = 8 with sd = 1). Additional calibrations include Strepsirrhini (mean Mya = 37 with sd = 3) (Seiffert, Simons et al. 2005) and Platyrrhini (mean Mya = 26 with sd = 3) (Takai, Anaya et al. 2000). The MCMC chain was run for 100,000,000 generations and sampled every 5,000 generations. In addition to performing the analysis a second time to ensure convergence had been reached, we used Tracer (Rambaut and Drummond 2007) to examine time-series plots to ensure that the runs had reached a stationary phase.

**Combining Morphological and Molecular Datasets**

There is currently no good way to combine taxon groups with small fractions of overlapping data, such as we have here for the extinct hominins and extant primates. Yet comparative phylogenetic statistical analysis requires a reference phylogeny. We approached this problem in three ways: combining datasets, making supertrees from separate molecular and morphological trees, and grafting trees. The supertree approach (see below) resulted in unusable trees. We therefore performed comparative analyses on the combined dataset trees and grafted trees.
**Combined Trees:** Bayesian MCMC analysis can efficiently deal with complex models resulting from combined datasets (Nylander, Ronquist et al. 2004), but is not immune to the problem of missing data. For example, we inferred a tree that included all species within the study, combining molecular and morphological datasets (Supporting Figure 1, legend at end of this document). Acceptance rates for chain swapping were very low (below 0.1), so the heated chains were cooled (temp=0.01; default is 0.2) to produce swapping acceptance rates that range from 10% to 70%. The average standard deviation of split frequencies between the MrBayes runs was less than 0.01, which indicates convergence. Including genetic data reduced posterior node support and caused changes in the topology within Hominini compared with the tree based on morphology alone. For example, *Ardipithecus ramidus* and *Pan troglodytes* grouped together with modest support in the combined tree. We also inferred a tree including only the taxa from the morphology dataset, but included molecular data for extant species. This tree resulted in a similar topology to the full combined dataset.

**Supertrees:** We also tried a supertree approach using the program PhySIC_IST (Scornavacca, Berry et al. 2008) to combine posterior morphology trees with posterior molecular trees one by one. As noted in that paper, small taxon overlap results in poorly resolved supertrees and this was our experience, too. Trees produced by this method were unusable.

**Grafting Trees:** Lastly, we grafted posterior trees from the morphological-only dataset onto the molecular trees. The morphology-only trees were pruned to exclude taxa outside the last common ancestor of *Pan* and *H. sapiens*. The branch lengths needed to be scaled to accord with the molecular tree. To do this we scaled the branch lengths of the morphology-only trees by dividing branches by the whole path length from *Pan* to *H. sapiens*, then multiplying by the molecular whole path length from *Pan* to *H. sapiens*. Next we pruned the *Pan - H. sapiens* clade from the molecular tree and grafted the rescaled morphology-only tree in its place. Finally, we replaced *H. sapiens* with the *H. sapiens - H. neanderthalensis* clade from the molecular tree. This procedure was performed on 1,000 trees from the
posterior distributions of the molecular and morphology trees (see SI Figure 1, legend at end of this document).

Differences Between the Combined, Grafted Trees, & Time Trees Do Not Affect the Results

Comparative analyses (see below) performed on the combined dataset trees (including trees in which the exaggerated branch lengths of *Paranthropus* were reduced by 50%), the grafted trees, and the time trees all produced similar results. As such, we report the grafted tree in the main text given its better resolution of the Hominini. Note that these issues do not affect our analysis of feeding time (because we lack feeding time data for extinct hominins). Also, note that some taxa, such as *Sahelanthropus*, shown in Figure 1 in the main text are absent in the comparative analysis tree (Supporting Figure 1) because we lack adequate data for their inclusion.

The Morphology Consensus Tree:

(Colobus_guereza:0.076892, Papio_anubis:0.273647, (Hylobates_lar:0.071884, Pongo_pygmaeus:0.256981, (Gorilla_gorilla:0.203993, (Pan_troglodytes:0.038132, (Sahelanthropus_tchad:0.185207, Ardipithecus_ramidus:0.084032, (Australopithecus_an:0.061546, ((Australopithecus_ga:0.072264, ((Kenyanthropus_p latyops:0.137273, (((Paranthropus_aethio:0.329054, Paranthropus_boisei:0.080671)0.58:0.121278, Paranthropus_robustus:0.109578)1.00:0.858837, (Homo_habilis:0.068153, (Homo_erectus:0.030902, Homo_sapiens:0.129412)0.95:0.083761)0.64:0.116069, Homo_rudolfensis:0.066463)0.69:0.203857)0.74:0.185139, Australopithecus_af:0.090067)0.96:0.238112)0.89:0.108304, Australopithecus_afaren:0.022796)0.97:0.157109)0.96:0.129868)0.93:0.127621)1.00:0.123666)1.00:0.193610)0.64:0.116069, Homo_rudolfensis:0.066463)0.69:0.203857)0.74:0.185139, Australopithecus_af:0.090067)0.96:0.238112)0.89:0.108304, Australopithecus_afaren:0.022796)0.97:0.157109)0.96:0.129868)0.93:0.127621)1.00:0.123666)1.00:0.193610)1.00:0.350060)1.00:0.139826);

The Combined Dataset Consensus Tree:

(Galeopterus_variegatus:0.572629, ((((((Colobus_guereza:0.006196, Colobus_polykomos:0.011145)1.00:0.028760, Colobus_angolensis:0.043320)1.00:0.125306, Piliocolobus_badius:0.010480)1.00:0.063930, (((Presbytis_comata:0.086090, Presbytis_melalophos:0.061845)1.00:0.088205, (Trachypithecus_cristatus:0.029723, Trachypithecus_observus:0.045376)0.65:0.009217, Trachypithecus_francoisi:0.089939)1.00:0.067429)0.98:0.029610, (Rhinopithecus_bieti:0.142092, Semnopithecus_entellus:0.045545, Trachypithecus_johnii:0.036832)1.00:0.101307)0.82:0.019028)0.93:0.021440)1.00:0.101092, ((((Papio_anubis:0.007581, Papio_cynocephalus:0.000889, Papio_hamadryas:0.006724)1.00:0.044813, Lophocebus_albigena:0.063785, Theropithecus_gelada:0.048942)1.00:0.065247, Cercocetus_galeritus:0.107681)0.92:0.027098, (((Macaca_fascicularis:0.059580, Macaca_fuscata:0.049010)1.00:0.024866, Macaca_raditla:0.052661)1.00:0.011405, Macaca_nigra:0.050138)1.00:0.058257)1.00:0.034534, (Cercopithecus_lhoesti:0.098273, Chlorocebus_aethiops:0.088391, Erythrocebus_patas:0.116878)1.00:0.006842)1.00:0.051962)1.00:0.097844)1.00:0.156748, (((Gorilla_gorilla:0.083975, Pan_troglodytes:0.035808, (((Homo_sapiens:0.011359, Homo_sapiens_neander:0.004540)0.66:0.006874, Homo_erectus:0.010844)0.79:0.009576, Homo_habilis:0.021097, Homo_rudolfensis:0.040316, (Paranthropus_aethio:0.110001, Paranthropus_boisei:0.027031, Paranthropus_robustus:0.043438)1.00:0.470104)0.54:0.030406, Australopithecus_af:0.051939, Kenyanthr
The Morphology and Molecular Graft Tree:

(Galeopterus_variegatus:0.571855,(Loris_tardigradus:0.479328,(Varecia_variegata:0.187989,(Hapalemur_griseus:0.0993858,Lemur_catta:0.0712347):0.0449186,(Eulemur_fulvus_albifrons:0.0341173,Eulemur_mongoz:0.0602102):0.107375):0.0566143):0.0743933,(Propithecus_leucopus:0.104946,Propithecus_verreauxi:0.0751012):0.0764752,(Avahi_laniger:0.175277,Indri_indri:0.181322):0.0229958):0.0626554):0.0328645):0.161253):0.108259,(Tarsius_bancanus:0.513338,((Callithrix_aurita:0.0485036,(Callithrix_kuhli:0.0121094,(Callithrix_geoffroyi:0.0135268,(Callithrix_jacchus:0.0037747),0.0307747):0.128567):0.0428129):0.0772135):0.00937192):0.0345879):0.0324569,((Saimiri_sciureus:0.273865,(Cebus_apella:0.073651),0.0160510,Loris_tardigradus:0.474861):0.0109133);
olfensis:0.00565532,(Homo_habilis:0.00565505,(Homo_erbuct:0.00256264,(Homo_sapiens:0.0118229,(Homo_sapiens_neander:0.0070205):0.00999482):0.0070205):0.00955302):0.0106872):0.0168868):0.0153977):0.0197686):0.00925477):0.0132753):0.0109733):0.00626541):0.0106427):0.0433387):0.0702403):0.0366899):0.110913,(((Piliocolobus_badius:0.104908,(Colobus_angolensis:0.0440045,(Colobus_guereza:0.00610861,Colobus_polykomos:0.0114185):0.0288955):0.126179):0.0647389,((Rhinopithecus_bieti:0.143255,(Semnopithecus_entellus:0.0458383,Trachypithecus_johnii:0.0366122):0.101573):0.0185167,((Presbytis_comata:0.0877418,Presbytis_melalophos:0.0609586):0.0898211,Trachypithecus_francoisi:0.0899324,Trachypithecus_crystalus:0.0298069,Trachypithecus_obscures:0.0458267):0.00936186):0.0666201):0.0298079):0.1014668):0.101017,((Cercopithecus_lhoesti:0.0980367,(Chlorocebus_aethiops:0.0890717,Erythrocebus_patas:0.117575):0.00654016):0.0520834,((Macaca_nigra:0.05026,(Macaca_radiata:0.0529066,(Macaca_fuscata:0.0497157):0.0251391):0.0117651):0.0590409,(Coccocebus_galeritus:0.107867,(Theropithecus_gelada:0.0491539,(Lophocebus_albigena:0.0641389,(Papio_cynocephalus:0.00927391,(Papio_anubis:0.00779222,Papio_hamadryas:0.00679791):0.00130645):0.0455528):0.0122448):0.0656008):0.0271141):0.0349646):0.0980995):0.157338):0.283231):0.2828):0.0324549);
The Combined Dataset Consensus Time Tree (outgroup removed):
The Morphology Consensus Time Tree:

Character Data

We extracted body mass (mean of male and female) and the percentage of the active day spent feeding from the literature (see Supplementary Table 1), being careful to distinguish feeding time from non-feeding components of feeding, such as searching for food. For these data adult mean values (both sexes) are reported. We removed *Loris tardigradus* from our dataset given that this species chews much more slowly than expected given its body and jaw size (Ross, Reed et al. 2009). Feeding time data were logit transformed (=log₁₀ (feeding_percentage / (100 - feeding_percentage)) - a standard practice for percentile data (Sokal and Rohlf 1995). Regressing log feeding time onto log body mass produces nearly identical results as regressing log (chew / (100 - chew)) onto body mass. However, the transformation was important because, when using untransformed data, impossible feeding times were sometimes predicted (e.g., >100%).

For the molar data, the occlusal surface area of the second lower molar was estimated by multiplying the buccolingual breadth by the mesiodistal length. Molar data were averaged for adult males and females. When available in the literature, we used an average of the trigonid (mesial portion of the molar) and the talonid (distal portion of the molar) buccolingual breadth. If no data were available from the lower second molar (mandibular), upper second molar (maxillary) measurements were used instead. Note that the dataset used to build the phylogeny contains characters derived from molar size (but not molar occlusal area), which is an acceptable procedure given that branch lengths are assumed to reflect rates of evolution in the character of interest.
Phylogenetic Comparative Methods

Feeding time data were logit transformed as noted above, and mass and molar size were log10 transformed. These characters were analyzed in the program BayesTraits (Pagel 1999) (http://www.evolution.rdg.ac.uk), which generates posterior distributions of phylogenetic generalized least square (PGLS) regression models. This method accounts for the non-independence among the characters that arises from common ancestry (Pagel 1997; Pagel 1999) by transforming the residuals with a variance-covariance matrix that is derived from the relevant phylogeny or from trees sampled from a Bayesian posterior probability distribution.

We first tested which model of character evolution best fits the data, model A or model B, using maximum likelihood. In BayesTraits, model A is a random walk with one parameter, the instantaneous variance of evolution. Model B has a bias parameter in addition to the variance parameter, making it a directional model of character evolution. Then the models of evolution and the regression parameters were co-estimated with lambda (\(\lambda\)), a parameter that scales the off-diagonal elements of the phylogenetic generalized least squares (PGLS) variance-covariance matrix and assesses the degree to which covariation among trait values follows the phylogeny (Pagel 1997; Pagel 1999; Freckleton, H. et al. 2002; Revell, Harmon et al. 2008). \(\lambda\) ranges from 0 (the data do not covary according to the tree) to 1, where the characters covary as implied by the phylogeny. The results from these analyses are given in Supporting Table 3 and 4.

We used the Akaike Information Criterion (AIC) to select among the models (see below). The AIC is defined as: 
\[
\text{AIC} = -2 \text{ (log likelihood)} + 2 K, \]
where the likelihood is the probability of the data given a model and K is the number of free parameters (Burnham and Anderson 2002). The model with the smallest AIC is the preferred model. \(\Delta\text{AIC} (\Delta_i)\) for each model is the difference between the AIC of the best model (smallest AIC) and each model’s AIC. To choose among models Akaike weights \((w_i)\) are calculated as 
\[
w_i = \frac{\exp(-\Delta_i/2)}{\Sigma(\exp(-\Delta_i/2))}.\]
According to the Akaike weights presented in Supporting
Table 3 and 4, we used random walk models of evolution and the ML estimate for $\lambda$ in PGLS regression models of molar size and feeding time.

The scaling parameter $\lambda$ (phylogenetic signal) was then sampled during the MCMC regression analysis, which produced posterior distributions of regression models (slopes, intercepts, and $\lambda$). We ran the analysis for 2,000,000 iterations sampling every 200 iterations with a burnin of 200,000. The rate deviation setting was adjusted so that acceptance values ranged between 0.2 and 0.4.

Based on the Bayesian phylogenetically-informed prediction method developed in Organ et al. (2007), we developed a phylogenetic outlier test. This test produces a posterior distribution of predictions for the dependent variable $\hat{y}$ in a new taxon given: (a) its value for the independent variable $x$, (b) the posterior distribution of regression models derived from the initial analysis, and (c) the phylogenetic tree. The uncertainty in the parameters of the regression model and the uncertainty of the prediction are summarized in the variance of the posterior predictive distribution. Phylogenetic information can move predictions off the regression line towards closely related sister taxa, thereby making them more precise, while accounting for phylogenetic uncertainty as opposed to conditioning the analysis on a single tree (Huelsenbeck, Rannala et al. 2000; Pagel and Lutzoni 2002). This aspect of the analysis is critical given the contention surrounding the phylogenetic tree of extinct hominins (Collard and Wood 2000; Finarelli and Clyde 2004; Strait and Grine 2004; White, WoldeGabriel et al. 2006; Gonzalez-Jose, Escapa et al. 2008; Wood and Lonergan 2008; Mounier, Marchal et al. 2009).

Because log-log regressions estimate the geometric mean as opposed to the arithmetic mean, we performed a correction when anti-logging the predictions by adding half the mean square error ($\text{MSE} = \text{SSE}/(n-p-1)$) to the prediction before the back transformation (Smith 1993; Hayes and Shonkwiler 2006). For a given species, the back transformed posterior predictive distribution of $\hat{y}$ is the plausible distribution of values given the regression model, the known character state ($x$), and the taxon’s phylogenetic position and branch lengths. If the observed value fell outside the 95% credible interval,
we took this as evidence that the value was an outlier. When the posterior predictive distribution strongly differs from a taxon’s known value in $y$, this is taken as evidence that a substantial amount of evolution in the trait has occurred in the taxon relative to related species that were included when generating the regression model – it is an evolutionary outlier for the trait. We apply this approach to study evolutionary singularities – i.e., evolutionary events or trends that occur along single branches, which are otherwise difficult to analyze using comparative approaches. However, approaches based on independent contrasts (McPeek 1995) and likelihood (Revell 2008) could be used to perform a similar tests. Our approach extends these in that it can both estimate phylogenetic signal and can easily accommodate phylogenetic uncertainly.

**Sensitivity Testing for Outlier Tests**

We explored the power to detect outliers in molar size within the extinct hominins by performing several additional tests as described above and in the main text. For example, using the combined data tree we predicted the molar size for *Gorilla gorilla* (posterior predictive mean = 309.6, $\sigma$ = 81.5, actual = 257.1, approximate p-value = 0.27) and *Ardipithecus ramidus* (posterior predictive mean = 159.4, $\sigma$ = 41.2, actual = 154.7, approximate p-value = 0.5), neither of which were hypothesized to be outliers for molar size and we obtained reasonably accurate predictions (neither were found to be phylogenetic outliers for this trait). We also predicted molar size for the genus *Paranthropus* (the robust australopithecines noted for their enlarged jaws and teeth) expecting them to be outliers. Indeed, we estimate that *P. robustus* (posterior predictive mean = 164.5, $\sigma$ = 70.6, actual = 260.62, approximate p-value = 0.06) and *P. boisei* (posterior predictive mean = 152.7, $\sigma$ = 64.5, actual = 377.4, approximate p-value = 0.013) were both phylogenetic outliers for molar size. It is possible that our results for *Homo* presented in the main text were contingent on the large molar size in *Paranthropus*, because they are inferred to be the sister group to *Homo*. To test this we inferred molar size for *Homo* and *Paranthropus*
simultaneously. Our Results remain unchanged. The only differences are slight and do not alter our conclusions.

References


Fig. S1. Integrated phylogeny for comparative analyses (cropped to show only the apes and species with molar and body mass data). (A) The phylogeny made from grafting the tree for the extinct hominids using morphology onto the extant molecular primate tree. (B) The phylogeny inferred from molecular and morphological data. (C) The time-calibrated phylogeny made from grafting the time tree for the extinct hominids using morphology onto the extant molecular primate tree. (D) The time-calibrated phylogeny inferred from molecular and morphological data. Labels at nodes are posterior probability support. All four distributions of trees were used to analyze trait evolution, although no differences were found among them. Some extinct hominids shown in Fig. 1 are not present here, because they were not included in the character analysis (because of inadequate molar or body size data).

Other Supporting Information Files

Si Appendix (PDF)
Table S1 (DOC)
Table S2 (DOC)
Table S3 (DOC)
Table S4 (DOC)