Application of a Hypothesis to Speciation in Hominidae

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Abstract

I have previously hypothesized that biological species are not the result of gradual changes in the genome or morphology as suggested by Darwin, but rather the result of punctuated major pericentric or paracentric inversions or other rearrangements (e.g., chromosome fusions) that prevent reproductive compatibility with the parent group. Following the rearrangement, a new nascent species can be formed through inbreeding within two generations consistent with the views of Goldschmidt. Applying this hypothesis to speciation in Hominidae (the great apes) suggests that (i) orangutans are close to the common ancestor of Hominidae; (ii) humans are close to the common ancestor of Hominoids, which was adapted for efficient all-terrain locomotion; (iii) gorillas and chimpanzees have passed through more species as they have adapted to a very specialized ecological niche in the tropical forest, and (iv) speciation events in Homo facilitated evolution of the human brain.

Key words
Evolution, Chimpanzee, Human, Species, Pericentric Inversion, Brain

Introduction

In a recent paper in this journal [1], I argue that biological speciation (i.e., reproductive isolation) is the result of common pericentric or paracentric inversions or rarer large scale chromosomal rearrangements (e.g., chromosome fusions or fractions) that have little or no effect on phenotype. Mutations of these types and magnitude are believed to adversely affect the metaphase alignment and/or anaphase segregation of chromosomes during the first few division of the fertilized egg [2-5]. Note that there are many other smaller or less strategically placed inversions in human chromosomes that probably do not interfere with reproduction or cause speciation [6]. A nascent new species is formed by inbreeding of the heterozygous clan members, leading to mutually fertile, homozygous offspring within two generations.

The nascent species resulting from these rearrangements then acquire minor mutations that vary the phenotype from the coexisting parental species [7]. Natural selection (as proposed by Wallace [8]) acting on the populations then selects the successful species for the specific habitat. The fittest phenotype eventually dominates in each habitat/ecosystem. It should be noted that the modern synthesis of evolutionary theory [9] does not recognize these inversions and fusions as speciation events, but rather interprets them as becoming fixed in species during Darwinian evolution (i.e., species created by progressive natural selection as implied by Darwin’s On the Origin of Species: By Means of Natural Selection) [10]. Without preliminary reproductive isolation, changes in morphology are likely very slow and easily reversible.

My hypothesis [1] draws a line between what a biologist might consider to be a species (based on reproductive compatibility) and what an anthropologist/paleontologist might consider to be a species based on morphology of fossils. It calls attention to the fact that within a biological species there may be substantial anatomical differences, while between species their might be almost no anatomical difference. The hypothesis might provide a framework for interpretation of paleontological observations.
An application of the hypothesis to Hominidae

Keep in mind that we only have access to the genomes of surviving species, but we can deduce the gross features of the genome of their most recent common ancestors, when there are two surviving species. Note that the frequency of the major mutations and formation of nascent species is much greater than the frequency of replacement of the parent species through natural selection. In fact, in a large population there are always nascent species [1]. Because reduced fertility with the parent group leading to speciation appears to be associated only with major mismatches in chromosome parity [1], the results of Yunis and Prakash [11-13] are adequate to identify the most likely speciation events in the Hominidae line. They identify 5 events (usually pericentric or paracentric inversions) in the ancestral line leading to Hominidae (>16 Ma). The orangutan (Pongo) line split first and has retained only 6 major events (in chromosomes 2q, 4, 8, 11, 17 and 20) in about 16 million years. Then, in the line leading to the surviving African apes, each chromosome except 6, 13, 19, 21, 22, and X was replaced by its mutant before the split of the gorillas (Gorilla). This implies a high rate of selective adaptation (i.e., a succession of 19 species in 7 million years during the Miocene radiation [14, 15 to 8 Ma]). The gorilla line has retained 9 major events (chromosomes 1, 4, 5, 8, 10, 12, 14, 16 and 17) over the last 6-8 million years. During the two to three million years immediately after the gorillas split [14, 15], three events (chromosomes 2p, 7 and 9) formed the common ancestor of chimpanzees (Pan) and humans (Homo). The chimpanzee line retained 7 major events (all pericentric inversions in chromosomes 4, 5, 9, 12, 15, 16 and 17) over the last 4 to 6 million years [15]. In the same period, the human line has retained only three major events (pericentric inversions in chromosomes 1 and 18 and the fusion of 2p and 2q to form human chromosome 2). I interpret these events (i.e., major mutations followed by slower replacement of one chromosome by its mutant in the surviving population) as the boundaries between successive (reproductively isolated) species.

The African apes have diverged genonomically and anatomically from their most recent common ancestor. If we look at the last common ancestor of the African apes that lived about 8 Ma [15], gorillas have gone through 9 major events, and chimpanzees have gone through 10 major events, but humans have only gone through 6 major events. I would argue that the adaptation of chimpanzees and gorillas to thrive in the dense tropical forest habitat was a radical departure from the primate line that leads to Homo sapiens; and, thus, required more speciation events to accomplish the deed. The common ancestor of the African apes appears to have been a world-traveling generalist with relatively upright stance and bipedal locomotion capable of crossing all sorts of land forms (across Europe, Asia and Africa during the Miocene [16, 17]) efficiently [18-21]. Homo sapiens have built on those ancestral traits, while the gorillas and chimpanzees have adapted to living exclusively in tropical rain forest. While Homo developed a larger brain, optimized all-terrain locomotion and adapted for cooling during high energy output by loss of hair [22]; the forest apes [23] have undergone convergent evolution reminiscent of the much earlier speciation of monkeys [24] more than 20 million years ago.

Tree-dwelling became an attractive alternative to plains-dwelling because of the escape from most large predators, available prey in the form of monkeys and, most important of all, the availability of high carbohydrate and vitamin-rich fruits. The primary down-side of moving into the jungle was insect-borne diseases, which were thwarted by hair over most of the forest ape’s body [25] and nesting high in insect-repellent trees [26]. The locomotion capabilities of Gorilla and Pan appear to have become specialized to the point where chimpanzees and bonobos have been isolated for millions of years by the Congo River in comparison to their ancestors who traversed the world.

Speciation and the human brain

Advanced intelligence is one of the hallmarks of our species not shared with other primates. It is clear that the human brain is much larger than that of chimpanzees or other members of Hominidae [27], and that even in very distant species, large brains seem to be correlated with intelligence [28]. There are two genes that seem to be closely associated with brain size [29]. The microcephalin group (located at 8p23.1) appears to have evolved during the Miocene (before the last common ancestor of the African apes) [29, 30], but it did not have much effect on brain size. These gene products (MCPH-1 to -4) appear to be necessary, but not sufficient for brain growth without producing tumors [31, 32]. Mutations in MCPH genes of humans result in brains the size of chimpanzees and/or dispose humans to various proliferation diseases by deregulation of the G2/M checkpoint [33-36].
The other gene associated with developmental expansion of the brain tissue is known as ASPM (located at 1q31.2-32.1). ASPM’s function appears to be related to cell proliferation, especially of neurons during development [37, 38]. This region of chromosome 1 was involved in a complex series of rearrangements culminating in a pericentric inversion in the Homo line about 3 Ma [39]. As described by Szamalek et al. [39] a duplication was followed by a transposition from 1q32 to 1q21; there was a inverted duplication in the p-arm; and finally these segments were involved in the major (putative speciation event) pericentric inversion between 1p11.2 and 1q21.1. The hypothesis applied here implies that these rearrangements isolated ASPM in a clan, which quickly formed a nascent species that allowed positive selection of ASPM. Interestingly, a similar chromosome 1 pericentric inversion is found the Gorilla lineage [11], which also experienced rapid evolution of ASPM [40]. Once the ASPM gene was isolated in a nascent species, it is believed to have taken about 2 million years to bring the gene to its modern form [40].

However, expansion of the brain cannot occur without changes in the skull and the female pelvis. These changes in development and/or adult phenotype were likely accomplished in other speciation events (chromosome 2 fusion and 18 inversion) [11]. According to Rightmire et al. [41] the skull changed slowly until 700,000 years ago (coinciding with perfection of the ASPM gene [40]) and modern human skull structure was not achieved until about 200,000 years ago. The skull was refined to a modern appearance a mere 35,000 years ago [41].

References

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