Chapter 1
Anthropogeny

Pascal Gagneux

Abstract Anthropogeny, "the study of the origin of humans" is an attempt to use all verifiable facts and ethical scientific methods to explain the origin of the species *Homo sapiens*. Only a transdisciplinary approach will allow to unravel the singularity that is the appearance of our species, the "planet-altering ape." Such transdisciplinarity will have to involve fields as varied as linguistics and psychology, biomedicine and neuroscience, physical and chemical sciences, comparative primatology, climate sciences and geology, archeology and paleontology with much support from computer science. Humans present a striking paradox as they combine an obvious mammalian and primate nature with a distinct combination of numerous biological and behavioral traits, making them spectacular outlier among the living world. The time depth of many of the processes that shaped our species represents a formidable obstacle. New fossils, archeological finds, ancient DNA technology, and comparative genomics are providing key new information. Anthropogenists are still facing a staggering list of humbling unknowns about the age of onset of key human innovations. These include but are not restricted to the following: symbolic capacity, personal name or kinship terms, language, home base use, fire use/cooking, pair bonding, awareness of paternal kinship networks, projectile weapon use, composite tool use, fiber use, bodily modifications, and death rituals. The human phenomenon reflects idiosyncratic concatenations of unlikely events. Key factors likely include both opportunities and constraints stemming from massive physical and cultural niche construction by our species that has increasingly taken its evolutionary fate in its own hands.

Keywords Human origins · Human evolution · Hominid · Hominin · Anthropogeny · Great ape · Niche construction · Theory of mind · Self-domestication

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P. Gagneux (✉)
Department of Pathology and Anthropology, University of California San Diego, La Jolla, CA, USA
e-mail: pgagneux@health.ucsd.edu

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1.1 Getting at the Origins of the Human Phenomenon

Questions about origins feature prominently in cosmologies of most human cultures. The study of the origin of our species or Anthropogeny has long fascinated philosophers and scientists.

***Anthropogeny** The investigation of the origin of man (humans) Oxford English Dictionary, 2006. First used in 1839 edition of Hooper's Med. Dict. and defined as "the study of the generation of man."

"Where do we come from?" and "How did we get here?" are the two questions driving anthropogeny. We have never been in a better position to attempt answering these questions. As we are approaching a clearer view of the timing and the location of our origin, we are still far from understanding the evolutionary singularity represented by the emergence of our question-asking species.

Huxley and Darwin initially predicted (Huxley 1863; Darwin 1871) that modern humans likely shared a last common ancestor with apes in Africa. Since then steady accumulation of hominid fossils in Africa, Asia, and Europe, combined with a wealth of molecular data now provides overwhelming evidence for a deeply rooted origin of our lineage in Africa. How did small Miocene apes evolve into bipedal, small-brained Pliocene hominids and then into tall, stone tool-using, running, and fire-controlling, ever larger-brained members of our genus *Homo*? A combination of factors, spanning the molecular, cellular, microbial, social, cultural, ecological, and climatic must have contributed to the peculiar trajectory of the hominin lineage. Modern Anthropogeny is focused on the circumstances and events that led to the appearance of our species between 200 and 100 kya in Africa and eventually followed by the almost complete replacement of all other hominin species in Europe and Asia.

To the best of our knowledge, the human species represents an evolutionary singularity. The study of human origins thus represents a historical exercise with a sample size of $n = 1$. As such, anthropogeny is an exercise in deep history (Smail 2008). For singular phenomena, one cannot rule out extremely rare or unusual events as causal factors. Getting at answers will require drawing on a large number of disciplines ranging from the molecular to the social and geophysical and benefitting most from comparative approaches (Fig. 1.1).

1.2 Our Evolutionary Roots

Humans are firmly rooted in the tree of life and share this planet with several closely related extant primate species. In stark contrast to their living relatives, humans can be characterized as a highly successful "weed species," having colonized the entire planet, replaced closely related species, and caused mass-extinctions everywhere we went (Diamond 1989). A combination of uniquely derived socio-cognitive

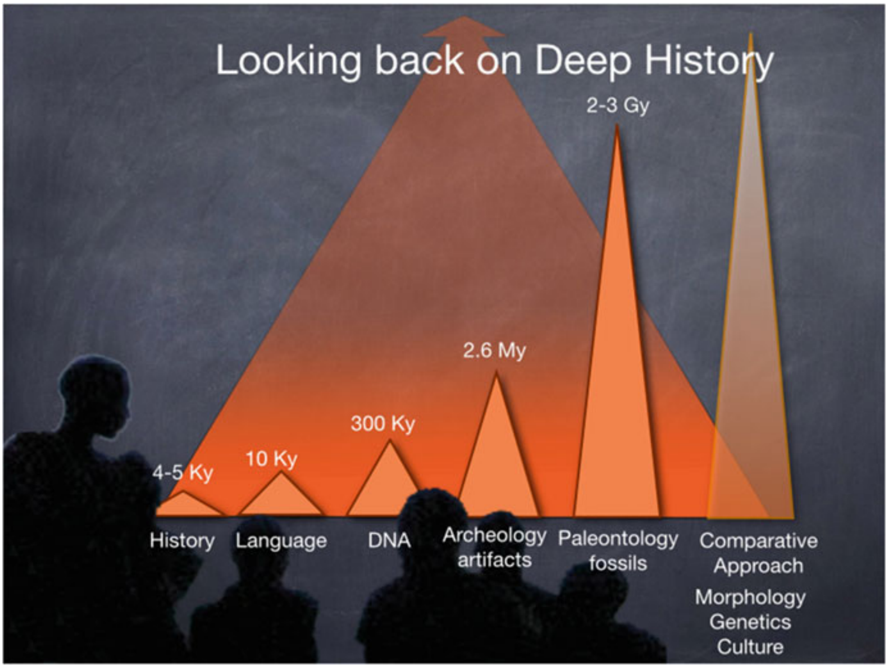


Fig. 1.1 The singularity of human evolution means that anthropogeny is first and foremost a historical enterprise. Different methodologies provide different time depth ranging from the <5 thousand years of written historical records to the billion year old fossil record. Comparative studies of genomes, phenotypes, and behavior represent our best chance at reconstructing the human story. Methods for deep history

adaptations, language, and technology catalyzed the powerful niche construction ability of our species and has directly contributed to this planetary take-over, also resulting in the endangered species status of all remaining non-human hominids (the “great apes”) (Kondgen et al. 2008). Several other primate species have evolved remarkably flexible ecologies, including baboons in Africa and macaques in Asia, but all of these continue to coexist as multiple closely related species (Winder 2014; Morales and Melnick 1998).

1.2.1 Homo Sapiens: *The Paradoxical Ape*

Complete genome data from multiple individuals of all extant ape species clearly indicate that two non-human primate species are more closely related to humans than either is to any other extant primate species. Traditionally, the notion of great apes (pongid) vs humans was based on skeletal anatomy. The fact that humans share a common ancestor with bonobos (*Pan paniscus*) and chimpanzees (*Pan troglodytes*) after the divergence of the lineage leading to gorillas (*Gorilla, gorilla*) nullifies the biological validity of the term “great apes/pongids” (Prado-Martinez et al. 2013). Despite its biological fallacy, the term “great ape” continues to be used and is rather useful when discussing the human phenomenon, given the many ways in which human biology and behavior have come to diverge from that of other hominids (including all living great apes). The close phylogenetic proximity of humans and the two species of Pan have even been used to argue that all three species should share a genus (Goodman et al. 1989, 1998). Soft tissue anatomy also groups humans and chimpanzees into a monophyletic group excluding gorillas and orangutans (Gibbs et al. 2000). Conversely, the long list of human-unique specializations from cell biology to cognition to social structure makes it unlikely that our species will be renamed “*Pan sapiens*” or that the two chimpanzees will be renamed “*Homo troglodytes*” and “*Homo paniscus*” any time soon. Humans can be safely considered to simultaneously be genetic apes and ecological “ex-apes” (Marks 2012).

1.2.2 Measuring Genetic Distance

How can we best express genetic or genomic similarity and how are we to interpret the meaning of such figures? Despite the linear nature of DNA sequences, genomes are far from linear and thus linear comparisons in % genetic difference have serious limitations. The initial DNA hybridization experiments (Sibley and Ahlquist 1987) excluded most heterochromatin. Taking into account the entirety of the genetic material there is closer to 5% total difference between human and the closest extant non-human genome (Britten 2002; Mikkelsen et al. 2005). Much of the genetic variation consists of structural variation including changes in cytogenetic organization, segmental duplications, and lineage-specific expansion and/or deletions (Gazave et al. 2011). The exact changes that make us human remain painfully elusive. They likely include: point mutations and positive selection in structural and regulatory regions; gains of function: via recently duplicated or partially duplicated genes, change in gene copy numbers, de novo genes, accelerated regions including RNA genes; losses of function: including deletions or lost expression of otherwise conserved mammalian genes. Changes in expression and splicing: including both transcription levels and locations. Rapid transcription factor evolution: by segmental duplication or positive selection. Also relevant are changes in transposable elements: their type, abundance, activity, suppression, and locations. Prime candidates for the genetic basis of humanness are alterations to gene expression networks in the brain and factors affecting growth rate and life history timing. However, testing human-specific genetic changes for their phenotypic effects remains far from trivial, and understanding their adaptive importance in the face of natural, sexual, and social selection is more difficult still. The quest for the genetic bases of humanness remains a fantastic challenge (Varki and Altheide 2005; O’Bleness et al. 2012). For an attempt at ongoing enumeration of such traits, please see the Matrix of Anthropogeny website of the Center for Academic Research and

Training in Anthropogeny (CARTA) (http://carta.anthropogeny.org/content/about-moca).

The fact that a few nucleotide changes at important functional sites of the genome, e.g. promoter region or transcription factor binding sites, can have drastic effects on development and phenotype has long prompted the hypothesis that relatively few regulatory changes would explain the drastic phenotypic differences between humans and apes (King and Wilson 1975). Comparative genomics have revealed ~2000 human accelerated regions (HARs) that seem enriched for functional elements such as enhancers (Pollard et al. 2006; Capra et al. 2013) and conserved regions uniquely deleted in humans (McLean et al. 2011; Lindblad-Toh et al. 2011). Similarly, human-specific duplication (HSDs) include a number of genes involved in neuronal proliferation, migration, and maturation (Nuttle et al. 2013). Of course, an important limitation remains in the uncertainty regarding the precise number and identity of functional elements and their interactions in the mammalian genome (The Encode Consortium 2012). Furthermore, given that even slight changes in the genome can profoundly affect function and with it the development of phenotypic traits, there is an obvious need for functional studies, which will mostly be limited to in vitro assays with hominid cells or studies of hominid DNA sequences in transgenic animal models (Sholtis and Noonan 2010; McLean et al. 2011).

1.2.3 Ancient Genome Data

More recently the access to ancient DNA from extinct and ancestral hominids found in temperate regions outside Africa has allowed advances in anthropogeny that few could have imagined just two decades ago (Shapiro and Hofreiter 2014). Paradoxically, anthropogeny has gone from an almost complete lack of fossils in Darwin's time, to fragmentary fossils but no DNA in most of the twentieth century, to more fossils and snippets of DNA, to thousands of complete genomes, including those of all living ape species and even fossil taxa like Neanderthals and Denisovan (the latter represented by a single finger bone and tooth). In an ironic twist of scientific history we now have whole genome data for taxa represented by only a single finger bone and a tooth (Meyer et al. 2012). Novel sources of ancient DNA include dental calculus, which also provides a wealth of information on ancient hominid diet and microbiomes (Warinner et al. 2015).

Clear evidence for limited introgression (Green et al. 2010; Reich et al. 2010; Prufer et al. 2014) combined with strong evidence for overall selection against most introgressed archaic DNA (Currat and Excoffier 2011) has had the few remaining multiregionalists claiming victory, while the out-of–Africa side feels confirmed by the rare exceptions of introgressed functional elements such as HLA alleles and EPAS1 in Tibetans (Abi-Rached et al. 2011; Huerta-Sanchez et al. 2014). The availability of two extinct hominid genomes is now also allowing the identification of very recent changes post-dating the divergence of the lineage leading toe

H. sapiens and the archaic Eurasian taxa of Neanderthal and Denisovan (Paabo 2014).

1.2.4 Limits to Detecting Ancient Selection

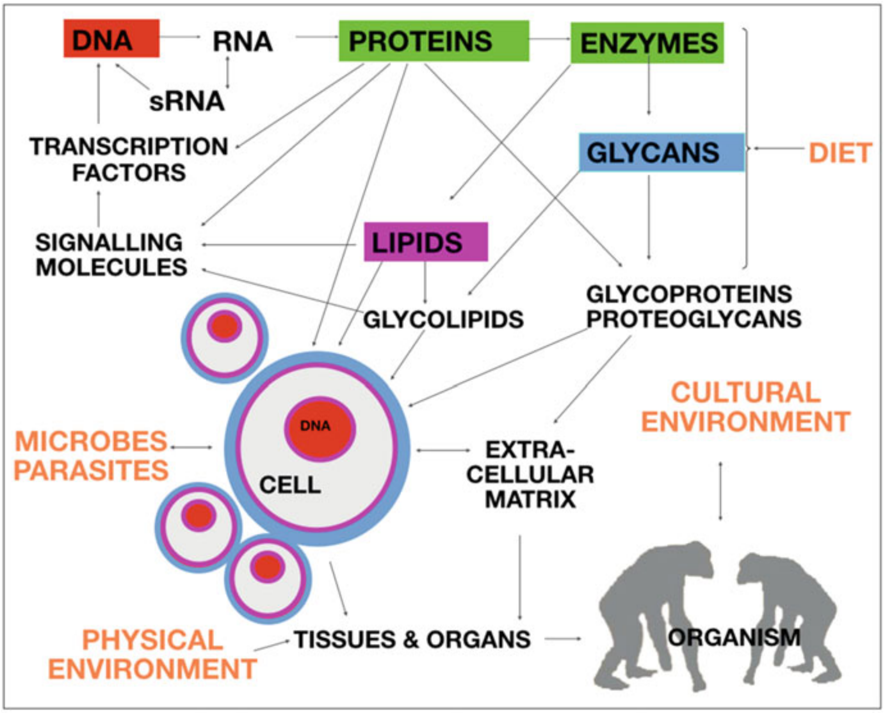
Ideally we would hope to find traces of past selection in areas of the genome responsible for unique modern human specializations. The irony is that the power to detect ancient selection in intra-specific sequence comparisons weakens substantially at just around the depth of time that modern humans appear on the scene (150 kya) (Granka et al. 2012; Voight et al. 2006).

Interpretations of this rapidly growing body of genomic data will crucially rely on independent investigation of countless phenomena ranging temporally from millisecond neuronal action potentials to million year geological epochs, and spatially from subatomic realms of stable isotopes to astronomical scales, affecting climate oscillation. It will also come to crucially rely on functional studies in cell culture and transgenic model animals. In addition, identifying the consequences in humans who carry deleterious mutations at human-specialized genetic loci will also help shed light on function in the absence of experiments.

The ongoing revelations about novel levels of complexity in genome organization and gene regulation make it difficult to clearly delineate where the genotype becomes phenotype. It is becoming clear that any stretch of DNA is already existing in a genomic environment comprising the location on a chromosome, chromatin structure, the identity of surrounding genetic elements (functional and non-functional “spacers”), and the presence of modifiers (Nadeau 2001). Non-coding RNAs and epigenetic modifications of DNA and histones are other dimensions blurring the genotype–phenotype boundary or forming a “code above the code.” Classical phenotypes range from fossil teeth and bone to anatomy, physiology, development, and behavior of living individuals. Explanations of the human phenomenon will have to include all classes of biomolecules, their interactions during development of each organism as well as inter-organismal interactions starting with prenatal mother–offspring interface to social interactions within and between social groups (Fig. 1.2).

1.2.5 Phenotypes Are More Than Nucleic Acids and Proteins

Humans and all other organisms consist of four major classes of biomolecules: nucleic acids, proteins, lipids, and glycans. The latter two are not produced in a template driven manner, like the proteins encoded in genes, but rather are metabolically encoded and also influenced by the organism’s diet and environment (Fig. 1.2). Lipids and glycans are also key components of extracellular tissues. Access to both is strongly affected by diet and the gut microbiome. An increased



adapted from Varki, A. (Di Fiore, 2006)

Fig. 1.2 Molecules in context. Not all biomolecules are encoded in a template driven manner in the genome. Lipids and glycans come from the environment via diet and are then metabolically altered by enzymatic pathways of the organism. An understanding of uniquely human phenotypes must take into account all four major classes of biomolecules including nucleic acids, proteins, lipids, and glycans (modified from Varki, unpublished). Molecules in context

understanding of uniquely human phenotypes depends on an inclusive molecular approach, which appreciates how these four classes of biomolecules combine and interact (Marth 2008). For example, it was recently discovered that histones are modified by the addition of a single sugar (O-N-Acetylglucosamine or O-GlcNAc) to histone tails (Sakabe et al. 2010). Levels of sugar nucleotide substrate for this “histone code” modifications are heavily influenced by diet (Wells et al. 2003) providing a direct link between environmental/dietary conditions and histone post-translational modification.

Phenotypic information on non-human primates including the “great apes” will be crucial for interpreting genetic data. Comparing phenotypes of extant species at levels ranging from molecules to societies while taking into account phylogeny as well as ontogeny continues to reveal important facets of human specializations and point to systems and pathways where experimental work is warranted (Fig. 1.3). The hominin lineage consists after all of populations of reproducing individuals. A correct reconstruction of phylogeny requires correct inference about which

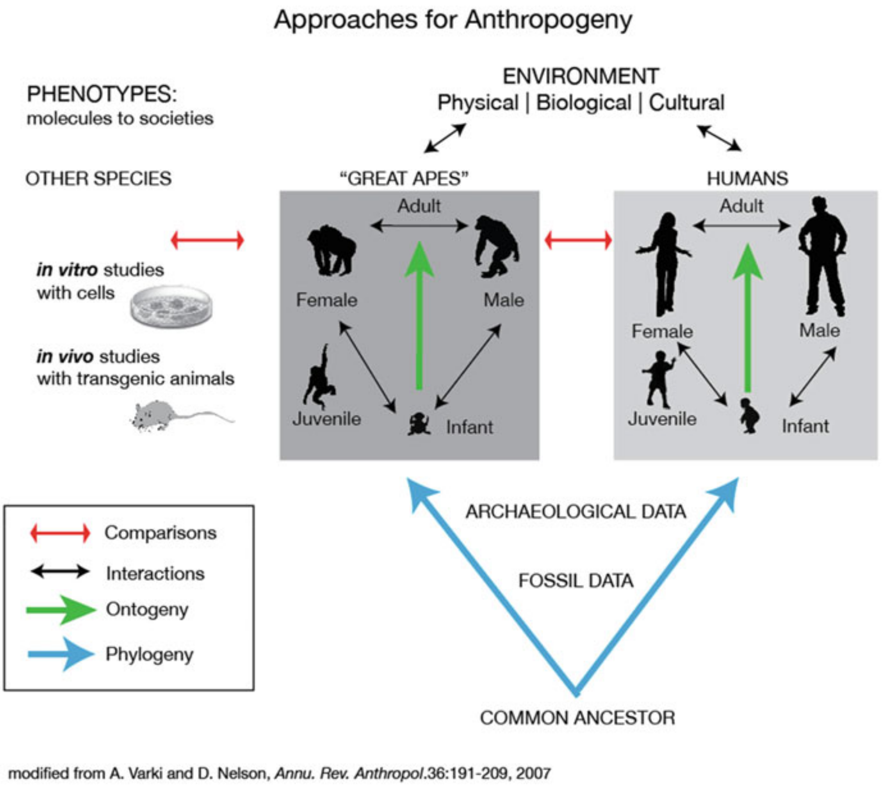


Fig. 1.3 Interdisciplinary approaches to anthropogeny. Paleontology provides crucial data on past life forms and their environments. Ancient DNA contributes key insights in the genetics of extinct and ancestral hominins. Comparative studies of human and great ape biology and behavior, including their ontogeny will continue to be key for identifying specializations of Homo sapiens. Such comparative studies should also include other species and be aided by in vitro studies using cells such as cell types derived from IPS cells obtained by minimally invasive ways from living individuals and experiments in transgenic model animals expressing manipulated to carry genetic material of interest (modified from Varki and Nelson 2007). Approaches for anthropogeny

populations continued to exchange genetic information. The classical view of phylogeny as a neat succession of bifurcations is complicated by the reality of hybridization (anastomosis/merging of lineages), which provides for networked phylogenies rather than neatly branched phylogenetic trees (Patterson et al. 2006; Reich et al. 2011; Jolly 2001). Availability of ancient DNA sequence from fossil and pre-fossil specimens is also opening up new avenues for directly measuring mutation rates (Fu et al. 2013; 2014).

1.3 Phenotypes: From Fossils to Past Behavior, Current Physiology, and Cognition

1.3.1 Fossil Data

Existing fossils clearly prove that bipedalism evolved early; that there were multiple bipedal lineages retaining excellent arboreal adaptations in Africa (White et al. 2009, Haile-Selassie et al. 2012); that the evolution of striding bipedalism came only more than two million years after the early bipedalism (Bramble and Lieberman 2004); that the expansion of cranial capacity came two million years ago (De Miguel and Henneberg 2001); that there was substantial anatomical variation among the first *Homo erectus (georgicus)* out of Africa (Lordkipanidze et al. 2013); that by 600 kya *Homo heidelbergensis* in Africa had reached cranial capacity comparable with modern humans (Conroy et al. 2000); that the continued expansion of the hominin cranium occurred despite increasing size constraints due to cephalo-pelvic disproportion at birth (Wells et al. 2012); that anatomically modern humans evolved 200–160 kya in East Africa (Fleagle et al. 2008, White et al. 2009). More fossils are badly needed but unfortunately very few field paleontology teams are enjoying stable financial support. The dearth of fossil representing the non-hominin (ape) lineages remains profoundly frustrating (McBrearty and Jablonski 2005; Suwa et al. 2007). The availability of powerful scanning technologies now allows studies on internal structures ranging from trabercular structure (Chirchir et al. 2015) to endocasts in breccia filled fossils such as *A. sediba* (Neubauer et al. 2012). Starch granules in tooth calculus (Henry et al. 2011) have allowed novel insights into the use of plant foods by Neanderthals and others.

Interpretation of the fossil record is also hampered by the tension between "lumpers," those who tend to group different fossils into the same taxon and "splitters" who tend to allocate each now fossil to its own taxon. A recent example is the reported large morphological variation among five *H. erectus* skulls from Dmanisi Georgia that all presumably represent a single species (Lordkipanidze et al. 2013) and the description of multiple taxa coexisting near Lake Turkana (Wood and Leakey 2011).

1.3.2 Archeological Data: Fossilized Behavior

Anthropogeny is first and foremost an African phenomenon. Behaviorally modern humans with fire, language, and projectile weapons colonized the entire planet and mostly replaced all other hominins (Henn et al. 2011). Much has been written about the "symbolic" watershed between "non-symbolic" ancestors and "fully symbolic," "behaviorally modern" humans. Tangible evidence for such a watershed remains very limited as there seem to be a few unequivocal tokens for "symbolic" behavior. Some of these, including shell beads and ochre for body paint long predate "behaviorally modern" humans (McBrearty and Brooks 2000), while others such as burials post-date their arrival (Gargett 1999). If burials are a clear sign of symbolic behavior, then such capacity might have evolved independently in Neanderthals and modern humans given the evidence for several Neanderthal burial sites across Europe and the Levant (Spikins et al. 2014).

Among the likely candidates for important impact on hominin genetics are the rise of the genus *Homo* to the place among top carnivores and its associated consumption of animal fat, use and reuse of home bases, the controlled use of fire, and cooking. Despite claims for the existence of home base use at more than one million years ago at Koobi Fora (Isaac et al. 1971), uncontested evidence is still pending (McBrearty and Brooks 2000; Brown et al. 2012). The cognitive specialization allowing for full theory of mind and language must include numerous genetic changes underlying neurodevelopment and brain function. These genetic changes contributed to a change in overall brain size and to complex reorganization and changes in overall connectivity.

1.3.3 Stable Isotopes, Paleoclimate, and Paleonutrition

Much information can be gleaned through the study of stable isotopes found in fossil material. Trophic levels, terrestrial versus marine diets, forest versus open grassland based diets are reflected in the ratio of stable isotopes of nitrogen and carbon and paleoclimate in reflected in oxygen and hydrogen isotopes (Schoeninger 2012; Bedaso et al. 2013). Plant wax biomarkers in sedimentary mud (sapropel), isotope composition of soil carbonate, and composition of fossil bovid fauna all point to an increase in more open vegetation over the last three million years (deMenocal 2011). The combination of stable isotope data with dental microwear data has allowed surprisingly detailed reconstruction of ancient hominid diets (Ungar and Sponheimer 2011). Finally microcharcoal in sediments from offshore or lake sediments can be powerful indicators of widespread burning, both natural and hominin in origins. Discerning the latter from the background rate of naturally ignited fires remains a big challenge (Bowman et al. 2011).

1.3.4 Learning from Living Foragers

There are a few remaining forager societies across the world, people who live entirely from gathering and hunting. Anthropologists and ethnographers studying these groups can glean powerful insights into the human condition prior to agriculture. Serious caveats include the important fact that these living societies do not represent ancient relics, and that they have routinely been pushed into degraded habitats not desirable for their pastoralist and agriculturalist neighbors. Nevertheless, behavioral patterns and cultural traits of these small-scale societies provide important information regarding past human life (Marlowe et al. 2014). Ethnographic, genetic, and linguistic data from such groups continues to inform our understanding of human biological and cultural evolution in crucial ways (Henn et al. 2011; Walker et al. 2011; Wiessner 2014; Tishkoff et al. 2007). Much interest exists in studying the microbiome of living foragers as examples of non-agricultural ecosystems. Life history studies on the Hadza of Tanzania were key for the development of the grandmother hypothesis (Kim et al. 2014). Information from non-agricultural societies also provides important insights about violent behavior and its determinants (Boehm 2012; Muller et al. 2009).

1.3.5 The Holocene Trap

Despite asking key questions about the Pleistocene, the wealth of data we have from the Holocene (including all of the neolithic behavioral records) unwittingly leads us to discuss more recent phenomena when trying to explain a much more ancient singularity. Our most cherished examples of cultural and behavioral adaptations shaping human genomes include lactase persistence and amylase copy number, both of which are firmly linked to neolithic times, i.e. the harvesting of milk from other mammals or feeding on grass grains, and do not shed light on the origins of our species (Tishkoff et al. 2007; Perry et al. 2007). These Holocene examples do however blatantly illustrate the power of behavioral and cultural adaptations for shaping human genetics. There is a need for considering cultural adaptations long predating the Neolithic, which might have similarly shaped our biology. How could the early use of fire and reuse of home bases have molded parts of our biology?

1.3.6 Biological Proxies for Past Behavior

DNA sequences encoding genes involved in reproductive behavior and their expression patterns allow a glimpse into past mating systems and are indicative of the presence of pair bonding (neotenous gene expression in male reproductive genes) (Saglican et al. 2014). This neotenous pattern mirrors clearly neotenous changes in gene expression networks in the brain (Somel et al. 2009). Similarly, sexual dimorphism or lack thereof in fossils can shed light on the degree of competition for mates. Recent work using digit ratios as proxy for in utero androgen exposure has generated interesting data with regard to past mating systems and the potential existence of alternative mating strategies in both sexes in humans (Wlodarski et al. 2015). The most unusual characteristics of our species, namely full theory of mind and language have no known biological counterparts that would survive in fossilized hard tissues (Povinelli and Preuss 1995).

Comparative medicine provides a long list of ailments apparently unique or unusual to our species (Varki et al. 2011). The ascertainment bias due to the two thousand plus years of history of human medicine but much younger medical knowledge of great apes needs to be kept in mind. A large number of diseases clearly affect humans differently. Major differences in immune system biology might underlie some of these disease differences, but how humans came to have such different immune systems remains an important unanswered question (Varki 2010). A further question is the degree to which derived genes represent a liability for disruption of proper neurodevelopment as evidenced by many human cognitive disorders. Studies of uniquely derived genes involved in human cognitive development and function and their disruption in individuals with intellectual disability are very promising in this respect (Hormozdiari et al. 2015).

1.3.7 The Crying Need for Phenotypic Data of Non-human Hominids

Natural selection operates mostly on individual phenotypes. Sadly, we only have limited information about the phenotypes of our closest living ape relatives. Opportunities for obtaining such information are rapidly vanishing with the closure of the last primate centers. The great ape sanctuaries across Africa offer some hope for continued access to great ape phenotypic studies (Farmer 2002). Common chimpanzees are the only “great ape” ever kept in captivity in significant numbers and even used for biomedical research. Captive chimpanzee populations are aging and biomedical research has come to near cessation with very few exceptions. Cell biology with induced pluripotent stem cells derived from minimally invasive samples (skin biopsies or milk teeth) offers some very promising avenues for studying cellular phenotypes including derived neuronal and other central nervous system cell types (Hrvoj-Mihic et al. 2014).

The use of non-human animal models also promises to produce important insights. Genetic changes including those in controlling regions such as HAR1 can be tested by transgenic expression in mouse (Capra et al. 2013; Prabhakar et al. 2008). Obviously, the lack of primate genomic background for such experiments in mice remains an important limitation. Recently established colonies of dwarf primates (marmosets) in China and Japan are intended to provide for transgenic primate experiments (Kishi et al. 2014).

Much of the human-specific biology takes place during development in utero, where experiments are ethically not possible in either apes or humans (Gagneux et al. 2005). Non-invasive imaging in humans and captive chimpanzees can provide extremely valuable insights such as the observation that the rate and velocity of chimpanzee brain decline well before birth while remaining steady in humans (Sakai et al. 2013). The schedule of myelination has also dramatically changed with an extension of mature myelination into the third decade of life for humans (Miller et al. 2012). Non-invasive imaging of human, chimpanzee, and macaque brains has revealed remarkable human-specific connectivity via the strongly lateralized arcuate fasciculus connecting Broca's and Wernicke's area (Rilling et al. 2008; Chen et al. 2013). Similarly, more detailed studies of cellular architecture in post-mortem brain samples are revealing striking differences between comparable regions in humans and "great apes" (Semendeferi et al. 2011). Most notably in regions involved in the limbic system and social cognition (Barger et al. 2014).

1.3.8 Niche Construction and Top-Down Effects

Complex neuro-behavioral phenotypes are subject to both, bottom-up regulation by genes affecting development and metabolism and top-down effects in the form of social and cultural input, which famously include diet, linguistic, and sociocultural input during a prolonged period of neuronal maturation in our species. How does the human genome encode propensity for language and a pattern of brain development that "expects" language input? Even more perplexing is the question about how such information underlying our linguistic capacities became internalized in the human germ line in the first place. Evidence for anatomical differences between brains of monolingual and second language learners would be further evidence of top-down effects (Klein et al. 2014; Mechelli et al. 2004).

A chimpanzee brain develops perfectly fine in the absence of language input, whereas a human brain does not reach its potential unless a child is spoken to (Greenough et al. 1987; Kuhl et al. 1992). It is striking that even apparently obvious biological traits such as bipedality appear to be subject to important learning and imitation for proper bipedal locomotion, despite the many anatomical adaptations to bipedality (Thelen 1995).

Among the top-down effects one could also consider the provocative idea of human "self-domestication," a form of social selection, against aggression within groups with important consequences for pro-social behavior and group function (Hare et al. 2012). Such a process could be in part responsible for the simultaneous selection of neotenous traits and shifts in developmental schedule typical of *Homo sapiens*. Delayed maturation, retention of juvenile characters, and heterochrony are all hallmarks of human development (Miller et al. 2012; Somel et al. 2009; Liu et al. 2012).

Humans are biologically dependent on cooked food as evidenced by the finding that female raw food eaters in modern societies frequently cease to ovulate (Carmody et al. 2011). Higher-level cognition cannot be explained outside the biological, social, and cultural contexts in which it evolved (Nunez et al. 2012). The cultural niche becomes a force in its own right, profoundly shaping human cognition and behavior. It is well conceivable that such higher-level niches have impacted the human genome differently than those of the "great apes" (Varki et al. 2008). To humans, fellow humans act as powerful "transcription factors" even more so than conspecifics do in other highly social species.

1.3.9 The Physical Niche

Exploitation of a large variety of landscapes was an early adaptation of hominins. It might have contributed to early bipedalism as a more efficient way of covering longer distances and gathering resources. It certainly contributed to a much wider set of food types consumed. Fire easily represents one of the most important cultural and technological breakthroughs of the hominin lineage. Vexingly, we still lack a firm evidence for the true age of this key innovation. Oldest evidence is currently at 1 mya (Wonderwerk Cave, South Africa) (Berna et al. 2012), but reasonably convincing arguments based on molar size reduction in the fossil record have been made for a role in the use of fire by early *Homo erectus* as early as 2 mya (Organ et al. 2011). The control of fire likely ushered in massive improvements in niche construction with profound effects on ecology, protection from predation, diet via cooking, and cognition via extended days and the social effects of social gatherings around fires (Wiessner 2014). It also provided novel technological opportunities by allowing altering of materials such as silcrete and compound adhesives (Brown et al. 2009, 2012). The phylogeny of head and body lice provides indirect evidence for early adoption of clothing by modern humans in Africa, a behavioral transition loaded with symbolic potential (Toups et al. 2011). The precise age of home base use is unknown, but the shift to repeated home base use (in contrast to daily new nests) would have dramatically altered the pathogen regime of our ancestors.

1.3.10 The Socio-Cognitive Niche

Human co-residence of multiple males and females but simultaneous widespread pair bonding is an arrangement not seen in any other primate. Pre-agricultural humans lived in small groups but these were likely part of extensive social networks linking such groups over generations. Pair bonding allows for increased confidence of paternity and through it to the establishment of male kinship networks that span individual social groups (Chapais 2013) allowing the evolution of “meta-group” social structure in humans as created by marriage patterns found across human cultures. Studies of marriage patterns in hunter-gatherers would indicate that human culture has been intricately implicated in marriage decisions from times long before agriculture (Walker et al. 2011). There is strong evidence for cultural effects on modern human genomes via different marriage rules in societies around the world with elevated lengths of runs of homozygosity in societies encouraging uncle-niece or first cousin marriages (Pemberton et al. 2012).

1.4 The Cultural Niche

Unlike the case with other, species human culture is ratcheting culture, whereby innovations are not only maintained across generations but can be further improved upon and even combined to form entire technologies (Dean et al. 2014). Human language is a powerful way of maintaining innovations and spreading these across social groups. Cognitive innovations such as beliefs about agency in nature and the supernatural become carried by language and are passed down through the generations. There is accumulating evidence that such beliefs can be very adaptive for both individuals and groups (Baumard and Boyer 2013). Rituals and norms can become powerfully anchored in local culture and enforced by institutions. Interestingly climatic and biological effects appear to affect both language and belief systems as the diversity is higher in the tropics for both religions and languages (Fincher and Thornhill 2008).

1.5 Language and Theory of Mind

Among the most important and species-specific social and cultural inputs in humans is language. This species-specific communication system simultaneously allows communication of experiences and ideas across individuals, time, and space, but also, rather paradoxiacally effectively precludes such communication across linguistic groups (Pagel 2009). Whether human language results from a saltationist event or from the combination of preexisting animal communication systems is a hotly debated issue. The same can be said about the question about the transition from no language to protolanguage via or with an important gestural component.

Much valuable insight continues to come from comparative animal psychology in the laboratory, the field, zoos or great ape sanctuaries (Herrmann et al. 2014; Subiaul et al. 2008), despite the fact that the extreme capacity of humans to envisage the mental life of others and to engage in shared “mental time travel” by using language has no, or at best very limited counterparts in other species.

Language allows for the establishment of widespread reputation, which introduces a completely novel factor in social behavior. Altruism towards non-kin, generosity, and even third-party punishment all can be highly favored by the existence and individual reputation and our awareness of it (Hardy and Van Vugt 2006). Chimpanzees can glean the generosity of other individual during observation of third-party interactions, but without language, they cannot spread that reputation beyond the actual observation (Subiaul et al. 2008). Efforts to find novel ways of studying language evolution based on syntax and phomenes are yielding some tantalizing insights similarities and differences between genetic and language evolution (Colonna et al. 2010; Creanza et al. 2015). While chimpanzee understands the psychology of others to a degree, they seem to lack a human-like theory of mind (Tomasello et al. 2003). The notion that there might have been a psychological threshold/barrier to full awareness of self and others (theory of mind) deserves special attention (Varki and Brower 2013), as it may help to explain why only one species of hominin was eventually left standing after exploiting its self-generated socio-cognitive niche to the fullest.

1.5.1 The Brain Needs the Body and the Group

The brainpower of our species undoubtedly underlies many of the cognitive specialization of *H. sapiens*. Currently, several genes with signatures of uniquely human changes and roles in neurodevelopment, including a handful dating to after the divergence of modern humans and Neanderthals are among the "hottest" candidates for getting at the genetics that make us humans (Paabo 2014).

Humans, however, are more than their large brains. Many of the genes involved in neurobiology have important functions for reproduction and immunity as well. It is important to consider in parallel that human mothers have to be able to gestate and give birth to large-headed babies against the constraints of a bipedal pelvis. The social system has to support mothers and their extremely altricial babies who carry on with a fetal rate of brain growth for a full year after birth. Such offspring are dependent on "mothers and others" especially once inter-birth interval shortens to where weaned offspring cannot find enough food on their own (Blaffer Hrdy 2009). Nutritional opportunities need to exist for the development of our expensive central nervous system with proposed necessary shift to higher trophic levels (top predator) (Hoberg et al. 2001), more marine resources, and/or cooking (Marean 2010; Organ et al. 2011).

1.6 Opportunities and Limitations

Anthropogenists are still facing a staggering list of humbling unknowns about the age of onset of key human innovations. These include but are not restricted to the following: symbolic capacity, personal name or kinship terms, language, home base use, fire use/cooking, pair bonding, awareness of paternal kinship networks, projectile weapon use, composite tool use, fiber use (strings, baskets, nets, hunting machines/traps, bow string, slingshot), bodily modifications (painting with pigments, scarifications, genital cutting, tattoos), and death rituals.

1.7 Open Minds, Closed Umbrellas

The human phenomenon likely reflects an idiosyncratic concatenation of unlikely events. Key factors likely include both opportunities and constraints stemming from massive physical and cultural niche construction by our species that has increasingly taken its own evolutionary fate in its own hands.

Famous umbrella hypotheses such as the "aquatic ape" or the "savannah ape" blatantly fail to account for the many human traits, which arose over a period of several million years (Langdon 1997).

Anthropogeny requires openness to least likely scenarios including ones not directly related to cognitive capacities, to name a few proposed candidates:

- Infection and immunity and their potential ramification for behavior and central nervous system development (Wang et al. 2012).
- Microbiomes, their establishment, evolutionary modification, and profound effects on the entire organism including mental function (Salvucci 2014).
- Climate and geophysical events (Mount Toba eruption) that can exert strong selection of human adaptability via culture and mental flexibility (Ambrose 1998; Calvin 2002).
- The interplay between stone tool manufacture, with strong lateralization of hand use and potential requirements for mental syntax (Stout and Chaminade 2012).
- The use of projectiles to hunt mobile prey and the importance of relative position, directionality, anticipation of motion as exaptation for syntax (Calvin 2001).
- Shifts in ecology allowing the lifting of energetic and nutrient limitations (Bradbury 2011; Organ et al. 2011) and opening of novel symbolic expressions (Duarte 2014; Henshilwood et al. 2011).

1.7.1 The Need for Transdisciplinarity

The human phenomenon includes wide ranges of spatial and temporal scales, from the subatomic (stable isotopes) to the astronomical (solar cycles and climate) and from the millisecond (neuronal action potential) to million years (paleontology). It also requires dealing with the deterministic when studying molecular mechanisms and the arbitrary when studying cultural attributes. Advances in understanding the human phenomenon will likely come from fresh perspectives originating from unexpected fields of research, involving researchers who do not shy away from difficult dialogues and collaborations. The lack of dialogue between sociocultural anthropologists and the physical and natural sciences represents an important hurdle for such transdisciplinary endeavors. The only hope forward is to promote interactions and willingness to refrain from mutual accusations over reductionism and scientism versus postmodernism and relativism. Human cultures and societies have played and continue to play important roles in shaping our biology, which in turn is part of any human cultural phenomenon.

1.8 Why Anthropogeny?

In these days of reduced funding for basic science and strong impetus on translational research, why engage in the exploration of the origins of the human phenomenon?

For one, questions about our origin are likely as old as our species and individuals not interested in their origins are very few. The study of our past deep history also promises to reveal important insights in how intricately involved humans themselves are in shaping their own biological destiny, long before the times of assisted reproduction. Such insights are bound to inform us in important ways about how we care for our young, how we make decisions and form moral views, how different societies use norms and sanctions to channel behaviors, and how different societies chose to interact. Anthropogeny will also provide important novel perspectives on human diseases and disabilities and potentially point to novel ways of preventing, treating, and managing these by understanding which factors in our past including some of the very features we celebrate as uniquely human achievements may predispose many of us for unnecessary suffering.

1.9 Note of Caution

In Ernst Haeckel's time, the lack of fossils prompted him to use fellow humans as "intermediary forms" between apes and Europeans in his Anthropogenie (Haeckel 1891). The study of our origins is loaded with such narcissistic bias and most of us will be tempted by findings with flattering implications about our own groups. Objectivity is heavily compromised when the object of study is our own origin (Marks 2012). Irrespective of whether this is a feeling of pride due to the perception of belonging to the more "original" groups or the more "derived" groups. Given the ugly history of early twentieth century anthropology and persisting attempts at classifying and ranking different human groups, it behooves any anthropogenist and student of the human genome to perpetually be on guard against Haeckel's specter of racist ideologies. After all, one of the hallmark characteristics of the human mind is how easily it adopts the parochial in-group/out-group paradigm (Bernhard et al. 2006). Luckily, that same characteristic can be exploited in advancing the effort to understand the human phenomenon as the hallmark of "our group" as a global species.

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