Human Evolution: Retrodictions and Predictions

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Human Evolution is a contentious topic. Understanding the human evolutionary past is complex enough; predicting the future of human evolution is nearly impossible. However, we can reconstruct events that led to the evolution of characteristics that have contributed to our success, and may hasten our extinction.

1. Introduction

Primates, including humans, are vision dominant mammals, largely arboreal, with unusually high levels of limb and dietary flexibility. Among primates, hominoids are the evolutionary group that includes humans and apes. All hominoids except humans practice a form of arboreal locomotion in which the body is positioned below rather than on top of a branch (suspension), and their brains are as large, or larger, than in any other primate. In hominids, the group that includes the great apes (orangutans, gorillas, chimpanzees and bonobos) and humans, there is a general slowing or delay in life history (lifespan, age at menarche, age of dental eruption and skeletal maturation, etc.), and a dramatic increase in brain and body size. All hominids are capable of extracting embedded, concealed or otherwise protected resources from the environment with a level of efficiency not generally seen in other primates, and all engage in intensive, prolonged, and complex forms of social interaction. Humans, of course, take all of these attributes to the extreme. If great apes are the gifted members of the primate community, humans are the super geniuses. We excel in information acquisition, processing and retrieval, and we are distinct from

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other hominids in being bipedal, permitting the development of greatly enhanced manipulative capabilities of the hands.

All of these attributes make humans the most impressive, and most dangerous, animal on the planet. In this chapter I will outline the major events in the evolutionary history of the primates that help explain the origins of the most important attributes that make us human. I will then consider the future course of human evolution, including the inevitability of extinction.

2. The Primate Fossil Record and the Origin of the Hominoidea

2.1 Early Primates

There is some debate about the age of the earliest primates, so I will begin my survey with the earliest easily recognizable primates, the adapiformes and the tarsiiformes. Adapiformes are primates mainly of Eocene age (about 56 to 35 million years ago, or Ma), although a few taxa persist into the late Miocene (roughly 10 Ma) [1]. Although very diverse in morphology and adaptation, they generally resemble living strepsirhines (lemurs, lorises and their kin). Tarsiiformes are also mainly Eocene, with a few taxa extending the range to about 20 Ma. Again, while highly diverse, tarsiiformes resemble living tarsiers, which belong to the haplorhines, to which monkeys, apes and humans belong as well [2].

Adapiformes are among the earliest primates to show characteristic features of living primates. Adapiformes had skulls with reduced snouts and eyes facing forward, reflecting the increasing importance of vision over the sense of smell. Their brains were small by modern primate standards but larger than most other mammals of similar size living at the same time. Their skeletons provide evidence of a somewhat mobile and powerfully grasping limb structure, and a long and flexible vertebral column.

Adapiformes were probably fairly agile in the trees, and had begun to develop enhanced eye-hand coordination, perhaps to improve their mobility in the challenging arboreal environment, or perhaps to enhance their ability to use the hands to acquire food items. Most adapiformes were fruit or leaf eaters.

Table1. Classification of the taxa described in this chapter.

- Primates
  - Strepsirhines
    - Adapiformes
    - Lemuriformes (lemurs and kin)
    - Lorisiformes (lorises and kin)
  - Haplorhines
    - Tarsiiformes (Tarsius)
    - Anthropoidea (monkeys, apes and humans)
      - Platyrrhini (New World monkeys)
      - Catarrhini (Old World monkeys, apes and humans)
        - Cercopithecoidea (Old World monkeys)
        - Hominoidea (apes and humans)
          - Hylobatidae (gibbons and siamangs)
          - Hominidae (great apes and humans)
            - Homininae (African apes and humans)
            - Ponginae (orangutan)

Tarsiiformes are also modern primate-like, but were generally smaller than adapiformes. Unlike most adapiformes, many tarsiiformes were insect or small vertebrate eaters, and may have used their large eyes and enhanced eye-hand coordination to capture prey.

Both of these groups of early primates appear to have dominated the arboreal environment at many localities. The features that define them as primates are the precursors to many uniquely human attributes, such as our large brains, highly manipulative hands, and mobile limbs. Paleoprimatologists disagree on which of these early primate groups is most closely related to anthropoids (New and Old World monkeys, apes and humans) [3-4]. There were many more events in the evolutionary history of the primates that led, by chance of course, to the origin of higher primates including humans.

2.2 Early Anthropoids

The oldest anthropoids are thought to date to the beginning of the middle Eocene, about 50 Ma [3]. The earliest anthropoids are recognized mainly by their dentition, which resembles living anthropoids in that the molar teeth are broader and have lower, more rounded cusps than in tarsiers or most strepsirhines. While the earliest anthropoids are more tarsier-like, eventually the mandibles would become more strongly built and fuse in the midline. These features distinguish modern anthropoids from other primates.

From the earliest anthropoids the two major groups of living anthropoids, the Platyrrhini or New World monkeys, and the Catarrhini or Old World monkeys, apes, and humans, would emerge. The origins of the New World monkeys are somewhat mysterious, as they live today only in Central and South America, which were not connected to North America at the time primates first appear in South America. But it is the origins of the catarrhines that are of special interest here. One of the best collections of fossil anthropoids comes from the famous Fayum deposits of Egypt [5]. Among these fossils are some of the earliest catarrhines.

2.3 Early Catarrhines

The most advanced of the Fayum anthropoids is the early catarrhine *Aegyptopithecus*, which had powerful jaws and low, rounded molars, a brain larger than would be typical in a strepsirhine and some further reduction in the snout. *Aegyptopithecus* is still quite primitive, and in many ways is intermediate between strepsirhines and more advanced catarrhines. Its limb structure, for example, while flexible as in living strepsirhines, lacks the increased mobility and overall elongation (especially the forelimb) present in more modern catarrhines. Over time, later early catarrhines, such as *Pliopithecus* from Europe, would develop more modern catarrhine characteristics, including a short snout, larger brain and long, highly mobile limbs [6].

2.4 Early Hominoids

Hominoids first appear in the fossil record in the early Miocene, at about 20 Ma, though a few specimens may date back to the Oligocene, about 26 Ma [7]. The best known of the protohominoids is *Proconsul,* present at many sites in Kenya. *Proconsul* has all the attributes of modern catarrhines, but only a few hominoid characteristics, including the absence of a tail (or the presence of a coccyx), and subtle indications of enhanced limb mobility [8-12]. *Proconsul* had powerful, grasping hands and feet, and some indications of encephalization (brain size increase) compared to most monkeys [13-16]. *Proconsul* probably ate soft, ripe fruits and moved through the environment as do living monkeys, on the top of branches. A protohominoid similar to *Proconsul* probably moved into Eurasia about 17 Ma, where the first specimens more closely resembling modern hominids appear. Several taxa are known with more powerful jaws, large teeth with thick enamel, but limbs still largely like those of *Proconsul.* The jaws and teeth may have permitted these new species to exploit a broader range of dietary resources [6].

3. The Evolution of Hominids

3.1 Early Hominids

By about 13 Ma hominoids appear with the hallmark of modern hominoids, highly mobile forelimbs capable of supporting body mass below branches. This, combined with the ability to exploit a wider range of resources that comes from having more powerful jaws, leads to the earliest hominids. The best known of the early hominids are *Dryopithecus* from Europe and *i pithecus* from South Asia. *Dryopithecus* is probably closely related to African apes and humans, while *i pithecus* is likely to be a close relative of the orangutan [17-18]. Both share many attributed with living great apes, including large bodies and brains, slower life histories, elongated faces with large front teeth and many other detailed resemblances to orangutans in the case of *i pithecus* and to African apes in the case of *Dryopithecus* [16 - 19]. The postcranial skeleton is better known in *Dryopithecus,* and includes typical hominoid features such as long arms and short legs, short, stiff backs, broad thoraxes, extremely mobile shoulders and elbows, and very powerfully grasping hands and feet [9].

The success of *Dryopithecus, i pithecus* and other late Miocene hominids was probably due at least in part to their enhanced cognitive abilities and flexible adaptations. During the late Miocene the Earth's climate was becoming more variable and unpredictable [20]. While most other mammals became increasingly specialized to exploit ever changing niches, hominids developed flexible strategies to confront ecological changes. With larger brains come more complex forms of behavior, including complex feeding techniques, more complex social interactions and enhanced communicative abilities. As these capacities become better developed, selection acts to increase their efficiency and effectiveness, leading to feedback loops or arms races resulting from competition among members of the population (figure 1) [21-24]. These developments set the stage for the immense increase in brain size that comes with the origin of the genus *o o.*

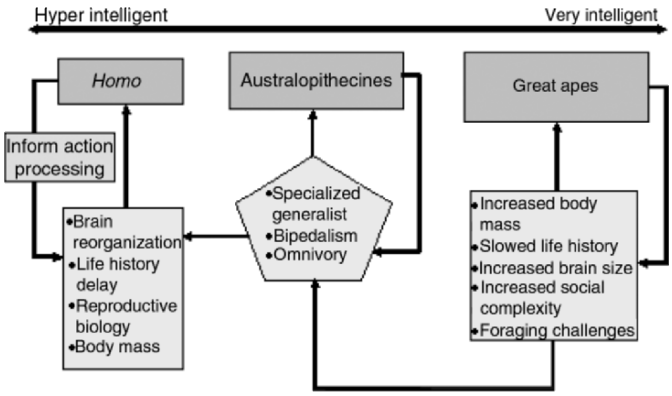

Fig. 1. Feedback loops among a variety of factors that contribute to the evolution of higher intelligence.

3.2 Early Humans

Dryopithecus, or a closely related species, is probably an ancestral to African apes and humans. While there is almost no fossil record of the African apes, many human taxa appear in the fossil record before the appearance of *o o* at about 2.5 Ma. The best known of these is *Austr lopithecus.* Australopithecines are chimpanzee sized fossil humans with brains only slightly larger than those of chimpanzees, and possible evidence of some degree of cortical reorganization [16, 25 - 29]. There is no direct evidence of tool use in australopithecines, though most presume that they had, at least, the tool using capacities of living chimpanzees. Chimpanzees use stones as tools and make tools from perishable materials that would not preserve in the fossil record [30 - 32].

The most important differences between chimpanzees and australopithecines are that australopithecines are bipedal and their jaws and teeth are massive and designed to exploit very hard and/or tough food items. Bipedalism, along with a persisting ability to use arboreal resources, allowed australopithecines to travel greater distances between forest patches, increasing their potential daily ranges. A massive masticatory apparatus probably allowed australopithecines to broaden their resource base, even beyond that of contemporaneous great apes.

3.3 Homo

Within the successful radiation of australopithecines there is the ancestor of the genus *o o,* although there is little agreement on the identity of this ancestor. The earliest specimens of *o o* are known from Ethiopia, Kenya and Malawi and are about 2.5 Ma, which is also the age of the earliest identifiable stone tools [33 - 37].

The earliest specimens of *o o* are fragmentary, but about 2 Ma more complete crania are known. These show that early *o o* (*o o h ilis* and *o o ru ol ensis* had significantly larger brains than australopithecines, and clearer evidence of reorganization. The later includes more marked cerebral asymmetries such as the development of a “Broca’s cap”, a bulge on the left frontal lobe in a region involved in spoken language in modern humans [38 - 39]. We can not know if enlargement in this region in early *o o* indicates spoken language competence or some other capacity that preceded language. Broca’s cap is adjacent on the cerebral cortex to the motor cortex region controlling movements of the arm and hand. It is possible that enlargement in this region is related initially to increasing manual dexterity or grip variety and strength, and was only secondarily co-opted for language production [40]. The simultaneous appearance of stone tools, Broca’s cap and early *o o* is probably not coincidental.

3.4 Later *Homo*

The evolution of *o o* is complex and includes many species over time, but for the purposes of this discussion it can be summarized by a few major trends. *o o erectus* and *o o erg ster* appear in Asia and Africa, respectively, between about 1.6 to 1.8 Ma, with larger brain and body masses than early *o o* [40 - 42]. By about 0.9 Ma *o o erectus* ranged from Europe to China in the north and from the Mediterranean to South Africa in the south. By about 0.8 Ma new species appear, the best known of which is *o o hei el ergensis.* Neandertals first appear about 0.25 Ma and Homo sapiens sapiens by at least 0.13 Ma and possibly as early as 0.2 Ma [42 - 45].

During the transition from early *o o* to modern humans, the main trends include fairly steady increases in brain size, reduction in the size of the jaws and teeth, geographic variability in body size, and, with modern humans, a general decrease in skeletal robustness.

3.5 The Biology/Technology Transition

The rate of increase in brain size begins to slow by about 0.5 Ma (figure 2). At the same time, thousands of localities are known around the world with millions of paleolithic artifacts. The rate of change in the complexity of these technologies, and in other aspects of the culture of prehistoric humans (settlement patterns, land use, hunting strategies, geographic distribution, etc.), is very different (figure 2).

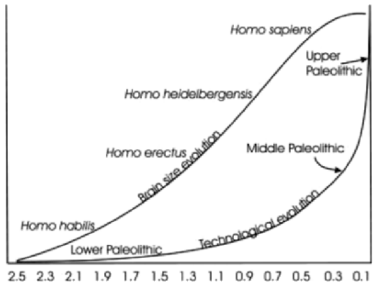

*Fig. 2. C*omparison of rates of change in biological and technological evolution. X axis units are millions of years.

Early stone tool technologies remain relatively unchanged for about 1 Ma. By about 1 Ma the pace of technological evolution accelerates. This rate of acceleration increases over time, reaching dramatic rates of change after about 0.2 Ma. The lower paleolithic time period, associated with Homo habilis, Homo erectus and their contemporaries, lasts about 2 Ma. The middle paleolithic, associated with the Neandertals, lasts about 0.2 Ma. The upper paleolithic, associated with modern humans, lasts about 0.035 [46]. In other words, each of the major archeological periods associated with prehistoric humans is about one order of magnitude shorter than the preceding period. Since the end of the paleolithic and the beginning of the agricultural revolution, about 12,000 years ago, the pace of technological change increased to unimaginable rates in comparison to the rate of cultural evolution during the period in which our brains evolved. It could be argued that the pace of technological change is reaching a point beyond our biological capacities to manage it.

3.6 Genetics of Human Evolution

It has taken about 7 Ma for humans and chimpanzees to accumulate about 1 to 2% genetic divergence, based on most measures, although there are between 20 and 40 million base pair differences between the two species [47]. Of these, it has recently been estimated that only about 70,000 have resulted in adaptive changes in protein coding sequence regions [47]. A few specific differences related to brain evolution have recently been identified. A mutation in a gene affecting myosin expression is thought by one group of researchers to have caused an overall reduction in the size and power of the jaws and muscles of mastication in humans, which they correlate to increases in brain size [48]. A number of other promising discoveries of genetic differences between apes and humans that may be correlated to important differences between the two have also been documented [49].

4. The Future "Evolution" of Humans

4.1 Beyond Biological Evolution?

It is often asserted that humans have moved beyond biological evolution, given the buffering effects of technology. Technology protects humans from the rigors of the natural environment, improves our minor imperfections, and permits individuals who would have died in the pre-industrial era to live productive lives. It has even been suggested that technology works against human evolution by allowing mutations that would lead to reduced fitness to be maintained in the population. This naïve view fails to consider the continuous effects of mutation and the fact that even the most deleterious alleles are maintained at low levels in all populations by simple Mendelian processes.

It is difficult to quantify the rate of evolution in current populations of humans. The fossil record provides ample evidence that humans, even with sophisticated technology, were still responding to environmental stresses with evolutionary innovations. Neandertals cared for their infirm and used technology to protect themselves from the elements, but they clearly changed over time [43, 46]. *o o loresiensis,* the recently discovered diminutive fossil human from Indonesia, underwent dramatic morphological changes from its putative *o o erectus* ancestor, despite a sophisticated technology. These changes, including a marked decrease in body size and a spectacular reduction in brain size, mirror those documented in classic cases of island biogeography, and show that humans respond to isolation in a manner similar to other mammals. Since the agricultural revolution, humans have become much less robust skeletally, and there is a trend toward reduction or loss of the last molar. But the time scale on which evolution operates makes it difficult to document ongoing biological evolution in humans.

Some current activities could conceivably lead to a reduction in genetic diversity within modern humans, precipitating either a speciation event, or more likely, a catastrophic event and possible extinction. Genetic screening during pregnancy has the potential to reduce genetic diversity by artificial selection of desirable characteristics in offspring. Dramatic declines in genetic diversity could leave humanity susceptible to pandemic outbreaks that could lead to extinction. Currently, screening consists largely of detecting genes or gene by-products that indicate the presence of genetic disorders. It is possible in the future that screening will evolve to the point where parents might have the ability to "customize" their offspring, allowing only those with a specific desired set of features (sex, height, weight, skin tone, IQ, etc.) continue in utero. While this may lead to a reduction in genetic diversity over time, mutation and recombination will continue to produce diversity, and recessive genes will persist in all populations. It seems unlikely to me that the number of genes that could be screened in the future will be significant relative to the total number of genes in the human genome.

Cloning, the ultimate in gene diversity reducing technology, if it becomes widespread, would place humanity in a precarious position. Even if human cloning becomes feasible and common, despite technical and ethical issues, it again seems unlikely to me that this form of reproductive technology would become any more widespread across all human populations than are current widely available technologies.

5. The One Confident Prediction about Human Evolution

All species eventually become extinct, at least among multicellular organisms. There are really two forms of extinction. Populations of a species may be isolated from other populations of the same species and, over time, evolve into a new species. The old species may persist for a time along with the new species. Or, a species may disappear without descendents. Either way, once the old species no longer exists, even if there is genetic continuity between it and the new species, it is considered to have become extinct.

Humans will surely follow one of these paths. It would be arrogant, and dangerous, to think otherwise. Ironically, the idea that we humans can think ourselves out of extinction makes it tempting to continue the policies and behaviors that demonstrate a callous disregard for the sustainable future of life on earth, and may precipitate our extinction. We can act to maximize the likelihood of the first option of extinction, that which leaves descendents. But we will become extinct either way. This is a natural phenomenon, and, as Shakespeare suggests, nothing to fear:

"Be cheerful, sir. Our revels now are ended. These our actors, as I foretold you, were all spirits and are melted into air, into thin air; And, like the baseless fabric of this vision, the cloud-capp'd towers, the gorgeous palaces, the solemn temples, the great globe itself, yea, all which it inherit, shall dissolve, and, like this insubstantial pageant faded, leave not a wrack behind. We are such stuff as dreams are made on, and our little life is rounded with a sleep."

Shakespeare, The Tempest.

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