

University of South Bohemia in České Budějovice
Faculty of Science

**Evolution of life history and behavior in Hominidae:
Towards phylogenetic reconstruction of the chimpanzee-
human last common ancestor**

RNDr. Thesis

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Annotation

The origin of the fundamental behavioral differences between humans and our closest living relatives is one of the central issues of evolutionary anthropology. In this study we performed a series of phylogenetic comparative analyses using 65 selected life-history and behavioral characters for all extant hominid species to reconstruct the ancestral character states of the last common ancestors of Hominidae, Homininae and Hominini (the chimpanzee-human last common ancestor). These analyses show that many fundamental behavioral and life-history attributes of hominids (including humans) are evidently ancient and likely inherited from the common ancestor of all hominids. On the other hand, numerous behaviors present in extant great apes represent their own terminal autapomorphies (both uniquely derived and homoplastic). We demonstrate that phylogenetic reconstruction of ancestral states is able to provide a detailed suite of behavioral, ecological and life-history characters for each hypothetical ancestor. The living great apes therefore play an important role for the identification of the traits found in the chimpanzee-human last common ancestor, some of which are likely to represent behaviors of the fossil hominins.

Declaration [in Czech]

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Pavel Duda is the first and corresponding author of the study. He conceived and designed the study with J. Zrzavý, collected the data, analyzed the data, prepared the artworks and co-wrote the paper with J. Zrzavý.

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Evolution of life history and behavior in Hominidae: Towards phylogenetic reconstruction of the chimpanzee–human last common ancestor

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ABSTRACT

The origin of the fundamental behavioral differences between humans and our closest living relatives is one of the central issues of evolutionary anthropology. The prominent, chimpanzee-based referential model of early hominin behavior has recently been challenged on the basis of broad multispecies comparisons and newly discovered fossil evidence. Here, we argue that while behavioral data on extant great apes are extremely relevant for reconstruction of ancestral behaviors, these behaviors should be reconstructed trait by trait using formal phylogenetic methods. Using the widely accepted hominoid phylogenetic tree, we perform a series of character optimization analyses using 65 selected life-history and behavioral characters for all extant hominid species. This analysis allows us to reconstruct the character states of the last common ancestors of Hominoidea, Hominidae, and the chimpanzee–human last common ancestor. Our analyses demonstrate that many fundamental behavioral and life-history attributes of hominids (including humans) are evidently ancient and likely inherited from the common ancestor of all hominids. However, numerous behaviors present in extant great apes represent their own terminal autapomorphies (both uniquely derived and homoplastic). Any evolutionary model that uses a single extant species to explain behavioral evolution of early hominins is therefore of limited use. In contrast, phylogenetic reconstruction of ancestral states is able to provide a detailed suite of behavioral, ecological and life-history characters for each hypothetical ancestor. The living great apes therefore play an important role for the confident identification of the traits found in the chimpanzee–human last common ancestor, some of which are likely to represent behaviors of the fossil hominins.

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Introduction

Reconstructing the ethology and ecology of the hypothetical chimpanzee–human last common ancestor ('CHLCA' hereinafter) and early hominins is among the central issues of evolutionary anthropology (e.g., Lovejoy, 1981; Tooby and DeVore, 1987; Stanford and Allen, 1991; McGrew, 2010a). The intense interest in this issue has resulted in several different approaches to modeling the behavior of extinct hominins (Stanford and Allen, 1991).

Non-referential modeling (also referred to as 'conceptual' or 'strategic' modeling) (Tooby and DeVore, 1987; Foley and Lee, 1989; Whiten et al., 2010) attempts to reconstruct the behavior of hypothetical ancestors using rules derived from evolutionary biology and behavioral ecology. These conceptual models are based on the

implicit assumption that only a limited number of possible behaviors or strategies exist given the morphology and physiology of the species and the prevailing environmental constraints. Given this assumption, one is able to 'predict' ancestral behavior on the basis of general evolutionary principles (Wrangham, 1987).

By contrast, referential modeling (e.g., McGrew, 1981) explicitly relies on knowledge of the ethology, ecology or cognitive skills of a particular species. Subsequent analyses use this reference species as a template for inferring the traits that are most likely ancestral to the condition of a second extant species. Such referential modeling could be based on homology (similarity through shared descent), e.g., a comparison of human ancestors with chimpanzees (McGrew, 1981), or analogy (similarity through shared but independently evolved ecological or social adaptations), e.g., a comparison of human ancestors with savanna baboons and their relatives (DeVore and Washburn, 1963; Jolly, 1970, 2001; Skybreak, 1984) or capuchin monkeys (Fernandes, 1991; Perry, 1997; Perry et al., 2003).

Throughout the last three decades, the gradual accumulation of data on great ape behavior and the full recognition of the human

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phylogenetic position within hominids has led to the extensive utilization of extant great apes, especially chimpanzees, as referential models for the evolutionary origins of human traits (Kinzey, 1987; Di Fiore and Rendall, 1994; Rendall and Di Fiore, 1995; Kappeler and Silk, 2010; Whiten et al., 2010). The sister-group relationship between the chimpanzee–bonobo (*Pan*) and human (*Homo*) clades became a logical basis for numerous evolutionary hypotheses (Wrangham and Pilbeam, 2001; Begun, 2004). The opinion that the CHLCA was not only morphologically but also behaviorally very similar to the present-day chimpanzee (*Pan troglodytes*) became a widely held opinion (Lovejoy, 1981; McGrew, 1981; Tanner, 1981; Sarich, 1992; Pilbeam, 1996; Stanford, 1996, 2012; Wrangham and Pilbeam, 2001; Begun, 2004; Pilbeam and Young, 2004). Indeed, the image of the chimpanzee as a proxy for the early human ancestor even penetrated the popular literature (Diamond, 1992; Wrangham and Peterson, 1996; Dawkins, 2004). While chimpanzee-based models encompassed virtually all aspects of hominization, including positional behavior, reproductive biology, hunting and intergroup violence (Tuttle, 1974; Lovejoy, 1981; Stanford, 1996; Wrangham and Peterson, 1996), bonobos (*Pan paniscus*) have been conspicuously neglected in this respect, despite being equally relevant for such inferences (De Waal, 1998; Sayers and Lovejoy, 2008). This has been ascribed to an unprecedented wealth of data on *P. troglodytes* and a lack of comparable data on *P. paniscus* (McGrew, 2010a).

Some researchers, however, promoted the utility of more distantly related great ape species for explaining various aspects of human biology. There have been arguments for gorillas (Geary and Flinn, 2001; Geary et al., 2011) as well as orangutans (Schwartz, 2004, 2005; Grehan, 2006; Crompton et al., 2008) as the best models for understanding the evolution of certain aspects of human behavior. Some studies attempt to choose explicitly between two referential models based on a quantification of human-like characters in two ape species. Wrangham and Pilbeam (2001) assessed the presence/absence of 12 behavioral traits in the two species of *Pan* and in *Homo*. These authors concluded that certain behaviors found in chimpanzees are the consequence of intense scramble competition (e.g., lethal raiding, group hunting or male dominance) and that these are good candidates for ancestral traits, whereas other behaviors found in bonobos are a result of relaxed scramble competition (e.g., relaxed intergroup interactions, egalitarian males or friendship among adult females) and are likely to be derived. More recently, Geary et al. (2011) identified modal patterns for 18 traits of life history and socio-ecology in chimpanzees, gorillas and modern human hunter–gatherers and quantified the relative number of changes required for the gorilla-like and the chimpanzee-like common ancestors to achieve the observed patterns of present-day hunter–gatherers. They concluded that the gorilla-like starting point provides a more parsimonious scenario of evolution of hominin behavior and social structure than does the chimpanzee-like one.

Behavioral data on great apes are undeniably of immense value for modeling human origins. As models, extant great apes cannot be replaced by inferences drawn from fossils of purported stem hominins (McGrew, 2010a; Whiten et al., 2010). The chimpanzees play a particularly important role in identifying the shared ecological and behavioral homologies of the *Pan–Homo* clade. It has been argued that the relatedness of chimpanzees to the hominin lineage makes their behaviors “phylogenetically relevant” (Pruetz and LaDuke, 2010: 646). However, it was suggested long ago that the CHLCA had to be biologically unique and therefore not necessarily best understood by direct analogy with any *single* extant species (Tooby and DeVore, 1987; Wrangham, 1987; Marlowe, 2005). Various authors (Rendall and Di Fiore, 1995; Marlowe, 2005; Sayers and Lovejoy, 2008; Lycett et al., 2009; Whiten et al.,

2010; Sayers et al., 2012) have suggested that the behaviors of the common ancestors within the Hominoidea should be reconstructed trait by trait using multispecies comparative data and making explicit use of phylogenetic methods, thus allowing the reconstructed ancestor to possess unique traits or combinations of traits.

Phylogenetic reconstruction of ancestral states can be considered a special subcategory of referential modeling (Wrangham, 1987; Moore, 1996; Whiten et al., 2010). It is among the standard tools used to understand the processes of evolutionary adaptation. Ancestral state reconstruction is used to infer the values of a trait for internal nodes of a phylogenetic tree (representing the hypothetical common ancestors) based on the trait values of the terminal (usually extant) species and a tree topology, possibly also with consideration of branch lengths (see Pagel, 1999; Salisbury and Kim, 2001; Mooers, 2004). Application of these methods in primatology and anthropology has been advocated (Rendall and Di Fiore, 1995; Whiten et al., 2010), although their potential has long been overlooked. This is likely to be because of the preconception that behavior may be inherently more prone to homoplasy or subject to different selection regimes than morphological and genetic traits (see Rendall and Di Fiore, 2007, for a review). However, there are numerous case studies (Paterson et al., 1995; McLennan and Mattern, 2001; Stuart and Currie, 2001; Zrzavý and Řičánková, 2004; Lycett et al., 2009) and meta-analyses (e.g., DeQueiroz and Wimberger, 1993) that, using various measures of character fit on phylogeny, demonstrate ecological and behavioral characters to be no less phylogenetically informative than morphological and molecular ones.

To date, there are several examples of the application of formal phylogenetic methods that can be drawn from the study of primate behavior. They include the evolution of social organization (Di Fiore and Rendall, 1994), male–female associations (van Schaik and Kappeler, 1997), color vision and coloration (Fernandez and Morris, 2007; Kamilar et al., 2012), food sharing (Jaeggi and van Schaik, 2011), and diet and seed dispersal abilities (Gómez and Verdú, 2012) in primates as a whole. More taxonomically restricted studies concern the evolution of facial complexity and sociality in New World monkeys (Santana et al., 2012), ovulation signaling in Anthroidea (Sillén-Tullberg and Møller, 1993) and Old World monkeys (Nunn, 1999), social structure in macaques (Thierry et al., 2000; Balasubramaniam et al., 2012), tickle-induced vocalization in great apes and humans (Davila Ross et al., 2009), and cultural behavior in chimpanzees (Lycett et al., 2007, 2009). Recently, formal phylogenetic methods were applied in a study of fossil hominin behavior and material culture (Lycett, 2007, 2009a,b; Organ et al., 2011). A specific subcategory of these studies is the application of the phylogenetic approach to modern human behavior and material and nonmaterial culture (e.g., Lipo et al., 2006; Jordan et al., 2009; Mace and Jordan, 2011; Walker et al., 2011).

Attempts to use phylogenetic approach for understanding the evolution of hominid behavior are relatively recent. Identifying a plausible suite of behaviors for the CHLCA through the comparison of behaviors of extant African apes has been a primary concern of the pioneering studies by Ghiglieri (1987) and Wrangham (1987). Importantly, these studies did not use formal phylogenetic methods, which were relatively undeveloped at the time. Instead, they reasoned that the traits shared across African apes are likely to have been present in the common ancestor as well because otherwise they must have evolved independently at least twice. The results of these two studies are highly consistent in identifying a similar set of behaviors, which include a polygynous mating system, female dispersal and weak female social bonds or male-dominated intergroup encounters. Further attempts to infer behaviors in the common ancestors of the hominid lineage using

similar logic are included in studies by Wrangham and Pilbeam (2001), Begun (2004), McGrew (2010a), and Geary et al. (2011).

Following these suggestions, we created a character set consisting of 65 characters for all seven extant hominid species (including humans) and for 12 outgroup species, including representatives of all hylobatid genera and selected well-studied species of cercopithecoidea primates. This character set has been framed to include human attributes that are frequently referred to in studies concerning the origin of human behavior, such as life-history characteristics, socio-sexual behavior, sexual morphology and socio-ecology, along with other behavioral characters such as cultural diversity, tool use, shelter construction and locomotion. We performed a series of maximum-parsimony (i.e., cladistic) and maximum-likelihood character optimization analyses (i.e., mapping the character states on the hominoid phylogenetic tree) in order to determine the best-supported sequences of evolutionary changes across characters. The aim of this study is to assess the amount of evolutionary change that characterizes the extant species and their ancestors, to reconstruct likely (and less likely) behaviors of the ancestors of the hominid (sub)clades with an emphasis on ancestral Hominidae (great apes), ancestral Homininae (African apes) and the CHLCA (the last common ancestor of Panini and Hominini) and to assign extant species attributes to phylogenetic ranks ('phylostrata') in order to evaluate how these ancestral phenotypes contribute to the behavioral suites of extant hominid species.

Materials and methods

Ingroup and outgroup taxa and adopted phylogeny

All seven extant great ape species (*P. troglodytes*, *P. paniscus*, *Gorilla gorilla*, *Gorilla beringei*, *Pongo pygmaeus* and *Pongo abelii*, plus *Homo sapiens*) were included in the analysis as ingroup terminal taxa. The species-level taxonomy from Groves (2001), Geissmann (2002), and Mootnick and Groves (2005) was used. The phylogenetic tree used for character optimization analyses was modified from Perelman et al. (2011). Two taxa not covered by Perelman et al. (2011) were added in agreement with previous studies: *G. beringei* as a sister species of *G. gorilla* (Shoshani et al., 1996; Groves, 2001) and *Hoolock hoolock* as a sister group of *Hylobates* (Roos and Geissmann, 2001; Chatterjee et al., 2009; Thinh et al., 2010; Wall et al., 2013; but see Israfil et al., 2011; Meyer et al., 2012; Springer et al., 2012).

In the phylogenetic classification adopted here (see Harrison, 2010; Wood, 2010; Wood and Harrison, 2011), all great apes (including humans) form the clade (family) Hominidae ('hominids'), and African ape species (*Gorilla*, *Pan*, *Homo*) form the clade (subfamily) Homininae ('hominines'). *Pan* species form the clade (tribe) Panini ('panins') and *Homo* and related genera fall into the clade Hominini ('hominins'), the latter having been referred to as 'family Hominidae' in older taxonomic conventions (the rest of great apes then having formed the paraphyletic 'family Pongidae'). The last common ancestor of panins and hominins, which is referred to in the literature as the 'chimpanzee–human last common ancestor' (LCA, CLCA, CHLCA or C/H LCA; Moore, 1996; Lovejoy, 2009, McGrew, 2010a), 'panin/hominin MRCA' (Wood and Harrison, 2011), 'concestor 1' (Dawkins, 2004), or '*Pan prior*' (Wrangham, 2001) is referred to here as the 'CHLCA'.

Altogether 12 species were used as outgroup species for the reconstruction of the deeper, namely, hominoid and catarrhine ancestors. The outgroups included four gibbon species (Hominoidea: Hylobatidae) representing all hylobatid genera: *Hylobates lar*, *H. hoolock*, *Symphalangus syndactylus* and *Nomascus concolor*, and eight well-sampled species of Old World monkeys

(Cercopithecoidea): three papionins (*Papio anubis*, *Theropithecus gelada*, and *Mandrillus sphinx*), two macaques (*Macaca mulatta* and *Macaca fuscata*), two cercopithecines (*Cercopithecus aethiops* and *Erythrocebus patas*) and one colobine (*Semnopithecus entellus*).

Note that any individual taxon could be viewed as an ingroup or outgroup depending on the scale of the analysis (e.g., orangutans are an ingroup for Hominidae but an outgroup for Homininae). The outgroup comparison is a simple method to determine the ancestral ingroup character state when the outgroup character states are invariant. The problem of a heterogeneous outgroup was first addressed by Maddison et al. (1984; see also Kitching et al., 1998): If two successive outgroup terminal taxa share the same single character state (forming a 'doublet'), then this character state is decisively present also in the ancestral node uniting ingroups with the nearest outgroup. Outgroups further out will have no effect on the ancestral state reconstruction. Thus, all outgroup character states beyond a nearest 'doublet' are irrelevant for ancestral state reconstruction. For example, the CHLCA is the node uniting the *Pan* species with their nearest outgroup, *Homo*. The CHLCA could be reconstructed decisively to include all character states shared by either *Pan* or *Homo* with any outgroup 'doublet' (i.e., either *Gorilla* + *Pongo*, or *Pongo* + Hylobatidae, or Hylobatidae + Cercopithecoidea). Otherwise, the CHLCA ancestral state is reconstructed as equivocal. Since all hominid ancestral nodes (Hominidae, Homininae, the CHLCA, as well as ancestral nodes of extant *Pongo*, *Gorilla* and *Pan*) are rooted by at least two successive outgroups (Cercopithecoidea and Hylobatidae for Hominidae; Cercopithecoidea, Hylobatidae, and *Pongo* for Homininae, etc.), the ancestral reconstructions can be considered well-founded. The ancestral ground pattern of Hominoidea (rooted exclusively by Cercopithecoidea) is less reliable, and the present character set is not at all suitable for reconstructing the ancestor of catarrhine primates (= Cercopithecoidea + Hominoidea clade).

To test whether reconstructed ancestral states in ingroup ancestral nodes are not affected by selection of particular cercopithecoidea species as outgroups, we experimentally modified the outgroup taxon sample. Two analyses were performed using maximum-likelihood optimization, 'binary' character set, tree with all branches equal in length). In the first analysis, the cercopithecoidea outgroup was reduced to the three species with the smallest amount of unknown and polymorphic character states, namely, one papionin (*M. mulatta*), one cercopithecine (*C. aethiops*) and one colobine (*S. entellus*), i.e., a taxon set representing one species from each of the three subclades of Cercopithecoidea. In the second analysis, the whole cercopithecoidea outgroup was excluded and only the four hylobatid species were used as the outgroup.

Character scoring

The character set is based on a large variety of literature sources (see Table 1; see Supplementary Online Material [SOM] for a detailed list of characters, character states and references). Characters were selected in order to cover the hominid 'biological' (i.e., life-history, socio-ecological and behavioral) traits that are particularly emphasized in human evolutionary studies. They included (i) life-history patterns (Mace, 2000; Hawkes and Paine, 2006; Robson and Wood, 2008), e.g., gestation length, neonatal weight, growth rate, infant development, weaning, puberty onset, age at first birth, interbirth interval, breeding seasonality, female post-reproductive lifespan, and maximum lifespan; (ii) socio-sexual behavior and sexual morphology (Lovejoy, 1981; Dixson, 1998), e.g., mating system, mating tactics, paternity success, mate choice and mate preferences, copulatory behaviors, sexual dimorphism and sexual adornments, genitalic morphology and reproductive physiology, and post-adolescent dispersal patterns

Table 1

List of characters. See SOM for details.

	Character	Number of character states	Character states
1.	Gestation length (months)	4	5–6 months; 6–7 months; 7–8 months; >8 months
2.	Neonate weight as a % of maternal weight	4	<3%; 3–5%; >5%; >10%
3.	Postnatal growth rate	4	Relatively very fast; relatively fast; accelerated; relatively slow
4.	Weaning age (cessation of breastfeeding)	4	<2 years; approx. 2–4 years; approx. 4–7 years; >7 years
5.	Age at the first molar eruption (years)	3	<2 years; 2–5 years; >5 years
6.	Age at the last molar eruption (years)	3	<8 years; approx. 8–12 years; approx. 20 years
7.	Onset of puberty	3	Less than 4 years; 6–10 years; noticeably varying, typically >10 years
8.	Age at the first female reproduction ^a	5	±5 years; ±10 years; approx. 11–15 years; approx. 16–21 years; >21 years
9.	Postponing first female reproduction	2	Early first reproduction; late first reproduction
10.	Interbirth interval ^a	5	1–3 years; 3–5 years; slightly prolonged (5–7 years); prolonged (6–8 years); strongly prolonged (>8 years)
11.	Seasonal breeding	2	Absent (year-round breeding); present (breeding season <200 days/year)
12.	Protracted post-reproductive (post-menopausal) female lifespan ^a	2	Absent; present
13.	Maximum lifespan ^a	5	<30 years; appr. 30–40 years; appr. 40–50 years; appr. 50–70 years; exceeding 70 years
14.	Philopatry (dispersal patterns)	3 ^b	Strict female philopatry; context-dependent dispersal; strict male philopatry
15.	Conjugal family as a social unit	2	Absent; present
16.	Social unit beyond family scope	2	Absent; present
17.	Male (father) presence within a group	2	Male (father) is unable to maintain proximity to a group; continuous presence of the male (father) within a group
18.	Social mating system	4 ^b	Monogamy; polygyny; multimale–multifemale (promiscuous); polyandry
19.	Male mating strategy	3 ^b	Possessive = mate guarding ^f ; consortship ^g ; opportunistic ^h
20.	Forced copulations (rape)	2	Absent (or not reported); present (reported, occurs regularly)
21.	Female mate choice (exerted preference for particular male(s))	2	Absent (female has a little opportunity to choose her mates); present (female is able to exert mate choice among resident males)
22.	Male mate preference (for female age, rank, or parity)	3 ^b	No apparent male preference reported; preference for older, higher-ranking, parous females; preference for younger (adolescent), nulliparous females
23.	Positive correlation of male rank and copulation rate	2	Absent; present
24.	Top-ranking (top-sire) ingroup male paternity success (%)	3	High (100–81%); limited (80–41%); low (less than 40%)
25.	Sexual dimorphism in body weight (male:female body weight ratio)	3	Insignificant (0.9:1 to 1.2:1); moderate (1.2:1 to 1.6:1); strong (1.6:1 to 2.6:1)
26.	Sexual dimorphism in canine size	3	Insignificant sexual dimorphism in canine size; male canines moderately larger than female canines; male canines markedly larger than female canines
27.	Sexual dimorphism in androgen-dependent sexual adornments of adult males ^c	2	Absent; present
28.	Sexual dichromatism	2	Absent; present
29.	Morphological–physiological–behavioral polymorphism of adult males	2	Absent (one adult male morph); present (two distinguishable adult sexually mature male morphs)
30.	Relative length of erected penis ^d	3	Short (>2); medium (0.5–2); long (<0.5)
31.	Baculum (os penis)	3	Absent; reduced/shortened; present
32.	Testes size ^e	4	Small (<0.25); medium (0.25–1.25); large (1.25–2.5); very large (>2.5)
33.	Copulatory plugs	2	Absent; present
34.	Ovulation	3 ^b	Well-detectable/advertized; likelihood of ovulation advertized, exact timing concealed; concealed/non-advertized
35.	Sexual skin swellings	3	Absent (or only slight tumescence of circum-vulval area); conspicuous swellings; exaggerated, prolonged or semipermanent swellings
36.	Mating initiation	2	Mount usually initiated by female approach or solicitation; mount usually initiated by male approach or courtship behavior
37.	Copulatory posture (type)	3 ^b	Dorso-ventral; ventro-ventral, male superior; ventro-ventral, female superior
38.	Copulatory posture (flexibility)	2	Fixed (invariably dorso-ventral); flexible
39.	Copulatory pattern	2	Single intromission; multiple intromission
40.	Intromission duration	4	Brief (<20 s); brief (<1 min); prolonged (>1.5 min); prolonged (>5 min)
41.	(Post)copulation calls (as a device of female social signaling)	2	Absent (not reported); present
42.	Mean (hourly) copulatory frequency	4	<0.01; <0.1; >0.1; >1
43.	Nocturnal copulations/mate guarding (sleeping together)	3	Absent; consortships occasionally continues at night, mates maintain proximity; present (prevailing and fundamental)
44.	Non-conceptive sexuality (functions)	3 ^b	Possibly paternity confusion; paternity confusion + exchange for favors; paternity confusion + female plotting
45.	Female intragroup relations, degree of cooperation among females	3 ^b	Relatively weak female bonds, only close kin support; significant cooperation among female kin; significant cooperation among female non-kin
46.	Male intragroup relations, male coalitions	3	Weak male bonds, no male coalitions; coalitions of two or more males occur occasionally; strong male bonds, characteristic tendency to form coalitions
47.	Intersexual relations	3 ^b	Males dominate females; no apparent dominance of one sex over another; females dominate males (and male status is acquired through female(s))
48.	Intergroup encounters, nature of intergroup relations	3 ^b	Affiliative ⁱ ; relatively peaceful ^j ; hostile ^k
49.	Sex-specific participation in intergroup encounters/territorial defense	2	Females are equally or more involved in intergroup encounters; males are more involved in intergroup encounters and play major role in territorial defense

(continued on next page)

Table 1 (continued)

	Character	Number of character states	Character states
50.	Stable all-male units (non-breeding groups)	2	Absent (all-male non-breeding groups have not been reported); present (all-male non-breeding or 'bachelor' groups have been reported)
51.	Multimale bisexual groups (inter-male tolerance)	2	Absent; present
52.	'Opposite-sex friendship' (special relationships between male and female)	2	Absent; present
53.	Infant (pre-weaning) mortality ^a	3	Up to 20%; 20–40%; over 40%
54.	Male-led infanticide ^a	4	Absent; rare (reported, occurs rarely); occasional (reported repeatedly, occurs occasionally); frequent (occurs regularly)
55.	Paternal care: protective function of an adult male	2	Infants receives no direct paternal protection; male (father) actively defends his offspring
56.	Paternal care: male–infant interactions	3	Virtually no male–infant interactions; occasional affiliation (play, some food sharing etc.); substantial paternal care ^l
57.	Paternal care: male (possible father) adopts weaned infant if mother dies	3	Absent; occasional; present
58.	Feeding/foraging pattern	2	Group foraging (members of the group maintain proximity during foraging and feeding); solitary foraging (group disperse during feeding and foraging)
59.	Diet	3 ^b	Folivorous (arboreal leaves or terrestrial herbaceous vegetation); frugivorous (ripe fruit); omnivorous ^m
60.	Meat proportion in diet/hunting of animal prey	4 ^b	Absent; occasional hunting or scavenging; present (cooperative arboreal hunting); present (cooperative terrestrial tool-assisted hunting)
61.	Cultural diversity (population-specific behavioral traditions)	2	Absent; present (local differences in tool use, plant use, vocal behavior etc.)
62.	Tool use ^a	4	Absent; simple (e.g., stone-handling, tool-assisted locomotion); sophisticated ⁿ ; elaborate ^o
63.	Shelter construction (nest building)	3	Shelter construction (nest building) absent; shelter construction (in form of overnight nest) present; construction of elaborate, semipermanent shelters
64.	Habitat	2	Mostly arboreal; mostly terrestrial
65.	Type of bipedalism	5 ^b	Obligate quadrupedalism; occasional bipedalism (semiplantigrade); occasional bipedalism ('midfoot/heel plantigrade'); occasional bipedalism (heel-strike plantigrade); obligate terrestrial bipedalism (and capability of running)

^a = non-additive/unordered character.

^b = scoring based exclusively on data from free-ranging populations.

^c = beard, mane, pelage, 'flanges', colored skin etc.

^d = head-body length [cm]:pars libera length [mm] ratio.

^e = mean combined testes weight [g]:mean body weight [kg] ratio.

^f = a male monopolizes a female within group.

^g = a male forms a short-term bond with a female, leaving the social group for some time.

^h = a male opportunistically mates with within-group females without restricting others to do so.

ⁱ = intergroup tolerance, peaceful intermingling, feeding, mating and infantine play etc.

^j = limited amount of non-lethal aggressive behaviors (agonistic interactions).

^k = harsh intergroup competition, lethal aggression (intercommunity killings) and genocide.

^l = strong affiliation, carrying, play, grooming and social learning etc.

^m = plant foods, mostly fruits, seeds and storage organs and animal foods.

ⁿ = tool kits including tool sets, tool composites and compound tools present.

^o = containers, complex tools and meta-tools present.

(philopatry); and (iii) socio-ecology (McGrew et al., 1996; Kappeler and Silk, 2010), e.g., social system, paternal investment, adoption, infanticide, intersexual and intrasexual relations, and coalitions and intragroup interactions. Several other characters that are of particular relevance for human evolutionary studies, such as cultural diversity (Wrangham et al., 1994; Lycett et al., 2009; Kappeler et al., 2010), tool use (McGrew, 2010a,b), shelter construction (Groves and Pi, 1985; Fruth and Hohmann, 1996; Anderson, 1998), feeding, diet, habitat use (Doran, 1996; Moore, 1996; Kaplan et al., 2000), and locomotion (Lovejoy, 1988; Crompton et al., 2008), were analyzed as well, in order to roughly characterize the ecology of the hypothetical ancestors.

Several traits that cannot be hypothesized as structurally homologous among the considered species (e.g., sexual adornments of adult males, concealed ovulation in females, cooperative hunting of animal prey and nest building) were also included in the character set. This was because they could represent nonhomologous morphological–physiological–behavioral responses to identical selective pressures (see Ghiglieri, 1987; Wrangham, 1987, for similar treatment of various aspects of social organization as

homologous phylogenetic characters; and Fernandez and Morris, 2007, for treatment of sexually selected aspects of primate morphology as homologous phylogenetic characters). Since the characters are not to be used for tree construction but for reconstruction of the ancestral ground patterns, they do not have to be fully logically independent. The parallel alternative formulation of partially overlapping characters could, in fact, be reciprocally illuminative: compare, e.g., #18 Social mating system and #19 Male mating strategy; #25 Sexual dimorphism in body weight and #26 Sexual dimorphism in canine size; #34 Ovulation and #35 Sexual skin swellings; #53 Infant mortality and #54 Male-led infanticide; #62 Tool use, and #63 Shelter construction (nest building) (see SOM for details).

Data from free-ranging populations of apes and monkeys were preferred over data from semi-free-ranging and captive groups. The behavior and life-history patterns exhibited by apes in captivity can differ from those observed in their free-ranging counterparts, showing a variety of behavioral abnormalities (Pazol and Bloomsmith, 1993; Lukas, 1999; Lukas et al., 2002; Birkett and Newton-Fisher, 2011). Different species are likely to respond in

different ways to captive environments, and no uniform response pattern should be expected across all primate species that are kept in zoos and laboratories (Hosey, 2005). For eight characters (#8 Age at the first female reproduction, #10 Interbirth interval, #12 Protracted post-reproductive female lifespan, #13 Maximum lifespan, #53 Infant mortality, #54 Male-led infanticide, #61 Cultural diversity, and #62 Tool use), the scoring of a 'prominent' character state in the 'monomorphic' character set was based exclusively on data from free-ranging populations. However, data derived from captive populations were taken into account and used for scoring of 'alternative' character states (see *Alternative character sets* below). Female life-history traits are subject to great variation in captivity in comparison with free-ranging populations. Captive females may exhibit life-history features not characteristic for free-ranging populations, such as post-reproductive lifespan (Atsalis and Margulis, 2006, 2008; see Walker and Herndon, 2008 for a review). Some behaviors are precluded by captive group management (e.g., infant mortality and infanticide) but may occur for different reasons (e.g., social stress due to overcrowding and lack of space). Moreover, cultural behavior and tool use are often stimulated by captive management (e.g., by different kinds of enrichment) and might be affected by interactions with a human audience.

For humans, data from foraging societies were considered along with the data from agricultural and industrial societies, as the modern foragers might not be useful models for the ancestral populations of *H. sapiens* (Lee and DeVore, 1968; Foley, 1988). Observed intraspecific diversity was covered using polymorphism coding (see below). No a priori hypotheses concerning evolutionary polarity of character states (plesiomorphic or apomorphic) were reflected in character scoring (e.g., '0' or '1') and the '0s' were, when applicable, used merely for absence of the trait in question, either ancestral or derived.

Direct human–ape comparison is problematic. Attempts to find ape homologs of human behavioral traits (such as controlled use of fire, language or artistic expression) can be misleading due to the extraordinary human capabilities for generating behavioral diversity without corresponding genetic change (Smith, 2011). Therefore, an alternative approach was chosen. Comparative biological data have been collected for all species of nonhuman great apes (and selected outgroups), and potential human homologs of these characters have been identified post hoc. However, the numbers of human phenotypic traits that have been analyzed from the phylogenetic point of view are beyond count (see, e.g., Varki and Altheide, 2005; Smith, 2011). As such, various hominid traits that might have played a role in framing the human condition are missing from the character set. Such traits might include, for example, 'capacity for self-recognition and self-awareness' (Gallup, 1982), 'propensity to contagious yawning' (Campbell and De Waal, 2011; Norscia and Palagi, 2011), 'conceptualization of fire' (Pruetz and LaDuke, 2010) and 'sibling availability and sibling relationships' (Geary et al., 2011).

The life-history characters were not scaled to body mass prior to analysis. Regressing traits of interest to body mass and using residuals as data in phylogenetic comparative analysis to uncover relationships between them necessarily makes the analysis biased (one of the 'deadly sins of comparative analysis' according to Freckleton, 2009). Moreover, different scaling methods tend to produce different results (Deaner et al., 2000). It is necessary to interpret the results of any character optimization analyses cautiously, and in the light of possible body mass effects.

The character set has been designed to reflect hominid life history and behavioral diversity, and character states of outgroup taxa were scored only to determine evolutionary polarity of hominid traits. Consequently, some character states for outgroup

species (e.g., aspects of social organization) were scored as polymorphic (due to overlap of character states defined primarily for hominids), or considered unknown or inapplicable (see SOM for details).

Alternative character sets

Primate species express substantial behavioral diversity and plasticity at both individual and population levels (Kappeler and van Schaik, 2002; Chapman and Rothman, 2009). Not surprisingly, this yields a high incidence of character polymorphism in character sets such as the ones used here. To begin to solve the problem of high intraspecific polymorphism and to mitigate the risks of spurious character state definition and character scoring, six character sets were created and analyzed separately.

- (1) In the basic 'polymorphic' character set, all character states reported by various studies for a given species were scored regardless of their quantitative distribution. This was done using the polymorphic scoring convention. The resulting character set comprised 25 binary and 40 multistate characters (see Tables 1 and 2). Of the multistate characters, 27 were additive (i.e., ordered; using Wagner optimization) and 13 nonadditive (i.e., unordered; using Fitch optimization).
- (2) In the 'monomorphic' character set, only the most frequent (common or prominent) character state was selected (see Table 2). Consider, for example, character #37 Copulatory posture for *H. sapiens* (Fig. 2). In the 'polymorphic' character set, all defined character states were scored, to reflect the entire cross-cultural and/or individual behavioral flexibility expressed by the human species. By contrast, in the 'monomorphic' character set, only the character state that is most common both cross-culturally and/or individually was scored (i.e., ventro-ventral copulation with a male on top; Kinsey et al., 1948; Ford and Beach, 1952; Dixon, 1998). The 'character polymorphism' does not always imply high intraspecific behavioral diversity. Sometimes the character state only reflects the diversity of previous authors' opinions (see SOM for 'prominent' and 'alternative' character states). So-called 'prominent' character states were identified based on the number of studies in support, year of publication (more recent studies were considered more reliable), nature of populations studied (free-ranging populations preferred) and polymorphism proportions (the character states most common cross-culturally and/or individually were selected).

In order to test the influence of preconceived opinions concerning hominoid evolution on the inferred evolutionary pattern, three 'biased' character sets were created using various permutations of the character scoring.

- (3) In the 'Pan-like' character set, humans and common chimpanzees (*P. troglodytes*) were scored as similar as possible (i.e., their observed intraspecific polymorphisms were limited to minimize the differences between the two species).
- (4) In the 'Gorilla-like' character set, interspecific polymorphisms in humans and western lowland gorillas (*G. gorilla*) were resolved to make the human–gorilla differences minimal.

For example, humans are polymorphic in character #48 Intergroup encounters. Human intergroup interactions range from invariably hostile intergroup encounters with occasional lethal violence (Nishida and Hiraiwa-Hasegawa, 1985; Goodall, 1986; Boesch et al., 2007; Sherrow and Amsler, 2007), shared with common chimpanzees (Wrangham, 1999; Wrangham et al., 2006;

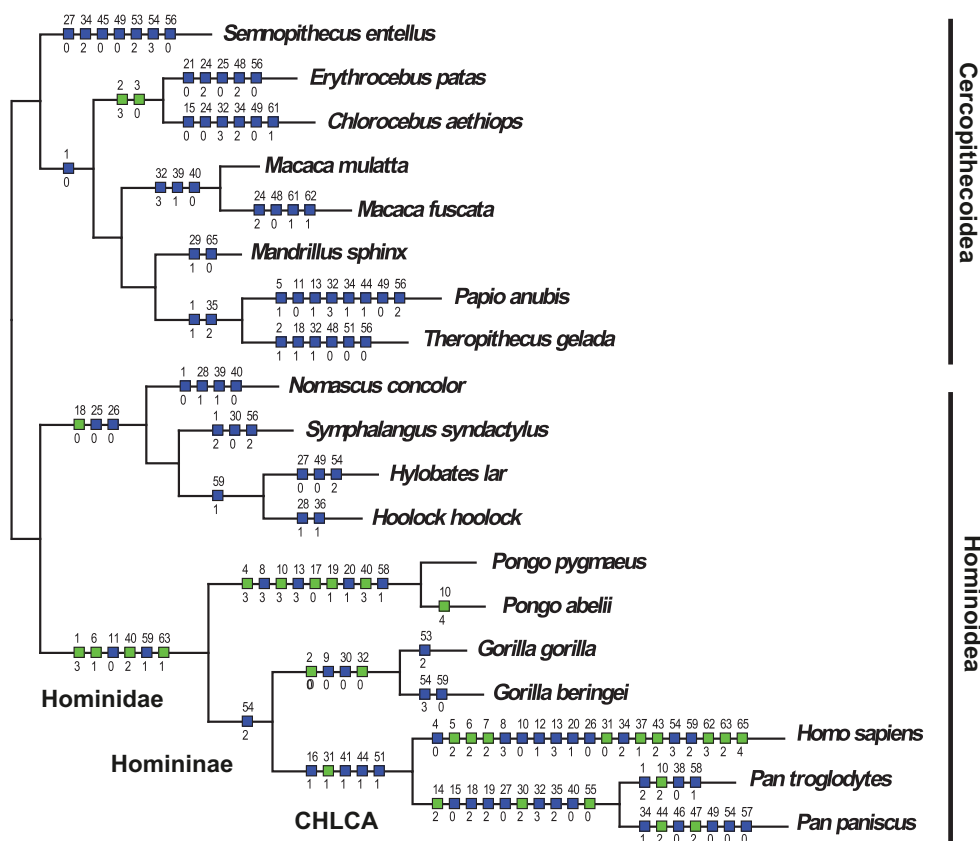


Figure 1. The amount of character change along internal and terminal branches of a tree (evolutionary derivation) based on maximum-parsimony character optimization and the ‘unambiguous’ optimization routine and the ‘monomorphic multistate’ character set (for results of optimization of other character sets see SOM). Blue rectangles represent homoplastic (parallel, convergent or reversal) apomorphies, green rectangles represent uniquely derived apomorphies. Numbers above each rectangle indicate character numbers, numbers below indicate character states (see Table 1 and List of characters in SOM). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

changes (i.e., shared character state due to causes other than common descent). The ensemble RI of the character set indicates the degree to which potential synapomorphies are exhibited on the internal branches of a tree, thus supporting the tree topology (Farris, 1989a,b; Kitching et al., 1998).

Evolutionary derivation

The six character sets were optimized on the widely accepted hominoid phylogeny (see Ingroup and outgroup taxa and phylogeny) using maximum-parsimony optimization, as implemented in NONA 2.0 (Goloboff, 1999). This allowed us to infer the amount of character change occurring along each internal and terminal branch of a tree (see Table 3; see Fig. 1 for visualization of amount of character change on a tree). This amount of change is hereinafter referred to as ‘evolutionary derivation’ (Miles and Dunham, 1993; compare ‘derivation load’ sensu Brinck, 1977; Andersen, 1979; see also Lovejoy et al., 2009, for itemizing evolutionary derivations of hominoid clades concerning skeletal morphology). The ‘unambiguous’ optimization routine was applied for inferring evolutionary derivations (UNAM: the character states are reconstructed as ‘ambiguous’ (?)) in cases when ‘slow’ and ‘fast’ optimization routines provide for different but equally parsimonious scenarios).

Phylogenetic reconstruction of ancestral states

Ancestral states for all 65 characters (from the ‘multistate’ character sets) and 77 characters (from the ‘binary’ character set)

were reconstructed using the widely accepted phylogenetic tree (see Ingroup and outgroup taxa and phylogeny) and the maximum-parsimony character optimization, utilizing three optimization routines: ‘fast’ (ACCTRAN: the character changes are placed as close to the root of the tree as possible, i.e., the number of parallelisms and convergences is minimized), ‘slow’ (DELTRAN: the character changes are assigned along branches as close to the tips as possible,

Table 3

Inferred amount of character change (evolutionary derivation) of individual species and their hypothetical ancestors, based on maximum-parsimony character optimization of the ‘polymorphic’ (a), ‘monomorphic’ (b), ‘Pan-like’ (c), ‘Gorilla-like’ (d), ‘uniquely-human’ (e) and ‘binary’ (f) character set, using the ‘unambiguous’ optimization routine. Number of homoplasies/true homologies that constitute evolutionary derivations is indicated in parentheses.

	a	b	c	d	e	f
Hominoidea	0 (0/0)	0 (0/0)	0 (0/0)	0 (0/0)	0 (0/0)	0 (0/0)
Hylobatidae	2 (1/1)	3 (2/1)	3 (2/1)	3 (2/1)	3 (3/0)	3 (2/1)
Hominidae	5 (1/4)	6 (2/4)	5 (1/4)	6 (2/4)	6 (2/4)	6 (2/4)
Pongo	10 (5/5)	9 (5/4)	9 (4/5)	9 (4/5)	8 (3/5)	8 (6/2)
Pongo pygmaeus	0 (0/0)	0 (0/0)	0 (0/0)	0 (0/0)	0 (0/0)	0 (0/0)
Pongo abelii	1 (0/1)	1 (0/1)	1 (0/1)	1 (0/1)	1 (0/1)	0 (0/0)
Homininae	1 (1/0)	1 (1/0)	1 (1/0)	1 (1/0)	1 (1/0)	1 (1/0)
Gorilla	5 (3/2)	4 (2/2)	5 (3/2)	3 (1/2)	5 (3/2)	2 (2/0)
Gorilla gorilla	0 (0/0)	1 (1/0)	1 (1/0)	0 (0/0)	1 (1/0)	1 (1/0)
Gorilla beringei	1 (1/0)	2 (2/0)	1 (1/0)	2 (2/0)	2 (2/0)	1 (1/0)
Hominini	5 (4/1)	5 (4/1)	9 (7/2)	5 (4/1)	7 (5/2)	5 (4/1)
Homo sapiens	12 (5/7)	19 (10/9)	13 (6/7)	13 (6/7)	23 (12/11)	14 (10/4)
Pan	9 (6/3)	10 (7/3)	8 (6/2)	12 (8/4)	6 (5/1)	8 (7/1)
Pan troglodytes	5 (4/1)	4 (3/1)	3 (3/0)	5 (4/1)	6 (6/0)	5 (5/0)
Pan paniscus	7 (5/2)	7 (5/2)	12 (8/4)	8 (6/2)	9 (6/3)	6 (3/3)

i.e., the number of reversals is minimized) and ‘unambiguous’ (see above).

In addition, the ancestral states of characters from the ‘multi-state monomorphic’ and ‘binary’ character sets were reconstructed using maximum-likelihood character optimization, as implemented in Mesquite 2.75 (Maddison and Maddison, 2011). The Markov k -state 1 parameter model (Mk1) that assumes an equal rate of change between all character states (Lewis, 2001) was used. The topology of the tree used in this analysis was combined from various sources based on different kinds of data, therefore no comparable branch lengths were available. As such, two alternative sets of branch lengths were used for maximum-likelihood optimization (SOM Table S.1): (i) all branch lengths were considered equal, the length of all branches having been arbitrarily set to 1 (‘all-equal’ hereinafter), (ii) branch lengths were based on maximum-likelihood estimates of nucleotide divergence, accepted from Perelman et al. (2011) (‘molecular-calibrated’ hereinafter). The lengths of branches leading to *H. hoolock* and to *G. beringei* (absent in Perelman et al., 2011) were arbitrarily set as equal to the lengths of branches leading to their sister taxa, i.e., to *H. lar* (a representative of the *Hylobates* spp.) and *G. gorilla*, respectively. The point of divergence of *G. beringei* was arbitrarily set to the midpoint of the branch leading to *G. gorilla* (see SOM Table S.1 for alternative sets of branch lengths and ‘molecular-calibrated’ branch lengths). Overall, four series of reconstructions were recovered, resulting from combinations of the two character sets (‘monomorphic multistate’ and ‘binary’) and two alternative sets of branch lengths (‘all-equal’ and ‘molecular-calibrated’).

The metric tree (phylogram) with ‘molecular-calibrated’ branch lengths has been preferred here to the time-calibrated ultrametric tree (chronogram) as an alternative to the tree with equal (= 1) branch lengths. Litsios and Salamin (2012) argued that inferring ancestral character states on time-calibrated trees could have deceiving results as it may not appropriately represent the evolution of species traits. Time-calibrated chronograms inherently include the false assumption that all sister taxa on the tree exhibit substitution rate homogeneity (i.e., identical rates of molecular evolution). Molecular-calibrated phylograms have been found most suitable for accurate reconstruction of ancestral states in various groups including primates (Litsios and Salamin, 2012), possibly because molecular substitution rates are a function of many

variables relating to life history (Fontanillas et al., 2007; Nikolaev et al., 2007; Thomas et al., 2010).

The statistical support for the ancestral state reconstructions was determined using a likelihood decision threshold of $T = 2$ (Schluter et al., 1997), indicating support at least 7.4 times greater for the character state in question than for the alternative character state(s). The reconstructed ancestral states in multistate characters were classified into four confidence categories as follows: (i) ‘confident’: a character state has a statistically significant support ($P < 0.05$) for its presence in an ancestor, based on the likelihood threshold of $T = 2$ (Schluter et al., 1997); (ii) ‘likely’: a character state has a nonsignificant support for its presence, being more supported than the sum of all alternatives; (iii) ‘debatable’: a character state has a nonsignificant support for its presence, being more supported than any single alternative (note that the confidence categories ‘likely’ and ‘debatable’ merge in binary characters); (iv) ‘unknown/speculative’: a character state unknown due to terminal polymorphism or data deficiency, equal support of two or more contradicting character states, or logical inconsistency between ancestral states inferred from various optimization analyses (Table 4; Figs. 2 and 3; SOM Table S.2).

Behavioral phylostratigraphy

Finally, the reconstructed ancestral states were used to assign individual attributes of extant species to nested ‘phylostrata’ that correspond to the successive phylogenetic nodes (= common ancestors). A ‘phylostratum’ (modified from Domazet-Lošo et al., 2007) can be considered a set of attributes of a species emerging in one of its successive common ancestors, giving phylogenetic (temporal) rank to every attribute in the character set (Fig. 4).

The evolution of the 65 characters present in four well-sampled extant species (*H. sapiens*, *P. troglodytes*, *G. gorilla* and *P. pygmaeus*) was reconstructed using the ‘monomorphic multistate’ character set and ‘fast’, ‘slow’ and ‘unambiguous’ MP optimization routines. The characters were then distributed into four ‘phylostrata’, representing the common ancestors of Hominae, Hominae, the CHLCA and the species’ own apomorphies. Character states of an extant species not matching any reconstructed ancestral state were considered novel (autapomorphic) in the given species. Only

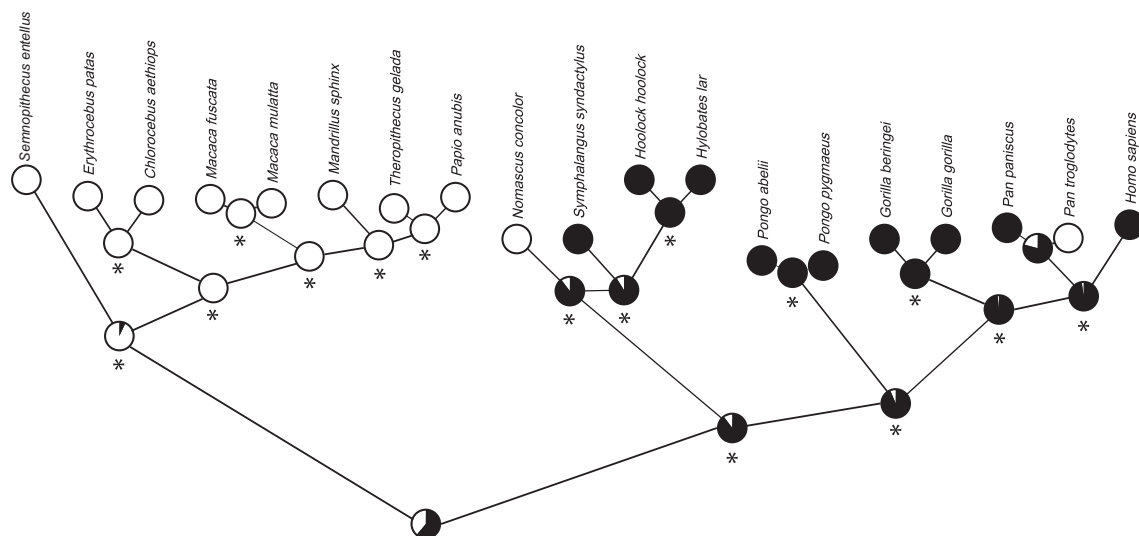


Figure 2. Reconstruction of ancestral states from the ‘binary’ character set, using maximum-likelihood character optimization, exemplified by character #37b Copulatory posture (ventro-ventral, male superior) with two character states: white = absent, black = present. Branch lengths were derived from the tree with ‘molecular-calibrated’ branch lengths. Areas of the pie charts indicate relative support for ancestral states. Significantly supported ancestral states are asterisked.

Table 4

The suite of selected life-history, socio-sexual and socio-ecological traits that characterized key common ancestors in Hominoidea, classified into four confidence categories based on maximum-likelihood support. Note that the reconstruction of the common ancestor of Hominoidea is less reliable (regardless of its statistical support) because only one outgroup (*Cercopithecoidea*) was used to determine the evolutionary polarity of character states.

	Hominoidea (last common ancestor of apes)	Hominidae (last common ancestor of great apes)	Homininae (last common ancestor of African apes)	CHLCA (chimpanzee–human last common ancestor)	Panini (last common ancestor of chimpanzee and bonobo)
'Confident'	Slow postnatal growth; first molar eruption at >3 years, last at <8 years; onset of puberty at 6–10 years; first female reproduction at around 10 years (postponed); interbirth interval <5 years; seasonal breeding; both sexes dispersal from natal groups; possessive and opportunistic male mating strategy; forced copulations absent; exerted female mate choice; sexual adornments of adult males present, sexual dichromatism absent; medium-size penis, baculum present medium-size testes; copulatory plugs absent; conspicuous sexual skin swellings; detectable ovulation; female-initiated matings; single intromission; weak male bonds, no male coalitions; multimale groups absent; infant (pre-weaning) mortality <40%; paternal protection present; group foraging; nest building absent	Gestation length >8 months; slow postnatal growth; first molar eruption at 2–5 years, last at 8–12 years; onset of puberty at 6–10 years; first female reproduction at 10–15 years (postponed); interbirth interval <5 years; year-round breeding; male-biased dispersal (female philopatry), both sexes dispersal; single male–multifemale mating system; possessive and opportunistic male mating strategy; exerted female mate choice; male preference for higher-ranking, parous females; strong sexual dimorphism in body and moderate sexual dimorphism in canine size, sexual adornments of adult males present; medium-size penis, baculum present; medium-size testes; copulatory plugs absent; female-initiated matings; flexible copulatory posture; single intromission; male dominance; multimale groups absent; infant (pre-weaning) mortality <40%; group foraging; cultural diversity (behavioral traditions) present, simple tools; nest building present	Gestation length >8 months; slow postnatal growth; first molar eruption at 2–5 years, last at 8–12 years; onset of puberty at 6–10 years; first female reproduction at 10–15 years (postponed); year-round breeding; female post-reproductive lifespan absent; maximum lifespan 40–50 years; female-biased dispersal (male philopatry), both sexes dispersal; single male–multifemale mating system; possessive and opportunistic male mating strategy; forced copulations absent; exerted female mate choice; male preference for higher-ranking, parous females; moderate sexual dimorphism in canine size, sexual adornments of adult males present; medium-size penis, baculum present; medium to small testes; copulatory plugs absent; sexual skin swellings absent or small; flexible copulatory posture; single, prolonged intromission (duration >1.5 min); male dominance; opposite-sex friendship (special relationships) present; infant (pre-weaning) mortality <40%; paternal care and paternal protection present; group foraging; no cooperative hunting; cultural diversity (behavioral traditions) present, simple tools; nest building present	Gestation length >8 months; first molar eruption at 2–5 years, last at 8–12 years; onset of puberty at 6–10 years; first female reproduction at 11–15 years (postponed); interbirth interval <5 years; year-round breeding; maximum lifespan 40–50 years; female-biased dispersal (male philopatry), both sexes dispersal; single male–multifemale mating system; possessive male mating strategy; exerted female mate choice; moderate sexual dimorphism in body weight and canine size; medium to long penis, baculum present (possibly reduced); copulatory plugs absent; sexual skin swellings absent or small; flexible copulatory posture; single, prolonged intromission (duration >1.5 min); male dominance; infant (pre-weaning) mortality <40%; paternal care and paternal protection present; group foraging; cultural diversity (behavioral traditions) present, simple tools; nest building present	Gestation length >8 months; slow postnatal growth; weaning at approx. 4–7 years; first molar eruption at 2–5 years, last at 8–12 years; onset of puberty at 6–10 years; first female reproduction at 11–15 years (postponed); year-round breeding; female-biased dispersal (male philopatry); multimale–multifemale (promiscuous) mating system; possessive and opportunistic male mating strategy; forced copulations absent; moderate sexual dimorphism in body weight and canine size, sexual adornments of adult males and male bimaturism absent; relatively long penis with reduced baculum; very large testes; exaggerated sexual swellings; male-initiated matings; single, brief intromission (duration <20 sec); (post)copulation calls present; high copulatory frequency; male dominance; multimale groups present; infant (pre-weaning) mortality <40%; direct paternal protection absent, occasional male–infant affiliation present; group foraging; frugivorous diet (ripe fruit eater); cultural diversity (behavioral traditions) present; nest building present
'Likely'	Medium-size neonates (3–10% of maternal weight); conjugal families and no semi-cohesive communities; single male–multifemale mating system; positive correlation of male rank and copulation rate; moderate sexual	Medium-size neonates (3–10% of maternal weight); female post-reproductive lifespan absent; maximum lifespan >40 years; female-biased dispersal (male philopatry); conjugal families and no semi-cohesive communities; forced copulations absent; sexual skin	Medium-size neonates (3–10% of maternal weight); weaning at approx. 4–7 years; interbirth interval 3–5 years; conjugal families and no semi-cohesive communities; positive correlation of male rank and copulation rate, high top-sire male mating success (100	Medium-size neonates (3–10% of maternal weight); weaning at approx. 4–7 years; female post-reproductive lifespan absent; conjugal families within semi-cohesive communities; opportunistic male mating strategy; forced copulations absent; positive correlation of	Medium-size neonates (3–10% of maternal weight); interbirth interval 3–5 years; no conjugal families and semi-cohesive communities; positive correlation of male rank and copulation rate, limited male paternity success (100–81%) (80–41%); advertized ovulation

Table 4 (continued)

	Hominoidea (last common ancestor of apes)	Hominidae (last common ancestor of great apes)	Homininae (last common ancestor of African apes)	CHLCA (chimpanzee–human last common ancestor)	Panini (last common ancestor of chimpanzee and bonobo)
	dimorphism in canine size; flexible copulatory posture; exchange of favors for sexual access present; moderately hostile intergroup encounters (limited amount of lethal intergroup violence), males more involved in territorial defense; no hunting and no meat in diet	swellings absent or small; positive correlation of male rank and copulation rate; prolonged intromission (duration >1.5 min); weak male bonds, no male coalitions	–81%); strong sexual dimorphism in body weight; detectable ovulation; female-initiated matings; medium copulatory frequency; female (kin) coalitions present, female non-kin coalitions absent; moderately hostile intergroup encounters (limited amount of lethal intergroup violence); regularly occurring infanticide	male rank and copulation rate, high top-sire male mating success (100–81%); sexual adornments of adult males present; medium-size testes; medium copulatory frequency; exchange of favors for sexual access present; moderately hostile intergroup encounters (limited amount of lethal intergroup violence); multimale groups present; regularly occurring infanticide; omnivorous diet	(exact timing possibly concealed due to semipermanent swellings); flexible copulatory posture (ventro-ventral, male superior posture present, female superior absent); occasional hunting of animal prey; simple tools
'Debatable'	Female-biased dispersal (male philopatry); high male paternity success (100–81%); insignificant to moderate sexual dimorphism in body weight, male bimaturation absent (one adult male morph); brief intromission (duration <1.5 min); low copulatory frequency; stable all-male non-breeding (bachelor) groups absent; infanticide absent or rare	Interbirth interval 1–3 years; maximum lifespan >50 years; high male paternity success (100–81%); male bimaturation present; low copulatory frequency; stable all-male non-breeding (bachelor) groups absent; infanticide absent or occurs rarely; omnivorous diet; hunting absent or occasional	Male bimaturation present; occasional male coalitions present; stable all-male non-breeding (bachelor) groups present, multimale groups absent; occasional infant adoption by male present; omnivorous diet; hunting absent or occasional	Interbirth interval 3–5 years; concealed ovulation; stable all-male non-breeding (bachelor) groups present; occasional infant adoption by male present; cooperative hunting of animal prey (habitat context unclear)	Strong male bonds, male coalitions present; stable all-male non-breeding (bachelor) groups present; regularly occurring infanticide; occasional infant adoption by male present; regular cooperative arboreal hunting of animal prey
'Unknown/ Speculative'	Gestation length; weaning age; female post-reproductive lifespan; maximum lifespan; male mate preference (for female age, rank, or parity); nature of female intragroup relations (cooperation and coalitions among female kin and non-kin); intersexual relations (intersexual dominance patterns); opposite-sex friendship (special relationships); paternal care (nature of male–infant interactions); infant adoption by male; dietary specialization; cultural diversity (behavioral traditions); tool use	Weaning age; ovulation detectability; nature of female intragroup relations (cooperation and coalitions among female kin and non-kin); nature of intergroup encounters and sex-specific participation in territorial defense; opposite-sex friendship (special relationships); paternal care and paternal protection; infant adoption by male	Sex-specific participation in territorial defense	Male mate preference; morphological–physiological behavioral polymorphism of adult males (male bimaturation); mating initiation (either female- or male-initiated); nature of female intragroup relations (cooperation and coalitions among female kin and non-kin); sex-specific participation in territorial defense; opposite-sex friendship (special relationships)	Female post-reproductive lifespan; exerted female mate choice; male mate preference; copulatory plugs; nature of female intragroup relations (cooperation and coalitions among female kin and non-kin); nature of intergroup encounters (severity of intergroup violence) and sex-specific participation in territorial defense; opposite-sex friendship (special relationships)

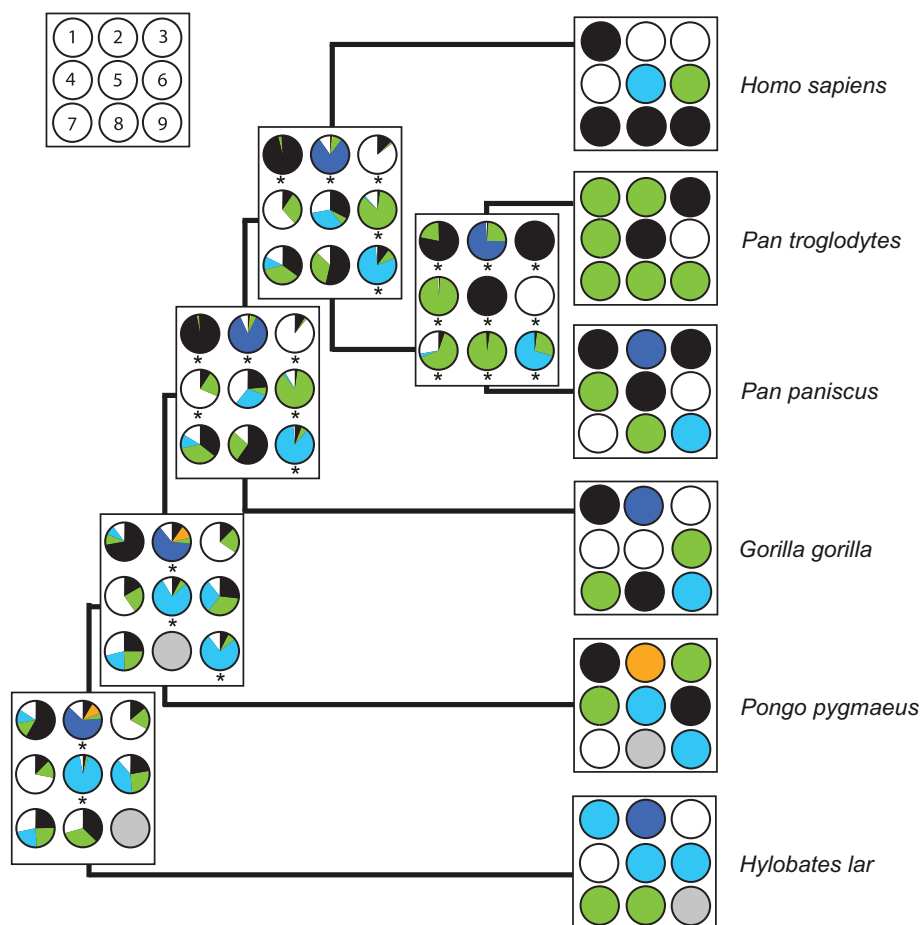


Figure 3. Reconstruction of ancestral states of selected characters using maximum-likelihood character optimization (the 'monomorphic multistate' character set and 'molecular-calibrated' branch lengths). The areas of the pie charts indicate relative support for individual ancestral states. Significantly supported ancestral states are asterisked. Selected characters: 1 = #1 Gestation length (white = 5–6 months, light blue = 6–7 months, green = 7–8 months, black = >8 months); 2 = #10 Interbirth interval (white = 1–3 years, light blue = 3–5 years, dark blue = 5–7 years, orange = 6–8 years, black = >8 years); 3 = #19 Male mating strategy (white = possessive, green = consortship, black = opportunistic); 4 = #24 Top-ranking (top-sire) ingroup male paternity success (white = high (100–81%), dark blue = limited (80–41%), black = low (less than 40%)); 5 = #32 Testes size (white = small, light blue = medium, green = large, black = very large); 6 = #40 Intromission duration (white = brief (<20 s), dark blue = brief (<1 min), green = prolonged (>1.5 min), black = prolonged (>5 min)); 7 = #54 Male-led infanticide (white = absent, light blue = rare, green = occasional, black = frequent); 8 = #56 Paternal care: male–infant interactions (white = virtually no male–infant interactions, dark blue = occasional affiliation, black = substantial paternal care, gray = unknown or inapplicable); 9 = #62 Tool use (white = absent, light blue = simple, green = sophisticated, black = elaborate, gray = unknown or inapplicable). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

positive matches between ancestral and extant species character states were considered (i.e., a pair of unknown or inapplicable character states was not considered a match).

Results and discussion

Phylogenetic properties of life-history, behavioral and ecological data

Homology criteria are elusive for life-history, behavioral and ecological traits. This is in part because these traits tend to be viewed as more context-dependent than morphological and molecular traits (Miller and Wenzel, 1995). However, the phylogenetic utility of a character (its 'secondary homology' sensu de Pinna, 1991) need not be speculative as it can be directly measured by indices of character fit on the tree.

Reconstructed evolutionary transitions among character states reveal multiple independent origins and losses of particular character states, suggesting numerous instances of parallel, convergent, and/or reversal character evolution in Hominidae (Fig. 1). However, the ensemble RI of the 'polymorphic' and 'monomorphic' character

sets (RI = 0.67 and 0.62, respectively) falls well within the range of RI values associated with other biological data sets, including those consisting of behavioral traits (Lycett et al., 2009). This suggests that primate (hominid) behavior and socio-ecology do not exhibit higher levels of homoplasy than other biological data sets. The highest possible fit (both consistency index $ci = 1$ and retention index $ri = 1$) was found in characters ##6, 7, 14, 17, 31, 43, 47, 55 and 63 (in both the 'monomorphic' and 'polymorphic' character sets), plus ##10, 19 and 45 in the 'polymorphic' character set only. Character state distribution for these characters (e.g., age at the last molar eruption, onset of puberty, presence of baculum and shelter construction) agrees well with phylogeny. These characters exhibited no convergences and/or reversals and their ancestral state reconstructions and thus might be labeled as highly confident. On the contrary, characters ##25, 34, 48 and 49 in both character sets, characters ##36 and 59 in the 'polymorphic' character set only and #45 in the 'monomorphic' character set only have $ri = 0$, indicating no contribution of these characters to reconstruction of the ancestral ground patterns. Character states for these characters (e.g., mating initiation, ovulation detectability, nature of female intragroup relations and intergroup encounters) exhibit high

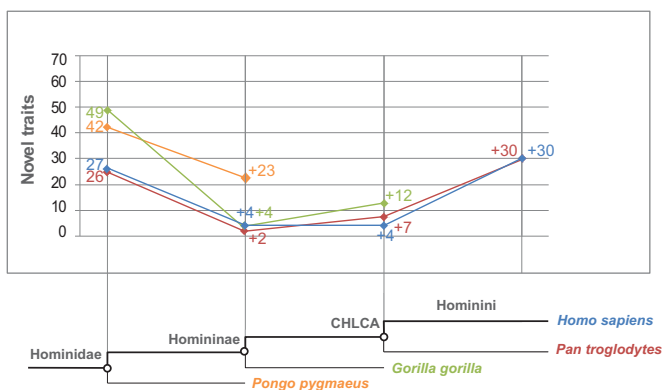


Figure 4. Phylostratigraphic map of four selected hominid species (*Homo sapiens*, *Pan troglodytes*, *Gorilla gorilla* and *Pongo pygmaeus*) describing the amount of evolutionary novelty (number of apomorphies) emerging in each phylostratum and retained in extant species, based on maximum-parsimony character optimization of the 'monomorphic multistate' character set and the 'slow' optimization routine. Four phylostrata correspond (from left to right) to the hypothetical common ancestors of Hominidae, Homininae, Hominini and to extant species. For example, out of 65 character states present in *Homo sapiens*, 27 are retained from the last common ancestor of Hominidae, four from the last common ancestor of Homininae, four from the CHLCA and 30 have originated in the human stem lineage after the human–chimpanzee split.

variation even between closely related taxonomic units. These characters exhibit mosaic evolution with a massive amount of homoplasy, due to intraspecific polymorphisms and interspecific variability (SOM Table S.2).

The different reconstruction methods (maximum-parsimony versus maximum-likelihood optimization) do not affect reconstructed ancestral states significantly. The ancestral states based on maximum-parsimony optimization are identical to those that are well supported by maximum-likelihood optimization on the tree with 'all-equal' branch lengths. However, maximum-parsimony reconstructions differ notably from the maximum-likelihood ones inferred from the tree with 'molecular-calibrated' branch lengths. Four characters (##22, 31, 54 and 60) are reconstructed with different ancestral state in the CHLCA (SOM Table S.2). This is due to the ability of maximum likelihood-based methods to take branch lengths into account (changes are more likely to occur on the long branches when their length is proportional to time).

By contrast, accounting for different branch lengths by using maximum likelihood-based methods can have dramatic effects on reconstructed ancestral states (Yang, 1996; Schluter et al., 1997; Cunningham, 1999; Pagel, 1999). When optimizing on the tree with 'all-equal' branch lengths, reconstructed hypothetical ancestors tend to possess the same character state as one of its direct extant descendant species. This is especially true of the last common ancestor of Hominidae, which in several instances possesses reconstructed ancestral states that are identical to character states possessed by orangutans. These states include forced copulations, extended lifespan, greatly prolonged intromission and absence of infanticide, which are rather unlikely to have characterized the common ancestor of all hominids. The reconstructions based on the tree with 'molecular-calibrated' branch lengths generally appear more realistic, although they have less statistical support, and should be considered more reliable given that molecular-calibrated phylograms were found to fit the assumptions of the ancestral character state more accurately (Litsios and Salamin, 2012). The number of characters with confident reconstruction of ancestral state decreased towards the root of the hominoid tree. This tendency was stronger when characters were optimized on the tree with 'molecular-calibrated' branch lengths than on the tree with 'all-equal' branch lengths, owing to long branches of the most basal hominids (orangutans) and their nearest outgroup (gibbons).

Even substantial changes of the outgroup sample have only a marginal impact on the suite of reconstructed ancestral states. Using two alternatives as outgroup samples (three cercopithecoids + hylobatids; hylobatids only), only two and five characters, respectively, were reconstructed with different ancestral states. These differences concerned only the deepest ingroup node, i.e., the ancestral Hominidae (great apes). Given that there are six ingroup ancestral nodes and 77 binary characters, the differences account for 0.43 and 1.01% of ancestral states. Most of these changes occurred when a character state for the outgroup species (gibbons) was unknown, so an outgroup was virtually absent. In some cases, however, the change occurred due to exclusion of an outgroup species with unknown or polymorphic character states, so the ancestral state that could not originally have been reconstructed unambiguously became resolved (see SOM for details).

General pattern of character evolution

Mapping the character states on the hominoid phylogenetic tree allowed to infer of the amount of character change along each internal and terminal branch of the hominoid tree (see Fig. 1). Comparison of results of MP character optimization using the 'unambiguous' optimization routine and five character sets revealed that the ratios of evolutionary derivation of individual tree branches remained similar (Table 3; SOM Fig. S.1). The only data set that stands apart is the 'uniquely-human' one (SOM Fig. S.1e). In this data set, the branch leading to *H. sapiens* is more than twice as long as any other branch. However, the 'uniquely-human' character set purposely describes humans as an exceedingly aberrant hominid by scoring only the most distinct human character states, even though the resulting set of character states is not representative of any existing human population.

Most evolutionary transitions occur on the branches leading to the ancestors of the extant hominid genera, not on the deeper branches of the hominoid tree (Fig. 1). Both gorilla species as well as both orangutan species diverged only slightly from the common ancestors of extant Gorillini and Ponginae, respectively. Gorillas are the least derived among the Hominidae. Also, the phylostratigraphic maps show that evolutionary patterns differ for the four hominid lineages (Fig. 4; SOM Fig. S.2). The retained plesiomorphic characters, originating as deep as in the common ancestor of all Hominidae, are still predominant in *P. pygmaeus* and *G. gorilla*, whereas *P. troglodytes* and *H. sapiens* are shown to be more derived (apomorphic) relative to the ancestral ground pattern.

H. sapiens is shown as the most derived of all hominid species. However, optimizations of all 'unbiased' character sets (i.e., 'multistate polymorphic', 'multistate monomorphic' and 'binary') show both chimpanzees and bonobos to be similarly distant from the CHLCA as humans (Table 3). Naturally, the actual level of evolutionary derivation (i.e., the amount of character change occurring along terminal branch of a tree) of any species could be manipulated by including numerous singularities (autapomorphies) of the species in question. The point of the present analysis is that some hominid species (chimpanzee, bonobo and human) are consistently indicated as highly derived relative to others (gorillas) when using a character set that includes traits emphasized in human evolutionary studies. Both *H. sapiens* and *P. troglodytes* are highly apomorphic, however, these apomorphies represent distinct attributes that evolved only after the *Pan*–*Homo* split (Figs. 1 and 4). Most attributes that characterize the *H. sapiens* in the character set are either unique apomorphies of the human lineage or retained plesiomorphies inherited from the last common ancestor of all hominids (Fig. 4). The inferred evolutionary pattern remains unchanged when optimizing various versions of the character set

(Table 3; SOM Fig. S.1), and whilst employing various optimization routines (SOM Fig. S.2). Attributes that have originated in the CHLCA and are still conserved in humans and/or chimpanzees (which would make *H. sapiens* a ‘third chimpanzee’ [Diamond, 1992] and *P. troglodytes* a suitable model of the CHLCA) are conspicuously less numerous.

The effects of tree topology on the outcome of character optimization are important and nontrivial. The chimpanzee and bonobo novelties are distributed along two successive branches (between CHLCA and *Pan* ancestor and between *Pan* ancestor and individual *Pan* species) whereas a comparable amount of novelties represent *H. sapiens* itself (see Fig. 1), simply because no other species of the hominin clade survived up to the present. The pectinate (i.e., asymmetrical, imbalanced) tree shape of the hominid phylogeny is indicative of numerous extinction events in the hominid lineage. Such extinction events are indeed known to have occurred in pongines (Harrison, 2010; Wood and Harrison, 2011), in basal African apes (Harrison, 2010) and also in hominins that used to be highly diversified and species-rich until very recently (Foley, 2005; and see Lahr and Foley, 2004; Bokma et al., 2012). Along with species diversity, considerable behavioral diversity has been lost, and we are unable to recover either. This problem is demonstrated by those traits that can be inferred from the fossil record, such as sexual dimorphism in body size. Reduction of sexual dimorphism in body size could have (according to the present analysis, based exclusively on extant species) taken place in the CHLCA or earlier, in the common ancestor of Homininae. The australopithecine fossils suggest, however, that CHLCA and stem hominins may have differed from both the present-day *Pan* species and modern humans in being highly sexually dimorphic (Lockwood et al., 1996, 2007; Rak et al., 2007; Spoor et al., 2007; Gordon et al., 2008; Van Arsdale and Wolpoff, 2013). This loss of size dimorphism must have occurred at least twice independently, in *Pan* and in *Homo*. The problem gets even more complicated if the recently unveiled *Ardipithecus ramidus*, which is nearly sexually monomorphic, is in fact a stem hominin (Lovejoy, 2009; Harrison, 2010). Patterns of sexual dimorphism and, by inference, the social structure in australopithecines and early *Homo* are still subject to debate (Kimbel and Deleuzene, 2009; Plavcan, 2012). Note that some discrepancies between reconstructed ancestral states and behavioral patterns inferred from the fossil record can be caused by a paucity of data and possible misinterpretation of the fossil record. This is possibly the case with dispersal patterns in early hominins and, by implication, in the CHLCA (see Koenig and Borries, 2012).

There are only a few life-history characters that seem to be more or less correlated with body size evolution (length of gestation, age of weaning, age of first reproduction, age of first and last molar eruption), but others (relative neonate body mass, neonate growth rate and interbirth interval) are not. This absence of clear correlation is especially evident for gorillas whose enlarged body size is joined with general life-history acceleration (early first reproduction of females, small neonates and rapid postnatal growth rate).

Reconstruction of the deep hominid ancestors

By performing a series of maximum-parsimony and maximum-likelihood character optimizations, all hypothetical ancestors of hominid species and clades have been reconstructed. The emphasis was put on the common ancestors of Hominidae (the great apes), Homininae (the African great apes), Panini (chimpanzees and bonobos) and the CHLCA (the last common ancestor of panins and hominins). The character state of the common ancestor of Hominoidea (apes) has only been reconstructed to provide additional information on the evolutionary polarity of hominid character states. Reconstruction of the hominoid ancestor itself should be

considered less reliable since it was rooted exclusively by a single sister clade, namely Cercopithecoidea. Note that, some of the ambiguously reconstructed (‘debatable’ or ‘unknown/speculative’) ancestral states could reflect real ancestral polymorphism, not just a lack of information.

According to present reconstructions, the hypothetical common ancestor of Hominidae (great apes) can be characterized by the following suite of life-history traits with significant support (Table 4, Figs. 2 and 3; see SOM Table S.2 for detailed list of ancestral reconstructions): gestation length over eight months accompanied by slow postnatal growth, first molar eruption at two to five years and last at eight to 12 years, puberty onset at six to 10 years, first female reproduction at 10–15 years, interbirth interval less than five (and probably less than three) years, non-seasonal breeding, and post-adolescent dispersal of both sexes depending on social and ecological context. Ancestral hominid socio-sexual and reproductive traits include a one-male/multifemale mating system with males employing possessive and opportunistic mating strategies, exerted female mate choice, male preference for older, higher-ranking females, strong sexual dimorphism in body weight and moderate sexual dimorphism in canine size, males possessing sexual adornments, medium-size penis with baculum, medium-size testes, no copulatory plugs, no (or only small) sexual swellings of adult females, female-initiated matings, flexible copulatory posture (see Fig. 2), single intromission and occasional nocturnal mate guarding. The remaining ancestral Hominidae traits in which we can be confident include male dominance, high degree of frugivory, regular shelter (nest) construction and simple tool use (see Fig. 3), as well as presence of cultural diversity (local behavioral traditions in tool use and extractive foraging, etc.).

Several other ancestral hominid traits were reconstructed with a lower degree of certainty. These traits include medium-size neonates (roughly between 3 and 10% of maternal weight), absence of female post-reproductive lifespan, maximum lifespan over 40 years, male bimaturism, female-biased post-adolescent dispersal, and absence of multimale–multifemale communities (i.e., no cohesive social units apart from one male–multifemale groups sensu Rodseth et al., 1991), absence of forced copulations, positive correlation of male rank and copulation rate with high paternity certainty of a top-ranking resident male (see Fig. 3), low copulatory frequency and prolonged intromission (with duration over 1.5 min), weak male bonds, no male coalitions, no stable all-male non-breeding groups, and no or only occasional hunting or scavenging on animal prey. The ancestral states that are uncertain for the last common ancestor of Hominidae include weaning age, ovulation detectability, cooperation and coalitions among female kin and non-kin, nature of intergroup encounters, sex-specific participation in territorial defense, presence of opposite-sex friendships, paternal care and paternal protection, infant adoption by males and degree of arboreality (Table 4).

The last common ancestor of Hominidae likely differed from the preceding common ancestor of Hominoidea (including also Hylobatidae) in possessing prolonged gestation, later weaning, non-seasonal breeding, delayed last molar eruption, male bimaturism, prolonged intromission, possibly less egalitarian intersexual relations (male dominance), higher degree of frugivory and shelter construction (nest building). The changes of life-history characters (gestation, weaning and molar eruption) might be associated with increase in body size.

Reconstructions suggest that the common ancestors of great apes (Hominidae) and African great apes (Homininae) were in most respects similar to each other in their patterns of life history and socio-ecology. The ancestor of the Homininae possibly differed from the preceding common ancestor by displaying female-biased dispersal and moderate sexual dimorphism (with male–female

body weight ratio from 1.2:1 to 1.6:1). Novel traits of the hominid ancestor also included higher copulatory frequency, higher intermale tolerance (while the existence of occasional male cooperation is debatable) and stable all-male non-breeding groups. Other likely novel traits included elevated frequency of male-led infanticide accompanied by paternal protection, paternal care (see Fig. 3), and occasional adoption of an infant by a male.

Five character complexes are worth commenting on in some detail:

- (i) Life-history data on Sumatran orangutans (*P. abelii*) collected by [Wich et al. \(2004\)](#) suggest that, compared with ancestral Hominidae, humans have undergone less of an increase in longevity than commonly assumed. These data also show that humans have experienced selection for earlier cessation of reproduction and shortening of interbirth interval. Our results support this view to some degree. Maximum-likelihood reconstruction of the last common ancestor of Hominidae, and all subsequent common ancestors in the hominid lineage, suggests high longevity (though lifespan below 50 years is more strongly supported than lifespan exceeding 50 years). Our reconstructions also suggest that age at first female reproduction occurs between 10 and 15 years, and that the interbirth interval is less than five years (Table 4 and SOM Table S.2). Thus, postponed age at first female reproduction and greatly prolonged interbirth interval (longer in Sumatran than Bornean orangutans; [Wich et al., 2004](#)) appear to be the apomorphies of *Pongo*. Slow growth and low rate of reproduction in orangutans is consistent with an extremely low rate of energy expenditure, unparalleled in primates ([Pontzer et al., 2010](#)). Orangutan life-history patterns can be a consequence of unique adaptive response to severe food shortages in their native Southeast Asian rainforests. ([Pontzer et al., 2010](#); [Russon, 2010](#); see also [Harrison and Chivers, 2007](#)).
- (ii) Recently patterns of genetic variation in various orangutan populations have confirmed male-biased dispersal in this species ([Morrogh-Bernard et al., 2010](#); [Nater et al., 2011](#); [van Noordwijk et al., 2012](#)), which contrasts to female-biased dispersal observed in African apes. [Morrogh-Bernard et al. \(2010\)](#) hypothesized that female philopatry might represent the ancestral state of early hominoids, since the female philopatry of orangutans is similar to female philopatry in Old World monkey species such as baboons (*Papio* ssp.) and vervets (*Chlorocebus aethiops*). To perceive the orangutan social system as a relict, female-retentive system ([Ghiglieri, 1987](#)) is tempting but debatable. Firstly, paleontological and paleoclimatological evidence ([Harrison and Chivers, 2007](#)), and long-term ethological studies ([van Schaik and van Hooff, 1996](#)) suggest that the orangutan social system has evolved only recently from a more or less gorilla-like basis. From this perspective, the ancestral social system of orangutans would have been characterized by higher gregariousness and a more terrestrial lifestyle ([Smith and Pilbeam, 1980](#)), accompanied by dispersal patterns more similar to those of African apes. Secondly, orangutans are not, strictly speaking, female-philopatric. Orangutan females only have shorter average dispersal distances than males ([van Schaik and van Hooff, 1996](#); [Morrogh-Bernard et al., 2010](#); [Nater et al., 2011](#)). Importantly, an opposite pattern was found in some species of gibbons, namely the siamang (*S. syndactylus*; [Lappan, 2007](#)), the white-handed gibbon (*H. lar*; [Brockelman et al., 1998](#)) and Kloss' gibbon (*Hylobates klossii*; [Tilson, 1981](#)). Genetic evidence suggests that shorter dispersal distances are common in siamang males, who frequently immigrate into groups immediately adjacent to the natal group. In contrast, females are characterized by longer dispersal distances ([Lappan, 2007](#)). Though the exact pattern of philopatry in gibbons and its social and life-history consequences are not clear ([Lappan, 2007](#)), both sexes disperse from their natal groups ([Leighton, 1987](#); [Brockelman et al., 1998](#); [Reichard and Barelli, 2008](#)). The results of our analyses suggest that the ancestral pattern of the last common ancestor of Hominidae (as well as of Homininae and the CHLCA) has been a context-dependent dispersal of both sexes, likely female-biased (though this was not significantly supported for the common ancestor of Hominidae; see Table 4 and SOM Table S.2). Reconstructed ancestral patterns suggest that while individuals of both sexes have emigrated from their natal groups, females might have had longer dispersal distances than males, whereas some males have stayed in their natal group for their whole life (as in gorillas; [Stokes et al., 2003](#); [Robbins et al., 2004](#); [Harcourt and Stewart, 2007](#)). Hence, the ancestral dispersal patterns were likely fluid, with a wider range of strategies employed, while the chimpanzee pattern of strict male-retention is derived ([Marlowe, 2004](#); [Koenig and Borries, 2012](#)). This conclusion contrasts with recent tentative reconstructions of dispersal strategies of Plio-Pleistocene hominins. *Australopithecus africanus* and *Paranthropus robustus* ([Copeland et al., 2011](#)) and *Homo neanderthalensis* were likely strictly male-philopatric ([Lalueza-Fox et al., 2011](#)), based on isotope and DNA analyses, respectively (see [Koenig and Borries, 2012](#), for discussion).
- (iii) A polygynous mating system (associated with possessive mating strategy and high paternity success of the top-ranking male; see Fig. 3) characterizes the whole sequence of ancestors in the hominid lineage, again, with the exception of the common ancestor of panins. The ancestral nature of this mating system is also supported by patterns of sexual dimorphism in extant as well as numerous extinct hominids, including members of the human stem lineage ([Lockwood et al., 1996](#); [Harrison and Chivers, 2007](#); [Lockwood et al., 2007](#); [Rak et al., 2007](#); [Spoor et al., 2007](#); [Van Arsdale and Wolpoff, 2013](#)), and by genes associated with sperm competition such as seminal protein genes and the prostate-specific transglutaminase gene ([Kingan et al., 2003](#); [Clark and Swanson, 2005](#); [Carnahan and Jensen-Seaman, 2008](#)). These genes are apparently nonfunctional in both gorilla species, suggesting that gorillas have had low sperm competition, and that their current polygynous mating system is therefore ancient. Similarly, orangutans show a longstanding stasis in the genes in question, which may be interpreted as evidence for an unchanging mating system after their divergence from the common ancestor of great apes. Chimpanzees and bonobos, on the other hand, show the fastest rate of evolution in these genes, which is indicative of selection for intense sperm competition ([Kingan et al., 2003](#); [Jensen-Seaman and Li, 2003](#)). Genetic data from humans could be interpreted as evidence for fluctuations between different mating systems or as a relaxed functional constraint in these proteins ([Carnahan and Jensen-Seaman, 2008](#)). The maintenance of functionality in these genes in the human lineage may also indicate that the ancestral human mating system was neither chimpanzee-like nor purely gorilla-like ([Carnahan and Jensen-Seaman, 2008](#)). Testes size, which might serve as a proxy for intensity of sperm competition, was reconstructed here as highly ambiguous in all common ancestors in the hominid lineage (see Fig. 3).
- (iv) The nature of female intragroup relations and the degree of cooperation among females is one of the traits in which the ancestral states are particularly difficult to infer. The only near certain conclusion is the absence of the bonobo-like pattern of

female relationships, which encompasses high cooperation and the affiliation of unrelated females ([Idani, 1991](#); [Parish and De Waal, 2000](#); [Furuichi, 2011](#)), strengthened by a frequent socio-sexual behavior ([Dixson, 1998](#)) and associated with female social dominance ([White, 1996](#); [Parish and De Waal, 2000](#); [Surbeck et al., 2011](#)). Various mutually exclusive characterizations of human female relationships can be found in the literature, ranging from kin-based cooperation ([Rodseth et al., 1991](#)) and conspicuous non-kin cooperation ([Taylor et al., 2000](#); [Marlowe, 2007](#)) to weak and uncooperative relations ([Hrdy, 1981](#); [Benenson et al., 2009](#)). The fundamental nature of female relationships is hard to assess in common chimpanzee due to females' largely solitary lifestyle ([Mitani, 2009](#)). The same applies to orangutans ([Galdikas, 1984](#); [van Schaik and van Hooff, 1996](#)). Moreover, there are notable differences between study sites in both chimpanzees ([Boesch and Boesch-Achermann, 2000](#); [Boesch et al., 2002](#); [Lehmann and Boesch, 2009](#)) and orangutans (compare [Knott et al., 2008](#), and [van Noordwijk et al., 2012](#)). In short, females of all hominids tend to express kin-based cooperation or at least greater tolerance towards female kin. This apparently applies to humans ([Rodseth et al., 1991](#)), and to some extent gorillas ([Bradley et al., 2007](#)) and possibly orangutans ([van Noordwijk et al., 2012](#)). In some species, however, female cooperation is effectively precluded by post-adolescent dispersal or a solitary lifestyle.

- (v) The presence of tool use and nest building behavior in the common ancestor of Hominidae is congruent with various lines of evidence. Besides *P. troglodytes*, orangutans are the most skilled tool users ([van Schaik and Knott, 2001](#); [van Schaik et al., 2003](#); [Krützen et al., 2011](#)). It is also possible that “their largely arboreal lifestyle curtails their technical expression,” because, as in chimpanzees, most tools are used while on the ground ([McGrew, 2010b](#): 580). Fossil evidence, morphology and behavior of present-day orangutans suggest that middle Pleistocene and Pliocene orangutan ancestors “would have been less arboreal, and more chimpanzee-like in their use of terrestrial habitats” ([Smith and Pilbeam, 1980](#): 447). The hypothesized terrestrial nature of orangutan ancestors could imply more frequent and more complex tool use in the past. Since patterns of tool use and tool production differ markedly among hominid species, some argue that the shared apomorphy of all hominids is not the tool use itself but the general ability for environmental problem solving ([McGrew, 1992](#); [Fruth and Hohmann, 1996](#)). Nest building behavior is shared in all great apes ([Fruth and Hohmann, 1996](#)) and, since it evinces conserved patterns of construction and function, some authors consider it homologous across hominid species, including humans ([Groves and Pi, 1985](#); [Fruth and Hohmann, 1996](#)). Both optimizations of the ‘multistate’ character set (on the tree with ‘all-equal’ and ‘molecular-calibrated’ branch lengths) suggest that nest building, tool use and cultural diversity (characters ##61–63; see Fig. 3) were present in all of the reconstructed common ancestors, but not in the common ancestor of all hominoids, in line with earlier suggestions ([Panger et al., 2002](#); [Whiten, 2011](#)). However, the reconstruction that is based on the behavior of free-ranging apes suggests that no ancestor in the hominid lineage, including the last common ancestor of chimpanzees and bonobos, exhibited the extensive technological skills and extensive tool kit (including tool sets, tool composites, and compound tools; [McGrew, 2010b](#)) found in present-day chimpanzees ([Lycett et al., 2009](#)). The evidence to date has outlined only a much smaller set of multiple-tradition cultures concerning tool use in *P. paniscus* ([Hohmann and Fruth, 2003](#); [Whiten, 2011](#)). On the

other hand, studies undertaken in captivity suggest that bonobos are capable of exhibiting technical skills comparable with *Pan troglodytes* ([Takeshita and Walraven, 1996](#); [Herrmann et al., 2008](#); [Gruber et al., 2010](#)). It is possible that bonobos have lost tool use in the wild not because they are cognitively incapable but because all relevant food sources can be acquired without the assistance of tools ([Hohmann and Fruth, 2003](#); [Gruber et al., 2010](#)). Further research and more precise analyses of technological skills in wild chimpanzee and bonobo communities are warranted ([Gruber et al., 2010](#); [Whiten, 2011](#)).

Evolutionary novelties of extant great ape genera

Numerous evolutionary novelties were found to originate in the lineages leading to extant hominid genera (see Fig. 1) instead of the deeper branches of the hominoid tree.

For orangutans, these include generally slow postnatal development (i.e., delayed first female reproduction, prolonged interbirth interval, postponed weaning and longer lifespan; [Wich et al., 2004](#)), ‘consortship’ as a prominent male mating strategy ([Schürmann, 1982](#); [Utami et al., 2002](#); [Knott et al., 2010](#)), the regular occurrence of forced copulations ([MacKinnon, 1974](#); [Knott and Kahlenberg, 2006](#); [Knott, 2009](#)), solitary lifestyle and inability of a dominant male to maintain long-term proximity to females ([Smith and Pilbeam, 1980](#); [van Schaik and van Hooff, 1996](#); [Harrison and Chivers, 2007](#)) accompanied by limited paternity certainty of the top-ranking resident male ([Utami et al., 2002](#); [Goossens et al., 2006](#)), ventro-ventral copulations (orangutans express, along with humans, the greatest flexibility of copulatory postures; [Dixson, 1998](#)) and greatly prolonged intromission ([Dixson and Anderson, 2004](#); [Stumpf et al., 2008](#)).

Gorillas are derived in life-history traits such as early first reproduction of females ([Harcourt and Stewart, 2007](#)), small neonates and rapid postnatal growth rate ([Leigh, 1994](#); [Robson and Wood, 2008](#)) that are tightly linked to higher reliance on vegetative foods (folivorous diet). Other derived traits include small testes (both absolutely and relatively) and a short penis ([Dixson and Anderson, 2004](#)) both linked to their social mating system. The origin of gorilla-like sexual dimorphism in body weight ([Frayr and Wolpoff, 1985](#); [Shoshani et al., 1996](#)) is uncertain. This trait would be interpreted as plesiomorphic for Hominidae if the evidence of strong sexual dimorphism in some extinct hominins ([Lockwood et al., 1996, 2007](#); [Rak et al., 2007](#); [Spoor et al., 2007](#); [Gordon et al., 2008](#); [Van Arsdale and Wolpoff, 2013](#)) was taken into account.

The true apomorphies of the last common ancestor of *Pan* include strict male philopatry ([Ghiglieri, 1987](#); [Rodseth et al., 1991](#); [Stanford, 1998](#)), disintegration of conjugal families ([Rodseth et al., 1991](#); [Chapais, 2010](#)), a multimale–multifemale social system and an opportunistic mating strategy ([Tutin, 1980](#); [Goodall, 1986](#); [Kano, 1992](#)), limited paternity success of the top-ranking male ([Constable et al., 2001](#); [Wroblewski et al., 2009](#); [Newton-Fisher et al., 2010](#)), absence of adult male sexual adornments ([Dixson, 1998](#)), an elongated penis with reduced baculum (possibly already reduced in the CHLCA), very large testes ([Dixson and Anderson, 2004](#)), exaggerated sexual skin swellings ([Dixson, 1998](#); [Nunn, 1999](#)) and advertised or semi-concealed ovulation ([Takahata et al., 1996](#); [Nunn, 1999](#); [Pawlowski, 1999](#); [Reichert et al., 2002](#)). Other apomorphies of the *Pan* ancestor likely included male-initiated copulations ([Goodall, 1986](#); [Kano, 1992](#); [Hashimoto and Furuichi, 2006](#)), reduced intromission duration ([Tutin, 1980](#); [Dixson and Anderson, 2004](#)) and higher copulatory frequency ([Dixson, 1998](#)). The numerous social structures and behavioral patterns of panins lack any clear analogs with other mammalian species ([Schwartz, 2004](#)). The remarkable similarity between the social structure of

chimpanzees and distantly related taxa such as spider monkeys demonstrates, however, that adaptive responses to the environment can produce remarkably similar social structures and behaviors (Chapman and Rothman, 2009; and see Di Fiore and Rendall, 1994). In the case of spider monkeys and chimpanzees, these include grouping pattern, lethal intergroup violence, female-directed intragroup aggression, and a reliance on similar food types (Chapman and Rothman, 2009). The number of unique chimpanzee traits as well as their similarities with very distantly related species question the validity of using chimpanzees as models to reconstruct the behavior and social structure of early hominins (Moore, 1996; Schwartz, 2004; Sayers and Lovejoy, 2008; Chapman and Rothman, 2009).

Both species of *Pan* can be further characterized by numerous species-specific apomorphies (Figs. 1 and 4). Apomorphies of the common chimpanzee include shortened gestation (Harcourt et al., 1980; Goodall, 1986; Robson and Wood, 2008), prolonged inter-birth interval (Galdikas and Wood, 1990; Wrangham et al., 1996; De Lathouwers and Van Elsacker, 2005; Robson and Wood, 2008), loss of copulatory posture flexibility (Dixson, 1998), increased hostility of intergroup encounters (Goodall, 1986; Wrangham, 1999; Wrangham et al., 2006) and more solitary lifestyle and foraging pattern (Chapman et al., 1994; Wrangham et al., 1996).

There has been a tendency to view *P. paniscus* as a 'generalized' great ape that might serve as a good model for the 'prototypic ape' (Zihlman et al., 1978; Zihlman, 1996), as well as to see bonobos as the more derived of the two species of *Pan* (Johnson, 1981; Latimer et al., 1981; and see Stanford, 1998). However, according to the present analyses, bonobos show a level of evolutionary derivation comparable with that of chimpanzees. Apomorphies of the bonobo (Fig. 1; SOM Fig. S.1) encompass exaggerated, semipermanent female swellings and semi-concealed ovulation (Kano, 1992; Wrangham, 1993; Reichert et al., 2002), intense sexual behavior that serves non-conceptive functions (Kano, 1992; Wrangham, 1993; Parish and De Waal, 2000), relatively weak male bonds and no male coalitions (White, 1996; Hohmann, 2001), female collective dominance and equal involvement of both sexes in intergroup encounters (White, 1996; Parish and De Waal, 2000; Surbeck et al., 2011), absence of male-led infanticide (Furuichi et al., 1998; Fowler and Hohmann, 2010; Furuichi, 2011) and absence of infant adoption by males (Geary, 2000).

The differences between chimpanzees and bonobos reflect different evolutionary pathways (Wrangham and Pilbeam, 2001) and could be attributed to selection against male aggression as a consequence of relaxed feeding competition: resulting in juvenilization and 'self-domestication' in the latter species (Wrangham and Pilbeam, 2001; Hare et al., 2012). Humans share important aspects of behavior with both chimpanzees and bonobos (Wrangham and Pilbeam, 2001). This might be entrenched in the species' genomes since incomplete lineage sorting exists between humans, chimpanzees and bonobos (Prüfer et al., 2012).

The chimpanzee–human last common ancestor

Our reconstructions suggest that the CHLCA differed from the last common ancestor of Homininae in the presence of communities consisting of less-related individuals, reduced sexual dimorphism in body weight (possibly in contradiction to the fossil evidence; see Lockwood et al., 2007; Rak et al., 2007; Gordon et al., 2008; see above), reduced baculum, presence of female (post)copulatory calls, presence of 'consortship' mating strategy, non-conceptive sexuality (e.g., paternity confusion and exchange of favors for sexual access), stronger male bonds and higher degree of male cooperation (male coalitions) and a likely

higher proportion of meat in the diet and regular hunting of animal prey.

The ambiguously reconstructed (unknown) ancestral states include degree of ovulation detectability, nature of female intra-group relations, intergroup encounters, presence of female post-reproductive lifespan, mating initiation, presence of female mate choice and male mate preference. While the absence of exaggerated sexual skin swellings in the common ancestors within the Hominoidea, including the CHLCA is a near certainty, the extent to which ovulation was concealed in the CHLCA is debatable. It is likely, however, that ovulation has been detectable by small swellings and by behavioral cues throughout the evolutionary history of hominids (Sayers and Lovejoy, 2008). The visual manifestation of ovulation was likely to be more subtle in the CHLCA (Pawlowski, 1999), and advertised ovulation of chimpanzees, semi-concealed ovulation in bonobos (Reichert et al., 2002) and concealed ovulation in humans represent distinct adaptations of the terminal lineages (Sillén-Tullberg and Møller, 1993; Nunn, 1999; Pawlowski, 1999).

The present reconstruction of the CHLCA (and also hominine, hominid, and hominoid ancestors) differs from preceding attempts to apply cladistic reasoning to hominid evolution (Ghiglieri, 1987; Wrangham, 1987). Admittedly, Wrangham's and Ghiglieri's studies identified a similar set of behaviors in the CHLCA, which included a polygynous mating system, female dispersal and weak female social bonds, and male-dominated intergroup encounters. However, the study by Ghiglieri (1987) also lacks data on important traits such as individual life histories and individual mating success, and his results arguably suffer from mischaracterization of several aspects of socio-ecology of particular hominid species. They include interpretation of orangutan social system as a relic, female-retentive system, similar to that of many Old World monkeys, interpretation of both chimpanzee and human social and mating systems as 'fusion–fission', 'community polygyny' and 'communal breeding', underrated male paternal investment by male gorillas (but likely overrated in bonobos) and likely an underrated role of nepotism in female gorillas as well as in humans (but clearly overrated in orangutans).

The process of hominization

Reconstructions suggest that numerous traits characterizing humans are, in fact, ancient and were already present the last common ancestor of Hominidae (some possibly inherited directly from the last common ancestor of Hominoidea; Table 4; Fig. 4; SOM fig. S.2.). These results have possible implications for speculations on the origin of seemingly unique traits of human social and sexual behavior. Various past (and recent) theories regarding the origin of human social and sexual behavior attempt to interpret these traits as adaptations resulting from selection pressures in action during the Plio-Pleistocene, after the split of the *Pan–Homo* lineages. These theories often rest upon the assumption that human behavior and socio-sexuality have evolved from a more or less chimpanzee-like basis (e.g., a promiscuous mating system and female sexual skin swellings) and then struggle to explain the subsequent transitions in the human lineage, e.g., from promiscuity to pair bonding (Gavrilets, 2012) or from advertised to concealed ovulation (Burley, 1979; Lovejoy, 1981; Daniels, 1983; Diamond, 1992). Some of the traits in question were already present in the CHLCA (Table 4; SOM Table S.2), and their origin likely dates back to the Miocene. Hence, these cannot be explained as adaptations resulting from selection pressures acting during human evolution. These ancient traits include slow postnatal growth rate (Robson and Wood, 2008), postponing the first female reproduction (Leigh, 2001;

Walker et al., 2006), relatively short interbirth interval of less than five years and year-round (non-seasonal) breeding (Hawkes and Paine, 2006), postnatal dispersal of both sexes that was female-biased (Marlowe, 2004, 2005; see above), conjugal families, polygynous mating system, male mate guarding and high paternity certainty (Buss, 2002, 2007; Simmons et al., 2004), sexual dimorphism in androgen-dependent sexual adornments, medium-sized penis and medium-sized testes (Dixson, 1998; Dixson and Anderson, 2004), absence of copulatory plugs (Dixson, 1998; Carnahan and Jensen-Seaman, 2008), absence of exaggerated sexual skin swellings (Nunn, 1999; Pawlowski, 1999), flexible copulatory posture and single, prolonged intromission (Dixson, 1998), paternal care (Hewlett, 1992; Geary, 2000) and cultural diversity (van Schaik et al., 2003; McGrew, 2010a; Whiten, 2011).

Of course, human apomorphies (i.e., traits that have likely originated in the human stem lineage only after *Pan–Homo* split) are also numerous (Figs. 1 and 4) with the long list of unique human adaptations definitely not covered by the present character set (see Varki and Altheide, 2005). Among the characters included in the present character set, the true human novelties encompass early age at weaning (Short, 1994; Sellen, 2001; Kennedy, 2005), delayed eruption of the first molar and completion of the permanent dentition (Smith et al., 1994; Macho, 2001; Robson and Wood, 2008), delayed onset of puberty (Mace, 2000; Parent et al., 2003), shortened interbirth interval (particularly among agricultural and industrialized populations; Short, 1994; Mace, 2000), protracted post-reproductive female lifespan (menopause; Hawkes et al., 1998; Mace, 2000; Hawkes, 2003) and extended lifespan (Kaplan et al., 2000; Mace, 2000; Robson and Wood, 2008). Apomorphic features of socio-sexual behavior include frequent forced copulations (Wrangham and Peterson, 1996; Thornhill and Palmer, 2000; Emery Thompson, 2009; Palombit, 2010), reduction of sexual dimorphism in canine size (Thoren et al., 2006), highly concealed ovulation (though ovulation has not been really advertised in any ancestor in the hominid lineage; Nunn, 1999; Pawlowski, 1999; Geary et al., 2011; see above), frequently employed ventro-ventral copulatory posture (Kinsey et al., 1948; Ford and Beach, 1952; Dixson, 1998), and prevailing nocturnal copulations (Dixson, 1998). Also important are frequent male infanticidal behavior (Daly and Wilson, 1985; Barrett et al., 2002), broadly omnivorous diet (Kaplan et al., 2000), manufacture and use of elaborate tools (Brown, 1991; McGrew, 2010a) and, of course, a unique type of bipedal locomotion (Lovejoy, 1988; Crompton et al., 2008).

Conclusions

While the first evolutionists remained intentionally vague concerning characteristics of ape–human ancestors (Huxley, 1863; Darwin, 1871), later researchers enthusiastically used living apes as explicit models for human evolution (see Tuttle, 1974, and Latimer et al., 1981, for review and criticism). The modeling techniques employed so far have been explicitly or implicitly based on preferred referential species and have attempted to answer the question of which extant species is (behaviorally) most similar to the common ancestor. However, as pointed out by Tooby and DeVore (1987) and Sayers and Lovejoy (2008), when an ape species is singled out for modeling human evolution, its similarities to modern humans are likely to be emphasized at the expense of critically important differences. Virtually every great ape species has been suggested to represent a behavioral relic (i.e., highly conserved, possessing retained features present in the last common ancestor of Hominidae) and by implication the single best available model for behavioral

evolution of early hominins. This has been said about orangutans (Ghiglieri, 1987; Schwartz, 2004, 2005; Grehan, 2006), gorillas (Geary and Flinn, 2001; Geary et al., 2011), chimpanzees (McGrew, 1981; Tanner, 1981) and bonobos (Zihlman et al., 1978).

In contrast, phylogenetic reconstruction of ancestral states does not use individual species as models. It only utilizes species traits' distribution as an indicator of their plesiomorphic (conserved) or apomorphic (derived) nature. It therefore allows the reconstructed hypothetical hominid ancestors to possess unique combinations of traits rather than assuming that early hominids behaved like a particular extant species (Wrangham, 1987). In addition (unlike non-referential modeling), cladistics treats individual traits independently and avoids relying on unified ecological and behavioral syndromes, the possible existence of which should be tested by independent analyses rather than imposed a priori (Rendall and Di Fiore, 1995).

The present analyses show that studies of living taxa can play an important role in identifying the potential homologies of hypothetical ancestors. Our analyses demonstrate that all extant great ape species are, to a varying extent, apomorphic and their common ancestors possessed unique suites of behaviors unparalleled in extant species. We suggest that the only great apes, if any, that could be viewed as behaviorally relictual are gorillas (in agreement with Geary et al., 2011). We conclude that many fundamental behavioral and life-history attributes of hominids, including humans, are ancient and likely inherited from the common ancestor of all hominids, although numerous behaviors present in extant great apes represent terminal autapomorphies, both uniquely derived and homoplastic. Any evolutionary model that uses a single extant great ape species as the direct proxy to explain behavioral evolution of early hominins is therefore of limited use. On the contrary, phylogenetic reconstruction is able to provide detailed suites of behavioral, ecological and life-history characters for the hypothetical ancestors (Table 4) that can be tested against independent evidence from the fossil record and behavioral ecology of non-hominoid models.

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Appendix A. Supplementary material

Supplementary material associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.jhevol.2013.07.009>.

References

- Andersen, N.M., 1979. Phylogenetic inference as applied to the study of evolutionary diversification of semiaquatic bugs (Hemiptera: Gerromorpha). *Syst. Zool.* 28, 554–578.
- Anderson, J.R., 1998. Sleep, sleeping sites, and sleep-related activities: awakening to their significance. *Am. J. Primatol.* 46, 63–75.
- Atsalis, S., Margulis, S.W., 2006. Sexual and hormonal cycles in geriatric *Gorilla gorilla gorilla*. *Int. J. Primatol.* 27, 1663–1687.
- Atsalis, S., Margulis, S.W., 2008. Primate reproductive aging: from lemurs to humans. In: Atsalis, S., Margulis, S.W., Hof, P.R. (Eds.), *Primate Reproductive Aging: Interdisciplinary Topics in Gerontology*, vol. 36. Karger, Basel, pp. 186–194.
- Baker, R.R., Bellis, M.A., 2007. *Human Sperm Competition: Copulation, Masturbation and Infidelity*. Springer, Berlin.
- Balasubramaniam, K.N., Dittmar, K., Berman, C., Butovskaya, M., Cooper, M.A., Majolo, B., Ogawa, H., Schino, G., Thierry, B., De Waal, F.B.M., 2012. Hierarchical steepness and phylogenetic models: phylogenetic signals in *Macaca*. *Anim. Behav.* 83, 1207–1218.
- Barrett, L., Dunbar, R.I.M., Lycett, J., 2002. *Human Evolutionary Psychology*. Palgrave Macmillan, London.
- Begun, D.R., 2004. Enhanced cognitive capacity as a contingent fact of hominid phylogeny. In: Russon, A.E., Begun, D.R. (Eds.), *The Evolution of Thought: Evolutionary Origins of Great Ape Intelligence*. Cambridge University Press, Cambridge, pp. 15–27.
- Benenson, J.F., Markovits, H., Fitzgerald, C., Geoffroy, D., Flemming, J., Kahlenberg, S.M., Wrangham, R.W., 2009. Males' greater tolerance of same-sex peers. *Psychol. Sci.* 20, 184–190.
- Betzig, L., 1995. Medieval monogamy. *J. Fam. Hist.* 20, 181–216.
- Birkett, L.P., Newton-Fisher, N.E., 2011. How abnormal is the behaviour of captive, zoo-living chimpanzees? *PLoS ONE* 6, e20101.
- Boesch, C., Boesch-Achermann, H., 2000. *The Chimpanzees of the Tai Forest*. Oxford University Press, Oxford.
- Boesch, C., Hohmann, G., Marchant, L. (Eds.), 2002. *Behavioral Diversity of Chimpanzees and Bonobos*. Cambridge University Press, Cambridge, pp. 156–167.
- Boesch, C., Head, J., Tagg, N., Arandjelovic, M., Vigilant, L., Robbins, M.M., 2007. Fatal chimpanzee attack in Loango National Park, Gabon. *Int. J. Primatol.* 28, 1025–1034.
- Bokma, F., van den Brink, V., Stadler, T., 2012. Unexpectedly many extinct hominins. *Evolution* 66, 2969–2974.
- Bradley, B.J., Doran-Sheehy, D.M., Lukas, D., Boesch, C., Vigilant, L., 2004. Dispersed male networks in western gorillas. *Curr. Biol.* 14, 510–513.
- Bradley, B.J., Doran-Sheehy, D.M., Vigilant, L., 2007. Potential for female kin associations in wild western gorillas despite female dispersal. *Proc. Zool. Soc. Lond.* 274, 2179–2185.
- Brinck, P., 1977. Evolution and taxonomy of *Andogyrus* Ochs (Coleoptera: Gyrinidae). *Insect Syst. Evol.* 8, 241–269.
- Brockelman, W.Y., Reichard, U., Treesucon, U., Raemaekers, J.J., 1998. Dispersal, pair formation and social structure in gibbons (*Hylobates lar*). *Behav. Ecol. Sociobiol.* 42, 329–339.
- Brown, D.E., 1991. *Human Universals*. McGraw-Hill, New York.
- Burley, N., 1979. The evolution of concealed ovulation. *Am. Nat.* 114, 835–858.
- Buss, D.M., 2002. Human mate guarding. *Neuroendocrinol. Lett. Spec. Issue* 23, 23–29.
- Buss, D.M., 2007. The evolution of human mating. *Acta Psychol. Sin.* 39, 502–512.
- Campbell, M.W., De Waal, F.B.M., 2011. Ingroup-outgroup bias in contagious yawning by chimpanzees supports link to empathy. *PLoS ONE* 6, e18283.
- Carnahan, S.J., Jensen-Seaman, M.I., 2008. Hominoid seminal protein evolution and ancestral mating behavior. *Am. J. Primatol.* 70, 939–948.
- Chapais, B., 2010. The deep structure of human society: primate origins and evolution. In: Kappeler, P.M., Silk, J.B. (Eds.), *Mind the Gap: Tracing the Origins of Human Universals*. Springer, Heidelberg, pp. 19–51.
- Chapman, C.A., Rothman, J.M., 2009. Within-species differences in primate social structure: evolution of plasticity and phylogenetic constraints. *Primates* 50, 12–22.
- Chapman, C.A., White, F.J., Wrangham, R.W., 1994. Party size in chimpanzees and bonobos. In: Wrangham, R.W., McGrew, W.C., De Waal, F.B.M., Heltne, P.G. (Eds.), *Chimpanzee Cultures*. Harvard University Press, Cambridge, pp. 41–58.
- Chatterjee, H.J., Ho, S.Y.W., Barnes, I., Groves, C., 2009. Estimating the phylogeny and divergence times of primates using a supermatrix approach. *BMC Evol. Biol.* 9, 259.
- Clark, N.L., Swanson, W.J., 2005. Pervasive adaptive evolution in primate seminal proteins. *PLoS Genet.* 1, e35.
- Constable, J.L., Ashley, M.V., Goodall, J., Pusey, A.E., 2001. Noninvasive paternity assignment in Gombe chimpanzees. *Mol. Ecol.* 10, 1279–1300.
- Copeland, S.R., Sponheimer, M., de Ruiter, D.J., Lee-Thorp, J.A., Codron, D., le Roux, P.J., Grimes, V., Richards, M.P., 2011. Strontium isotope evidence for landscape use by early hominins. *Nature* 474, 76–78.
- Crofoot, M.C., Wrangham, R.W., 2010. Intergroup aggression in primates and humans: the case for a unified theory. In: Kappeler, P.M., Silk, J.B. (Eds.), *Mind the Gap: Tracing the Origins of Human Universals*. Springer, Heidelberg, pp. 171–197.
- Crompton, R.H., Vereecke, E.E., Thorpe, S.K.S., 2008. Locomotion and posture from the common hominoid ancestor to fully modern hominins, with special reference to the last common panin/hominin ancestor. *J. Anat.* 212, 501–543.
- Cunningham, C.W., 1999. Some limitations of ancestral character state reconstruction when testing evolutionary hypotheses. *Syst. Biol.* 48, 665–674.
- Daly, M., Wilson, M., 1985. Child abuse and other risks of not living with both parents. *Ethol. Sociobiol.* 6, 155–176.
- Daniels, D., 1983. The evolution of concealed ovulation and self-deception. *Ethol. Sociobiol.* 4, 69–87.
- Darwin, C., 1871. *The Descent of Man and Selection in Relation to Sex*. Murray, London.
- Davila Ross, M., Owren, M.J., Zimmermann, E., 2009. Reconstructing the evolution of laughter in great apes and humans. *Curr. Biol.* 19, 1106–1111.
- Dawkins, R., 2004. *The Ancestor's Tale: A Pilgrimage to the Dawn of Life*. Houghton-Mifflin, Boston.
- De Lathouwers, M., Van Elsacker, L., 2005. Reproductive parameters of female *Pan paniscus* and *Pan troglodytes*: quality versus quantity. *Int. J. Primatol.* 26, 55–71.
- de Pinna, M.C.C., 1991. Concepts and tests of homology in the cladistic paradigm. *Cladistics* 7, 367–394.
- De Waal, F.B.M., 1998. Reply to Stanford (1998). *Curr. Anthropol.* 39, 407–408.
- Deaner, R.O., Nunn, C.L., van Schaik, C.P., 2000. Comparative tests of primate cognition: different scaling methods produce different results. *Brain Behav. Evol.* 55, 44–52.
- DeQueiroz, A., Wimberger, P.H., 1993. The usefulness of behavior for phylogeny estimation: levels of homoplasy in behavioral and morphological characters. *Evolution* 47, 46–60.
- DeVore, I., Washburn, L.S., 1963. Baboon ecology and human evolution. In: Howel, C.F., Bourlière, F. (Eds.), *African Ecology and Human Evolution*. Aldine, New York, pp. 335–367.
- Di Fiore, A.F., Rendall, D., 1994. Evolution of social organization: a reappraisal for primates by using phylogenetic methods. *Proc. Natl. Acad. Sci.* 91, 9941–9945.
- Diamond, J.M., 1992. *The Third Chimpanzee: The Evolution and Future of the Human Animal*. Harper Collins, New York.
- Dixon, A.F., 1998. *Primate Sexuality: Comparative Studies of the Prosimians, Monkeys, Apes, and Human Beings*. Oxford University Press, New York.
- Dixon, A.F., Anderson, M.J., 2004. Sexual behavior, reproductive physiology and sperm competition in male mammals. *Physiol. Behav.* 83, 361–371.
- Domazet-Lošo, T., Brajkovic, J., Tautz, D., 2007. A phylostratigraphy approach to uncover the genomic history of major adaptations in metazoan lineages. *Trends Genet.* 23, 533–539.
- Doran, D.M., 1996. Comparative positional behavior of the African apes. In: McGrew, W.C., Marchant, L.F., Nishida, T. (Eds.), *Great Ape Societies*. Cambridge University Press, Cambridge, pp. 213–224.
- Emery Thompson, M., 2009. Human rape: revising evolutionary perspectives. In: Muller, M.N., Wrangham, R.W. (Eds.), *Sexual Coercion in Primates and Humans: An Evolutionary Perspective on Male Aggression Against Females*. Harvard University Press, Cambridge, pp. 346–374.
- Farris, J.S., 1989a. The retention index and homoplasy excess. *Syst. Zool.* 38, 406–407.
- Farris, J.S., 1989b. The retention index and the rescaled consistency index. *Cladistics* 5, 417–419.
- Fernandes, M.E.B., 1991. Tool use and predation of oysters (*Crassostrea rhizophorae*) by the tufted capuchin, *Cebus apella apella*, in brackish water mangrove swamp. *Primates* 32, 529–531.
- Fernandez, A.A., Morris, M.R., 2007. Sexual selection and trichromatic color vision in primates: statistical support for the preexisting-bias hypothesis. *Am. Nat.* 170, 10–20.
- Foley, R., 1988. Hominids, humans and hunter-gatherers: an evolutionary perspective. In: Ingold, T., Riches, D., Woodburn, J. (Eds.), *Hunters and Gatherers: History, Evolution and Social Change*. St. Martin's Press, New York, pp. 207–221.
- Foley, R., 2005. Species diversity in human evolution: challenges and opportunities. *Trans. R. Soc. South Afr.* 60, 67–72.
- Foley, R.A., Lee, P.C., 1989. Finite social space, evolutionary pathways and reconstructing hominid behavior. *Science* 243, 901–906.
- Fontanillas, E., Welch, J.J., Thomas, J.A., Bromham, L., 2007. The influence of body size and net diversification rate on molecular evolution during the radiation of animal phyla. *BMC Evol. Biol.* 7, 95.
- Ford, C.S., Beach, F.A., 1952. *Patterns of Sexual Behavior*. Eyre and Spottiswoode, London.
- Fowler, A., Hohmann, G., 2010. Cannibalism in wild bonobos (*Pan paniscus*) at Lui Kotale. *Am. J. Primatol.* 72, 509–514.
- Frayer, D.W., Wolpoff, M.H., 1985. Sexual dimorphism. *A. Rev. Anthropol.* 14, 429–473.
- Freckleton, R.P., 2009. The seven deadly sins in comparative analysis. *J. Evol. Biol.* 22, 1367–1375.
- Fruth, B., Hohmann, G., 1996. Nest building behavior in the great apes: the great leap forward? In: McGrew, W.C., Marchant, L.F., Nishida, T. (Eds.), *Great Ape Societies*. Cambridge University Press, Cambridge, pp. 225–240.
- Furuichi, T., 2011. Female contributions to the peaceful nature of bonobo society. *Evol. Anthropol.* 20, 131–142.
- Furuichi, T., Idani, G., Ihobe, H., Kuroda, S., Kitamura, K., Mori, A., Enomoto, T., Okayasu, N., Hashimoto, C., Kano, T., 1998. Population dynamics of wild bonobos (*Pan paniscus*) at Wamba. *Int. J. Primatol.* 19, 1029–1043.
- Galdikas, B.M.F., 1984. Adult female sociality among wild orangutans at Tanjung Puting Reserve. In: Small, M.F. (Ed.), *Female Primates: Studies by Women Primatologists*. Alan R. Liss, New York, pp. 217–235.
- Galdikas, B.M.F., Wood, J.W., 1990. Birth spacing patterns in humans and apes. *Am. J. Phys. Anthropol.* 83, 185–191.

- Gallup, G.G., 1982. Self-awareness and the emergence of mind in primates. *Am. J. Primatol.* 2, 237–248.
- Gavrillets, S., 2012. Human origins and the transition from promiscuity to pair-bonding. *Proc. Natl. Acad. Sci.* 109, 9923–9928.
- Geary, D.C., 2000. Evolution and proximate expression of human paternal investment. *Psychol. Bull.* 126, 55–77.
- Geary, D.C., Flinn, M.V., 2001. Evolution of human parental behavior and the human family. *Parent-Sci. Pract.* 1, 5–61.
- Geary, D.C., Bailey, D.H., Oxford, J., 2011. Reflections on the human family. In: Salmon, C., Shackelford, T. (Eds.), *The Oxford Handbook of Evolutionary Family Psychology*. Oxford University Press, New York, pp. 365–385.
- Geissmann, T., 2002. Taxonomy and evolution of gibbons. *Evol. Anthropol.* S1, 28–31.
- Ghiglieri, M.P., 1987. Sociobiology of the great apes and the hominid ancestor. *J. Hum. Evol.* 16, 319–357.
- Goloboff, P., 1999. NONA (NO NAME) ver. 2.0. Tucumán, Argentina.
- Gómez, J.M., Verdú, M., 2012. Mutualism with plants drives primate diversification. *Syst. Biol.* 61, 567–577.
- Goodall, J., 1986. *The Chimpanzees of Gombe: Patterns of Behavior*. Harvard University Press, Cambridge.
- Goossens, B., Setchell, J.M., James, S.S., Funk, S.M., Chickhi, L., Abulani, A., Ancrenaz, M., Lackman-Ancrenaz, I., Bruford, M.W., 2006. Philopatry and reproductive success in Bornean orang-utans (*Pongo pygmaeus*). *Mol. Ecol.* 15, 2577–2588.
- Gordon, A.D., Green, D.J., Richmond, B.G., 2008. Strong postcranial size dimorphism in *Australopithecus afarensis*: results from two new resampling methods for multivariate data sets with missing data. *Am. J. Phys. Anthropol.* 135, 311–328.
- Gréhan, J.R., 2006. Mona Lisa smile, the morphological enigma of human and great ape evolution. *Anat. Rec.* 289B, 139–157.
- Groves, C.P., 2001. *Primate Taxonomy*. Smithsonian Institution Press, Washington.
- Groves, C.P., Pi, J.S., 1985. From ape's nest to human fix-point. *Man Lond.* 20, 22–47.
- Gruber, T., Clay, Z., Zuberbühler, K., 2010. A comparison of bonobo and chimpanzee tool use: evidence for a female bias in the *Pan* lineage. *Anim. Behav.* 80, 1023–1033.
- Harcourt, A.H., Stewart, K.J., 2007. *Gorilla Society: Conflict, Compromise and Cooperation Between the Sexes*. The University of Chicago Press, Chicago.
- Harcourt, A.H., Fossey, D., Stewart, K.J., Watts, D.P., 1980. Reproduction in wild gorillas and some comparisons with chimpanzees. *J. Reprod. Fertil.* 28 (Suppl), 59–70.
- Hare, B., Wobber, V., Wrangham, R., 2012. The self-domestication hypothesis: evolution of bonobo psychology is due to selection against aggression. *Anim. Behav.* 83, 573–585.
- Harrison, M.E., Chivers, D.J., 2007. The orangutan mating system and the unflanged male: a product of increased food stress during the late Miocene and Pliocene? *J. Hum. Evol.* 52, 275–293.
- Harrison, T., 2010. Apes among the tangled branches of human origins. *Science* 327, 532–534.
- Hashimoto, C., Furuichi, T., 2006. Comparison of behavioral sequence of copulation between chimpanzees and bonobos. *Primates* 47, 51–55.
- Hawkes, K., 2003. Grandmothers and the evolution of human longevity. *Am. J. Hum. Biol.* 15, 380–400.
- Hawkes, K., Paine, R. (Eds.), 2006. *The Evolution of Human Life History*. School of American Research Press, Santa Fe.
- Hawkes, K., O'Connell, J.F., Jones, N.G.B., Alvarez, H., Charkov, E.L., 1998. Grandmothering, menopause, and the evolution of human life histories. *Proc. Natl. Acad. Sci.* 95, 1336–1339.
- Herrmann, E., Wobber, V., Call, J., 2008. Great apes' (*Pan troglodytes*, *Pan paniscus*, *Gorilla gorilla*, *Pongo pygmaeus*) understanding of tool functional properties after limited experience. *J. Comp. Psychol.* 122, 220–230.
- Hewlett, B.S., 1992. *Father–Child Relations: Cultural and Biosocial Contexts*. Aldine de Gruyter, New York.
- Hohmann, G., 2001. Association and social interactions between strangers and residents in bonobos (*Pan paniscus*). *Primates* 42, 91–99.
- Hohmann, G., Fruth, B., 2003. Culture in bonobos? Between-species and within species variation in behavior. *Curr. Anthropol.* 44, 563–571.
- Hosey, G.R., 2005. How does the zoo environment affect the behaviour of captive primates? *Appl. Anim. Behav. Sci.* 90, 107–109.
- Hrdy, S.B., 1981. *The Woman that Never Evolved*. Harvard University Press, Cambridge.
- Huxley, T.H., 1863. *Evidence as to Man's Place in Nature*. Williams and Norgate, London.
- Idani, G., 1991. Social relationships between immigrant and resident bonobo (*Pan paniscus*) females at Wamba. *Folia Primatol.* 57, 83–95.
- Israfil, H., Zehr, S.M., Mootnick, A.R., Ruvolo, C.M., Steiper, M.E., 2011. Unresolved molecular phylogenies of gibbons and siamangs (Family: Hylobatidae) based on mitochondrial, Y-linked, and X-linked loci indicate a rapid Miocene radiation or sudden vicariance event. *Mol. Phylogenet. Evol.* 58, 447–455.
- Jaeggi, A.V., van Schaik, C.P., 2011. The evolution of food sharing in primates. *Behav. Ecol. Sociobiol.* 65, 2125–2140.
- Jeffery, K.J., Abernethy, K.A., Tutin, C.E.G., Anthony, N.A., Bruford, M.W., 2007. Who killed Porthos? Genetic tracking of a gorilla death. *Integr. Zool.* 2, 111–119.
- Jensen-Seaman, M.I., Li, W.H., 2003. Evolution of the hominoid semenogelin genes, the major proteins of ejaculated semen. *J. Mol. Evol.* 57, 261–270.
- Johnson, S., 1981. Bonobos: are they generalized hominid prototypes or specialized insular dwarfs? *Curr. Anthropol.* 22, 363–365.
- Jolly, C.J., 1970. The seed-eaters: a new model of hominid differentiation based on a baboon analogy. *Man* 5, 5–28.
- Jolly, C.J., 2001. A proper study of mankind: analogies from the papionin monkeys and their implications for human evolution. *Yearb. Phys. Anthropol.* 44, 177–204.
- Jordan, F.M., Gray, R.D., Greenhill, S.J., Mace, R., 2009. Matrilocal residence is ancestral in Austronesian societies. *Proc. R. Soc. B-Biol. Sci.* 276, 1957–1964.
- Kamilar, J., Heesy, C.P., Bradley, B.J., 2012. Did trichromatic color vision and red hair color coevolve in primates? *Am. J. Primatol.* 75, 740–751.
- Kano, T., 1992. *The Last Ape: Pygmy Chimpanzee Behavior and Ecology*. Stanford University Press, Stanford.
- Kaplan, H., Hill, K., Lancaster, J., Hurtado, A.M., 2000. Theory of human life history evolution: diet, intelligence, and longevity. *Evol. Anthropol.* 9, 156–185.
- Kappeler, P.M., Silk, J.B. (Eds.), 2010. *Mind the Gap: Tracing the Origins of Human Universals*. Springer, Heidelberg.
- Kappeler, P.M., van Schaik, C.P., 2002. Evolution of primate social systems. *Int. J. Primatol.* 23, 707–740.
- Kappeler, P.M., Silk, J.S., Burkart, J.M., van Schaik, C.P., 2010. Primate behavior and human universals: exploring the gap. In: Kappeler, P.M., Silk, J.B. (Eds.), *Mind the Gap: Tracing the Origins of Human Universals*. Springer, Heidelberg, pp. 3–18.
- Kennedy, G.E., 2005. From ape's dilemma to weanling's dilemma: early weaning and its evolutionary context. *J. Hum. Evol.* 48, 123–145.
- Kimbel, W.H., Deleuzene, L.K., 2009. "Lucy" redux: a review of research on *Australopithecus afarensis*. *Yearb. Phys. Anthropol.* 52, 2–48.
- Kingan, S.B., Tatar, M., Rand, D.M., 2003. Reduced polymorphism in the chimpanzee semen coagulating protein Semenogelin I. *J. Mol. Evol.* 57, 159–169.
- Kinsey, A.C., Pomeroy, W.B., Martin, C.E., 1948. *Sexual Behavior in the Human Male*. W. B. Saunders Co., Philadelphia.
- Kinzey, R.W. (Ed.), 1987. *The Evolution of Human Behavior: Primate Models*. State University of New York Press, Albany.
- Kitching, J., Forey, P.L., Humphries, C.J., Williams, D.M., 1998. *Cladistics: The Theory and Practice of Parsimony Analysis*. Oxford University Press, Oxford.
- Knott, C.D., 2009. Orangutans: sexual coercion without sexual violence. In: Muller, M.N., Wrangham, R.W. (Eds.), *Sexual Coercion in Primates and Humans: An Evolutionary Perspective on Male Aggression Against Females*. Harvard University Press, Cambridge, pp. 81–111.
- Knott, C.D., Kahlenberg, S., 2006. Orangutans in perspective: forced copulations and female mating resistance. In: Bearder, S., Campbell, C.J., Fuentes, A., MacKinnon, K.C., Panger, M. (Eds.), *Primates in Perspective*. Oxford University Press, Oxford, pp. 290–305.
- Knott, C.D., Beaudrot, L., Snaith, T., White, S., Tschauner, H., Planasky, G., 2008. Female–female competition in Bornean orangutans. *Int. J. Primatol.* 29, 975–997.
- Knott, C.D., Thompson, M.E., Stumpf, R.M., McIntyre, M.H., 2010. Female reproductive strategies in orangutans, evidence for female choice and counterstrategies to infanticide in a species with frequent sexual coercion. *Proc. R. Soc. B-Biol. Sci.* 277, 105–113.
- Koenig, A., Borries, C., 2012. Hominoid dispersal patterns and human evolution. *Evol. Anthropol.* 21, 108–112.
- Krützen, M., Willems, E.P., van Schaik, C.P., 2011. Culture and geographic variation in orangutan behaviour. *Curr. Biol.* 2, 1808–1812.
- Lahr, M.M., Foley, R., 2004. Human evolution writ small. *Nature* 431, 1043–1044.
- Lalueza-Fox, C., Rosas, A., Estalrich, A., Gigli, E., Campos, P.F., García-Taberner, A., García-Vargas, S., Sánchez-Quinto, F., Ramírez, O., Civit, S., Bastir, M., Huguet, R., Santamaría, D., Gilbert, M.T.P., Willerslev, E., de la Rasilla, M., 2011. Genetic evidence for patrilocal mating behavior among Neandertal groups. *Proc. Natl. Acad. Sci.* 108, 250–253.
- Lappan, S., 2007. Patterns of dispersal in Sumatran siamangs (*Symphalangus syndactylus*): preliminary mtDNA evidence suggests more frequent male than female dispersal to adjacent groups. *Am. J. Primatol.* 69, 692–698.
- Latimer, B., White, T., Kimbel, W., Johanson, D., Lovejoy, C.O., 1981. The pygmy chimpanzee is not a living missing link in human evolution. *J. Hum. Evol.* 10, 475–488.
- Lee, R.B., DeVore, I., 1968. Problems in the study of hunters and gatherers. In: Lee, R.B., DeVore, I. (Eds.), *Man the Hunter*. Aldine, Chicago, pp. 5–12.
- Lehmann, J., Boesch, C., 2009. Sociality of the dispersing sex: the nature of social bonds in West African female chimpanzees, *Pan troglodytes*. *Anim. Behav.* 77, 377–387.
- Leigh, S.R., 1994. Ontogenetic correlates of diet in anthropoid primates. *Am. J. Phys. Anthropol.* 94, 499–522.
- Leigh, S.R., 2001. Evolution of human growth. *Evol. Anthropol.* 10, 223–236.
- Leighton, D.R., 1987. Gibbons: territoriality and monogamy. In: Smuts, B., Cheney, D.L., Seyfarth, R.M., Wrangham, R.W., Struhsaker, T.T. (Eds.), *Primate Societies*. University of Chicago Press, Chicago, pp. 135–145.
- Lewis, P.O., 2001. A likelihood approach to estimating phylogeny from discrete morphological character data. *Syst. Biol.* 50, 913–925.
- Lipo, C.P., O'Brien, M.J., Collard, M., Shennan, S. (Eds.), 2006. *Mapping Our Ancestors: Phylogenetic Approaches in Anthropology and Prehistory*. Aldine de Gruyter, New York.
- Litsios, G., Salamin, N., 2012. Effects of phylogenetic signal on ancestral state reconstruction. *Syst. Biol.* 61, 533–538.
- Lockwood, C.A., Richmond, B.G., Jungers, W.L., Kimbel, W.H., 1996. Randomization procedures and sexual dimorphism in *Australopithecus afarensis*. *J. Hum. Evol.* 31, 537–548.
- Lockwood, C.A., Menter, C.G., Moggi-Cecchi, J., Keyser, A.W., 2007. Extended male growth in a fossil hominin species. *Science* 318, 1443–1446.
- Lovejoy, C.O., 1981. The origin of man. *Science* 211, 341–350.
- Lovejoy, C.O., 1988. Evolution of human walking. *Sci. Am.* 259, 118–125.

- Lovejoy, C.O., 2009. Reexamining human origins in light of *Ardipithecus ramidus*. *Science* 326, 74e1–74e8.
- Lovejoy, C.O., Suwa, G., Simpson, S.W., Matternes, J.H., White, T.D., 2009. The great divides: *Ardipithecus ramidus* reveals the postcrania of our last common ancestors with African apes. *Science* 326, 100–106.
- Lukas, K.E., 1999. A review of nutritional and motivational factors contributing to the performance of regurgitation and reingestion in captive lowland gorillas (*Gorilla gorilla gorilla*). *Appl. Anim. Behav. Sci.* 63, 237–249.
- Lukas, K.E., Barkauskas, R.T., Maher, S.A., Jacobs, B.A., Bauman, J.E., Henderson, A.J., Calcagno, J.M., 2002. Longitudinal study of delayed reproductive success in a pair of white-cheeked gibbons (*Hylobates leucogenys*). *Zoo Biol.* 21, 413–434.
- Lycett, S.J., 2007. Why is there a lack of Mode 3 Levallois technologies in East Asia? A phylogenetic test of the Movius–Schick hypothesis. *J. Anthropol. Archaeol.* 26, 541–575.
- Lycett, S.J., 2009a. Understanding ancient hominid dispersals using artefactual data: a phylogeographic analysis of Acheulean handaxes. *PLoS ONE*, 1–6.
- Lycett, S.J., 2009b. Are Victoria West cores 'proto-Levallois'? A phylogenetic assessment. *J. Hum. Evol.* 56, 175–191.
- Lycett, S.J., Collard, M., McGrew, W.C., 2007. Phylogenetic analyses of behavior support existence of culture among wild chimpanzees. *Proc. Natl. Acad. Sci.* 104, 17588–17592.
- Lycett, S.J., Collard, M., McGrew, W.C., 2009. Cladistic analyses of behavioural variation in wild *Pan troglodytes*: exploring the chimpanzee culture hypothesis. *J. Hum. Evol.* 57, 337–349.
- Mace, R., 2000. Evolutionary ecology of human life history. *Anim. Behav.* 59, 1–10.
- Mace, R., Jordan, F.M., 2011. Macro-evolutionary studies of cultural diversity: a review of adaptation empirical studies of cultural transmission and cultural adaptation. *Phil. Trans. R. Soc. B* 366, 402–411.
- Macho, G.A., 2001. Primate molar crown formation times and life history evolution revisited. *Am. J. Primatol.* 55, 189–201.
- MacKinnon, J.R., 1974. The behavior and ecology of wild orangutans (*Pongo pygmaeus*). *Anim. Behav.* 22, 3–74.
- Maddison, W.P., Maddison, D.R., 2011. Mesquite: a Modular System for Evolutionary Analysis. Version 2.75. <http://mesquiteproject.org>.
- Maddison, W.P., Donoghue, M.J., Maddison, D.R., 1984. Outgroup analysis and parsimony. *Syst. Zool.* 33, 83–103.
- Marlowe, F.W., 2004. Marital residence among foragers. *Curr. Anthropol.* 45, 277–284.
- Marlowe, F.W., 2005. Hunter–gatherers and human evolution. *Evol. Anthropol.* 14, 54–67.
- Marlowe, F.W., 2007. Hunting and gathering: the human sexual division of foraging labor. *Cross-Cult. Res.* 41, 170–195.
- McGrew, W.C., 1981. The female chimpanzee as a human evolutionary prototype. In: Dahlberg, F. (Ed.), *Woman the Gatherer*. Yale University Press, New Haven, pp. 35–73.
- McGrew, W.C., 1992. *Chimpanzee Material Culture: Implications for Human Evolution*. Cambridge University Press, Cambridge.
- McGrew, W.C., 2010a. In search of the last common ancestor: new findings on wild chimpanzees. *Phil. Trans. R. Soc. B* 365, 3267–3276.
- McGrew, W.C., 2010b. Chimpanzee technology. *Science* 328, 579–580.
- McGrew, W.C., Marchant, L.F., Nishida, T., 1996. *Great Ape Societies*. Cambridge University Press, Cambridge.
- McLennan, D.A., Mattern, M.Y., 2001. The phylogeny of the Gasterosteidae: combining behavioral and morphological data sets. *Cladistics* 17, 11–27.
- Meyer, T.J., McLain, A.T., Oldenburg, J.M., Faulk, C., Bourgeois, M.G., Conlin, E.M., Mootnick, A.R., de Jong, P.J., Roos, C., Carbone, L., Batzer, M.A., 2012. An Alu-based phylogeny of gibbons (Hylobatidae). *Mol. Biol. Evol.* 29, 3441–3450.
- Miles, D.B., Dunham, A.E., 1993. Historical perspectives in ecology and evolutionary biology: the use of phylogenetic comparative analyses. *A. Rev. Ecol. Syst.* 24, 587–619.
- Miller, J.S., Wenzel, J.W., 1995. Ecological characters and phylogeny. *A. Rev. Entomol.* 40, 389–415.
- Mitani, J.C., 2009. Cooperation and competition in chimpanzees: current understanding and future challenges. *Evol. Anthropol.* 18, 215–227.
- Mooers, A.O., 2004. Effects of tree shape on the accuracy of maximum likelihood-based ancestor reconstructions. *Syst. Biol.* 53, 809–814.
- Moore, J., 1996. Savanna chimpanzees, referential models and the last common ancestor. In: McGrew, W.C., Marchant, L.F., Nishida, T. (Eds.), *Great Ape Societies*. University of Cambridge Press, Cambridge, pp. 275–292.
- Mootnick, A., Groves, C., 2005. A new generic name for the hooleck gibbon (Hylobatidae). *Int. J. Primatol.* 26, 971–976.
- Morrogh-Bernard, H.C., Morf, N.V., Chivers, D.J., Krützen, M., 2010. Dispersal patterns of orang-utans (*Pongo* spp.) in a Bornean peat-swamp forest. *Int. J. Primatol.* 32, 362–376.
- Nater, A., Nietlisbach, P., Arora, N., van Schaik, C.P., van Noordwijk, M.A., Willems, E.P., Singleton, I., Wich, S.A., Goossens, B., Warren, K.S., Verschoor, E.J., Perwitasari-Farajallah, D., Pamungkas, J., Krützen, M., 2011. Sex-biased dispersal and volcanic activities shaped phylogeographic patterns of extant orangutans (genus *Pongo*). *Mol. Biol. Evol.* 28, 2275–2288.
- Newton-Fisher, N.E., Emery Thompson, M., Reynolds, V., Boesch, C., Vigilant, L., 2010. Paternity and social rank in wild chimpanzees (*Pan troglodytes*) from the Budongo Forest, Uganda. *Am. J. Phys. Anthropol.* 142, 417–428.
- Nikolaev, S.I., Montoya-Burgos, J.L., Popadin, K., Parand, L., Margulies, E.H., Antonarakis, S.E., 2007. Life-history traits drive the evolutionary rates of mammalian coding and noncoding genomic elements. *Proc. Natl. Acad. Sci.* 104, 20443–20448.
- Nishida, T., Hiraiwa-Hasegawa, M., 1985. Responses to a stranger mother–son pair in the wild chimpanzee: a case report. *Primates* 26, 1–13.
- Norscia, I., Palagi, E., 2011. Yawn contagion and empathy in *Homo sapiens*. *PLoS ONE* 6, e28472.
- Nunn, C.L., 1999. The evolution of exaggerated sexual swellings in primates and the graded-signal hypothesis. *Anim. Behav.* 58, 229–246.
- Organ, C., Nunn, C.L., Machanda, Z., Wrangham, R.W., 2011. Phylogenetic rate shifts in feeding time during the evolution of *Homo*. *Proc. Natl. Acad. Sci.* 108, 14555–14559.
- Pagel, M., 1999. The maximum likelihood approach to reconstructing ancestral character states of discrete characters on phylogenies. *Syst. Biol.* 48, 612–622.
- Palombit, R.A., 2010. Conflict and bonding between the sexes. In: Kappeler, P.M., Silk, J.B. (Eds.), *Mind the Gap: Tracing the Origins of Human Universals*. Springer, Heidelberg, pp. 53–83.
- Panger, M.A., Brooks, A.S., Richmond, B.G., Wood, B., 2002. Older than the Oldowan? Rethinking the emergence of hominin tool use. *Evol. Anthropol.* 11, 234–245.
- Parent, A.S., Teilmann, A.J., Skakkebaek, N.E., Toppari, J., Bourguignon, J.-P., 2003. The timing of normal puberty and the age limits of sexual precocity: variations around the world, secular trends, and changes after migration. *Endocr. Rev.* 24, 668–693.
- Parish, A.R., De Waal, F.B.M., 2000. The other “closest living relative” – how bonobos (*Pan paniscus*) challenge traditional assumptions about females, dominance, intra- and intersexual interactions, and hominid evolution. *Ann. N.Y. Acad. Sci.* 907, 97–113.
- Paterson, A.M., Wallis, G.P., Gray, R.D., 1995. Penguins, petrels, and parsimony: does cladistic analysis of behavior reflect seabird phylogeny? *Evolution* 49, 974–989.
- Pawłowski, B., 1999. Loss of oestrus and concealed ovulation in human evolution. *Curr. Anthropol.* 40, 257–276.
- Pazol, K.A., Bloomsith, M.A., 1993. The development of stereotyped body rocking in chimpanzees (*Pan troglodytes*) reared in a variety of nursery settings. *Anim. Welf.* 2, 113–129.
- Perelman, P., Johnson, W.E., Roos, C., Seuánez, H.N., Horvath, J.E., Moreira, M.A.M., Kessing, B., Pontius, J., Roelke, M., Rumpler, Y., Schneider, M.P.C., Silva, A., O'Brien, S.J., Pecon-Slatery, J., 2011. A molecular phylogeny of living primates. *PLoS Genet.* 7, e1001342.
- Perry, S., 1997. Male female social relationships in wild white faced capuchins (*Cebus capucinus*). *Behaviour* 134, 477–510.
- Perry, S.E., Panger, M., Rose, L.M., Baker, M., Gros-Louis, J., Jack, K., MacKinnon, K.C., Manson, J., Fedigan, L., Pyle, K., 2003. Social conventions in wild white-faced capuchin monkeys: evidence for behavioral traditions in a neotropical primate. *Curr. Anthropol.* 44, 241–268.
- Pilbeam, D., 1996. Genetic and morphological records of the Hominoidea and hominoid origins: a synthesis. *Mol. Phylogenet. Evol.* 5, 155–168.
- Pilbeam, D., Young, N., 2004. Hominoid evolution: synthesizing disparate data. *C. R. Palevol.* 3, 305–321.
- Plavcan, J.M., 2012. Body size, size variation, and sexual size dimorphism in early *Homo*. *Curr. Anthropol.* 53 (S6), S409–S423.
- Pontzer, H., Raichlen, D.A., Shumaker, R.W., Ocobock, C., Wich, S.A., 2010. Metabolic adaptation for low energy throughput in orangutans. *Proc. Natl. Acad. Sci.* 107, 14048–14052.
- Pruetz, J.D., LaDuke, T.C., 2010. Brief communication: reaction to fire by savanna chimpanzees (*Pan troglodytes verus*) at Fongoli, Senegal: conceptualization of “fire behavior” and the case for a chimpanzee model. *Am. J. Phys. Anthropol.* 141, 646–650.
- Prüfer, K., Munch, K., Hellmann, I., Akagi, K., Miller, J.R., Walenz, B., Koren, S., Sutton, G., Kodira, C., Winer, R., Knight, J.R., Mullikin, J.C., Meader, S.J., Ponting, C.P., Lunter, G., Higashino, S., Hobolth, A., Dutheil, J., Karakoc, E., Alkan, C., Sajjadian, S., Catchchio, C.R., Ventura, M., Marques-Bonet, T., Eichler, E.E., André, C., Atencia, R., Mugisha, L., Junhold, J., Patterson, N., Siebauer, M., Good, J.M., Fischer, A., Ptak, S.E., Lachmann, M., Symer, D.E., Mailund, T., Schierup, M.H., Andrés, A.M., Kelso, J., Pääbo, S., 2012. The bonobo genome compared with the chimpanzee and human genomes. *Nature* 486, 527–531.
- Rak, Y., Ginzburg, A., Geffen, E., 2007. Gorilla-like anatomy on *Australopithecus afarensis* mandibles suggests *Au. afarensis* link to robust australopithecids. *Proc. Natl. Acad. Sci.* 104, 6568–6572.
- Reichard, U.H., Barelli, C., 2008. Life history and reproductive strategies of *Khao Yai Hylobates lar*: implications for social evolution in apes. *Int. J. Primatol.* 29, 823–844.
- Reichert, K.E., Heistermann, M., Hodges, K.J., Boesch, C., Hochmann, G., 2002. What females tell males about their reproductive status: are morphological and behavioural cues reliable signal of ovulation in bonobos (*Pan paniscus*)? *Ethology* 108, 583–600.
- Rendall, D., Di Fiore, A.F., 1995. The road less traveled: phylogenetic perspectives in primatology. *Evol. Anthropol.* 5, 43–52.
- Rendall, D., Di Fiore, A.F., 2007. Homoplasy, homology, and the perceived special status of behavior in evolution. *J. Hum. Evol.* 52, 504–521.
- Robbins, M.M., Bermejo, M., Cipolletta, C., Magliocca, F., Parnell, R.J., Stokes, E., 2004. Social structure and life history patterns in western gorillas (*Gorilla gorilla gorilla*). *Am. J. Primatol.* 64, 145–159.
- Robson, S.L., Wood, B., 2008. Hominin life history: reconstruction and evolution. *J. Anat.* 212, 394–425.
- Rodseth, L., Wrangham, R.W., Harrigan, A.M., Smuts, B.B., 1991. The human community as a primate society. *Curr. Anthropol.* 32, 221–254.

- Roos, C., Geissmann, T., 2001. Molecular phylogeny of the major hylobatid divisions. *Mol. Phylogenet. Evol.* 19, 486–494.
- Russon, A.E., 2010. Life history: the energy-efficient orangutan. *Curr. Biol.* 20, 981–983.
- Salisbury, B.A., Kim, J., 2001. Ancestral state estimation and taxon sampling density. *Syst. Biol.* 50, 557–564.
- Santana, S.E., Alfaro, J.L., Alfaro, M.E., 2012. Adaptive evolution of facial colour patterns in Neotropical primates. *Proc. R. Soc. B* 279, 2204–2211.
- Sarich, V.M., 1992. Immunological evidence on primates. In: Jones, S., Martin, R., Pilbeam, D. (Eds.), *The Cambridge Encyclopedia of Human Evolution*. Cambridge University Press, Cambridge, pp. 303–306.
- Sayers, K., Lovejoy, C.O., 2008. The chimpanzee has no clothes – a critical examination of *Pan troglodytes* in models of human evolution. *Curr. Anthropol.* 49, 87–114.
- Sayers, K., Raghanti, M.A., Lovejoy, C.O., 2012. Human evolution and the chimpanzee referential doctrine. *A. Rev. Anthropol.* 41, 119–138.
- Schluter, D., Price, T., Mooers, A.O., Ludwig, D., 1997. Likelihood of ancestor states in adaptive radiation. *Evolution* 51, 1699–1711.
- Schürmann, C.L., 1982. Courtship and mating behavior of wild orangutans in Sumatra. In: Chiarelli, A.B., Corrucini, R.S. (Eds.), *Primate Behavior and Sociobiology*. Springer Verlag, Berlin, pp. 129–135.
- Schwartz, J.H., 2004. Trying to make chimpanzees into humans. *Hist. Phil. Life Sci.* 26, 271–277.
- Schwartz, J.H., 2005. *The Red Ape: Orangutans and the Human Origins*. Westview Press, Cambridge.
- Sellen, D., 2001. Comparison of infant feeding patterns reported for nonindustrial populations with current recommendations. *J. Nutr.* 3, 2707–2715.
- Sherron, H.M., Amsler, S.J., 2007. New intercommunity infanticides by the chimpanzees of Ngogo, Kibale National Park, Uganda. *Int. J. Primatol.* 28, 9–22.
- Short, R.V., 1994. Human reproduction in an evolutionary context. *Hum. Reprod. Evol.* 709, 416–425.
- Shoshani, J., Groves, C.P., Simons, E.L., Gunnell, G.F., 1996. Primate phylogeny: morphological versus molecular results. *Mol. Phylogenet. Evol.* 5, 102–154.
- Sillén-Tullberg, B., Möller, A.P., 1993. The relationship between concealed ovulation and mating systems in anthropoid primates: a phylogenetic analysis. *Am. Nat.* 141, 1–25.
- Simmons, L.W., Firman, R.C., Rhodes, G., Peters, M., 2004. Human sperm competition: testis size, sperm production, and rates of extrapair copulations. *Anim. Behav.* 68, 297–302.
- Skybreak, A., 1984. *Of Primeval Steps and Future Leaps: An Essay on the Emergence of Human Beings, the Source of Women's Oppression and the Road to Emancipation*. Banner, Chicago.
- Smith, B.H., Crummett, T.L., Brandt, K.L., 1994. Ages of eruption of primate teeth: a compendium for aging individuals and comparing life histories. *Yearb. Phys. Anthropol.* 37, 177–231.
- Smith, E.A., 2011. Endless forms: human behavioural diversity and evolved universals. *Phil. Trans. R. Soc. B* 366, 325–332.
- Smith, R.J., Pilbeam, D.R., 1980. Evolution of the orangutan. *Nature* 284, 447–448.
- Spoor, F., Leakey, M.G., Gathogo, P.N., Brown, F.H., Antón, S.C., McDougall, I., Kiarie, C., Manthi, F.K., Leakey, L.N., 2007. Implications of new early *Homo* fossils from Ileret, east of Lake Turkana, Kenya. *Nature* 448, 688–691.
- Springer, M.S., Meredith, R.W., Gatesy, J., Emerling, C.A., Park, J., Rabosky, D.L., Stadler, T., Steiner, C., Ryder, O.A., Janečka, J.E., Fisher, C.A., Murphy, W.J., 2012. Macroevolutionary dynamics and historical biogeography of primate diversification inferred from a supermatrix. *PLoS ONE* 7, e45921.
- Stanford, C.B., 1996. The hunting ecology of wild chimpanzees: implications for the evolutionary ecology of Pliocene hominids. *Am. Anthropol.* 98, 96–113.
- Stanford, C.B., 1998. The social behavior of chimpanzees and bonobos – empirical evidence and shifting assumptions. *Curr. Anthropol.* 39, 399–420.
- Stanford, C.B., 2012. Chimpanzees and the behavior of *Ardipithecus ramidus*. *Annu. Rev. Anthropol.* 41, 139–149.
- Stanford, C.B., Allen, J.S., 1991. On strategic storytelling: current models of human behavioral evolution. *Curr. Anthropol.* 32, 58–61.
- Stokes, E.J., Parnell, R.J., Olejniczak, C., 2003. Female dispersal and reproductive success in wild western lowland gorillas (*Gorilla gorilla gorilla*). *Behav. Ecol. Sociobiol.* 54, 329–339.
- Stuart, A.E., Currie, D.C., 2001. Using caddisfly (Trichoptera) case-building behaviour in higher level phylogeny reconstruction. *Can. J. Zool.* 79, 1842–1854.
- Stumpf, R.M., Emery Thompson, M., Knott, C., 2008. A comparison of female mating strategies in *Pan troglodytes* and *Pongo* spp. *Int. J. Primatol.* 29, 865–884.
- Surbeck, M., Mundry, R., Hohmann, G., 2011. Mothers matter! Maternal support, dominance status and mating success in male bonobos (*Pan paniscus*). *Proc. R. Soc. Lond. B* 278, 590–598.
- Takahata, Y., Ihobe, H., Idani, G., 1996. Comparing copulations of chimpanzees and bonobos: do females exhibit proceptivity or receptivity? In: McGrew, W.C., Marchant, L.F., Nishida, T. (Eds.), *Great Ape Societies*. Cambridge University Press, Cambridge, pp. 146–155.
- Takeshita, H., Walraven, V., 1996. A comparative study of the variety and complexity of object manipulation in captive chimpanzees (*Pan troglodytes*) and bonobos (*Pan paniscus*). *Primates* 37, 423–441.
- Tanner, N.M., 1981. *On Becoming Human*. Cambridge University Press, Cambridge.
- Taylor, S.E., Klein, L.C., Lewis, B.P., Gruenewald, T.L., Gurung, R.A., Updegraff, J.A., 2000. Biobehavioral responses to stress in females: tend-and-befriend, not fight-or-flight. *Psychol. Rev.* 107, 411–429.
- Thierry, B., Iwaniuk, A.N., Pellis, S.M., 2000. The influence of phylogeny on the social behaviour of macaques (Primates: Cercopithecidae, Genus *Macaca*). *Ethology* 106, 713–728.
- Thinh, V.N., Mootnick, A.R., Grossmann, T., Li, M., Ziegler, T., Agil, M., Moisson, P., Nadler, T., Walter, L., Roos, C., 2010. Mitochondrial evidence for multiple radiations in the evolutionary history of small apes. *BMC Evol. Biol.* 10, 74.
- Thomas, J.A., Welch, J.J., Lanfear, R., Bromham, L., 2010. A generation time effect on the rate of molecular evolution in invertebrates. *Mol. Biol. Evol.* 27, 1173–1180.
- Thoren, S., Lindenfors, P., Kappeler, P.M., 2006. Phylogenetic analyses of dimorphism in primates: evidence for stronger selection on canine size than on body size. *Am. J. Phys. Anthropol.* 130, 50–59.
- Thornhill, R., Palmer, C.T., 2000. *A Natural History of Rape: Biological Bases of Sexual Coercion*. MIT Press, Cambridge.
- Tilson, R.L., 1981. Family formation strategies of Kloss' gibbons. *Folia Primatol.* 35, 259–287.
- Tooby, J., DeVore, I., 1987. The reconstruction of hominid behavioral evolution through strategic modeling. In: Kinzey, W.G. (Ed.), *The Evolution of Human Behavior: Primate Models*. State University of New York Press, Albany, pp. 183–238.
- Tutin, C.E.G., 1980. Reproductive behaviour of wild chimpanzees in the Gombe National Park, Tanzania. *J. Reprod. Fertil.* 28, 43–57.
- Tutin, C.E.G., 1996. Ranging and social structure of lowland gorillas in the Lopé Reserve, Gabon. In: McGrew, W.C., Marchant, L.F., Nishida, T. (Eds.), *Great Ape Societies*. Cambridge University Press, Cambridge, pp. 58–69.
- Tuttle, R.H., 1974. Darwin's apes, dental apes, and the descent of man: normal science in evolutionary anthropology. *Curr. Anthropol.* 15, 389–398.
- Utami, S.S., Goossens, B., Bruford, M.W., de Ruiter, J.R., van Hooft, J.A.R.A.M., 2002. Male bimaturism and reproductive success in Sumatran orang-utans. *Behav. Ecol.* 13, 643–652.
- Van Arsdale, A.P., Wolpoff, M.H., 2013. A single lineage in early Pleistocene *Homo*: size variation continuity in early Pleistocene *Homo* crania from East Africa and Georgia. *Evolution* 67, 841–850.
- van Noordwijk, M.A., Arora, N., Willems, E.P., Dunkel, L.P., Amda, R.N., Mardianah, N., Ackermann, C., Krützen, M., van Schaik, C.P., 2012. Female philopatry and its social benefits among Bornean orangutans. *Behav. Ecol. Sociobiol.* 66, 823–834.
- van Schaik, C.P., Kappeler, P.M., 1997. Infanticide risk and the evolution of male–female association in primates. *Proc. R. Soc. Lond. B* 264, 1687–1694.
- van Schaik, C.P., Knott, C.D., 2001. Geographic variation in tool use on *Neesia* fruits in orangutans. *Am. J. Phys. Anthropol.* 144, 331–342.
- van Schaik, C.P., van Hooft, J.A.R.A.M., 1996. Toward an understanding of the orangutan's social system. In: McGrew, W.C., Marchant, L.F., Nishida, T. (Eds.), *Great Ape Societies*. Cambridge University Press, Cambridge, pp. 3–15.
- van Schaik, C.P., Ancrenaz, M., Borgen, G., Galdikas, B.F.M., Knott, C.D., Singleton, I., Suzuki, A., Utami, S.S., Merrill, M., 2003. Orangutan cultures and the evolution of material culture. *Science* 299, 102–105.
- Varki, A., Altheide, T., 2005. Comparing the human and chimpanzee genomes: searching for needles in a haystack. *Genome Res.* 15, 1746–1758.
- Walker, M.L., Herndon, J.G., 2008. Menopause in nonhuman primates? *Biol. Reprod.* 79, 398–406.
- Walker, R., Hill, K., Burger, O., Hurtado, A.M., 2006. Life in the slow lane revisited: ontogenetic separation between chimpanzees and humans. *Am. J. Phys. Anthropol.* 129, 577–583.
- Walker, R.S., Hill, K.R., Flinn, M.V., Ellsworth, R.M., 2011. Evolutionary history of hunter–gatherer marriage practices. *PLoS ONE* 6, e19066.
- Wall, J.D., Kim, S.K., Luca, F., Carbone, L., Mootnick, A.R., de Jong, P.J., Di Rienzo, A., 2013. Incomplete lineage sorting is common in extant gibbon genera. *PLoS ONE* 8, e53682.
- White, F.J., 1996. Comparative socio-ecology of *Pan paniscus*. In: McGrew, W.C., Marchant, L.F., Nishida, T. (Eds.), *Great Ape Societies*. Cambridge University Press, Cambridge, pp. 29–41.
- Whiten, A., 2011. The scope of culture in chimpanzees, humans and ancestral apes. *Phil. Trans. R. Soc. B* 366, 997–1007.
- Whiten, A., McGrew, W.C., Aiello, L.C., Boesch, C., Boyd, R., Byrne, R.W., Dunbar, R.I.M., Matsuzawa, T., Silk, J.B., Tomasello, M., van Schaik, C.P., Wrangham, R.W., 2010. Studying extant species to model our past. *Science* 327, 410.
- Wich, S.A., Utami-Atmoko, S.S., Setia, T.M., Rijksen, C., Schürmann, C., van Hooft, J.A.R.A.M., van Schaik, C.P., 2004. Life history of wild Sumatran orangutans (*Pongo abelii*). *J. Hum. Evol.* 47, 385–398.
- Wilson, M., Daly, M., 1992. The man who mistook his wife for a chattel. In: Barkow, J., Cosmides, L., Tooby, J. (Eds.), *The Adapted Mind: Evolutionary Psychology and the Generation of Culture*. Oxford University Press, New York, pp. 289–322.
- Wood, B., 2010. Reconstructing human evolution: achievements, challenges, and opportunities. *Proc. Natl. Acad. Sci.* 107, 8902–8909.
- Wood, B., Harrison, T., 2011. The evolutionary context of the first hominins. *Nature* 470, 347–352.
- Wrangham, R.W., 1987. The significance of African apes for reconstructing human social evolution. In: Kinzey, W.G. (Ed.), *The Evolution of Human Behavior: Primate Models*. State University of New York Press, Albany, pp. 51–71.
- Wrangham, R.W., 1993. The evolution of sexuality in chimpanzees and bonobos. *Hum. Nature-Int. Bios.* 4, 47–79.
- Wrangham, R.W., 1999. Evolution of coalitionary killing. *Yearb. Phys. Anthropol.* 42, 1–30.

- Wrangham, R.W., 2001. Out of the *Pan*, into the fire: how our ancestors' evolution depended on what they ate. In: De Waal, F.B.M. (Ed.), *Tree of Origin: What Primate Behavior Can Tell Us About Human Social Evolution*. Harvard University Press, Cambridge, pp. 119–143.
- Wrangham, R.W., Peterson, D., 1996. *Demonic Males*. Houghton-Mifflin, Boston.
- Wrangham, R.W., Pilbeam, D., 2001. African apes as time machines. In: Galdikas, B.M.F., Briggs, N., Sheeran, L.K., Shapiro, G.L., Goodall, J. (Eds.), *All Apes Great and Small, Chimpanzees, Bonobos, and Gorillas*, vol. 1. Plenum/Kluwer, New York, pp. 5–18.
- Wrangham, R.W., McGrew, W.C., De Waal, F.B.M., Heltne, P.G. (Eds.), 1994. *Chimpanzee Cultures*. Harvard University Press, Cambridge.
- Wrangham, R.W., Chapman, C.A., Clark-Arcadi, A.P., Isabirye-Basuta, G., 1996. Social ecology of Kanyawara chimpanzees: implications for understanding the costs of great ape groups. In: McGrew, W.C., Marchant, L.F., Nishida, T. (Eds.), *Great Ape Societies*. Cambridge University Press, Cambridge, pp. 45–57.
- Wrangham, R.W., Wilson, M.L., Muller, M.N., 2006. Comparative rates of violence in chimpanzees and humans. *Primates* 47, 14–26.
- Wroblewski, E.E., Murray, C.M., Keele, B.F., Schumacher-Stankey, J.C., Hahn, B.H., Pusey, A.E., 2009. Male dominance rank and reproductive success in chimpanzees, *Pan troglodytes schweinfurthii*. *Anim. Behav.* 77, 873–885.
- Yang, Z., 1996. Phylogenetic analysis using parsimony and likelihood methods. *J. Mol. Evol.* 42, 294–307.
- Zihlman, A., 1996. Reconstructions reconsidered: chimpanzee models and human evolution. In: McGrew, W.C., Marchant, L.F., Nishida, T. (Eds.), *Great Ape Societies*. Cambridge University Press, Cambridge.
- Zihlman, A.L., Cronin, J.B., Cramer, D.L., Sarich, V.M., 1978. Pygmy chimpanzee as a possible prototype for the common ancestor of humans, chimpanzees, and gorillas. *Nature* 275, 744–746.
- Zrzavý, J., Ričánková, V., 2004. Phylogeny of recent Canidae (Mammalia, Carnivora): relative reliability and utility of morphological and molecular datasets. *Zool. Scr.* 33, 311–333.