FEATURE ARTICLE

Why Are Chimps Still Chimps?

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Abstract

Teachers may be posed with such questions as, "If we evolved from chimps, why are there still chimps?" We provide teachers with answers to this and related questions in the context of the latest genetic, fossil, and behavioral evidence. We also provide references they can use to further students' understanding of human evolution and evolution in general. In the process, we highlight recent discoveries in paleontology, molecular evolution, and comparative genomics. Modern chimps and humans shared a now extinct common ancestor that was neither a chimp nor a human – in other words, humans did not evolve from chimps – and, though chimps are humans' closest living relatives, we are characterized by distinct evolutionary histories.

Key Words: *Anagenesis; bonobo; brain; chimpanzee; cladogenesis; evolution; human evolution.*

Biology educators, whether they teach in high schools or in colleges and universities, may get a question similar to the one in our title. How should they respond? Such questions can provide excellent teaching moments. In the following pages, we provide answers to this and related questions. Our main point: Chimps are still around today because humans did not evolve from living chimps[1] – both humans and chimps evolved from a now extinct common ancestor. To better understand the distinct evolutionary histories of humans and chimps, we must begin with a discussion of two evolutionary patterns: anagenesis and cladogenesis.

> *Chimps are still around today because humans did not evolve from living chimps.*

Question: Did humans evolve in a "straight line," with one species evolving into another?

Answer: Evolution does not just proceed along a straight line; it also branches.

Key concepts: Anagenesis and Cladogenesis

Anagenesis is an identifiable pattern, or outcome, characterized by directional evolutionary changes within a single lineage. By contrast, cladogenesis (branching evolution) leads to the origin of two or more lineages from a common ancestor (Figure 1) (Futuyma, 2009). Evolutionary biologists consider cladogenesis a much more important pattern in the generation of biological diversity than anagenesis.[2] In the strictest sense, cladogenesis results in two new sister species, and the common ancestor is considered to have gone extinct. The data strongly indicate that the lineages represented today by living humans and living chimps diverged via cladogenesis; fossil and genetic evidence shows that the two lineages diverged from a common ancestor ~6 million years ago. The term "common ancestor" refers to a set of ancestral populations, not a single individual, that split to give rise to two sets of populations. In the present case, one of these sets evolved to become modern-day humans, while the other evolved to become modern-day chimps. With regard to terminology, we recommend referring to the common ancestors of living chimps, living humans, and all the extinct species that are ancestral to them as "fossil apes" or "ancestral apes" so that these ancestral species are clearly distinguished from living apes. We hope that this language will help dispel the incorrect idea that humans evolved from living chimps.

Multiple lines of evidence support the hypothesis that cladogenesis and anagenesis occurred within the human lineage after the initial split between the human and chimp lineages. Species known from the human fossil record are believed to have originated from ancestral forms primarily via lineage splitting, but also via anagenetic change (e.g., Kimbel et al., 2006; Dunsworth, 2010; McNulty, 2010).

With an understanding of cladogenesis and anagenesis, students can better appreciate the distinction between descent from a common ancestor and relationships among coexisting modern species.

[1] Two living species are commonly referred to as chimpanzees: *Pan troglodytes* (the common chimpanzee) and *P. paniscus* (the bobobo). When we are talking about both living species, either with or without their extinct fossil relatives, we will refer to them as chimps.

[2] There are some exceptions, however; for example, Stuessy et al. (2006) have argued that anagenetic evolutionary processes have been particularly important in the evolution of some plant species on oceanic islands.

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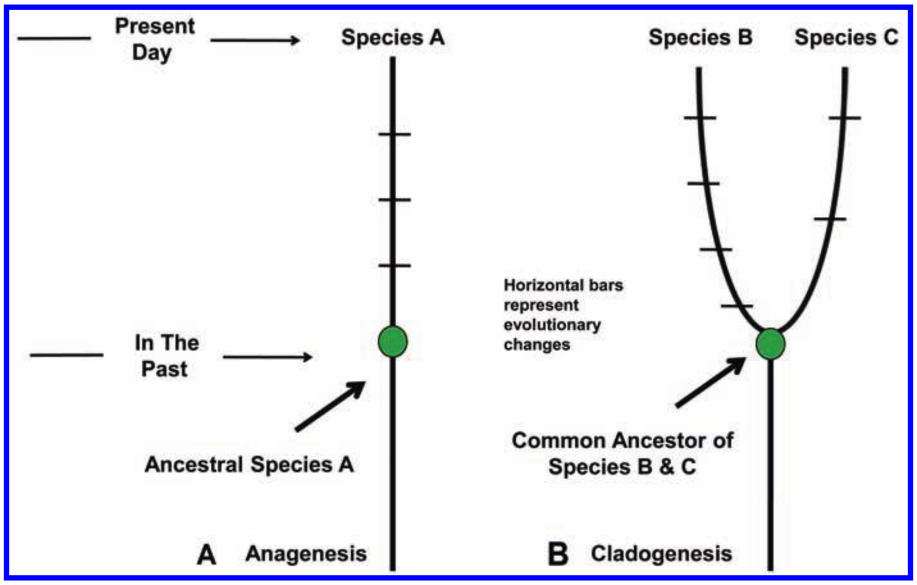

Figure 1. (A) Anagenesis versus (B) cladogenesis. (A) Anagenic evolution occurs within and is constrained to a single lineage. For example, an ancestral flock of seagulls might change over time, evolving the gray wing tips and increased mean flight speed observed in present-day Species A. (B) Cladogenesis involves lineage splitting, leading to two new lineages. For example, present-day Species B and Species C may have evolved from a common ancestral species that was split apart by the appearance of a new river or some other vicariant event. This resulted in two groups, now separated, where there was once one. Evolutionary changes can now occur independently in these two resulting lineages.

Question: Did humans evolve from chimps?

Answer: No. Just as you and your cousins share a common ancestor who lived hundreds of years ago and are long dead, all living humans share a common ancestor with all living chimps that lived millions of years ago, and that common ancestor no longer exists.

Key concepts: Common Ancestor vs. Living Relative or Evolutionary Cousin

It is important to introduce the concept of evolutionary cousins to help clear up misconceptions about humans evolving from modern chimps. In addition to this analogy being familiar to students, "the notion that living species are cousins, and neither ancestors nor descendants of each other, is one of the most important understandings for students to acquire" (Miekle & Scott, 2010, p. 574). Note that this statement reflects the fact that diversification of species occurs via cladogenesis, as described earlier. Explaining the difference between a student's living relative in the same generation (a distant cousin) and the dead relative from a few generations ago that the student and his or her cousin share (a great-great-grandparent) is an effective method for introducing the concept of a common ancestor. With this analogy, students can better grasp the notion that they did not descend from living apes, just as they did not descend from their cousins. Students can also be introduced to the concept of close versus distant relatives; just as a student and his or her sibling are genetically more closely related to each other than either is to a cousin, humans and chimps are genetically closer to each other than either is to monkeys or any other species of ape. This should help correct the related misconception that evolution is always linear. As Dougherty (2011) suggests, this can be a teachable moment: present to your students a series of incorrect statements based on common misconceptions, and ask them to find the errors and rewrite the statements to be correct.

Question: How similar are chimps and humans?

Answer: It depends on what feature you are looking at.

Before discussing the changes that have occurred along the human and chimp lineages since humans and chimps diverged, we need to discuss the currently observable similarities and differences between living chimps and humans. Notably, the relative brain size of humans is significantly larger than that of any other primate, including chimps (Striedter, 2005). Further, human intellectual capabilities surpass those of chimps, as does the complexity of human communication and cultural practice. In addition, chimps and humans differ substantially in overall body anatomy.

What does genetics say about similarities and differences between humans and chimps? At the chromosome level, humans and chimps are very similar. How can we tell? After being treated by various stains, chromosomes in a karyotype acquire a banding pattern that is somewhat similar to the barcodes one uses at the supermarket to identify products. The banding patterns of human and chimp chromosomes highlight their chromosomal similarities and differences. With one exception, chimp and human chromosomes can be paired up such that each human chromosome has a corresponding chimp chromosome. The exception to this is human chromosome number 2. Human cells have 23 pairs of chromosomes in the nucleus (numbered 1–22 and including the sex chromosomes, X and/or Y). Chimps have 24 pairs of chromosomes. Based on the chromosomal banding patterns and from the fact that other nonhuman primates share the chimp chromosome pattern, biologists hypothesize that two of the chromosomes in the human–chimp common ancestor population ultimately fused into one chromosome somewhere along the human lineage. DNA evidence has confirmed the fusion hypothesis. In fact, biologists know the exact position on the chromosome – down to the nucleotide! – where the fusion occurred (Hillier et al., 2005). Humans and chimps also share similarities in the sequence of nucleotides in their DNA. Comparing base changes at single nucleotide sites, humans and chimps differ by 1.2%. The DNA sequences of humans and chimps also differ in small insertions and deletions; these differences bring the total difference between human and chimp DNA molecules to about 3–4% (see Johnson, 2007, and references within). Still, even the 1.2% difference works out to about 40 million single nucleotide differences between humans and chimps (Johnson, 2007; Taylor, 2009).

Question: Have humans evolved more than chimps?

Answer: It depends on what trait or gene you are considering. For brain-related traits and genes, human DNA has generally shown more evolutionary change than chimp DNA.

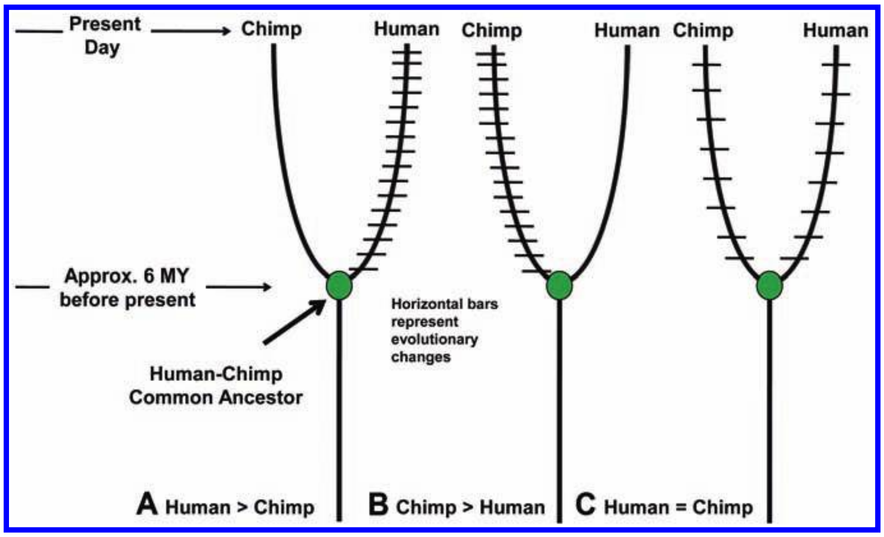

Figure 2. Three hypotheses for relative degrees of evolutionary change in the human and chimp lineages since their divergence from a common ancestor. Phylogenetic trees depicting three distinct possibilities for phenotypic evolution subsequent to the divergence of humans and chimps from their most recent common ancestor (MRCA). (A) Humans have experienced a higher evolutionary rate than chimps since the time of their divergence from the MRCA. The chimp is thus more similar than humans to their MRCA. (B) Chimps have experienced a higher evolutionary rate than humans since the time of their divergence from the MRCA. The chimp is thus more similar than humans to their MRCA. (C) Equal evolutionary rates across both lineages – both humans and chimps differ from their MRCA by an equivalent amount, which may be large or small.

Let's consider three possibilities regarding relative evolutionary rates between the human and chimp lineages since they diverged from their common ancestor (Figure 2). Scenario I: More evolutionary change has occurred within the human lineage since the split. Scenario II: More evolutionary change has occurred within the chimp lineage since the split. Scenario III: Since the split of the lineages, the amount of evolutionary change has been roughly equal in each of the lineages. Scenarios I and II represent two ends of a continuum, and Scenario III represents a midpoint.

The common ancestor of humans and chimps likely had a brain that was very much like the brains of living chimps in both size and function. (Modern human brains are about four times the size of modern chimp brains.) Thus, brain structure and function would present evidence of evolution occurring under Scenario I. That is, more change in the physical features of the brain has occurred within the human lineage (see box).

If we assume that DNA sequence differences accumulate as a function of time, then, because human and chimp lineages have been diverging for the same amount of evolutionary time, we would expect that the same amount of evolutionary change has occurred in each lineage (Scenario III). Such a pattern has been seen in some DNA sequences. For example, Chen and Li (2001) found that parts of DNA in-between genes evolved at similar rates in humans and in chimps.

There is a third possibility: more evolution along the chimp lineage (Scenario II). Biologists are now increasingly able to detect the signature of adaptive evolution acting on particular genes (Johnson, 2007). This information can be used to address whether adaptive evolution has been more prevalent in certain lineages, such as the human one, as compared with others. Considering just the 14,000 genes that encode proteins, 233 of these genes show the signature of having undergone adaptive evolution in the lineage leading from the human–chimp common ancestor to chimps. By contrast, only 154 underwent adaptive evolution in the lineage leading from the human–chimp common ancestor to humans (Bakewell et al., 2007). On the basis of this information, we come to the potentially counterintuitive conclusion that more adaptive evolution has occurred within the chimp lineage than in the human lineage. Two of the possible reasons for this pattern are that more generations have occurred within the chimp than in the human lineage, and that selection is more efficient in the chimp lineage because chimps historically had larger population sizes than humans (Chen & Li, 2001). See Futuyma (2009) for an explanation regarding why natural selection is more efficient in larger populations.

Many of the adaptive evolutionary changes that have occurred since humans and chimps split have nothing to do with the brain, but instead involve changes in the immune system, reproductive functions, and other biological processes. In those cases (above), faster evolution occurred in the chimp lineage. When we look at the changes that have occurred for genes that have major roles in the brain, a different picture emerges. During the past decade, biologists have discovered several genes that (1) are involved in brain formation and/or language and (2) show molecular signatures that they underwent selection-driven evolution in the human lineage (reviewed in Johnson, 2007).

One of these genes is FOXP2. Humans who carry mutations in FOXP2 have difficulty in speech, especially in articulating complex words. These people also have other difficulties in coordinating movements and show clear differences in various brain scans when compared with the general population (reviewed in Johnson, 2007; Taylor, 2009). FOXP2 shows a highly unusual pattern; of the three genetic differences that alter the amino acids in its protein, two differences have evolved since the human and chimp lineages diverged. Such a pattern is highly statistically unlikely to occur by chance. These and other data strongly suggest that natural selection has operated on this gene that affects language and brain activity since the lineages diverged, and possibly within the past 100,000 years (Johnson, 2007; Taylor, 2009). Two other genes, ASPM and Microcephalin, which influence brain size, also show a clear pattern that they have evolved via natural selection within the human lineage (Johnson, 2007; Taylor, 2009). No genes such as these that affect brains have been found to show adaptive evolution occurring on the chimp lineage since it split from the human lineage.

Of course, genetic changes that alter the structure of proteins are not the only type of genetic changes that occur. Also of importance are regulatory mutations, which lead to changes in when, where, and how much protein is put into a particular cell. Regulatory mutations alter gene expression, not gene structure. In 1975, King and Wilson predicted that regulatory changes could have a

Why did brain size increase within the human lineage?

Perhaps the most remarkable difference between humans and our ape relatives is our brain. On average, the human brain is ~1500 cm^3 (1.5 L), whereas those of chimps and gorillas are ~400 cm^3. In addition to being larger than those of the nonhuman primates, our brains are organized differently. Notably, human brains have disproportionately more space devoted to the neocortex, the location where most higher-level cognitive functions occur (Striedter, 2005). The fossil record also shows brain size evolving in several steps: the brains of *Australopithecus* species are smaller than brains in the earliest species of the genus *Homo*, and the most ancient species of *Homo* had brains that were considerably smaller than more recent fossil species in the genus (Dunsworth, 2010).

What explains this large change in brain size and stucture? Hypotheses abound in the literature, with no definitive answer. However, there are a number of plausible explanations.

First, we must distinguish between (1) the processes that led to brain size increases as a result of relaxed selection against larger brains and (2) those that actively favored increases in brain size. Relaxed selection, the elimination or substantial weakening of a source of natural selection, can be an important factor leading to change in natural populations (Lahti et al., 2009). For instance, suppose zebras are under threat from predation by lions. If, for some reason, lions disappeared, then that source of selection would be relaxed. The relaxation of this selective pressure might influence the evolution of zebras along a different trajectory than that constrained by lion predation.

Similarly, relaxed selection may have permitted evolutionary change in the human lineage. Dietary changes are often presented as explanations for the increase in brain size. A notable example is an increase in meat eating. Our ancestors started eating considerable quantities of meat about 2.5 million years ago. Some have hypothesized that meat eating was associated with a noticeable increase in brain size (Aiello & Wheeler, 1995; Babbitt et al., 2011), but the jury is still out. Meat not only provides animal protein, but also creatine, an important molecule for long-term energy storage in the brain (Babbitt et al., 2011; Pfefferle et al., 2011). The switch to meat and other changes probably made it easier for our ancestors to evolve larger brains because such changes relaxed selective constraints on energetic requirements. By contrast, the lack of extensive meat eating by the ancestors of chimps may be one reason why they did not evolve larger brains.

Relaxed selection, however, cannot be the whole story behind brain evolution. There must have been some factor or factors that made increased brain size advantageous for survival and/or reproduction. Scientists must hypothesize that such an advantage occurred because brains are costly. First, they are energetically expensive; our brains account for one-fifth of our metabolic needs, even though they are only about 2% of our weight (Dunbar, 1998). Our large brains also make birthing difficult; indeed, the human gestation period is reduced and brain growth continues throughout infancy, owing to constraints by the mother's pelvic morphology. Such large costs require that larger brains provided some large advantage or increase in reproductive success.

One popular explanation is that some feature of the social environment of our ancestors provided a selective advantage to individuals with larger brains. Strong support for this explanation is that social group size of different primates is tightly correlated with brain size (Dunbar, 1998). Perhaps larger brains evolved because individuals with refined cognitive skills were better able to keep track of information in the group and to use that information to their advantage (Dunbar, 1998). Another possibility is sexual selection: perhaps males and females preferred mates that were more skilled. Geoffrey Miller (2000) proposed that such sexual selection may be responsible for such traits as language, music, and the arts.

much more profound effect on the organism than changes in the building-block proteins themselves. In the past few years, biologists have confirmed this prediction: regulatory mutations can (and do) have major effects.

What is known about regulatory mutations within the human and chimp lineages? In one of the first studies to examine relative rates of gene expression in humans, chimps, and macaques (a monkey), Enard et al. (2002) observed equivalent levels of gene expression in the blood and liver of these three primates but noted a marked increase in gene expression in the human neocortex. Since the publication of Enard's study, more studies on differences in gene regulation between humans and chimps have been done. For example, Cáceres et al. (2003) and Preuss et al. (2004) found higher levels of gene expression in human brains than in the brains of nonhuman primates. Further work by Haygood et al. (2007) began to characterize differences in the actual promoter regions of genes involved in nutrition and neural pathways.

More recently, Greg Wray and his colleagues at Duke University have been comparing how glucose is allocated differentially to the brains and muscles of different primates (as measured by the numbers and activities of a set of glucose transporter proteins; see Zimmer, 2011), presumably in response to diet type. Wray's group found that the relative numbers of glucose transporters for the brain has gone up in the human lineage, whereas the number of glucose transporters for body muscles has decreased. This is in direct contrast to observations made in chimps in which the muscle transporters are abundant and the brain transporters are comparatively fewer in number. This study, combined with other work recently published by the Wray lab on the phosphocreatine cycle (Pfefferle et al., 2011), supports the idea that metabolic adaptations evolved in humans in response to dietary shifts and subsequently allowed "bigger brains" to form.

In summary, although it appears that overall evolutionary rates in the human and chimp lineages have been roughly equivalent since the time of the human–chimp split, certain types of evolutionary changes have occurred predominantly in the human lineage. These changes have frequently occurred at the level of gene regulation and appear to have occurred in biological features that involve the human brain.

Question: What can we infer about the common ancestor of humans and chimps?
Answer: For most physical traits, especially brain size, the common ancestor looked more like a chimp than a human.

Consider all of the members of the superfamily Hominoidea (hominoids) – the group that includes all the apes that are living today and all of the tailless primates that have lived in the past. Among the homonoids, humans and our recent fossil ancestors are the most flat-faced (orthognathic), large-brained, and small-toothed. Modern chimps are much more like fossil apes, gorillas, orangutans, and gibbons than are humans. Parsimony (the task of finding the simplest explanation that fits the data) tells us that modern humans have uniquely derived traits not shared with any other hominoids – and these traits set us apart from chimps. Given the similarities between modern chimps and other fossil and nonhuman apes, scientists hypothesize that modern chimps are much more similar to the human–chimp common ancestor than are modern humans. Also supporting this hypothesis is the fossil record within the human lineage; the oldest fossils that present evidence of bipedal behavior belong to individuals with relatively prognathic faces (Jaws projecting forward), larger canines, and smaller brains. So the earliest bipeds (hominins) looked significantly more like fossil apes than modern humans do.

From the above, we can draw these conclusions: (1) the distinct evolutionary lineages leading to modern humans and modern chimps evolved, initially, from an ape population characterized by prognathic faces, relatively small brains compared with body size, and relatively large canines; (2) the earliest members of the chimp and human lineages were extremely similar to each other, but distinct enough to be considered separate species; (3) the descendants of the earliest chimps remained similar in form and function to the ancestral form, such that modern chimps are relatively similar to fossil apes and other nonhuman living apes; and (4) evolution within the human lineage is characterized by more change than that of the chimp lineage, such that modern humans can be distinguished from all other living and extinct hominoids in many ways.

Paleoanthropologists can develop hypotheses about other aspects of the ancestral populations from which humans and chimps descended, such as locomotor and social behaviors and habitats. For instance, recent studies using carbon isotopes of ancestral environments (Cerling et al., 2011) enable scientists to make inferences about the proportions of woody versus open habitat at various times during the history of our lineage. Future discoveries of fossils from the late Miocene (Just before and during the time when chimps and humans diverged) will provide evidence to test these hypotheses.

Question: What does the chimp fossil record tell us about chimp evolution?
Answer: Not much, as there are very few known fossil chimps. The reasons for this dearth of fossils are many and varied.

One of the reasons scientists face difficulty making inferences about the nature of the common ancestor of chimps and humans is that in contrast to the rich record of fossils within the human lineage, the first discovery of a chimp fossil was reported only 7 years ago (McBrearty & Jablonski, 2005). This fossil occurrence consists of three teeth, all probably from the same individual (two incisors and a molar); the wear on all three teeth indicates that this fossil chimp was about 7 years old when it died. The incisors are nearly identical to living chimp teeth except for having shorter tooth roots. The scientists who identified and described these fossil teeth are reluctant to assign these teeth to either *Pan troglodytes* (the common chimpanzee) or *P. paniscus* (the bonobo) but suggest that they have more similarities to the former – or that they may be a new species of chimp altogether. Unfortunately, these teeth provide little information about fossil chimp body size, ecology, or behavior. The only other possible chimp fossil that has been published is a fragmentary right proximal femur (top part of the leg upper bone) from southwestern Uganda, originally collected in 1961 and assigned to *Homo sapiens* (DeSilva et al., 2006). Recent reanalysis of this fossil suggests that it may be a chimp fossil. This fossil, however, is large for a chimp. Moreover, much of the anatomy that distinguishes living humans from chimps is not preserved in this fossil.

Why is the chimp fossil record so sparse? As McBrearty and Jablonski (2005) noted, living chimps prefer wooded environments. Because there is a relationship between bone preservation and soil pH, forests are less likely to provide good bone preservation and fossilization environments (e.g., Gordon & Buikstra, 1981). Cote (2004) suggested that preservation bias, small fossil samples, and a lack of fossils samples from western and central Africa and in paleohabitats like tropical forests where early chimps probably lived may be at least partly to blame for the scarce record of chimp fossils. Another possibility is that chimp fossils were misidentified as hominins (the fossil femur from Uganda is a possible case). Perhaps more chimp fossils are already in museum collections waiting for rediscovery.

Question: What can we infer about chimp evolution by looking at living chimp species?
Answer: Differences between the two living chimp species (the common chimpanzee and the bonobo) show that chimps have evolved substantially since they diverged from humans.

Despite the meager chimp fossil record, we can infer that significant evolutionary change has occurred within the chimp lineage after the human–chimp split. Among the evidence that supports such chimp evolution is the existence of two species of chimps, the common chimpanzee and the bonobo. These species differ in morphology and behavior but are much more closely genetically related to each other than either is to humans (deWaal, 2005; Johnson, 2007). Any differences that have accumulated between these chimp species must have evolved within the chimp lineage after the split from the human lineage.

The lineages leading to common chimpanzees and bonobos split ~2 million years ago (de Waal, 2005), approximately one-third of the time since the human and chimp lineages split. These two species show striking morphological differences, including those of head size and shape, body proportions and coloring, female breast differences (bonobos are more like humans in this regard, compared with the flat-chested chimpanzees), and gait (de Waal, 2005). De Waal (2005:7) uses an analogy to describe this level of difference: "A bonobo is physically as different from a chimpanzee as a Concorde is from a Boeing 747…."

Even more dramatic are the behavioral differences – common chimps will display violent behavior more often than bonobos, and bonobos are more sexually active than common chimps (de Waal, 1995, 2005). An experiment illustrates these differences: Parish (1994) presented a simulated termite mound (with food) to groups of both common chimpanzees and bonobos. In the groups of the common chimpanzees, one dominant male monopolized the resources. By contrast, the female bonobos controlled access to the food and negotiated distribution of the resources by the use of sexual encounters.

Was the common ancestor of the two chimp species more like the common chimpanzee or more like the bonobo (or perhaps in-between)? We don't know – but we know that significant evolution has occurred since the split of these two chimp species, because the two chimp species differ in obvious ways from each other.

○ Conclusions

If humans evolved from chimps, why are there still chimps? The two major misconceptions this question reflects are that evolution is (1) always linear and (2) innately progressive. The common depiction of evolution as a linear progression throughout which ape-like creatures become more like modern humans is a gross simplification (see Gould, 1989, for further discussion of the iconography). Along these lines, we encourage educators to find images of human and ape family trees in which the human–chimp common ancestor is depicted as an illustration, rather than those that use photographs of chimps to represent this common ancestor – reinforcing the very misconception we are trying to avoid. As we discussed, much of evolution results in a pattern known as cladogenesis; this involves processes that have given rise to the tree-like pattern of the diversity of life. Moreover, evolution does not necessarily equate to progress, as change is not always progressive (Ruse, 1996). It is incorrect to speak of living organisms as more (or less) evolved than other living organisms. Chimps are just as evolved as humans. The lineages leading to chimps and humans split from one another some 6 million years ago; since then, each has taken its own path.

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