Human Evolution as a Theoretical Model for an Extended Evolutionary Synthesis

Adam Van Arsdale

Abstract Humans have occupied a paradoxical position within the history of evolutionary studies. On one end, humans have been central to both the academic motivation of the field and the public tensions surrounding evolution. Simultaneously, humans have been cast aside as a poor model organism for understanding the processes that underlie evolutionary theory. As a result, anthropologists who work within an evolutionary context, often chided as being two decades behind mainstream biology, have come to occupy a unique position with respect to the understanding of how evolution operates on humans. Incorporating theoretical developments from a diverse set of related evolutionary fields, biological anthropologists have begun to gather empirical data on the unique evolutionary processes that have shaped our own evolutionary path. Some of the important components that have emerged in human evolutionary studies—biocultural feedback systems, culturally mediated niche construction, and technological ratchet effects—have shed new light not only on how human evolution has proceeded but also on the range of capabilities of evolution more broadly. While not rejecting traditional neo-Darwinian theory and the importance of genetic inheritance, these new developments have highlighted the tremendous complexity afforded by the cumulative action of both selective and neutral evolutionary forces across a range of inheritance modes. Rather than a poor evolutionary model, many of these evolutionary processes are best, or perhaps only, observable in humans. The traits which have structured critical transitions in our hominin past—encephalization, expanded childhood development, and generative language—open up new windows into thinking about an Extended Evolutionary Synthesis.

Keywords Hominin evolution • *Homo erectus* • Darwinism • Modern synthesis • Encephalization

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1 Background

In Charles Darwin's *On the Origin of Species* (1859: 488), he famously limits his references to human evolution to a single line near the end of the volume, writing that through the study of evolution, "light will be thrown on the origin of man and his history." Twelve years later, with the publication of *The Descent of Man* (1871), Darwin expands on human evolution in much greater detail, using it as an opportunity to develop the concept of sexual selection. However, even in this work, Darwin begins on a cautionary note:

> When we confine our attention to any one form, we are deprived of the weighty arguments derived from the nature of the affinities which connect together whole groups of organisms—their geographical distribution in past and present times, and their geological succession (Darwin 1871: 1).

Darwin's awareness of the significance for humanity in understanding the evolution of humans, coupled with his reticence to focus exclusively on humans as a model for evolution, provides an interesting framing for the question considered in this essay. There exists a great deal of interest and curiosity in the knowledge of our shared human evolutionary past but considerable apprehension in reversing the equation and considering what humans can help us understand about how evolution operates. We use evolution to understand our origins as a species, but what does the story of our own evolution reveal about the forces of evolutionary change?

Today, it is unusual to find a researcher whose specialization is the behavioral and morphological evolution of humanity in a biology department (human genetics as a focus in molecular biology being a notable exception). Instead, researchers who focus on human evolution are more often found in departments of anthropology, anatomy divisions of medical schools, or more recent incarnations such as departments of human evolutionary biology.

This contemporary dynamic is the result of an evolution within scientific fields of evolutionary study and was not always the case. As Strier (2016) notes, Section H (Anthropology) of the American Association for the Advancement of Science (AAAS) dates back to 1882. The American Anthropological Association (AAA), the largest association of anthropologists in the world, grew out of AAAS in 1902. The American Association of Physical Anthropologists (AAPA), the largest association of anthropologists whose study is focused on humans and grounded in evolutionary theory, also took origin from the AAAS. First proposed in 1924, a newly chartered AAPA held joint meetings with the AAAS in 1930, and met jointly with both AAAS and the AAA in 1932 (Strier 2016). These facts illustrate the evolutionary origin of the scientific study of human evolution within the broader natural science and evolutionary studies academic realm.

Indeed, several evolutionary biologists intimately connected with the Modern Synthesis were directly involved in the major conversations on human evolution as late as the mid-twentieth century (Smocovitis 2012). Among his endlessly prolific works, Ernst Mayr wrote on the "*Taxonomic categories in fossil hominids*" (1950).

When anthropologist Frank Livingstone provided the first formal critique of the biological race concept in 1962, the respondent on the paper was Theodosius Dobzhansky (Livingstone and Dobzhansky 1962). Again, outside genetics, it is rare to find those points of overlap not just in theory, but in subject, within biology and anthropology today. Stephen Jay Gould's voluminous *The Structure of Evolutionary Theory* (2002), as one example of this trend, only makes passing reference to hominid evolution in its more than 1300 pages.

The drift of human evolutionary studies away from mainstream evolutionary research, or vice versa, in the period after World War II is understandable (Barkan 1996). The revelations of the atrocities of science engineered under the National Socialist regime of Germany, especially those focused on human subjects, made public by the Nuremberg Trials were a watershed moment in twentieth-century human biology (Marks 2008). Given the historical focus of anthropology on race, and the prominence of race-based perspectives on human evolution within anthropology prior to WWII, it is easy to understand the movement away from studies focused on humans in mainstream biology (Washburn 1951; Caspari 2009).

The resistance to E. O. Wilson's *Sociobiology: The New Synthesis* (1975) from areas of the social sciences critical of any hint of biological determinism only furthered this trend (Sahlins 1976; Lieberman 1989; see also Alcock 2017). Humans are too complex to distinguish between genetic and environmental ("cultural") effects. We live too long to look at trans-generational changes in allele frequencies. The data needed to study evolution for humans is too messy. Humans, quite simply, are not a good model organism for the study of evolution. Or so the logic went.

Despite the sidelining of humans within evolutionary studies, humans remain a major focus of the public facing side of evolutionary studies (Plutzer and Berkman 2008). Major fossils relevant for human evolution are disproportionately represented on the covers of *Science* and *Nature*. Documentaries on evolution rarely bypass, and more often than not highlight as a central topic, human evolution. While often devoting entire spacious halls to narratives of human evolution, organisms like *Drosophila* or *Caenorhabditis elegans* (or even *Mus musculus*) rarely get the public coverage warranted by their importance within the scientific process itself.

On the more controversial side of things, it is the evolution of humans, rather than evolutionary theory more broadly, which often raises legal and political challenges to the teaching of evolution or public acceptance of evolution (Lynn et al. 2017). Likewise, the acceptance of scientific knowledge itself, regardless of its evolutionary content, often is strongly correlated with one's understanding of the application of evolution to humans (Pobiner 2016).

In the time period that human evolution has drifted away from the center of evolutionary studies, traditional biological sciences have also been involved in critical self-examination of its foundational framework (Laland et al. 2014). These debates encompass a broad range of topics and developments within the fields of evolutionary studies but can be summarized as discontentment (or a lack of discontentment) with the traditional gene-centric view of the Modern Synthesis (Blute 2017; Laland 2017). For some researchers, the major developments within evolutionary theory over the past 80 years—neutral theory, renewed engagement with evolutionary perspectives on development, epigenetics and complex genomic structure, and hierarchically structured plasticity—have shifted the main focus of evolutionary causation away from natural selection and raised questions as to whether the traditional neo-Darwinian framework remains the best approach to understanding and presenting the action of evolution (Jablonka and Lamb 2014). These are not, it should be pointed out, arguments that "evolution is wrong" but instead are arguments about where the focus is placed on the processes of evolutionary change through time.

Conversations around this issue are equally fascinating and frustrating (Pigliucci 2007, 2017; Szathmáry 2015). On the one hand, it is possible that these conversations can highlight the extraordinary capacity of evolution to create complex patterns of variation in a seemingly endless and changing number of ways (Pigliucci 2008; Jablonka and Lamb 2014). On the other hand, some see these efforts as undermining public understanding of evolution, unnecessarily focusing on ephemeral "exceptions" rather than central tendencies in evolution, and potentially prioritizing novel theoretical perspectives over interpretation of basic observational data (Wray and Hoekstra 2014; Futuyma 2015).

Mindful of the cautionary note sounded by Darwin at the beginning of this essay, in what will follow I will nevertheless argue that this is a unique and important moment to reconsider the role that human evolution plays in the mainstream of evolutionary biology (Fuentes 2016). The unique trajectory of our own evolutionary past highlights both the possibilities and the limitations of an Extended Evolutionary Synthesis. There is compelling evidence that specific changes in our evolutionary past, beginning with the emergence of the genus *Homo*, initiated a fairly unique manifestation of neo-Darwinian processes involving multiple modes of trans-generational inheritance with significant evolutionary consequences. And yet, the specific nature of the changes that have occurred in humans highlights the exceptional status of the circumstances under which humans evolved, perhaps thereby serving as the exception that proves the rule when it comes to the need for new theoretical understandings of evolution, as opposed to simply new ways of understanding existing theory and data.

2 Humans as a Model Organism in Evolutionary Studies

At the heart of many of the discussions around a "new" Evolutionary Synthesis are varying views about how well integrated are emerging bodies of theory in ecology and evolution (Laland et al. 2015), with a healthy smattering of discussion of demography (Lowe et al. 2017) and development added to the mix (Gilbert et al. 2015). As it happens, multiple lines of evidence associated with recent human evolution highlight the critical role played by changing patterns of demography, development, and ecology in shaping our own evolutionary trajectory. As such, an examination of recent human evolution provides a valuable lens into ongoing and active debates about the nature of evolutionary theory.

The particular importance of humans in this discussion can be observed by focusing on the nature of the evolutionary transition at two major points in our past. Traditionally, narratives of human evolution (scientific or public) tend to focus on two transitions: the origin of hominins and the last common ancestor with extant apes (e.g., Gibbons 2007) and the African origin of "modern" *Homo sapiens* toward the end of the Pleistocene (Stringer 2012). These two evolutionary transitions are certainly important, but for the purposes here, a more telling perspective comes from examining the emergence of the genus *Homo*, sometime around 2 million years ago (and *Homo erectus sensu lato*, in particular), and the widespread shift to agricultural subsistence systems over the past 12,000 years. These transitions encompass a significant shift in the pattern of human evolution in the case of the origin of *Homo* and a major ecological change with the origin of agricultural food systems that highlights the magnitude of the evolutionary frame shift that has occurred in our lineage.

2.1 The Origin of **Homo**

The transition from *Australopithecus* to *Homo* is one marked by fairly subtle changes in morphology but changes that have a profound effect on the ecology of subsequent hominins and the ensuing pattern of evolution seen in humans and our ancestors (McHenry and Coffing 2000). In particular, the transition from *Australopithecus* to *Homo* involves the evolutionary investment in mechanisms that enhance plasticity and enable long-term changes to the basic pattern of human evolution.

Most anthropologists place the origin of *Homo* somewhere in East Africa near the Pliocene–Pleistocene transition (e.g., Villmoare et al. 2015; Schrenk et al. 2015). However, current consensus is lacking on the exact nature, both taxonomic and biological, of these earliest specimens, sometimes referred to simply as early *Homo* (Wood and Collard 1999; Wolpoff 1999; Van Arsdale and Wolpoff 2013; Berger 2013; Antón et al. 2014) As such, it is more useful to focus on the less controversial initial appearance of *Homo erectus*, also likely in East Africa (Antón 2003; Spoor et al. 2007), though perhaps most clearly evident in its earliest appearance with fossil material from the site of Dmanisi, Georgia, at approximately 1.8 MA (Lordkipanidze et al. 2007, 2013; Van Arsdale and Lordkipanidze 2012). *Homo erectus* presents the convergence of several morphological and behavioral traits seen heterogeneously in earlier hominin fossils, including the diverse assemblage of potential early *Homo* fossils.

Morphologically, an evolutionary shift from Australopithecines to *Homo erectus* can be seen across several broad features. One of the clearest distinguishing features of *Homo erectus* is an expanded body size, particularly involving elongated hind limbs (Rose 1984; Walker and Leakey 1993; Antón 2003; Lordkipanidze et al. 2007). The Nariokotome partial skeleton, dating to roughly 1.6 MA, provides a near complete glimpse of an extremely long-legged individual that would have been in the vicinity of six feet in height as an adult (Walker and Leakey 1993; Dean and Smith 2009). The longer limbs of *Homo erectus* have been associated with greater long-distance locomotor efficiency (Steudel-Numbers 2006; Pontzer et al. 2010; Pontzer 2012). This attribute appears to have been associated with the utilization of a broader range of food resources, including higher quality food resources relative to earlier hominins (Walker 1981; Organ et al. 2011).

Further evidence of a dietary shift toward higher quality food resources comes from the reduced masticatory apparatus in *Homo erectus* relative to earlier hominins. This reduction includes significantly reduced post-canine dentition (Wood 1992; Gabunia and Vekua 1995; Kaifu 2006; Suwa et al. 2007; Zaim et al. 2011), an increase in the gracility of the mandibular corpus (Rightmire 1981; Antón 2003; Van Arsdale and Lordkipanidze 2012), reduced temporal fossa size corresponding to a reduced temporalis muscle (Wolpoff 1975; Demes and Creel 1988), and a possible shift in the biomechanics of hominin chewing (Teaford et al. 2002). There is at least some evidence for a genetic basis to this suite of masticatory changes in the form of a nonsense mutation to *MYH16* gene in the human lineage dating to the Plio-Pleistocene boundary, though additional research needs to be done to confirm this link (Stedman et al. 2004).

Importantly, the reduction in masticatory apparatus, particularly in the cranial musculature and post-canine dentition, is not limited to *Homo erectus* at this time. *Australopithecus sediba* from South Africa, possibly concurrent with the earliest *Homo erectus* in East Africa, also shows a reduced masticatory apparatus, but absent many of the other changes seen in *Homo erectus*, most notably a lack of brain expansion (Berger et al. 2010). The presence of coexisting hominin lineages in the Lower Pleistocene, but featuring a different combination of traits, provides a natural test for the significance of the combination of traits present in *Homo erectus* and distinguishes the eventual evolutionary success of *Homo erectus* relative to these other lineages.

The focus on higher quality food resources was conditioned on the utilization of cultural technology, including intentionally flaked stone tools. Recent findings have pushed the earliest appearance of stone tools to at least 3.3 million years (Harmand et al. 2015), but by the time of *Homo erectus*, tool technologies have taken on aspects of complexity involving form, acquisition, specialization, and usage, which highlight a dynamically changing role within *Homo erectus* ecology (Shipman and Walker 1989; Braun et al. 2009; Ferring et al. 2011; Hovers and Braun 2009). This ecological shift included a broadening, or at least increased variability, in the diet (Ungar et al. 2006), as well as an increase in energetic quality (Leonard and Robertson 1992). The reduction in masticatory capabilities seen in *Homo erectus*, particularly when compared to contemporary and possibly sympatric robust Australopithecine lineages, highlights the important role of stone tool technology in separating the ecological niche of these two lineages.

The convergence of larger body size, reduced masticatory apparatus, and improved dietary quality (aided by the application of cultural technology) all relate to the most significant feature of *Homo erectus*, an increase in the size and encephalization of the brain. Beginning just after 2 million years ago, some members of the hominin lineage begin displaying an absolute and relatively larger brain (Ruff et al. 1997; Antón 2003; Lee and Wolpoff 2003; Rightmire 2004; Baab 2008). In addition to an expansion in absolute and relative brain size, fossil endocasts reveal evidence of a shift toward a more human-like brain morphology (Falk 1987; Bruner and Holloway 2010; Berger et al. 2015).

Changes to the brain observed in *Homo erectus* also reflect related changes to development, life history, and ecology of this species. The brain is an energetically expensive tissue that expands in *Homo erectus* without an associated change in basal metabolic rate (Aiello and Wheeler 1995; Aiello 2007). The ecological transition to higher quality food resources thus appears to be a necessary precursor for adequately fueling an expanded brain, consistent with the emerging evidence of complex tool use in earlier Pliocene hominins (McPherron et al. 2010; Harmand et al. 2015) and, in a less durable fashion, nonhuman primates (Van Schaik et al. 1999; Whiten et al. 1999; Matsuzawa 2008). Again, the contrast between the dietary ecology of *Homo erectus* and the contemporaneous robust Australopithecines is telling. *Homo erectus* appears to have fully committed, with both an encephalized brain and a reduced gut, to a more intensified, high-quality, diet. The contemporaneous Australopithecines, no doubt also engaged in diverse dietary strategies, retained the ability, likely fully realized in species like *Australopithecus boisei*, of targeting low-quality, high-volume food resources (Cerling et al. 2011). This contrast is helpful not only in highlighting the different niche in *Homo* but also in identifying the points of departure in the evolutionary trajectory in *Homo*. It is difficult to imagine a later member of the genus *Homo* biologically specializing in low-quality food resources without the aid of the kinds of cultural technology we see in contemporary farming populations (see below).

The transition to a relatively larger brain required not only an ecological shift but also a life history change. Relative to nonhuman primates or earlier hominins, *Homo erectus* had a more rapid pattern of brain growth after birth in addition to an overall extended period of brain development (Leigh 2006; DeSilva and Lesnik 2008; Snodgrass et al. 2009; DeSilva 2011; Grabowski 2016). Developing larger brains in infants and toddlers more rapidly and for a longer period of time requires a subsequent change in parental, and particularly maternal, investment (Aiello and Key 2002; Aiello and Wells 2002; Ellison 2009; Dunsworth et al. 2012). The expansion and increasing energetic investment in early development in *Homo erectus*, coupled with the increased energetic demands and higher quality diet, all attest to an overall energetic/ecological intensification within *Homo erectus* relative to earlier hominins and nonhuman primates.

The above changes in *Homo erectus* are all supported by morphological evidence from the existing hominin fossil record or material evidence in the Plio-Pleistocene archaeological record. However, they also gesture toward a set of behavioral changes that are harder to directly examine in the fossil and archaeological record but also have at least circumstantial support. These behavioral changes—population expansion and dispersal, decreasing mortality, increasing social complexity, and increasing behavioral plasticity—all have tremendous importance for how the pattern of evolution and the underlying processes are inferred for our shared, recent evolutionary past.

The least contentious consequence of the above changes in *Homo erectus* is an overall expansion in the geographic range of *Homo erectus* relative to earlier hominins. In a relatively narrow window of time between 1.8 and 1.6 million years ago, hominins (and generally considered to be *Homo erectus*) expand from an exclusively African fossil clade to one found in the Caucasus (Dmanisi), China (Nihewan Basin), and Indonesia (Java) (Swisher et al. 1994; Sémah et al. 2000; Gabunia et al. 2001; Zhu et al. 2004). After evolving in Africa for at least 3 million years, within a short window of time, *Homo erectus* becomes the first hominin to expand outside of Africa, occupying a range of habitats that dramatically expands the existing range of seasonality (both temperature and humidity) and ecosystems occupied by earlier hominins (Tappen 2009; Potts and Teague 2010).

Another subtle shift that occurs with *Homo erectus* is evidence of a reduction in the rate of adult mortality. Analysis of hominin dental remains throughout the Plio-Pleistocene identifies a small but significant increase in the fraction of adult remains that might be considered "older adults" at the time of death as opposed to young adults (Caspari and Lee 2004). Even a slight change in patterns of adult mortality may have led to significantly different dynamics structured around life history, including the potential for an associated increase in longevity (O'Connell et al. 1999). The effects of an increase in adult survivorship could be compounded by the geographic expansion observed in *Homo erectus* and the potential increase in the number of accessible and suitable environments for occupation. More populations with more individuals living longer create a greater number of natural laboratories for processes of evolution to operate.

There is also direct evidence at the site of Dmanisi for increased longevity in *Homo erectus* with the presence of a completely edentulous specimen, showing extensive resorption of both the mandibular and maxillary alveolar regions, indicating sustained survival in the absence of a functioning masticatory apparatus (Lordkipanidze et al. 2006; Van Arsdale and Lordkipanidze 2012). This specimen is not sufficient to argue directly for social care in early *Homo erectus*, but it does provide the earliest evidence in humans of the potential to survive with some combination of cultural technology. This view is consistent with the evidence associated with the energetic demands of pregnancy and childhood development, as well as the acquisition of large-sized prey (Bunn 2001), of an overall uptick in the intensity and significance of social networks of hominins.

2.2 Pleistocene Hominin Evolution

The evolutionary changes associated with *Homo erectus* described above, viewed individually, may be considered unremarkable. However, when viewed in conjunction with the evidence drawn from the archaeological record indicating changing behavioral patterns, they provide compelling evidence of a significant change in the properties that define the pattern of human evolution. More importantly, this pattern can be observed by looking at the Pleistocene fossil and archaeological record that

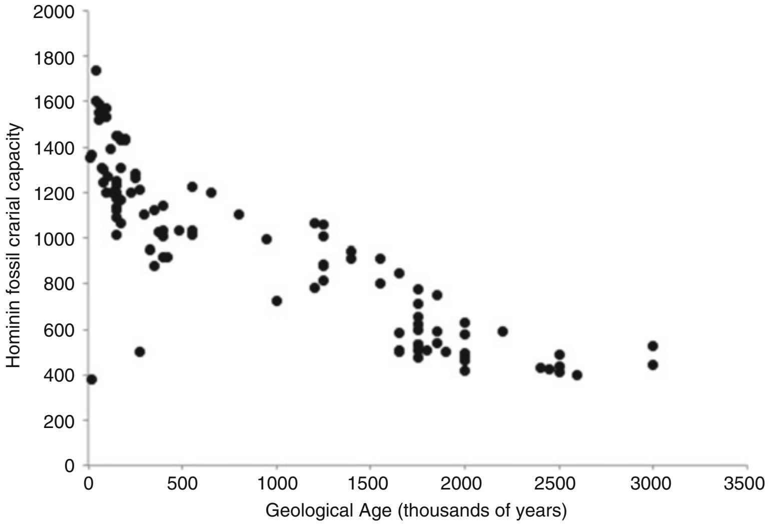

Fig. 1 Pleistocene hominin cranial capacity of major fossil specimens across the Pleistocene. The initial evidence of encephalization begins shortly after 2 million years ago, concurrent with the origin of *Homo erectus*, marking the onset of a trend that continues until about 30,000 years ago

follows the origin of *Homo erectus*, suggesting that the evolutionary changes associated with humans are durable across a geological timeframe.

What makes the transition to *Homo* noteworthy is the extent to which the brain becomes both a focus of evolutionary pressure and a mechanism for establishing the evolutionary landscape governing hominins in the Pleistocene. The behavioral, technological, and dietary changes that predate the origin of *Homo erectus* indicate the beginning of a shift in at least some Australopithecines to a higher quality diet, involving more intensive extraction of food resources (presumably relatively scarce fat components, in particular). At a certain point, however, evident by at least 1.8 million years ago in *Homo erectus*, this led to the onset of a clear pattern of brain expansion seen throughout Pleistocene hominins (see Fig. 1).

The gradual expansion in hominin brain size throughout the Pleistocene is paralleled by other transitions that reflect the impact and scope of this change. The most significant trends are those indicating increased demographic potential (Caspari and Lee 2004), increasing cultural complexity (McBrearty and Brooks 2000), and increasing habitat range and diversity (Dennell and Roebroeks 2005; Finlayson 2005).

As the brain became a more important part of the hominin ecological adaptation, it simultaneously became a more efficacious mechanism for the transmission of evolutionarily relevant information across generations and between individuals. The brain takes on a dual importance in Pleistocene hominins as both a shaper of phenotype, and therefore target for selective processes, and at the same time a nongenetic alternative hereditary system. Increasing social complexity, coupled with extended periods of childhood development and elevated cognitive abilities, establishes an increasingly durable pathway for the transmission of behavioral, and potentially symbolic, forms of evolutionary information. As others have noted, in this scenario, the brain becomes positioned as the fulcrum in an evolutionary "ratchet" model of human cognition and culture (Tomasello 1999; Tennie et al. 2009).

What exactly is being "ratcheted" up in the above model of human evolution is up for interpretation, particularly when the amorphous term of "culture" is invoked? An examination of the fossil evidence is helpful. Brain size is, of course, one thing that is steadily increasing, along with the aforementioned demographic increases, range expansion, and technological complexity. But another way of viewing this scenario is that it is the breadth of the hominin niche itself that is being expanded. As cognitively mediated technology/culture becomes a more important aspect of phenotype in hominins, the range of conditions under which hominins might persist also expands. Importantly, this expansion in niche and phenotypic plasticity is at least partially mediated by nongenetic modes of transmission. The development of new tool technologies allows for procurement of different kinds of food resources (Wilkins et al. 2012). The application of fire to food processing allows for enhanced nutrient extraction from the environment (Attwell et al. 2015). The long-range exchange of material goods helps facilitate cultural and technological practices across a wider range of environments (Langley and Street 2013). These kinds of traditions develop, propagate, and change on the basis of cultural factors, not genetic ones.

It is reasonable to ask whether or not these patterns are supported by an analysis of the cranial morphology in Pleistocene hominins. Does the pattern of niche expansion in Pleistocene hominins fit the predictions associated with a dramatic shift in the pattern of human evolution and is such a change visible in the hominin fossil record?

In order to address this question, the below analysis looks at the pattern of cranial variation observed across 143 Plio-Pleistocene hominin fossils, a sample representing the majority of the well-preserved cranial specimens available for study at this time (Table 1). A diverse array of views exist as to the appropriate taxonomic classification of these specimens individually and the number and identity of the taxonomic groups to which they belong. As a starting point, this study builds off recent genetic evidence that suggests anatomically modern *Homo sapiens* admixed with multiple populations of archaic hominins, including at a minimum Neandertals and Denisovans (Sankararaman et al. 2016; Wall and Brandt 2016; Nielsen et al. 2017). Assuming that the admixture between *Homo sapiens* and these archaic populations reflects a theoretical maximum amount of genetic divergence, patterned across time and space, through which an evolutionarily continuous lineage can be maintained, the combined *Homo sapiens*–Neandertal sample is used as a lens to evaluate the pattern of cranial variation observed throughout the remainder of the Pleistocene.

The 143 cranial specimens used in this study are variable in their degree of preservation. In order to maximize the comparability of pairs of specimens, up to 188 cranial measurements were used for comparison, with a minimum threshold for inclusion in the study of 20 measurements. For each specimen pair, an average

Table 1 List of cranial specimens

Amud 1	La Chaise 2	Skhul 5
Arago 21	Laetoli 18	Skhul 6
Atapuerca 5	Lantian	Skhul 9
Biache	Lazaret 1	Spy 1
Bodo	LB 1	Spy 2
Ceprano	Maba	Solo 1
Chao Hu	MH 1	Solo 3
Chesowanja 1	MK 1	Solo 4
Daka	MK 9	Solo 5
Dali	MK 37	Solo 6
Dmanisi 2280	Narmada	Solo 8
Dmanisi 2282	Ndutu	Solo 9
Dmanisi 2700	OH 5	Solo 10
Dmanisi 3444	OH 9	Solo 11
Ehringsdorf	OH 12	SK 12
Eliye Springs	OH 13	SK 13
Florisbad	OH 16	SK 46
Fontechevade	OH 24	SK 47
Herto 16/1	Omo 1	SK 48
Herto 16/5	Omo 2	SK 49
Hexian	Petralona	SK 52
Jebel Irhoud 1	Qafzeh 3	SK 79
Jebel Irhoud 2	Qafzeh 5	SK 80
Jinniushan	Qafzeh 6	SK 83STS 5
Kabwe	Qafzeh 7	STS 13
Kanjera 1	Qafzeh 9	STS 17
KNM-WT 15000	Qafzeh 11	STS 19
KNM-WT 17000	Saccopastore 1	STS 22
KNM-WT 17400	Saccopastore 2	STS 52
KNM-ER 406	Saldanha	STS 53
KNM-ER 732	Sale	STS 71
KNM-ER 1470	Saltzgitter	STS 1511
KNM-ER 1590	Sambungmachan 1	STW 52
KNM-ER 1805	Sambungmachan 3	STW 252
KNM-ER 1813	Sambungmachan 4	STW 505
KNM-ER 3732	Sangiran 2	Steinheim
KNM-ER 3733	Sangiran 3	Swanscombe
KNM-ER 3883	Sangiran 4	Reilingen
KNM-ER 13750	Sangiran 10	Tabun 1
Krapina A	Sangiran 12	Trinil 1
Krapina B	Sangiran 17	Vértesszolos
Krapina C	Shanidar 1	ZKD D1
Krapina D	Shanidar 2	ZKD E1

(continued)

Table 1 (continued)

Krapina E	Shanidar 4	ZKD H3
Krapina 16	Shanidar 5	ZKD L1
Kromdraai	Skhul 2	ZKD L2
La Chaise 0	Skhul 4	ZKD L3
		Zuttiyeh

normalized pairwise distance was calculated on the basis of mutually preserved homologous measurements:

$$\frac{1}{n}\left[\sum_{1}^{n}\left(\text{abs}(x_a - x_b)\ast\sum_{1}^{z}\frac{\text{abs}(x_1 - x_z)}{\mu_z}\right]\right.$$

A conservative taxonomic scheme was employed, consisting of a mixed *Homo sapiens*–Neandertal sample, specimens assigned to *Homo heidelbergensis*, *Homo erectus*, and five species of Australopithecines (*A. africanus, A. sediba*, *A. aethiopicus*, *A. boisei*, *A. robustus*).

Figure 2 displays the results of a pairwise comparison of cranial variation of Pliocene and Pleistocene hominin crania.

A number of interesting results emerge from this analysis. First, while there is considerable noise within the pairwise comparisons for any given group (more on that below), the mean for those groups assigned to Pleistocene *Homo* fit a linear model through time. In contrast, the samples of pairwise Australopithecine comparisons, in aggregate, are consistently elevated from this trend in their degree of morphological divergence.

In this analysis, *Homo sapiens*, Neandertals, *Homo heidelbergensis*, and *Homo erectus* do not show major gaps or discontinuities suggestive of a significant change in the overall pattern of evolution. In contrast, the division between *Homo* and *Australopithecus* is marked by such a discontinuity, as shown by a secondary analysis of these results. If the 95th percentile of variation observed in the *Homo sapiens*–Neandertal sample is used as a guide for the expected level of morphological variation within an evolving lineage, it is possible to explore the percentage of pairs in each group of pairwise comparisons that exceeds that level (Table 2). The significance of these values is assessed via a resampling approach that generates an expected level of variation for a randomly resampled set of pairwise comparisons equivalent in sample size to that observed in this study. None of the pairwise samples within *Homo* show a significant fraction of highly divergent pairwise comparisons (though they do show an increasingly amount of variation as the temporal gap increases). In contrast, all of the available Australopithecine comparisons show statistically significant fractions of pairwise comparisons that are more divergent than the observed 95th percentile of *Homo sapiens*–Neandertal comparisons.

The apparent “noise” in Fig. 2 might also be indicative of the strong effects of genetic drift on shaping aspects of Pleistocene hominin crania morphology. This result has been suggested by previous research (Ackermann and Cheverud 2004; Roseman 2016) and likely reflects the strong evolutionary constraint imposed on Pleistocene hominins given their demographic limitations. Parsing the data from

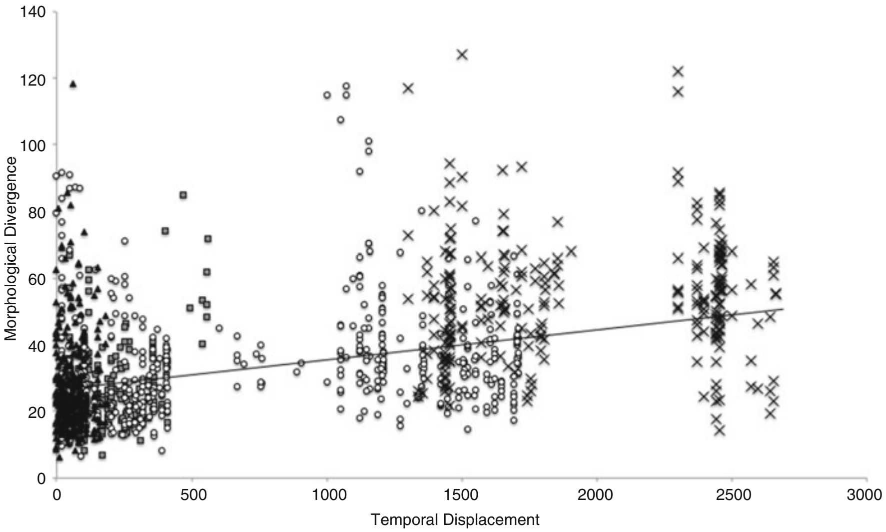

Fig. 2 Morphological divergence in a sample of 1201 pairwise comparisons of Plio-Pleistocene hominin crania. The *y*-axis displays the degree to which any pair of crania differ on the basis of homologous linear measurements. The *x*-axis depicts the best estimate of the temporal distance separating the pair of fossils. Solid triangles indicate pairwise comparisons from a mixed *Homo sapiens*–Neandertal sample. Gray squares include pairwise comparisons between *Homo sapiens*–Neandertals and *Homo heidelbergensis* specimens. Open circles include pairwise comparisons between *Homo sapiens*–Neandertals and *Homo erectus* specimens. The trendline depicts a model of the expected level of divergence given an estimated temporal displacement between any two specimens. The trendline intersects nearly exactly with the mean morphological and temporal divergence in the samples including pairwise comparisons with *Homo heidelbergensis* and *Homo erectus*. Pairwise comparisons involving specimens assigned to *Australopithecus* (*A. africanus*, *A. robustus*, *A. boisei*) are displayed with a gray X. Relative to comparisons with *Homo*, these pairings show substantially elevated levels of morphological divergence

above more closely, within pairwise groupings there exists a significant relationship between morphological variation and geographic separation, in addition to the association with temporal displacement. This observation adds an additional ripple to the evolutionary pattern evident in the morphology of Pleistocene *Homo*, highlighting the significant constraint imposed by demographic constraint and geographic isolation on hominin populations. Thus, alongside the strong argument for continuous selection acting on the associated pattern of encephalization, genetic drift is likely playing a major and ongoing role in shaping aspects of cranial morphology.

The concordant patterns of change seen in Pleistocene hominins can be understood as part of a novel emergent evolutionary pattern in *Homo*, centered on the brain as both an adaptive and hereditary element. Even while populations of hominins are expanding into diverse and distant environments in the Pleistocene, they show consistent trends in morphological variation, particularly centered around aspects of neurocranial size and structure. This is true, despite the evidence of an expanded role for genetic drift in shaping patterns of population differentiation. That these semi-isolated populations are not fissioning off into distinct

Table 2 Results of pairwise cranial analysis

	A. africanus	*A. robustus*	*A. boisei*	*H. erectus*	*H. heidel.*	Neandertal	*H. sapiens*
A. africanus		65	41	228	78	99	83
A. robustus	0		37	158	57	73	68
A. boisei	21.95	16.22		160	44	65	61
H. erectus	50.88**	47.37**	33.75**		347	525	479
H. heidel.	65.38**	45.61**	47.73**	10.37		132	117
Neandertal	54.55**	28.75**	49.23**	12.38	6.82		169
H. sapiens	56.63**	30.88**	50.26**	12.11	9.40	5.92	

The numbers above the diagonal reflect the number of pairwise comparisons that met the threshold for having at least 20 homologous measurements available for comparison. The numbers below the diagonal are the percentage of pairwise comparisons that exhibited morphological differences greater than the 95th percentile of observed variation in Neandertal–*Homo sapiens* pairings. Asterisks indicate significant differences on the basis of a resampling analysis morphological lineages attests to the expanding hominin niche and its power in reducing the development of long-term reproductive barriers.

While it is difficult to directly identify a mechanism for causation with the encephalization of the Pleistocene hominin brain, it is nearly impossible to avoid its association with increasing social and technological complexity. More advanced cultural and technological capabilities allowed hominins to expand and persist across a greater range of environments. The expansion of hominins into new environments in the Pleistocene does not correlate strongly with significant morphological change; rather, it appears to be driven by increasing plasticity associated with the application of cognitive resources to novel environmental challenges. Hominins in the Pleistocene are able to adapt, increasingly, by creating novel cognitive/cultural/technological variants specifically directed toward environmental challenges, rather than depending on the creation of such novel variation via purely genetic processes.

The Pleistocene archaeological record attests to not just greater cognitive complexity in tool construction but also an increased emphasis on the mechanisms associated with the transmission of that complexity across generations. Tools become more complex throughout the Pleistocene—including a diversification of tool types, materials, and construction technologies—but they also become more consistent in form. Reconstructions of the cognitive processes associated with Pleistocene tool construction attest to the active learning and instruction processes necessary for successful replication of elements of the archaeological record (Nowell and Davidson 2010; Bruner 2014).

The knowledge produced by cognitive archaeology parallels developmental psychology literature contrasting humans and nonhuman primates (Want and Harris 2002; Hare and Tomasello 2005). Humans are extraordinarily good active learners and teachers. The human brain places sensory information from the environment into complex semantic structures in a hypothesis-like manner. In this capacity, the Pleistocene hominin brain acts as an alternative hereditary system, conveying evolutionarily relevant information associated with the construction of phenotype, and thereby subject to evolutionary forces, including natural selection.

2.3 The Origin of Domestication

While the origin of *Homo* appears to include both a morphological and related ecological shift, the transition to domestication-based lifestyles and subsistence strategies in human populations appears to be largely ecological (though with the possibility for substantial lagging morphological changes in response). Importantly, the transition to agriculture is best explained as a direct product, and indeed continuation, of the pattern enabled by the origin of *Homo* (Zeder 2006).

By the end of the Pleistocene, hominin populations, still predicated on subsistence level foraging, had occupied the majority of available environments within Eurasia and Africa. Technological and cultural developments had enabled populations to overcome a wide range of climatic and ecological barriers (Roebroeks and Villa 2011; Boivin et al. 2013; Glantz et al. 2016). Evidence based on faunal exploitation shows that population levels in many of these regions were increasing, a finding consistent with the gradual changes in mortality patterns that began with *Homo erectus* (Stiner et al. 1999). Facing such circumstances, populations in the Late Pleistocene began to show evidence of increased exploitation of marginal plant resources, including the precursors of eventual domesticates (Henry et al. 2011).

Out of this, comes the major transition to domestication-based food resources. Within 10,000 years, less than 1000 generations for humans, the vast majority of the world's people go from a foraging-based food economy to a sedentary, domesticated food economy. The scale of the transition, and its implications for human evolution, is enormous.

It should further be noted that the transition to domestication-based subsistence strategies is not just a major event in human evolutionary history but also a major event in the history of the planet. The emerging utilization of the "Anthropocene" as a concept and time period to understand and focus attention on the consequences of human processes on the world can largely be tied into the transition to agricultural and pastoral food systems (Smith and Zeder 2013).

Like the transition to *Homo*, the establishment of domesticated food systems in human societies is conditioned on both the evolvability of cognitive and genetic systems. However, more so than the transition to *Homo*, this transition is clearly driven by cognitive/technological changes outside of the strict constraints of the human genotype/phenotype complex. Without a doubt, the transition has had and continues to have substantial genetic changes, many of which are implicated in contemporary issues of human health (Cordain et al. 2005). However, the change to a domestication-based food economy was not, itself, predicated on any specifically arising beneficial genetic mutation.

The origin of agriculture is the most significant and widespread example of the utility and importance of an Extended Evolutionary Synthesis for human evolutionary studies. The transition from a subsistence-foraging based ecology to one predicated on domestication is the most significant ecological change in the past 5 million years of hominin evolution. And yet, unlike the origin of *Homo* (or *Homo erectus sensu lato*), it does not correspond with major morphological changes in humans. It also does not evolve in association with a single population but rather occurs independently and in rapid succession across populations in the Near East, Northeast Africa, South Asia, East Asia, and Central and South America. Likewise, it is not associated with a single set of environmental conditions. Instead, what it is associated with is a broadly shared and incredibly flexible human niche, the product of nearly 2 million years of evolution in the genus *Homo*.

Some researchers view the morphological changes associated with the genus *Homo* as a transition in which the emerging hominin brain, and all of its associated cultural technology, comes to replace hominin teeth in their role in energy procurement. In a similar vein, the emergence of agricultural systems represents a wholesale shift of food procurement away from the evolved hominin physiology and onto the hominin environment itself. This hereditary systems associated with the development of agricultural systems are, functionally, cultural (or in Jablonka's nomenclature, symbolic) modes of inheritance.

Interestingly, the focus on domestication as a "cultural phenomenon" is implicit within the historical placement of the study of agricultural origins largely in the archaeological realm, rather than the realm of physical anthropology. In other words, this transition has historically been viewed as a cultural transition in evolution, rather than a biological or genetic transition. This perspective has changed dramatically in recent years given the wealth of ancient genomic data from early agriculturalists, pastoralists, and their predecessors (Haak et al. 2005; Bramanti et al. 2009; Skoglund et al. 2012). A new wave of emerging biological anthropological and genetic research is highlighting the complex demographic and genetic relationship, including genetic components of fitness, between pre-agricultural populations and the agricultural populations that came to replace them almost in their entirety (Skoglund et al. 2014; Racimo et al. 2015).

One way of viewing the evolutionary pattern of humans in the Pleistocene is as a 2-million-year transition period, beginning with the onset of encephalization in *Homo erectus*, and culminating with the ecological transition to agriculture. To be sure, the transition to agriculture does not mark the end of human evolution (Hawks et al. 2007), but rather that permanent establishment of a robust system of evolutionary inheritance running parallel to genetic heredity. The population growth observed in agricultural populations pushed human populations across the threshold of the demographic challenge faced by human and nonhuman primates up to this point (Excoffier and Schneider 1999; Bocquet-Appel 2011). Large brains, even those of nonhuman primates, take a long time to develop with evolutionary costs associated with delayed reproduction and longer interbirth intervals. While hominin evolution has, since its beginning, been marked by steps toward greater reproductive potential in comparison to non-hominin primates (Lovejoy 1981, 2009), population persistence on the order of millennia is likely only a consistent product of the agricultural revolution. The cumulative effects of long-term cultural-technological transmission across generations, critically dependent on long-term population stability and persistence, are therefore only firmly established in the human record over the last 10,000–15,000 years. While the transition to agricultural food production might have had negative effects on overall human population health, it greatly expanded human reproductive potential at the population level (Armelagos et al. 1991). Thus, while the brain is uniquely positioned to be both a mechanism for generating phenotypic novelty and a means of trans-generational transmission, it is biologically constrained in critical ways by processes of development and demography.

3 The Limits and Possibilities of an Extended Evolutionary Synthesis

This essay began with the argument that humans might serve as an important model for examining the need to rethink evolutionary theory given ongoing debates within evolutionary biology. The argument above outlines how the evolution of the human brain over the Pleistocene opens the door to an expanded set of evolutionary processes. The brain's role in shaping patterns of phenotypic plasticity and the subsequent expansion of the human ecological niche, coupled with the role of the brain in constructing a durable mode of transmission via social learning, is a fairly unique evolutionary dynamic. As Pleistocene hominins became more dependent on the brain to facilitate socially and technologically enabled ecological strategies, hominins became better learners, better teachers, and more creative, canalizing a kind of symbolic/behavioral mode of transmission. The human brain is fairly exceptional in its size, degree of complexity, and duration of development by mammalian standards. And yet the properties that gave rise to the human brain are not so unique.

The evolutionary changes that gave rise to *Homo erectus* were predicated on a complex developmental physiology that is broadly shared across mammals. While there appears to be clear evidence of selection favoring encephalization throughout the Pleistocene, many of the identified selective variants in the human genome over the past 50,000 years are associated with regulatory and epigenetic systems (Akey 2009). As Esposito (2017) notes, such interactions are not non-Darwinian so much as they defy the mechanistic interpretations of Darwinian processes often associated with representations in the Modern Evolutionary Synthesis. Nor should they be expected to be limited to any particular lineage given the deep homology of these inherited regulatory and developmental systems. Another key element of the hominin pattern of evolution throughout the Pleistocene is the way in which development is malleable to the traditional forces of Darwinian evolution. Yet, as MacCord and Maienschein (2017) make clear, developmental approaches to understanding biology might have their own historical trajectory but are not inconsistent with the overarching historical trajectory or theoretical groundings of the varied nature of Darwinism (see also Bowler 2017; Levit and Hossfeld 2017; Loison and Herring 2017).

But it is also worth considering the limitations on the human example for understanding of broader patterns of evolution. Many of the critiques of an Extended Evolutionary Synthesis focus on the ephemeral nature of emergent, "non-Darwinian," evolutionary processes in model organisms. In the human case, the power of alternative modes of evolutionary inheritance is fundamentally and significantly limited by demographic constraints. Despite the brain serving as a kind of Swiss army knife of adaptation, hominin populations nearly everywhere they are found, throughout the Pleistocene, were likely always vulnerable to localized extinction. Areas were occupied and then unoccupied for long periods of time. New technological patterns emerged, were lost, and then emerged (seemingly independently) again. Even the emergence of seemingly fundamentally altering technologies, like the controlled use of fire, was not enough to overcome the long-term evolutionary drag of genetic drift on populations extremely limited by their demographic scale (Sandgathe et al. 2011).

And yet, in the human example, the demographic constraints on human populations in the Pleistocene reflect an essential component of the expanded evolutionary processes in hominin evolution. The very features that make human behavioral/symbolic inheritance more durable than the emergent properties of other exceptional organisms simultaneously limited human evolutionary potential. Alternative modes of inheritance predicated on the properties of the hominin brain would not be possible, or at least not have sustained, long-term effects, without long periods of pre-adult development and intense dedication of evolutionary resources to child-rearing. But these are the very traits that limit the demographic potential of Pleistocene hominin populations. Even in the Late Pleistocene, as populations are developing more and more complex forms of cultural technology and occupying a greater range of environments, they remain vulnerable to population extinction and replacement. Thus, the Pleistocene human evolutionary record is marked by the many remainders, both fossil and archaeological, of side branches to the human evolution story, positioned somewhere between the population and species level (Slatkin and Racimo 2016).

The key disruption in human evolution, after the emergence of the genus *Homo*, is the origin of agricultural systems. In many ways, this evolutionary transition, massive in its long-term scope, highlights the complex ways in which we frame discussions of Darwinian or non-Darwinian processes. Historically, this transition has been viewed as “cultural” in the sense that it is not predicated on a genetic change, but this view is incomplete. Genetic change in its most traditional understanding (the Modern Synthesis) is a critical part of this transition, even if it is not the primary driver of the shift toward agricultural food production. Likewise, the “cultural” processes of inheritance associated with the transition do not behave in ways fundamentally dissimilar to genetically inherited and maintained properties, recognizing the complex ways in which genotypic variation becomes expressed. The human transmission to a domesticated mode of subsistence marked the beginning of a new epoch on the planet, the Anthropocene, appropriately reflecting the scope and magnitude of the change our species has and continues to produce. The changes wrought by humans to environments across the globe and the evolutionary trajectory of other organisms are not fully unique in the history of the planet but are certainly exceptional enough to highlight how rare such a transition is likely to be in our planet’s evolutionary past.

Looking back at the broader picture, every species on the planet is the product of a unique set of evolutionary events. By taking a comparative approach to understanding the diversity of biological life on the planet, evolutionary scientists have produced reliable and durable theories for the nature of evolutionary change. While the understanding of evolutionary processes, both in the broad context and in specific cases, is constantly being refined by new research, our basic knowledge of the principles of evolutionary change remains grounded in the basic tenets laid out by Darwin himself. Biological variation exists, some of that variation is transferred from one generation to the next, and a variety of natural processes sort that variation through time in regular and predictable ways. Contained within those basic ideas, however, are vast areas open to complexity. Some of this complexity is focused on how variation is shaped throughout the life of an organism via processes of development. Some of this complexity relates to the ways in which variation might be transferred across generations. And still other complexities can be found in how exactly evolutionary processes act, and with what strength, to shape those patterns of variation. As Delisle points out (2017), even the architects of the Modern Synthesis focused not only on distinct areas of this broad paradigm but came to different interpretations about which questions and processes were foundationally important for the understanding of evolution's action. As such, rather than reveal the need for a paradigm shift, the period of self-reflexivity that evolutionary biology is currently engaged in might instead highlight the variable understandings of Darwinian processes (neo- or other) that exist and, in many ways, have always been a part of the field of evolutionary biology.

In this context, the study of a single lineage, such as humans and our evolutionary predecessors, affords the opportunity to explore the boundary conditions of existing theory more than offer a paradigmatic shift in thinking. The above essay argues that now is an appropriate time to more broadly engage humans as a model organism within evolutionary studies. For reasons both scientific and political, humans are often positioned at the center of descriptive conversations about evolution but rarely the subjects of research on evolutionary processes and theory. This is a missed opportunity to improve basic literacy around issues of evolution and science, as well as a missed opportunity to incorporate one of the more remarkable and well-documented organisms into broader evolutionary thinking.

The human example highlights the continuing entanglement between process and structure in evolutionary studies. Even as structures of significance for human evolution become more and more grounded in the social domain created by complex cognitive and technological capabilities, they remain grounded in processes of descent and modification. Human evolutionary studies, drawing from the diverse historical fields of thought—archaeology, anthropology, anatomy, genetics—each with their own realms of data, are uniquely positioned to interrogate questions at this intersection.

References

Ackermann RR, Cheverud JM (2004) Detecting genetic drift versus selection in human evolution. Proc Natl Acad Sci 101(52):17946–17951

Aiello LC, Wheeler P (1995) The expensive-tissue hypothesis: the brain and the digestive system in human and primate evolution. Curr Anthropol 36(2):199–221

Aiello LC (2007) Notes on the implications of the expensive tissue hypothesis for human biological and social evolution. In: Roebroeks W (ed) Guts and brains. Leiden University Press, Leiden, pp 17–28

Aiello LC, Key C (2002) Energetic consequences of being a Homo erectus female. Am J Hum Biol 14(5):551–565

Aiello LC, Wells JCK (2002) Energetics and the evolution of the genus Homo. Annu Rev Anthropol 31(1):323–338

Akey JM (2009) Constructing genomic maps of positive selection in humans: where do we go from here? Genome Res 19(5):711–722

Alcock J (2017) The behavioral sciences and sociobiology: a Darwinian approach. In: Delisle RG (ed) The Darwinian tradition in context: research programs in evolutionary biology. Springer, Cham, pp 37–60

Antón SC (2003) Natural history of Homo erectus. Am J Phys Anthropol 122(S37):126–170

Antón SC, Potts R, Aiello LC (2014) Evolution of early Homo: an integrated biological perspective. Science 345(6192):1236828

Armelagos GJ, Goodman AH, Jacobs KH (1991) The origins of agriculture: population growth during a period of declining health. Popul Environ 13(1):9–22

Attwell L, Kovarovic K, Kendal JR (2015) Fire in the Plio-Pleistocene: the functions of hominin fire use, and the mechanistic, developmental and evolutionary consequences. J Anthropol Sci 93:1–20

Baab KL (2008) The taxonomic implications of cranial shape variation in *Homo erectus*. J Hum Evol 54(6):827–847

Barkan E (1996) The politics of the science of race: Ashley Montagu and UNESCO's anti-racist declarations. Race and other misadventures: essays in honor of Ashley Montagu in his ninetieth year. General Hall, New York

Berger LR, de Ruiter DJ, Churchill SE, Carlson KJ, Dirks P, Kibii JM (2010) Australopithecus sediba: a new species of Homo-like australopith from South Africa. Science 328(5975):195–204

Berger LR (2013) The mosaic nature of Australopithecus sediba. Science 340(6129):163–165

Berger LR et al (2015) *Homo naledi*, a new species of the genus Homo from the Dinaledi Chamber, South Africa. elife 4:e09560

Blute M (2017) Three modes of evolution by natural selection and drift: a new or an extended evolutionary synthesis? Biol Theor 12(2):67–71

Boivin N et al (2013) Human dispersal across diverse environments of Asia during the Upper Pleistocene. Quat Int 300:32–47

Bocquet-Appel JP (2011) When the world's population took off: the springboard of the Neolithic Demographic Transition. Science 333(6042):560–561

Bowler PJ (2017) Alternatives to Darwinism in the early twentieth century. In: Delisle RG (ed) The Darwinian tradition in context: research programs in evolutionary biology. Springer, Cham, pp 195–218

Bramanti B et al (2009) Genetic discontinuity between local hunter-gatherers and central Europe's first farmers. Science 326(5949):137–140

Braun DR et al (2009) Raw material quality and Oldowan hominin toolstone preferences: evidence from Kanjera South, Kenya. J Archaeol Sci 36(7):1605–1614

Bruner E, Holloway RL (2010) A bivariate approach to the widening of the frontal lobes in the genus *Homo*. J Hum Evol 58(2):138–146

Bruner E (ed) (2014) Human paleoneurology, vol 3. Springer, New York

Bunn HT (2001) Hunting, power scavenging, and butchering by Hadza foragers and by Plio-Pleistocene Homo. Meat-eating and human evolution. Oxford University Press, Oxford

Caspari R, Lee SH (2004) Older age becomes common late in human evolution. Proc Natl Acad Sci USA 101(30):10895–10900

Caspari R (2009) 1918: three perspectives on race and human variation. Am J Phys Anthropol 139 (1):5–15

Cerling TE et al (2011) Diet of Paranthropus boisei in the early Pleistocene of East Africa. Proc Natl Acad Sci 108(23):9337–9341

Cordain L et al (2005) Origins and evolution of the Western diet: health implications for the 21st century. Am J Clin Nutr 81(2):341–354

Darwin C (1859) On the origin of species by means of natural selection, or the preservation of favoured races in the struggle for life. John Murray, London

Darwin C (1871) Sexual selection and the descent of man. John Murray, London

Dean MC, Smith BH (2009) Growth and development of the Nariokotome youth, KNM-WT 15000. In: Grine FE, Fleagle JG, Leakey RE (eds) The first humans – origin and early evolution of the genus Homo. Springer, Dordrecht, pp 101–120

Delisle RG (2017) From Charles Darwin to the evolutionary synthesis: weak and diffused connections only. In: Delisle RG (ed) The Darwinian tradition in context: research programs in evolutionary biology. Springer, Cham, pp 133–168

Dennell R, Roebroeks W (2005) An Asian perspective on early human dispersal from Africa. Nature 438(7071):1099–1104

Demes B, Creel N (1988) Bite force, diet, and cranial morphology of fossil hominids. J Hum Evol 17:657–670

DeSilva JM, Lesnik JJ (2008) Brain size at birth throughout human evolution: a new method for estimating neonatal brain size in hominins. J Hum Evol 55(6):1064–1074

DeSilva JM (2011) A shift toward birthing relatively large infants early in human evolution. Proc Natl Acad Sci 108(3):1022–1027

Dunsworth HM et al (2012) Metabolic hypothesis for human altriciality. Proc Natl Acad Sci 109 (38):15212–15216

Ellison PT (2009) On fertile ground: a natural history of human reproduction. Harvard University Press, Cambridge

Esposito M (2017) The organismal synthesis: holistic science and developmental evolution in the English-speaking world, 1915–1954. In: Delisle RG (ed) The Darwinian tradition in context: research programs in evolutionary biology. Springer, Cham, pp 219–242

Excoffier L, Schneider S (1999) Why hunter-gatherer populations do not show signs of Pleistocene demographic expansions. Proc Natl Acad Sci 96(19):10597–10602

Falk D (1987) Hominid paleoneurology. Annu Rev Anthropol 16(1):13–28

Ferring R et al (2011) Earliest human occupations at Dmanisi (Georgian Caucasus) dated to 1.85–1.78 Ma. Proc Natl Acad Sci 108(26):10432–10436

Finlayson C (2005) Biogeography and evolution of the genus Homo. Trends Ecol Evol 20 (8):457–463

Fuentes A (2016) The extended evolutionary synthesis, ethnography, and the human niche: toward an integrated anthropology. Curr Anthropol 57(S13):S13–S26

Futuyma DJ (2015) Can modern evolutionary theory explain macroevolution? In: Serrelli E, Gontier N (eds) Macroevolution. Springer, Cham, pp 29–85

Gabunia L, Vekua A (1995) A plio-pleistocene hominid from Dmanisi, East Georgia, Caucasus. Nature 373(6514):509

Gabunia L et al (2001) Dmanisi and dispersal. Evol Anthropol 10(5):158–170

Gibbons A (2007) The first human. Anchor, New York

Gilbert SF, Bosch TCG, Ledón-Rettig C (2015) Eco-Evo-Devo: developmental symbiosis and developmental plasticity as evolutionary agents. Nat Rev Genet 16(10):611–622

Glantz M, Van Arsdale AP, Temirbekov S, Beeton T (2016) How to survive the glacial apocalypse: Hominin mobility strategies in late Pleistocene Central Asia. Quat Int. https://doi.org/10.1016/j.quaint.2016.06.037

Gould SJ (2002) The structure of evolutionary theory. Harvard University Press, Cambridge

Grabowski M (2016) From bigger brains to bigger bodies: the correlated evolution of human brain and body size. Curr Anthropol 57(2):174–196

Haak W, Forster P, Bramanti B, Matsumura S, Brandt G, Tänzer M, Villems R, Renfrew C, Gronenborn D, Alt KW, Burger J (2005) Ancient DNA from the first European farmers in 7500-year-old Neolithic sites. Science 310(5750):1016–1018

Hare B, Tomasello M (2005) Human-like social skills in dogs? Trends Cogn Sci 9(9):439–444

Harmand S, Lewis JE, Feibel CS, Lepre CJ, Prat S, Lenoble A, Boës X, Quinn RL, Brenet M, Arroyo A, Taylor N, Clément S, Daver G, Brugal JP, Leakey L, Mortlock RA, Wright JD, Lokorodi S, Kirwa C, Kent DV, Roche H (2015) 3.3-million-year-old stone tools from Lomekwi 3, West Turkana, Kenya. Nature 521(7552):310

Hawks J et al (2007) Recent acceleration of human adaptive evolution. Proc Natl Acad Sci 104 (52):20753–20758

Henry AG, Brooks AS, Piperno DR (2011) Microfossils in calculus demonstrate consumption of plants and cooked foods in Neanderthal diets (Shanidar III, Iraq; Spy I and II, Belgium). Proc Natl Acad Sci 108(2):486–491

Hovers E, Braun DR (eds) (2009) Interdisciplinary approaches to the Oldowan. Springer, Dordrecht

Jablonka E, Lamb MJ (2014) Evolution in four dimensions, revised edition: Genetic, epigenetic, behavioral, and symbolic variation in the history of life. MIT Press, Cambridge

Kaifu Y (2006) Advanced dental reduction in Javanese Homo erectus. Anthropol Sci 114 (1):35–43

Laland K, Wray GA, Hoekstra HE (2014) Does evolutionary theory need a rethink? Nature 514 (7521):161

Laland K, Uller T, Feldman MW, Sterelny K, Müller GB, Moczek A, Jablonka E, Odling-Smee J (2015) The extended evolutionary synthesis: its structure, assumptions and predictions. Proc R Soc B 282(1813):1–14

Laland K (2017) Schism and synthesis at the royal society. Trends Ecol Evol 32(5):316–317

Langley MC, Street M (2013) Long range inland–coastal networks during the Late Magdalenian: evidence for individual acquisition of marine resources at Andernach-Martinsberg, German Central Rhineland. J Hum Evol 64(5):457–465

Lee SH, Wolpoff MH (2003) The pattern of evolution in Pleistocene human brain size. Paleobiology 29(2):186–196

Leigh SR (2006) Brain ontogeny and life history in Homo erectus. J Hum Evol 50(1):104–108

Leonard WR, Robertson ML (1992) Nutritional requirements and human evolution: a bioenergetics model. Am J Hum Biol 4(2):179–195

Levit GS, Hossfeld U (2017) Major research traditions in 20th century evolutionary biology: the relations of Germany's Darwinism with them. In: Delisle RG (ed) The Darwinian tradition in context: research programs in evolutionary biology. Springer, Cham, pp 169–194

Lieberman L (1989) A discipline divided: Acceptance of human sociobiological concepts in anthropology. Curr Anthropol 30(5):676–682

Livingstone FB, Dobzhansky T (1962) On the non-existence of human races. Curr Anthropol 3:279–281

Loison L, Herring E (2017) Lamarckian research programs in French biology (1900–1970). In: Delisle RG (ed) The Darwinian tradition in context: research programs in evolutionary biology. Springer, Cham, pp 243–270

Lordkipanidze D, Vekua A, Ferring R, Rightmire GP, Zollikofer CPE, Ponde de León MS, Agusti J, Kiladze G, Mouskhelishvili A, Nioradze M, Tappen M (2006) A fourth hominin skull from Dmanisi, Georgia. Anat Rec 288(11):1146–1157

Lordkipanidze D, Jashashvili T, Vekua A, Ponce de León MS, Zollikofer CPE, Rightmire GP, Pontzer H, Ferring R, Oms O, Tappen M, Bukhsianidze M, Agusti J, Kahlke R, Kiladze G, Martinez-Navarro B, Mouskhelishvili A, Nioradze M, Rook L (2007) Postcranial evidence from early Homo from Dmanisi, Georgia. Nature 449(7160):305–310

Lordkipanidze D, Ponce de León MS, Margvelashvili A, Rak Y, Rightmire GP, Vekua A, Zollikofer CPE (2013) A complete skull from Dmanisi, Georgia, and the evolutionary biology of early Homo. Science 342(6156):326–331

Lovejoy CO (1981) The origin of man. Science 211(4480):341–350

Lovejoy CO (2009) Reexamining human origins in light of *Ardipithecus ramidus*. Science 326 (5949):74e1–74e8

Lowe WH, Kovach RP, Allendorf FW (2017) Population genetics and demography unite ecology and evolution. Trends Ecol Evol 32(2):141–152

Lynn CD, Glaze AL, Evans WA, Reed LK (eds) (2017) Evolution education in the American South: culture, politics, and resources in and around Alabama. Palgrave Macmillan, New York

MacCord K, Maienschein J (2017) Cells, development, and evolution: teeth studies at the intersection of fields. In: Delisle RG (ed) The Darwinian tradition in context: research programs in evolutionary biology. Springer, Cham, pp 289–308

Marks J (2008) Race across the physical-cultural divide in American anthropology. In: Kublick H (ed) A new history of anthropology. Blackwell, Hoboken, pp 242–258

Matsuzawa T (2008) Primate foundations of human intelligence: a view of tool use in nonhuman primates and fossil hominids. In: Matsuzawa T (ed) Primate origins of human cognition and behavior. Springer, Tokyo, pp 3–25

Mayr E (1950) Taxonomic categories in fossil hominids. Cold Spring Harb Symp Quant Biol 15:109–118

McBrearty S, Brooks AS (2000) The revolution that wasn't: a new interpretation of the origin of modern human behavior. J Hum Evol 39(5):453–563

McHenry HM, Coffing K (2000) Australopithecus to Homo: transformations in body and mind. Annu Rev Anthropol 29(1):125–146

McPherron SP, Alemseged Z, Marean CW, Wynn JG, Reed D, Geraads D, Bobe R, Béarat HA (2010) Evidence for stone-tool-assisted consumption of animal tissues before 3.39 million years ago at Dikika, Ethiopia. Nature 466(7308):857–860

Nielsen R, Akey JM, Jakobsson M, Pritchard JK, Tishkoff S, Willerslev E (2017) Tracing the peopling of the world through genomics. Nature 541(7637):302–310

Nowell A, Davidson I (2010) Stone tools and the evolution of human cognition. University Press of Colorado, Boulder

O'Connell JF, Hawkes K, Blurton Jones NG (1999) Grandmothering and the evolution of *Homo erectus*. J Hum Evol 36(5):461–485

Organ C, Nunn CL, Machanda Z, Wrangham RW (2011) Phylogenetic rate shifts in feeding time during the evolution of *Homo*. Proc Natl Acad Sci 108(35):14555–14559

Pigliucci M (2007) Do we need an extended evolutionary synthesis? Evolution 61(12):2743–2749

Pigliucci M (2008) Is evolvability evolvable? Nat Rev Genet 9(1):75–82

Pigliucci M (2017) Darwinism after the modern synthesis. In: Delisle RG (ed) The Darwinian tradition in context: research programs in evolutionary biology. Springer, Cham, pp 89–104

Plutzer E, Berkman M (2008) Trends evolution, creationism, and the teaching of human origins in schools. Public Opin Q 72(3):540–553

Pobiner B (2016) Accepting, understanding, teaching, and learning (human) evolution: obstacles and opportunities. Am J Phys Anthropol 159(S61):S232–S274

Pontzer H et al (2010) Locomotor anatomy and biomechanics of the Dmanisi hominins. J Hum Evol 58(6):492–504

Pontzer H (2012) Ecological energetics in early Homo. Curr Anthropol 53(S6):S346–S358

Potts R, Teague R (2010) Behavioral and environmental background to 'Out-of-Africa I' and the arrival of *Homo erectus* in East Asia. In: Fleagle JG (ed) Out of Africa I. Springer, Dordrecht, pp 67–85

Racimo F, Sankararaman S, Nielsen R, Huerta-Sánchez E (2015) Evidence for archaic adaptive introgression in humans. Nat Rev Genet 16(6):359–371

Rightmire GP (1981) Patterns in the evolution of Homo erectus. Paleobiology 7(2):241–246

Rightmire GP (2004) Brain size and encephalization in early to Mid-Pleistocene Homo. Am J Phys Anthropol 124(2):109–123

Roebroeks W, Villa P (2011) On the earliest evidence for habitual use of fire in Europe. Proc Natl Acad Sci 108(13):5209–5214

Rose MD (1984) A hominine hip bone, KNM-ER 3228, from East Lake Turkana, Kenya. Am J Phys Anthropol 63(4):371–378

Roseman CC (2016) Random genetic drift, natural selection, and noise in human cranial evolution. Am J Phys Anthropol 160(4):582–592

Ruff CB, Trinkaus E, Holliday TW (1997) Body mass and encephalization in Pleistocene *Homo*. Nature 387(6629):173

Sahlins MD (1976) The use and abuse of biology: an anthropological critique of sociobiology. University of Michigan Press, Ann Arbor

Sandgathe DM, Dibble HL, Goldberg P, McPherron SP, Turq A, Niven L, Hodgkins J (2011) On the role of fire in Neandertal adaptations in Western Europe: evidence from Pech de l'Azé IV and Roc de Marsal, France. PaleoAnthropology 216–242

Sankararaman S, Mallick S, Patterson N, Reich D (2016) The combined landscape of Denisovan and Neanderthal ancestry in present-day humans. Curr Biol 26(9):1241–1247

Schrenk F, Kullmer O, Bromage T (2015) The earliest putative Homo fossils. In: Henke W, Tattersall I (eds) Handbook of paleoanthropology. Springer, Berlin, pp 2145–2165

Sémah F, Saleki H, Falguères C, Féraud G, Djubiantono T (2000) Did early man reach Java during the Late Pliocene? J Archaeol Sci 27(9):763–769

Shipman P, Walker A (1989) The costs of becoming a predator. J Hum Evol 18(4):373–392

Slatkin M, Racimo F (2016) Ancient DNA and human history. Proc Natl Acad Sci 113 (23):6380–6387

Skoglund P, Malmström H, Raghavan M, Stora J, Hall P, Willerslev E, Gilbert TP, Götherström A, Jakobsson M (2012) Origins and genetic legacy of Neolithic farmers and hunter-gatherers in Europe. Science 336(6080):466–469

Skoglund P et al (2014) Genomic diversity and admixture differs for Stone-Age Scandinavian foragers and farmers. Science 344(6185):747–750

Smith BD, Zeder MA (2013) The onset of the Anthropocene. Anthropocene 4:8–13

Smocovitis VB (2012) Humanizing evolution: anthropology, the evolutionary synthesis, and the prehistory of biological anthropology, 1927–1962. Curr Anthropol 53(S5):S108–S125

Snodgrass JJ, Leonard WR, Robertson ML (2009) The energetics of encephalization in early hominids. In: Hublin JJ, Richards M (eds) The evolution of hominin diets. Springer, Dordrecht, pp 15–29

Spoor F, Leakey MG, Gathogo PN, Brown FH, Antón SC, McDougall I, Kiarie C, Manthi FK, Leakey LN (2007) Implications of new early Homo fossils from Ileret, east of Lake Turkana, Kenya. Nature 448(7154):688–691

Stedman HH, Kozyak BW, Nelson A, Thesier DM, Su LT, Low DW, Bridges CR, Shrager JB, Minugh-Purvis N, Mitchell MA (2004) Myosin gene mutation correlates with anatomical changes in the human lineage. Nature 428(6981):415–418

Steudel-Numbers KL (2006) Energetics in Homo erectus and other early hominins: the consequences of increased lower-limb length. J Hum Evol 51(5):445–453

Stiner MC, Munro ND, Surovell TA, Tchernov E, Bar-Yosef O (1999) Paleolithic population growth pulses evidenced by small animal exploitation. Science 283(5399):190–194

Strier KB (2016) Why biological anthropologists should identify as anthropologists: The meaning of membership in the AAA and the AAAS. Am J Phys Anthropol 161(1):3–5

Stringer C (2012) Lone survivors: how we came to be the only humans on earth. Macmillan, New York

Suwa G, Asfaw B, Haile-Selassie Y, White T, Katoh S, Woldegabriel G, Hart WK, Nakaya H, Beyene Y (2007) Early Pleistocene Homo erectus fossils from Konso, southern Ethiopia. Anthropol Sci 115(2):133–151

Swisher CC, Curtis GH, Jacob T, Getty AG, Suprijo A (1994) Age of the earliest known hominids in Java, Indonesia. Science 263(5150):1118–1122

Szathmáry E (2015) Toward major evolutionary transitions theory 2.0. Proc Natl Acad Sci 112 (33):10104–10111

Tappen M (2009) The wisdom of the aged and out of Africa I. In: Shea J, Lieberman D (eds) Transitions in prehistory: essays in honor of Ofer Bar Yosef. Oxbow, Oakville, pp 24–41

Teaford MF, Ungar PS, Grine FE (2002) Paleontological evidence for the diets of African Plio-Pleistocene hominins with special reference to early Homo. Human diet: its origin and evolution. Bergin & Garvey, London, pp 143–166

Tennie C, Call J, Tomasello M (2009) Ratcheting up the ratchet: on the evolution of cumulative culture. Philos Trans R Soc Lond B Biol Sci 364(1528):2405–2415

Tomasello M (1999) The human adaptation for culture. Annu Rev Anthropol 28(1):509–529

Ungar PS, Grine FE, Teaford MF (2006) Diet in early Homo: a review of the evidence and a new model of adaptive versatility. Annu Rev Anthropol 35:209–228

Van Arsdale AP, Lordkipanidze D (2012) A quantitative assessment of mandibular variation in the Dmanisi hominins. PaleoAnthropology 134–144

Van Arsdale AP, Wolpoff MH (2013) A single lineage in early Pleistocene Homo: size variation continuity in early Pleistocene Homo crania from East Africa and Georgia. Evolution 67 (3):841–850

Van Schaik CP, Deaner RO, Merrill MY (1999) The conditions for tool use in primates: implications for the evolution of material culture. J Hum Evol 36(6):719–741

Villmoare B, Kimbel WH, Seyoum C, Campisano CJ, DiMaggio EN, Rowan J, Braun DR, Arrowsmith JR, Reed KE (2015) Early Homo at 2.8 Ma from Ledi-Geraru, Afar, Ethiopia. Science 347(6228):1352–1355

Walker A (1981) Dietary hypotheses and human evolution. Philos Trans R Soc Lond B Biol Sci 292(1057):57–64

Walker A, Leakey RE (1993) The Nariokotome Homo erectus skeleton. Harvard University Press, Cambridge

Wall JD, Brandt DYC (2016) Archaic admixture in human history. Curr Opin Genet Dev 41:93–97

Want SC, Harris PL (2002) How do children ape? Applying concepts from the study of non-human primates to the developmental study of ‘imitation in children. Dev Sci 5(1):1–14

Washburn SL (1951) Section of anthropology: the new physical anthropology. Trans NY Acad Sci 13(7), Series II):298–304

Wilkins J, Schoville BJ, Brown KS, Chazan M (2012) Evidence for early hafted hunting technology. Science 338(6109):942–946

Whiten A, Goodall J, McGrew WC, Nishida T, Reynolds V, Sugiyama Y, Tutin CEG, Wrangham RW, Boesch C (1999) Cultures in chimpanzees. Nature 399(6737):682–685

Wilson EO (1975) Sociobiology: the new synthesis. Harvard Belknap, Cambridge

Wolpoff MH (1975) Some aspects of human mandibular evolution. In: McNamara JA (ed) Determinants of mandibular form and growth. Craniofacial growth series monograph. Center for Human Growth and Development, Ann Arbor, vol 4, pp 1–64

Wolpoff MH (1999) Paleoanthropology. McGraw-Hill Humanities, Social Sciences & World Languages, Boston

Wood B (1992) Origin and evolution of the genus Homo. Nature 355(6363):783

Wood B, Collard M (1999) The human genus. Science 284(5411):65–71

Wray GA, Hoekstra HE (2014) Does evolutionary theory need a rethink?-COUNTERPOINT No, all is well. Nature 516:161–164

Zaim Y, Ciochon RL, Polanski JM, Grine FE, Bettis EA, Rizal Y, Franciscus RG, Larick RR, Heizler M, Eaves KL, Marsh HE (2011) New 1.5 million-year-old Homo erectus maxilla from Sangiran (Central Java, Indonesia). J Hum Evol 61(4):363–376

Zeder M (ed) (2006) Documenting domestication: new genetic and archaeological paradigms. University of California Press, Berkeley

Zhu RX, Potts R, Xie F, Hoffman KA, Deng CL, Shi CD, Pan YX, Wang HQ, Shi RP, Wang YC, Shi GH, Wu NQ (2004) New evidence on the earliest human presence at high northern latitudes in northeast Asia. Nature 431(7008):559–562