

The emergence of complexity and novelty in the human fossil record

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Abstract

Outside of possible evidence for more complex social practices (e.g. longevity post-trauma, preserved infant remains), the fossil record of human evolution is limited in its ability to address the transition towards transcendental forms of wisdom. Indeed, it is difficult to equate our modern intellectual condition with deep past biological indicators at all. Nonetheless, arguably the best and most visible evidence for biological changes that might be precursors to these abilities are in the form of increasing complexity and/or novelty. We see these patterns in the hominin fossil record most strongly at the emergence and diversification of our genus, and in the Middle to Late Pleistocene record with the emergence of our species. Here we will first give a brief overview of the human fossil record, and will then focus on these two time periods, and the question of what produces such complexity/novelty.

The hominin fossil record: in brief

Hominin evolution has occurred over the course of the last six million years or so (Figure 1). The earliest fossil hominins – including australopiths and other early taxa, restricted entirely to Africa – are diverse in terms of their morphology, but have in common (non-human) ape-sized bodies and brains. Presumably, their behavioural repertoire was also ape-like in most respects, with the possible exception of the role that an increasingly bipedal locomotive repertoire played in their ability to navigate their environments and access resources. The emergence of our genus *Homo* marks the beginning of fairly substantial changes in

both cranial and postcranial morphology, along with an abundant record of formalised tool manufacture and other cultural developments. The genus *Homo* is also characterized by a significant amount of morphological diversity, a phenomenon central to the longstanding debate around the origin and evolution of *Homo*.¹ The earliest fossil that has been attributed to *Homo* comes from Ledi-Geraru, Ethiopia, dated to approximately 2.8 million years ago (Ma).² Between 2.8 and 2.0 Ma, the fossil record of *Homo* is sparse, represented by a handful of gnathic (maxilla, mandible, teeth) remains, and only increases in bone representivity, sample size and species diversity after 2.0 Ma. We currently have at least three taxa of early *Homo* – *H. habilis*, *H. rudolfensis*, *H. erectus* – that overlap temporally and in some cases geographically. There also appears to be considerable variation within at least some taxa, as highlighted in the large and highly variable sample of *H. erectus* from Dmanisi, Georgia.³ At ~1.8Ma, this Georgian *H. erectus* sample marks the first appearance of our lineage outside of Africa and the beginning of its spread into other parts of the world.⁴

Once *H. erectus* left Africa they moved fairly quickly, arriving in Southeast Asia not long after their initial emergence. In this taxon we see a general trend of smaller teeth and increasing (though variable) brain size, with many individuals having brain sizes in the range of living humans. In general, they are characterised by modern body proportions, a more sophisticated tool kit and increased hunting, and the ability to live in many and more diverse environments. There is, however, quite a lot of morphological variability across individuals and regions, and indeed there is some disagreement about whether this taxon represents two (or more) taxa. *H. erectus* persists for more than one and a half million years, until just less than 200 thousand years ago in some regions, occupying sites across Africa and the more southerly portions of Asia (e.g. Georgia, China, Java). It is well-accepted that *H. erectus* – and/or its descendants – is broadly ancestral to us, though that does not necessarily mean that all *H. erectus* populations contributed to our ancestry. Indeed, the period from around one million years onwards becomes increasingly complex

¹ see Susan Antón et al., *Evolution of early Homo: an integrated biological perspective* (2014); Bernard Wood, *Origin and evolution of the genus Homo* (1992); Bernard Wood and Jennifer Baker, *Evolution in the genus Homo* (2011)

² Brian Villmoare et al., *Early Homo at 2.8 Ma from Ledi-Geraru, Afar, Ethiopia* (2015)

³ David Lordkipanidze et al., *A complete skull from Dmanisi, Georgia, and the evolutionary biology of early Homo* (2013); Fred Spoor et al., *Reconstructed Homo habilis type OH 7 suggests deep-rooted species diversity in early Homo* (2015)

⁴ David Lordkipanidze et al., *A complete skull from Dmanisi, Georgia, and the evolutionary biology of early Homo* (2013)

in terms of potential taxon diversity, as well as our understanding of human origins. What is clear is that we see multiple lineages – verified by genetic studies – that indicate branching during this time period. This branching results in regional variants of human ancestors in Africa, Europe, the Middle East and Asia. Out of this diversity, the human species ultimately arises, with people who begin to look essentially like us clearly present in the fossil record by the time we get to the end of the Pleistocene.

Morphological novelty and its complex origins

We now want to turn to this question of the evolution of new forms that have novel attributes or appear to be more complex than previous forms. This is particularly relevant to the topic of this book because there has been a tendency to interpret new things, especially when they appear to be more complex than previous things, as the product of selection acting to create such complexity and novelty. (A good example of this is the production of bigger and more complex brains; large brains are generally interpreted as resulting from selection for increased intelligence or other cognitive abilities.) Although no evolutionary biologist would frame these changes in the language of ‘progress’, we nonetheless tend to attribute them to adaptive change that moves in a progressive way towards our current state (e.g. better able to navigate changing environments, more capable of communication, “ultimate invader”). As an example of the latter, a dominant narrative regarding the emergence of modern people frames the entire conversation as one of increasing abilities progressing towards the modern condition, e.g. more complex cognition leading to more advanced behaviours, better weapons, and ultimately the conquering of the world.⁵ In the context of palaeoanthropology more broadly, this adaptationist approach (the tendency to assume adaptive explanations for describing organismal traits, without any consideration of alternative evolutionary explanations⁶) manifests itself in the causal explanations given to describe major transitions and morphological diversity present in the human fossil record, overlooking, and to some extent disregarding, the potential contributions made by other evolutionary processes such as genetic drift and gene flow.

⁵ ‘The most invasive species of all’ Scientific American, August, 2015.

⁶ see discussion in Stephen Jay Gould, and Richard Lewontin, *The spandrels of San Marco and the Panglossian paradigm: a critique of the adaptationist programme* (1979)

However, while there is no doubt that the emergence of our genus is characterised broadly by novelty/innovation and what might be interpreted as increasing complexity, many of these key elements that have traditionally served as signatures of precisely this – things such as increased brain size, formalised tool use, and an essentially human-like mode of locomotion – do not appear as a package, but instead emerge at different points in time and are associated with different taxa. The earliest stone tools actually pre-date the evolution of *Homo* by half a million years⁷; their manufacturers are still unknown, though the best candidate is likely *Australopithecus afarensis* given its geographic and temporal proximity. Similarly, although there may be signatures of changing brain morphology in very late australopiths, early *Homo* cranial material shows little change from the australopiths, with brain size making its first significant leap with *H. erectus*. It is with *H. erectus* that we also see a largely modern postcranial skeleton (though it is important to note that the postcranial fossil record of other early *Homo* is poor).

Adding additional complexity to this picture, the co-existence of multiple taxa at different points in time, and the re-evolution of small brains in multiple contexts⁸, challenge a linear notion of the emergence of *Homo*-like morphology. For example, in 2003 and 2004, several hominin fossil specimens were recovered from the Liang Bau cave on the island of Flores, Indonesia.⁹ Most (but not all) researchers agree that these specimens are representative of a new hominin species named *Homo floresiensis*.¹⁰ Despite their recent age of ~ 100-60 thousand years ago (ka), these individuals are small-brained (417 cm³) and small-bodied. They also overlap temporally with the appearance of modern *Homo sapiens* in the broader region, while at the same time displaying a number of ancestral traits indicative of early *Homo*.¹¹ Similarly, in late

⁷ Sonia Harmand et al., *3.3-million-year-old stone tools from Lomekwi 3, West Turkana, Kenya* (2015)

⁸ Lee Berger et al., *A new species of the Genus Homo from the Dinaledi Chamber, South Africa* (2015); Peter Brown et al., *A new small-bodied hominin from the Late Pleistocene of Flores, Indonesia* (2004)

⁹ Peter Brown et al., *A new small-bodied hominin from the Late Pleistocene of Flores, Indonesia* (2004); Michael Morwood et al., *Further evidence for small-bodied hominins from the Late Pleistocene of Flores, Indonesia* (2005)

¹⁰ For example: Debbie Argue et al., *Homo floresiensis: a cladistic analysis* (2009); Peter Brown et al., *A new small-bodied hominin from the Late Pleistocene of Flores, Indonesia* (2004); Peter Brown and Tomoko Maeda, *Liang Bua Homo floresiensis mandibles and mandibular teeth: a contribution to the comparative morphology of a new hominin species* (2009); Dean Falk et al., *The brain of LB1, Homo floresiensis* (2005); Adam Gordon et al., *The Homo floresiensis cranium (LB1): Size, scaling, and early Homo affinities* (2008); William Jungers et al., *Descriptions of the lower limb skeleton of Homo floresiensis* (2009a); William Jungers et al., *The foot of Homo floresiensis* (2009b); Michael Morwood and William Jungers, *Conclusions: implications of the Liang Bua excavations for hominin evolution and biogeography* (2009); Matthew Tocheri et al., *The primitive wrist of Homo floresiensis and its implications for hominin evolution* (2007)

¹¹ Peter Brown et al., *A new small-bodied hominin from the Late Pleistocene of Flores, Indonesia* (2004); Adam Gordon et al., *The Homo floresiensis cranium (LB1): Size, scaling, and early Homo affinities* (2008); Michael Morwood et al., *Further evidence for small-bodied hominins from the Late Pleistocene of Flores, Indonesia* (2005); Michael Morwood and William Jungers,

2013, a new species of fossil hominin, *Homo naledi*, was recovered from the Dinaledi Chamber in the Rising Star cave system in South Africa.¹² With a cranial capacity ranging between 465 and 560 cm³, *Homo naledi* lends further support to the idea that a large brain size cannot be regarded as a defining character of *Homo*. It's recent date of between 335 and 236 ka¹³ parallels the situation in Flores¹⁴, indicating that small brains, in conjunction with “early *Homo*-like” cranial morphology, persisted into recent time periods. The numerous possible phylogenetic scenarios and evolutionary relationships between these two species and both early and later *Homo* pose an interesting alternative to the traditional linear view of the evolution of *Homo*. Furthermore, these findings have provided us with evidence that small brains and “early *Homo*-like” cranial morphology evolved at multiple times in multiple contexts, even persisting into recent time periods. Collectively, these data support the idea that the emergence of *Homo* was not straightforward, and may have been characterized by multiple lineages, and defined by evolutionary innovation and experimentation.¹⁵ In such a scenario, what we identify as *Homo*-like morphology could have evolved repeatedly, in different contexts or at different times.

But the question is not so much when novelty, innovation and complexity appear, but rather why and how. Does it say anything about adaptive (directional) change – i.e. can we apply meaning to why these morphologies evolved? Are they changes that cause an organism to be better suited to its environment? The answer to these questions is sometimes, but not always. This is because the emergence of complexity and novelty also occurs through chance (i.e. genetic drift) and gene exchange, making it difficult to point to either as indications of adaptive change in innate human capabilities.

Genetic drift as a producer of morphological diversity

Conclusions: implications of the Liang Bua excavations for hominin evolution and biogeography (2009); Richard Roberts et al., *Geochronology of cave deposits at Liang Bua and of adjacent river terraces in the Wae Racang valley, western Flores, Indonesia* (2009); Thomas Sutikna et al., *Revised stratigraphy and chronology for Homo floresiensis at Liang Bua in Indonesia* (2016)

¹² Lee Berger et al., *A new species of the Genus Homo from the Dinaledi Chamber, South Africa* (2015)

¹³ Paul Dirks et al., *The age of Homo naledi and associated sediments in the Rising Star Cave, South Africa* (2017)

¹⁴ For example: Peter Brown et al., *A new small-bodied hominin from the Late Pleistocene of Flores, Indonesia* (2004)

¹⁵ Susan Antón et al., *Evolution of early Homo: an integrated biological perspective* (2014)

Sewall Wright, the cofounder of population genetics, hypothesised that genetic drift, acting in small populations, may be an important force driving evolutionary change.¹⁶ Since then, many researchers, especially in the palaeontological community, have debated the significance of this process for the diversification of populations over a large timeframe, most preferring to attribute phenotypic change to the process of natural selection. However, in 1953, George G. Simpson considered the possible effect that genetic drift may have had on morphological evolution in the fossil record, by introducing the theoretical model of adaptive zones for driving rapid evolution. He hypothesised that these zones were dominated by stabilizing selection, but that genetic drift may have played an important role when these adaptive zones were traversed.¹⁷ In addition, Eldredge and Gould (1972), applying Mayr's (1963) model of geographic speciation to the fossil record, considered the role of random genetic drift in species formation. They theorised that species diversification occurred almost exclusively in isolated populations, of small sample size, undergoing habitat fragmentation.¹⁸ In 1976, Russell Lande highlighted the limitations of these conceptual models for objectively evaluating the relative roles of drift and selection in macroevolution. He attributed this to the lack of a testable, phenotype applicable, mathematical model for assessing the evolutionary processes underlying the diversification of phenotypic characters.¹⁹ As a result, from 1976-1979, Lande published a series of statistical models to evaluate the null hypothesis of evolution by genetic drift.²⁰ These models, rooted in predictions about evolutionary rates and constant heritability, are functions of population variation, effective population size and time since divergence. Importantly, the overarching model asserts that in the evaluation of phenotypic change in populations within an evolutionary context, patterns of within-population variability are central players as they provide the material on which evolution works to diversify populations.

¹⁶ Sewall Wright, *Evolution in Mendelian populations* (1931) Sewall Wright, *The roles of mutation, inbreeding, crossbreeding, and selection in evolution* (1932)

¹⁷ George Simpson, *The Major Features of Evolution* (1953)

¹⁸ Niles Eldredge, and Stephan Gould., 'Punctuated equilibria: an alternative to phyletic gradualism.' in *Models in Paleobiology*, edited by T. Schopf (1972)

¹⁹ Russell Lande, *Natural selection and random genetic drift in phenotypic evolution* (1976)

²⁰ Russell Lande, *Natural selection and random genetic drift in phenotypic evolution* (1976); Russell Lande, *Statistical tests for natural selection on quantitative characters* (1977); Russell Lande, *Quantitative genetic analysis of multivariate evolution, applied to brain: body size allometry* (1979)

Since then, a number of theoretical advancements in the field of evolutionary quantitative genetics have provided the basis for the development of a suite of novel approaches for understanding evolutionary process in phenotypic evolution and diversification. These approaches have been successfully applied in a number of studies of both extant and extinct animals for evaluating the evolutionary processes underlying population divergence. For example, in 1988, Lofsvold tested the null hypothesis of genetic drift in differentiating three populations of deer mice (*Peromyscus*). His analyses produced an overall rejection of drift, indicating the possibility of selection acting to differentiate these taxa.²¹ Ackermann and Cheverud (2002) investigated the evolutionary processes underlying craniofacial diversity among 12 species of tamarin (*Saguinus*), detecting a deviation from the neutral model. In contrast, the majority of the variation within each of these groups was shown to be consistent with genetic drift.²² Similarly, Marriog and Cheverud (2004) assessed the relative roles of genetic drift and selection for producing the cranial diversity among all living New World monkeys. The majority of their analyses produced rejections of drift, indicating that most of these groups underwent adaptive diversification.²³ However, some of their comparisons of species within genera were indeed consistent with the neutral model. They postulate that the mixture of drift and selection detected in this lineage is consistent with Simpson's (1953) adaptive zone hypothesis. A more recent study of hominoid (ape) cranial evolution using the Lande approach detected strong stabilizing selection acting on cranial diversity within the ape lineage, with only a few instances of neutral diversification and directional selection identified.²⁴ As for living humans, a number of studies have tested whether the patterns we see in cranial diversity across different human populations is due to natural selection or neutral evolution, and have shown, overwhelmingly, that the majority of global cranial diversity can be accounted for by non-adaptive processes.²⁵ This pattern is also evident in

²¹ David Lofsvold, *Quantitative genetics of morphological differentiation in Peromyscus. II. Analysis of selection and drift* (1988)

²² Rebecca Ackermann and James Cheverud, *Discerning evolutionary processes in patterns of tamarin (genus Saguinus) craniofacial variation* (2002)

²³ Gabriel Marriog and James Cheverud, *Did natural selection or genetic drift produce the cranial diversification of neotropical monkeys?* (2004)

²⁴ Lauren Schroeder and Noreen von Cramon-Taubadel, *The evolution of hominoid cranial diversity: A quantitative genetic approach* (2017)

²⁵ Marcia Ponce de León, et al. *Human bony labyrinth is an indicator of population history and dispersal from Africa* (2018); Charles Roseman, *Detecting interregionally diversifying natural selection on modern human cranial form by using matched molecular and morphometric data* (2004); Charles Roseman and Timothy Weaver, *Molecules versus morphology? Not for the human cranium* (2007); Noreen von Cramon-Taubadel, *Evolutionary insights into global patterns of human cranial diversity: population history, climatic and dietary effects* (2014)

pelvis shape.²⁶ However, a study of the postcranial skeleton in a global human sample (specifically long bones) detects a strong signal of natural selection acting on a number of traits related to body form.²⁷

In terms of human evolution, Ackermann and Cheverud (2004) published the first direct application of the Lande model to the human fossil record. Their results showed that, while genetic drift may account for facial diversity during the evolution of the genus *Homo*, selection may have played an important role in diversifying hominin facial morphology between the australopiths and *Homo*.²⁸ Since then, there have been a series of studies of the crania and mandibles of all fossil *Homo* – from the earliest *H. habilis* material until the recent (pre-modern) past – investigating the relative role of genetic drift versus selection in shaping cranial morphology.²⁹ These studies collectively suggest that a large amount of the variation we see across these taxa – including variation in neurocranial (brain) size and shape – is consistent with genetic drift acting to diversify taxa, invoking a strong role for random chance causing the emergence of new forms, likely acting in small populations. This is true even when very small-brained *H. erectus* and *H. naledi* individuals are included in the analyses.³⁰ Because molecular change over evolutionary timeframes occurs predominantly through neutral processes,³¹ it should not be surprising that morphological change in human evolution is consistent with drift. When we do see evidence for selection, it is not associated with our big brains, but rather with our mouths, especially in the Dmanisi hominins, the oldest known fossil *Homo* specimens outside of Africa, suggesting that dietary adaptations are an important driver of change as these hominins adapted to different environments. In this light, recent suggestions that brain size and shape differences may poorly define *Homo* are intriguing.³² This does not mean that having a larger brain did not ultimately provide benefits, but that it did not necessarily evolve initially for that purpose. Because these models test for deviations in patterns of cranial variation (covariance), what this

²⁶ Lia Betti et al., *Global geometric morphometric analyses of the human pelvis reveal substantial neutral population history effects, even across sexes* (2013)

²⁷ Kristen Savall et al., *Constraint, natural selection, and the evolution of human body form* (2016)

²⁸ Rebecca Ackermann and James Cheverud, *Detecting genetic drift versus selection in human evolution* (2004)

²⁹ Rebecca Ackermann and James Cheverud, *Detecting genetic drift versus selection in human evolution* (2004); Lauren Schroeder et al., *Characterizing the evolutionary path (s) to early Homo* (2014); Lauren Schroeder and Rebecca Ackermann, *Evolutionary processes shaping diversity across the Homo lineage* (2017); Timothy Weaver et al., *Were neandertal and modern human cranial differences produced by natural selection or genetic drift?* (2007)

³⁰ Lauren Schroeder and Rebecca Ackermann, *Evolutionary processes shaping diversity across the Homo lineage* (2017)

³¹ Motoo Kimura, *Evolutionary rate at the molecular level* (1968); Motoo Kimura, *The neutral theory of molecular evolution: a review of recent evidence* (1991)

³² Fred Spoor et al., *Reconstructed Homo habilis type OH 7 suggests deep-rooted species diversity in early Homo* (2015)

result is also saying is that it is fairly easy to evolve bigger (or smaller) brains through chance effects because the patterns of variation (covariance) need not be altered. It might be interesting to consider this in light of the association – or lack thereof – between brain size and technology in the hominin record. Another significant finding by Schroeder and Ackermann (2017) is the lack of any major selective pressures detected between the crania of *Homo sapiens* from Middle Pleistocene *Homo*, indicating that selection does not need to be invoked to explain the cranial differentiation of *Homo sapiens* from Middle Pleistocene *Homo*. This result is similar to the findings of Weaver et al. (2007) who show that stochastic evolutionary processes can explain the cranial differences between Neanderthals and modern humans. Taken together, these results may also provide further evidence for a “lengthy process model” of modern human origins,³³ which hypothesizes that no discrete evolutionary event occurred between ~100 to 200 ka, suggesting morphological continuity from the later Middle Pleistocene to the emergence of early anatomically modern *Homo sapiens*.

Gene flow as a producer of novelty

Interpretations of the emergence of new traits, whether complex or innovative, are also complicated by hybridization and resultant gene exchange between divergent lineages. The consequences of gene exchange vary widely, but can include the evolution of novel phenotypes – both true novelty and new combinations of traits – and the evolution of new species.³⁴ Recent studies of baboons, gorillas, marmosets, wildebeest, and mice have begun to lay the foundation for understanding hybrid morphology.³⁵ In particular, Ackermann and colleagues (2006, 2014), identify a package of anomalous morphological traits (dental and sutural) found at high frequency in a hybrid population of olive and yellow baboons of known-pedigree. This hybrid package is also present in recent and Pleistocene ground

³³ Timothy Weaver, *Did a discrete event 200,000–100,000 years ago produce modern humans?* (2012)

³⁴ Michael Arnold, *Natural hybridization as an evolutionary process* (1992); Ole Seehausen, *Hybridization and adaptive radiation* (2004)

³⁵ Rebecca Ackermann et al., *Identifying the morphological signatures of hybridization in primate and human evolution* (2006); Rebecca Ackermann et al., *Further evidence for phenotypic signatures of hybridization in descendant baboon populations* (2014); Rebecca Ackermann and Jacqueline Bishop, *Morphological and molecular evidence reveals recent hybridization between gorilla taxa* (2010); Lisieux Fuzessy et al., *Morphological variation in wild marmosets (*Callithrix penicillata* and *C. geoffroyi*) and their hybrids* (2014); Kerryn Warren et al., *Craniomandibular form and body size variation of first generation mouse hybrids: A model for hominin hybridization* (2018)

squirrel hybrids³⁶, wildebeest hybrids³⁷, gorillas³⁸, and in a purported beluga-narwhal hybrid³⁹, suggesting that this skeletal signature may characterize mammalian hybridization more generally. In addition, hybrids often display transgressive morphologies and high intra-group morphological variability or heterosis (e.g. baboons⁴⁰, wildebeest⁴¹, marmosets⁴², mice⁴³). Even though some of these traits have been identified in hominin fossil specimens, more controlled research from additional extant model organisms is required for statistical and empirical application of the hybrid model to the fossil record.⁴⁴ In this manner, hybridization stands as an important producer of evolutionary innovation; in certain circumstances such innovation/novelty can result in increased adaptive fitness and evolutionary success.⁴⁵

In the case of human evolution, gene exchange has occurred repeatedly in our past and the above-mentioned research on the phenotype suggests that the role and frequency of gene flow has been underestimated in the hominin fossil record. To date, gene flow in our lineage has been demonstrated using both morphological approaches (as above⁴⁶) and also ancient DNA studies⁴⁷. This DNA evidence indicates that the lineages (e.g. Neanderthal, Denisovan, African) known to play a role in modern human ancestry diverged relatively recently, during the past one million years or so⁴⁸, and that hybridization

³⁶ Thomas Goodwin, *Supernumerary teeth in Pleistocene, recent, and hybrid individuals of the *Spermophilus richardsonii* complex (Sauridae)* (1998)

³⁷ Rebecca Ackermann, *Phenotypic traits of primate hybrids: recognizing admixture in the fossil record* (2010)

³⁸ Rebecca Ackermann and Jacqueline Bishop, *Morphological and molecular evidence reveals recent hybridization between gorilla taxa* (2010)

³⁹ Mads Heide-Jørgensen and Randall Reeves, *Description of an anomalous monodontid skull from west Greenland: a possible hybrid?* (1993)

⁴⁰ Rebecca Ackermann et al., *Identifying the morphological signatures of hybridization in primate and human evolution* (2006); Rebecca Ackermann et al., *Further evidence for phenotypic signatures of hybridization in descendant baboon populations* (2014)

⁴¹ Rebecca Ackermann, *Phenotypic traits of primate hybrids: recognizing admixture in the fossil record* (2010)

⁴² Lisieux Fuzessy et al., *Morphological variation in wild marmosets (*Callithrix penicillata* and *C. geoffroyi*) and their hybrids* (2014)

⁴³ Kerry Warren et al., *Craniomandibular form and body size variation of first generation mouse hybrids: A model for hominin hybridization* (2018)

⁴⁴ Rebecca Ackermann et al., *Identifying the morphological signatures of hybridization in primate and human evolution* (2006); Rebecca Ackermann et al., *Further evidence for phenotypic signatures of hybridization in descendant baboon populations* (2014)

⁴⁵ Michael Arnold and Axel Meyer, *Natural hybridization in primates: one evolutionary mechanism* (2006); Ole Seehausen et al., *Genomics and the origin of species* (2014)

⁴⁶ For example: Rebecca Ackermann, *Phenotypic traits of primate hybrids: recognizing admixture in the fossil record* (2010); Rebecca Ackermann et al., *The hybrid origin of “modern” humans* (2016); Kerry A. Warren et al., *Craniomandibular form and body size variation of first generation mouse hybrids: A model for hominin hybridization* (2018)

⁴⁷ For example: Richard Green et al., *A draft sequence of the Neanderthal genome* (2010)

⁴⁸ Johannes Krause et al., *The complete mitochondrial DNA genome of an unknown hominin from southern Siberia* (2010); Kay Prüfer et al., *The complete genome sequence of a Neanderthal from the Altai Mountains* (2014)

between these lineages has occurred repeatedly⁴⁹. The resultant gene exchange is reflected in some living people today, who have ancestry derived from multiple lineages. This portrayal is consistent with scenarios – argued for decades – that present a complex picture of our origins on the basis of fossil morphology⁵⁰ and earlier genetic studies⁵¹. Again, we find ourselves in a situation where novelty – including morphological traits such as large overall size and changes in tooth morphology⁵²– can emerge through non-adaptive means. And again, this does not mean that many of the acquired and retained traits are not ultimately adaptive (e.g. skin pigmentation diversity as a product of natural selection affecting the levels of pigment (melanin) in the skin relative to levels of ultraviolet radiation from the sun⁵³), but that they did not arise as an adaptation as one group diverged from an ancestral condition.

Summary: Adaptation is not a prerequisite for morphological complexity

To sum, human evolution is increasingly being shown to have occurred through a complicated interplay of evolutionary forces, working together to produce change over time. Whereas in the past researchers have tended to frame such change, and especially the evolution of new and more complex forms, in an adaptive context, we now know that neutral (chance) processes and gene exchange have played substantial roles in the production of hominin diversity (Table 1). It is plausible that some of our capabilities as a species that we associate with the modern condition, including many of the things discussed in this volume, and potentially including cultural capabilities, emerged through chance or reticulate processes of gene exchange (e.g. rather than by a scenario where one group in one region evolved adaptively superior abilities and replaced another). Moreover, the repeat history of reticulate (versus branching) evolution (Figure 1), particularly over the past million years, but possibly further in the past, makes it very difficult to point to one place and time for “humanness”. We therefore must be cautious in our interpretation of changes we see in the fossil past, including the emergence of traits we consider surrogates for the remarkable intellectual capabilities of our species.

⁴⁹ Richard Green et al. *A draft sequence of the Neandertal genome* (2010); Qiaomei Fu et al., *Genome sequence of a 45,000-year-old modern human from western Siberia* (2014); Kay Prüfer et al., *The complete genome sequence of a Neanderthal from the Altai Mountains* (2014); Qiaomei Fu et al., *An early modern human from Romania with a recent Neanderthal ancestor* (2015)

⁵⁰ For example: Rachel Caspari and Milford Wolpoff, *The process of modern human origins* (2013); Erik Trinkaus, *Early modern humans* (2005); Xinzhi Wu, *On the origin of modern humans in China* (2004)

⁵¹ For example: Alan Templeton, *Out of Africa again and again* (2002)

⁵² See for example: Rebecca Ackermann, *Phenotypic traits of primate hybrids: recognizing admixture in the fossil record* (2010)

⁵³ Nina Jablonski and George Chaplin, *The evolution of human skin coloration* (2010)

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Figure 1. A braided stream metaphor depicting the evolution of our lineage. Repeat divergence and remerger, via adaptive and non-adaptive evolutionary processes, produce both novelty and complexity.

Table 1. Current evidence for evolutionary processes acting during human evolution between pairs of taxa.*

	Natural selection	Genetic drift	Gene flow	References
<i>Homo neanderthalensis</i> – <i>Homo sapiens</i>	Brain volume	Cranium	Genetic data	Fu et al. 2014; Fu et al. 2015; Green et al. 2010; Kuhlwilm et al. 2016; Weaver et al. 2007
<i>Homo neanderthalensis</i> – Denisovans	Unknown	Unknown	Genetic data	Prüfer et al. 2017
Denisovans – <i>Homo sapiens</i>	Unknown	Unknown	Genetic data	Huerta-Sánchez et al. 2014; Krause et al. 2010; Prüfer et al. 2017; Reich et al. 2010
Early <i>Homo</i> – Dmanisi hominins	Maxilla Mandible	Midface Neurocranium	Unknown	Schroeder and Ackermann 2017
<i>Homo erectus</i> – <i>Homo naledi</i>	Unknown	Cranium Mandible	Unknown	Schroeder and Ackermann 2017
Early <i>Homo</i> – <i>Homo erectus</i>	Mandible Maxilla Brain volume	Midface Neurocranium Teeth	Unknown	Gómez-Robles et al. 2017; Schroeder and Ackermann 2017
<i>Australopithecus sediba</i> – early <i>Homo</i>	Mandible Neurocranium	Face	Unknown	Schroeder et al. 2014
<i>Australopithecus africanus</i> – <i>Australopithecus sediba</i>	Maxilla Temporal	Upper face Mandible Neurocranium	Unknown	Schroeder et al. 2014
<i>Australopithecus africanus</i> – early <i>Homo</i>	Upper orbit Zygomatics Brain volume	Mandible Midface Neurocranium Teeth	Unknown	Gómez-Robles et al. 2017; Schroeder et al. 2014
<i>Australopithecus africanus</i> – <i>Paranthropus robustus</i>	Zygomatics Brain volume	Midface Neurocranial shape Teeth	Unknown	Ackermann and Cheverud 2004; Gómez-Robles et al. 2017; Hlazo et al. 2018
<i>Paranthropus aethiopicus</i> – <i>Paranthropus boisei</i>	Brain volume	Midface Frontal Neurocranium Teeth	Unknown	Ackermann and Cheverud 2004; Gómez-Robles et al. 2017; Hlazo et al. 2018
<i>Paranthropus aethiopicus</i> – <i>Paranthropus robustus</i>	Temporal Brain volume	Midface Frontal Neurocranium Teeth	Unknown	Ackermann and Cheverud 2004; Gómez-Robles et al. 2017; Hlazo et al. 2018

<i>Paranthropus boisei</i> – <i>Paranthropus robustus</i>	Mandible Palate Brain volume	Midface Neurocranium Teeth	Unknown	Ackermann and Cheverud 2004; Gómez-Robles et al. 2017; Hlazo et al. 2018
<i>Australopithecus afarensis</i> – early <i>Homo</i>	Os coxa Brain volume	Neurocranial shape Teeth	Unknown	Gómez-Robles et al. 2017; Grabowski and Roseman 2015

*Evidence of genetic drift or natural selection indicates diversification between taxa; evidence of gene flow indicates gene exchange and hybridization.