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The Evolution of Human Origins

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The Evolution of Human Origins

ABSTRACT Because humans are the product of our evolutionary past, learning how we evolved is fundamental to all anthropological investigations. We now realize that reconstructing why unique human attributes evolved requires an understanding of our starting point, but this is a relatively recent perspective. One hundred years ago, the question of human origins was identical to that of hominin origins. Accepting *Australopithecus* into human ancestry, coupled with the modern synthesis of evolution, led anthropologists to consider humans as products of natural selection. They realized that increased intelligence did not initially distinguish our lineage, and that early hominins were apelike in many ways. *Australopithecus* brought bipedality, and brain expansion came with *Homo*. Because the human mind and behavior are products of evolution, we must reconstruct the selective pressures that shaped our lineage in order to understand ourselves today. Paleoanthropology, as with all anthropology, is becoming ever more question oriented, drawing on many areas of inquiry. [Keywords: human origins, human evolution, history, data, theory]

HUMAN ORIGINS RESEARCH CREATES a temporal foundation for anthropology. Why and how our lineage began determined what was to follow in the course of human evolution. Early adaptations set the stage for later changes and opened up new evolutionary avenues that subsequent hominins were able to follow.¹ Our ability to understand and predict why modern humans look and behave the way we do today depends on our knowledge of the evolutionary pressures that shaped our developing lineage. To fully appreciate why and how humans evolved, it is critical to learn more about our earliest ancestors. Human behavior, the domain of sociocultural anthropology, is a product of our evolved mind and evolutionary past. Had we evolved different neural capacities to respond to different selective pressures during our evolutionary history, we would have very different behavioral tendencies and abilities today.

Understanding why we think, feel, and behave the way we do depends on an understanding of why we evolved the way we did. This knowledge arms us with the knowledge and ability to develop and apply useful social intervention worldwide and to cope with modern social issues. Uncovering more hard evidence of our evolutionary past helps us to emphasize the common thread that unites humanity and the shared past that shaped all of us.

Our current conceptions about the sequence of changes that shaped human evolution are relatively recent (Bowler 1986; Goodenough 2002; Krogman 1976; Reader 1988; Shipman 2001; Spencer 1979, 1997), although many specific hypotheses are rooted in early-20th-century ideas. In

the early 1900s, we did not understand the sequence of acquisitions of unique human attributes. The most common idea was that big brains were what initially set us apart from apes. Assuming that our large brains paved the way for our many other unique attributes requires a very different reconstruction of why we are the way we are than does the pattern of events we now see in the human fossil record. We now have a clearer understanding of the timing of acquisition of human characteristics, allowing us to more accurately reconstruct why we are the way we are today.

With the discovery of the Taung *Australopithecus africanus* child in 1924 (Dart 1925), the modern consensus on our place in primate evolution as well as our history began to take hold. Taung confirmed hints from *Pithecanthropus* (Dubois 1894) that brain expansion was not what initially set us apart from apes, a pattern substantiated by numerous subsequent discoveries. We now realize that the selective pressures that produced the first hominins differed from those that produced our genus, *Homo*, and from those that produced our species, *Homo sapiens* (see also Goodenough 2002).

Not only has our knowledge of the available facts about human evolution changed over the past 100 years but so too has the approach physical anthropologists have taken to answer the questions of human evolution. Facts do not speak for themselves. Without interpretive frameworks and methodologies to systematically ask and answer questions about the available facts, we can make no progress toward accurately interpreting them. The modern synthesis of evolution was incorporated into physical

anthropology by about 1950, led by Sherwood L. Washburn and others. This began the modern trend of approaching the interpretation of hominin fossils from a truly Darwinian perspective (Bowler 1986). Without this theoretical shift, the significance of the Taung specimen and other early hominin fossils may never have been fully appreciated.

Since that time, remarkable developments in molecular biology, primatology, behavioral ecology, and developmental biology have provided critical new ways to develop and test hypotheses about what the fossil record means. We now have a much more complex and biologically accurate picture of several diverse hominin radiations and realize that many of the distinctively human traits appeared at different times undoubtedly for different reasons.

100 YEARS AGO: EARLY IDEAS AND THEIR LEGACIES

In 1903, the question about the origin of our species, *Homo sapiens*, was the same as the question of the origin of the hominin radiation. At this time, we had no idea of how humans fit into the primate order, what steps in the transitions hominins underwent from an unknown ancestral form to become human, how our ancestors were similar to or different from us, or what the time frame was for this process. Only a handful of hominoid fossils were known, namely *Dryopithecus* (Lartet 1856), *Sivapithecus* (Lydekker 1886), *Pithecanthropus* (Dubois 1894), and several Neandertal specimens. There was no scientific consensus on what these specimens revealed about human evolution, or how these taxa were related to modern humans. Still, some of the early ideas about their meaning have had lasting legacies on developments throughout the century. Many issues currently being raised in the literature had their origins in the early parts of the last century: a Eurasian origin of hominins (Begun et al. 1997; Mathews 1914; Stewart and Disotell 1998), the position of the lunate brain sulcus on the Taung endocast (Dart 1925; Falk 1980, 1983, 1991; Holloway 1981, 1985, 1991; Keith 1931), the recognition of the prevalence of parallelisms and convergences (termed "homoplasy") in hominoid evolution (Begun et al. 1997; Larson 1988; Le Gros Clark 1936), and how similar the last common ancestor of chimps and humans may have been to any modern genus (Begun 1994; Darwin 1871; Haeckel 1883; Huxley 1863; Keith 1929a, 1931; Lamarck 1809; Latimer et al. 1981; Mivart 1873; Munro 1897; Osborn 1927; Sarmiento 1994; Wallace 1889; Weinert 1932; Wrangham 1999; Zihlman 1978).

By the early 1900s, many researchers had recognized the link between apes and humans (e.g., Darwin 1871; Haeckel 1883, 1907; Hooton 1931; Huxley 1863, Lamarck 1809; Nuttall 1904; Schwalbe 1904). There was little consensus on whether we passed through a great apelike stage (Gregory 1927a, 1927b, 1930, 1934; Huxley 1863), or if our ancestor was more primitive in some fashion even than modern apes (e.g., Hill-Tout 1921; Klaatsch 1902; Mivart 1873; Munro 1897; Osborn 1927; Wallace 1889; Weinert

1932; Wood Jones 1929). Today both views have been validated. We recognize that *Australopithecus* species differ from both extant apes and humans in significant ways, and that the last common ancestor of apes and hominins was a great ape but not necessarily like any particular modern species. The variation among fossil and living taxa reminds us that our ancestors were part of a radiation of taxa, and that, often, species share traits in parallel rather than because of common descent. The fossils also remind us that modern great apes have evolved throughout the Plio-Pleistocene as well. The discovery of the earliest putative hominins yet found—the 5.8 to 4.4-million-year-old *Ardipithecus ramidus* (Haile-Selassie 2001; White et al. 1994, 1995) and six-million-year-old *Orrorin tugenensis* (Senut et al. 2001) and *Sahelanthropus* (Brunet et al. 2002) fossils—reiterate this point, as they do not look exactly like African apes either although they are close in time to the last common ancestor.

In the early part of the 20th century, ideas on the pattern of hominin evolution and the order in which we acquired our distinctive human characteristics also varied. Eugene Dubois's (1894) *Pithecanthropus* fossil displayed a relatively small cranial capacity with a fully modern femur (Shipman 2001). This specimen was the first real indication that encephalization was not the initial adaptation of the human lineage, as Chevalier de Lamarck (1809), Charles Darwin (1871), Robert Munro (1897), and others had proposed. The fact that the *Pithecanthropus* skullcap and femur were not associated was unknown then, however (Shipman 2001). That bipedality was the fundamental adaptive shift of the hominins is now well documented, but at that time it was a relatively unpopular opinion (but see Gregory 1916, 1934; Miller 1920; Morton 1926; Schwalbe 1904; Shipman 2001; Weinert 1932).

The viewpoint of these researchers, that humans passed through *Pithecanthropus* and Neandertal stages, implied a linear pattern of evolution with no branching. The single-species hypothesis enjoyed considerable popularity in academic circles for much of the 20th century. The reason for this was partly because of the idea that humans are somehow different from other lineages of mammals, and views on human evolution were not necessarily even Darwinian in nature. More recently, the enduring appeal of the single-species hypothesis was based more on the concept of Occam's razor, that the simplest explanation for relationships among fossil hominins is in a linear progression until it could be demonstrated otherwise. Beginning with the discovery of *Zinjanthropus* in the 1950s, and more *Australopithecus* and early *Homo* fossils by the 1970s, mounting fossil evidence has demonstrated otherwise and has refuted the single-species hypothesis. It is no longer possible for even the most extreme lumpers to fit all hominin fossils into a single evolving lineage.

In the early 1900s, however, most scholars regarded *Pithecanthropus* and Neandertals as not ancestral to modern humans (Boule 1921; Elliot Smith 1931; Keith 1929a, 1931; Le Gros Clark 1934; Smith Woodward 1935; Vallois

1954), a concept essentially the same as the one later termed the pre-*sapiens* idea by Vallois (1954). The bulk of support for this idea was not necessarily based on science but, rather, came from orthogenists, who considered encephalization to have been the initial adaptation of humans (e.g., Osborn 1927; Elliot Smith 1931; Le Gros Clark 1934). The Piltdown *Eoanthropus dawsoni* discovery (Dawson and Smith Woodward 1913) temporarily bolstered this position by appearing to provide a fully encephalized individual with a modern human braincase shape with a primitive dentition. *Pithecanthropus* then must be relegated to a side branch of the human family tree. This pre-*sapiens* hypothesis was the initial recognition that the human family tree is bushy, not linear, as Watson (1928) argued it should be based on comparisons most mammalian taxa. A bushy family tree was also suggested by early interpretations of human racial variation, often used to also suggest that multiple species of hominins existed even today (reviews in Shipman 1994; Wolpoff and Caspari 1997). The pre-*sapiens* idea was significant because it recognized that hominin ancestors may not have been like any living species, paving the way for incorporation of all later fossil discoveries into the hominin family tree, none of which are a perfect blend of ape and human features.

THE TAUNG DISCOVERY

Dart's discovery of the Taung child in 1924 (Dart 1925) was arguably the most important fossil find of the past century. There were three really significant things about Taung that partly served to delay its acceptance as a human ancestor. In addition, these things helped form later ideas about not only what our ancestors looked like but also where they first appeared and what environment they inhabited.

First, and the most obvious, was the fact that Taung had an apelike brain size with upright posture and a humanlike dentition, the opposite signal from the widely accepted large-brained Piltdown specimen that had fit the orthogenists' ideas so neatly. Instead, Taung supported Dubois's contention that *Pithecanthropus* reflected the order or acquisition of human characters. Taung, in a sense, verified *Pithecanthropus*, which then began to become widely accepted as a human ancestor. Taung's surprising suite of characters was not a major problem for most proponents of the pre-*sapiens* idea, however, because according to most scholars, the known hominin fossils already occupied evolutionary side branches, and so Taung could, too.

A more significant problem of Taung than its morphology was its geographical location. Most researchers were convinced that our ancestry stemmed from Asia, not Africa, as was argued by scholars such as Haeckel and Dubois. (Black 1925; Gregory 1922; Mathews 1914; Osborn 1927; Smith Woodward 1935). Darwin had argued for an African origin, but this was not the predominant opinion at the time. William D. Mathews's work on mammalian origins

led Henry Fairfield Osborn, and many others, to be convinced that all modern mammalian radiations, including humans, must have stemmed from Asia based on patterns of similarity among American, European, and African faunas. Florentino Ameghino (1908) argued for human origins in the New World, but Aleš Hrdlička quickly falsified Ameghino's ideas by applying careful, comparative craniometric analysis to Ameghino's alleged human ancestor skulls from Argentina (Spencer 1979). This New World idea was bolstered temporarily by the *Hesperopithecus* tooth found in Nebraska (Osborn 1922) until it was shown to be that of a peccary. Hermann Klaatsch (1902) had even argued for an Australian origin, although this idea never received much support. More credibly, Davidson Black's discovery of *Sinanthropus* (now referred to "*Homo erectus*") fossils from Choukoutien in the mid-twenties seemed to support the Asian origin hypothesis, as did *Pithecanthropus*.

One real benefit of the Asian origins hypothesis was that it led Osborn to help Roy Chapman Andrews conduct the Central Asiatic Expeditions (Gallenkamp 2001). These were the first large interdisciplinary paleontological expeditions, not unlike modern ones, equipped with paleontologists, photographers, natural historians, geologists, and faunal and paleoecological experts, among others. The expeditions produced no hominins, of course, but were wildly successful in producing dinosaurs and early mammals. They formed an early model of paleontological fieldwork that resembles the teams assembled today.

The fact that Taung was found in Africa, therefore, did not fit the prevailing view. Most researchers who doubted the validity of Taung as a human ancestor at the time were not convinced until further *Australopithecus* discoveries were made. Even Robert Broom's announcement of the Sterkfontein *Australopithecus* fossils in 1936 and the subsequent Congress on Early Man in Philadelphia in 1937 was not enough to convince many scholars, especially as Piltdown had not been factually refuted at this point. It was only when Broom and G. W. H. Schepers's detailed monograph appeared (1946), and the Piltdown fossil was widely discredited (Weiner et al. 1953), that many researchers finally accepted *Australopithecus* as a probable human ancestor and accepted the pattern of human evolution that it implied (Bowler 1986). Still, the idea of encephalization defining the human lineage did not go away, for after finally accepting *Australopithecus* as a hominin, Sir Arthur Keith (1948) immediately proposed the cerebral Rubicon (that there was a fundamental threshold increase in intelligence defining humans and our recent ancestors from apes and earlier hominins) to salvage encephalization as a defining human character.

The third aspect of Taung that was noteworthy was its association with a savanna fauna, with no evidence of the forested environment that most scholars had predicted. The savannah association of Taung, when *Australopithecus* was finally accepted as a human ancestor, led to the long-standing hypothesis that earliest hominins evolved in or along with an expanding savannah environment. Most

hypotheses to explain why the earliest documented adaptive shifts of the hominin lineage, namely bipedality and the hominin craniodental complex, have revolved around a savannah setting. With the discovery of mixed paleoenvironments for *A. anamensis* and *A. afarensis*, and the wooded settings of *Sahelanthropus*, *Ardipithecus*, and *Orrorin*, we are now back to a forest-origin interpretation today, but the savanna hypothesis was influential for many years.

The discovery of Taung's savannah setting immediately began to provoke some of the earliest adaptive explanations for hominin diversification. Most early interpretations of human evolution had not focused on adaptive explanations for events in human evolution (but see Darwin 1871; Keith 1923, 1929b, 1931; and discussions in Bowler 1986; Reader 1988; and Shipman 2001). Right away, Sollas hypothesized that early hominins evolved as hunters on the plains (Bowler 1986). Gerritt S. Miller Jr. (1928) suggested that hominins were part of a local adaptive radiation, driven to become terrestrial by selection. Beginning with Taung, and picking up steam with the acceptance of *Australopithecus* and *Homo erectus* as parts of human evolutionary history in the 1930s, most researchers began to agree that bipedality and, perhaps, a dietary shift were initial adaptations that caused hominins to diverge from our ape forebears.

THE MODERN SYNTHESIS OF EVOLUTION

Equally important to the mounting fossil evidence was the theoretical revolution of the modern synthesis of evolution in biology. Dobzhansky, Thomas Henry Huxley, Mayr, and George Gaylord Simpson's syntheses of genetics and evolution in the late thirties and early forties stressed the importance of adaptation in shaping individuals and species and refocused the biological world on Darwinism. Using this new approach, seeing humans as the product of evolution by natural selection, changed paleoanthropology. *Australopithecines* had been an "anticipated stage in human evolution" (Washburn 1950:67). Once *australopithecines* were on our branch of the tree, the question of hominin origins became distinct from that of human origins, salvaging the idea of intelligence as the mark of humanity, so important for many. The set of questions we deal with today was born at this time.

Without the revitalization of Darwinism that accompanied the new synthesis, even the expanded set of *Australopithecus* fossils may not have had the impact they did on changing prevailing views of early human evolution. Even Louis Leakey's discoveries of *Zinjanthropus* and *Homo* at Olduvai Gorge might have been explained away without this theoretical shift.

Before this time, most approaches to interpreting human evolution relied on a more poorly defined tendency for progression within one or several lineages of higher primates. Some researchers thus far explicitly had considered that humans were the products of natural selection, but many had not, nor had they considered the selective

pressures that shaped the human form in depth. There were a few exceptions, but they were in the minority of approaches in the early 1900s.

BUILDING THE CURRENT PERSPECTIVE

Armed with the theoretical advances encompassed in the modern synthesis and mounting fossil evidence, the modern approach to the study of human origins began. Rather than a single ape-human transition, there are now several major adaptive shifts to explain (Goodenough 2002). The first of these shifts occurred at the beginning of the hominin clade. We do not know much about this transition yet, but new fossils like *Sahelanthropus*, *Orrorin*, or *Ardipithecus* that are close to the ape-human divergence time will undoubtedly reveal more information about it than ever before. Because each of these early genera share different sets of characteristics with later hominins, we cannot yet be certain which is ancestral to later hominins, or which are simply close relatives. Studies over the next few years, however, stand to reveal much about what set our specific lineage apart from all others.

By 4.2 million years ago, with the appearance of *Australopithecus*, early hominins were committed bipeds with reduced canines and anterior teeth, but thick-enameled cheek teeth, and massive body size sexual dimorphism (Ward et al. 2001). Bipedality and its corollary adaptations led early hominins like *Australopithecus* and *Kenyanthropus* (Leakey et al. 2001) to radiate. Bipedality also provided important preadaptations facilitating the appearance of the genus *Homo*. It may have been a factor in the earlier radiation that included *Sahelanthropus*, *Orrorin*, or *Ardipithecus*, and as these new fossils undergo further analysis, we will learn more about this. *Homo* ushered in the next adaptive phase, with its humanlike body plan, larger brain, systematic meat eating, decreased sexual dimorphism, stereotypic stone tool technologies, and, possibly, rudimentary language and life history changes. There appears to be yet another major behavioral transition accompanying the appearance of anatomically modern humans. Each of these transitions, and the many others in between, depends on the stage preceding it. Inferring that *Homo* evolved from a highly polygynous toolmaker and meat eater involves a different hypothesis about selective pressures than from a monogamous vegetarian, for example. As we refine our knowledge about each fossil hominin taxon, we will be able to refine our hypotheses about what pattern of selection produced the others, including ourselves.

Just as with the modern synthesis, fields outside of the traditional core anthropological subdisciplines, such as genetics and other branches of molecular biology, geology, primatology, and behavioral ecology, have provided many of our most important advances in the study of hominin origins.

Molecular Biology

After George H. F. Nuttall in 1904, Morris Goodman (1963) and, subsequently, Vincent M. Sarich and Allan C. Wilson (1967) and others, began a long series of molecular studies that have provided extremely important information on a number of fronts. Importantly, they have revealed that we are most closely related to chimps and bonobos, and that great apes do not belong to a single Pongid clade (but see discussion in Marks 2002). This discovery is the most significant ever made for enabling us to generate more accurate hypotheses about our ancestry. Knowing that *Pan* species are our closest living relatives allows us to compare chimps to hominins and to more accurately develop hypotheses as to what the last common ancestor might have been like.

Another critical contribution of molecular biology to the study of human origins has been the application of molecular clocks. Timing is essential to our interpretations of various fossils; a fossil cannot belong to a lineage it pre-dates. Molecular phylogenies and divergence times form important starting points for developing evolutionary hypotheses we use to interpret the fossil record and evolutionary trajectories in anthropology, and in all branches of biology. Molecular clocks have revealed that the chimp-human split occurred somewhere between ten and four, and more likely five to seven, million years ago, closely following the split of this common chimp-human ancestor from the gorilla clade. Thus, fossils like *Sahelanthropus* (six–seven m.y.a.), *Ororin* (six m.y.a.), or *Ardipithecus* (5.8–4.4 m.y.a.) are clearly close in time to the chimp-human split, and whatever their specific evolutionary relations turn out to be will be highly significant in informing us about the split.

Falsifying the hypothesis that all apes belong to a single clade alters the balance of parsimony for interpreting the evolutionary development of ape and human features. For example, when we thought that chimps and gorillas belonged to the same clade, we were uncertain whether the last common ancestor of African apes and humans was a knuckle walker. For them to have evolved, it independently would be less parsimonious than if the African ape-human ancestor were a knuckle walker. We also realize now, however, that evolution does not always take the most parsimonious course. Using the same taxa, for example, we know that a reduction in body mass sexual dimorphism has occurred twice, once in *Pan* and once in hominins, probably in early *Homo*, because all pre-*Homo* hominins have high levels of body mass dimorphism in which males were twice the weight of females, like gorillas and orangutans. Parsimony can be a powerful tool but is simply another way to generate hypotheses to be tested with functional, developmental, or other data.

Phylogeny and Cladistics

The rise of Emil Hans Willi Hennig's (1966) cladistic methodology in biology has been a mixed blessing but has

given us a renewed appreciation of phylogenetic systematics. It cannot identify ancestors and tends to influence interpretations of bushy clades over linear ones disproportionately but provides a framework for making systematic hypotheses based on molecular and morphological data. Our focus has shifted from examining overall similarities to looking for shared derived characters and changes from the putative primitive condition within a clade.

Because of extensive fieldwork during the past hundred years, we know that extant hominoids are only a relict sample of the diversity of apes that have existed. Without including data from the almost thirty genera of Miocene and Pliocene apes known, our ability to accurately reconstruct the character states of ancestral taxa is severely limited (Begun et al. 1997). The importance of parsimony in determining the phylogenies on which our evolutionary reconstructions depend means that we must continue to maximize the amount of data we consider and continue to assess the quality of those data. Fossils must be placed into phylogenetic context in order to interpret vectors of change within lineages and the pattern of selection that shaped these lineages. Several significant changes in our thinking have come from studies of Miocene apes. Early apes like *Proconsul* were quite different postcranially from extant great apes and had a more monkeylike build, including even limb lengths and long, flexible torsos (Ward 1993). Extant apes all share a suite of features to enhance their abilities for effective below-branch arboreality, including short, stiff torsos, long forelimbs, and short hindlimbs. These traits have always been assumed to be primitive for all extant great apes. The discovery that *Sivapithecus* may be more primitive in many ways from its sister taxon *Pongo* (Pilbeam et al. 1990) means that oranges and African apes may have evolved this suite of features in parallel. This suggests that it is possible that the common African ape and human ancestor may also have been more generalized than supposed. Thus, for the question of human origins and hominin ancestry, the many Miocene apes that have been discovered are of increasing significance. Incorporating these into our phylogenetic considerations may well alter the balance of parsimony in regard to many features of hominoid biology and behavior, altering our reconstructions of the ancestor from which earliest hominins evolved, and, thus, our hypotheses about the direction selection took to produce our lineage. This line of inquiry will be pivotal in years to come.

The hominin fossil record itself has grown exponentially. We have pushed back the fossil record to nearly when the last common ancestor should be found. Putative hominins *Ardipithecus ramidus* (Haile-Selassie 2001) is 5.8 million years old, and *Ororin tugenensis* (Senut et al. 2001) and *Sahelanthropus tchadensis* (Vignaud et al. 2002) are at least six million years old. These taxa have the possibility to revolutionize our understandings once again. They will help us define the vectors of morphological change (Simpson 1953) characterizing the origin and early evolution of our lineage, giving us a baseline from which to develop

and test hypotheses about why it occurred. Because they each share different suites of traits with later hominins, determining which is the ancestor and which are sister taxa will provide important information on the trajectory of earliest hominin evolution.

Coupling the molecular and morphological data on living and fossil apes will help us reconstruct the character states of the last common ancestor. This will provide a critical baseline for reconstructing vectors of morphological change (Simpson 1953) within the hominin clade, enables us to hypothesize about what selective pressures caused these changes and begin to answer *why* lineages evolved the way they did. Perhaps the most important case that highlights this issue is the interpretation of the primitive, apelike traits retained in the *Australopithecus* skeleton (reviewed in Ward 2002). These can be interpreted as evolutionary holdovers of no current adaptive value (summarized in Latimer 1991) or as traits retained by stabilizing selection for arboreal abilities (summarized in Susman and Stern 1991). In order to infer the adaptive value of these traits, we must consider the vector of selection evident in the *Australopithecus* lineage. The fact that the *Australopithecus* skeleton had undergone numerous modifications to enhance the effectiveness of bipedal progression at the expense of arboreal capabilities tells us that traveling bipedally was of much greater value in determining the reproductive success of the immediate ancestors of *Australopithecus*, and, likely, individual members of the *Australopithecus* species themselves.

Skeletal Biology

Recent developments in skeletal biology and ontogeny reveal that only traveling, not simply standing, bipedality results in tissue strains of sufficient magnitude to induce the characteristic hominin morphologies (reviewed in Carter and Beaupre 2001) and provide sufficient selective disadvantages to individuals not suited to withstand the mechanical demands of bipedal locomotion. Therefore, only models explaining why bipedality evolved that involve bipedal travel are viable, and not those that would invoke stationary bipedal postures alone.

The adaptive value of primitive, apelike traits—such as longer, more curved phalanges—in *Australopithecus* is more difficult to interpret than are derived ones and have been the subject of considerable debate over the locomotor behavior of *Australopithecus* (reviewed in Stern 2000; Ward 2002). Our understanding of bone biology may help inform us about the reason some of these traits are present in *Australopithecus*. We are beginning now to understand better the role of activity in shaping bones throughout development. We are learning to use this information to interpret the selective history of animals as revealed in more tightly genetically constrained aspects of bone and also to interpret activity patterns of individual animals based on aspects of the skeleton that reflect the loads borne during growth. For example, we know that the appearance of a

valgus angle of the femur depends on walking bipedally, and without walking humans never develop it (Duren 2001; Duren and Ward 1995). So, this angle in *Australopithecus* femora indicates that they did, indeed, walk bipedally. The presence of other features under tighter apparent genetic control, such as the lack of an abductable hallux or a short, flaring pelvis, indicates a long-term history of selection for bipedal locomotion. So, we know that not only was *Australopithecus* selected to be bipedal, they actually behaved bipedally as well. If a bony feature is influenced ontogenetically by climbing trees, its presence can be used to infer the behavior of that individual. We would then be able to use this trait to infer whether or not individual *Australopithecus* were regularly climbing trees. We will still not know whether this enhanced their reproductive success, but it will give us an idea of their behaviors. This will be an important avenue of inquiry in the future and is likely to provide significant insight into interpreting the behavior and adaptations of our ancestors in coming years.

Geology, Taphonomy, and Paleoecology

The development and eventual refinement of potassium-argon and argon-argon dating methods, coupled with detailed stratigraphic work in the Turkana basin and with faunal correlations at the South African cave sites, has provided us with an accurate and detailed temporal sequence of the earliest hominin fossils. Placing each fossil specimen in an accurate temporal position allows us to evaluate possible contemporaneity of individuals and to see diachronic changes within and among taxa. We now know that *Kenyanthropus* and *Australopithecus* were contemporaneous (Leakey et al. 2001), so if their morphology differs significantly, as it may, they must represent different branches of the tree. Similarly, we know that *Australopithecus garhi*, *A. robustus*, *A. aethiopicus*, and *Homo* and *Australopithecus habilis* and coexisted in time. Without good information on the timing of these taxa, we could never be certain about the existence of a bushy, or linear, family tree.

Hand in hand with geological developments has been the relatively new science of taphonomy, which has allowed us to reconstruct depositional environments and make more accurate inferences from them. Paleoenvironmental reconstructions have increasingly entered into the spotlight for understanding the context of human evolution. These have led to important hypotheses about the role of environments in shaping hominin species, and in patterns of speciation and extinction. We realize that the earliest hominins did not live in open savannah environments but in more mixed or wooded settings, and so the split from the apes did not occur as a direct consequence of a retreat of the forests (Brunet et al. 2002; Wolde Gabriel et al. 1994; Wynn 2000). We also know that a major environmental shift did occur in the late Miocene with the appearance of C4 grasses (Cerling et al. 1997; Morgan et al.

1994; Quade et al. 1989; Quade et al. 1992) affecting many mammalian lineages, and, perhaps, hominins as well (Leakey et al. 2001; Ward et al. 2001).

Primatology and Behavioral Ecology

Along with the important work on reconstructing the morphology of the last common ancestor has come a wealth of information from primatology and behavioral ecology. Features shared between chimpanzees, bonobos, and humans are likely to have been present in the last common ancestor of the three, such as some level of male philopatry; a certain level of intelligence and, perhaps, rudimentary tool use; highly complex interpersonal interactions; and at least some level of coalitionary behavior. For this reason, continued detailed studies of chimpanzee and, particularly, bonobo behavior are particularly important. Primatological studies can address behavioral questions on which the fossil record is silent and likely to remain so.

Behavioral ecology has given us morphological correlates of behavior, not only with diet and locomotion but also the relationship between social behavior and sexual dimorphisms. These are tools we rely on heavily to understand the fossil record. Primatological comparisons have led to some of the most influential theories about how hominins evolved, such as Clifford J. Jolly's seed-eating hypothesis (1970), C. Owen Lovejoy's origin of man (1981), all of the work on hunting and human evolution (e.g., Dart 1953; Hill 1982; Stanford 2000; Washburn and Lancaster 1968; Wrangham et al. 1999), and others. These disciplines have given us important hypotheses to test using the fossil record, and the opportunity to test hypotheses about the biological significance of anatomical characteristics.

By observing the morphology of the earliest fossil ancestors and applying behavioral ecological knowledge, we have begun to make reasonable inferences not only on the adaptive repertoires of each taxon but also about what features accompanied the onset of bipedality, at least in *Australopithecus* so far. The thick enamel of *A. anamensis* teeth (also seen in *Orrorin*) compared with the thin enamel of *Ar. ramidus* and African apes may suggest a shift in dietary emphasis toward eating harder or more abrasive foods, while retaining an ability to process softer fruits (Teaford and Ungar 2000). *Australopithecus* would have been able to process foods with a more variable set of material properties than can African apes, perhaps widening the dietary niches and microhabitats that they were capable of exploiting. The presence of high levels of body mass dimorphism is associated with polygynous social systems in all anthropoids (see Plavcan 2000) and would seem to contradict the hypothesis that these early hominins had a pair-bonded social system (Lovejoy 1981), even in light of reduced canine dimorphism (Plavcan 2000). Large body size appears to have retained an advantage for males while canine size did not, suggesting an altered emphasis on

strategies of male-male combat rather than an elimination of such competition. Thus, dietary and social behavior shifts do accompany bipedality, and the task remains to explain how.

Developmental Biology and Genetics

Developmental biology and developmental genetics are beginning to play a more central role in our interpretations of morphology. Since Hill-Tout's (1921), Smith Woodward's (1935), and others' attempts to use ontogenetic development to reconstruct phylogeny, morphologists have been intrigued by relationships between ontogeny and phylogeny. We have long realized that potential developmental links among structures could affect our functional and phylogenetic interpretations of these structures; we have been unable to test many hypotheses about any such relationships because of the general lack of understanding of the regulation of growth in primates, or almost any animals, on a sufficiently detailed level. Exciting new developments in the genetics of segmentation and limb and craniofacial development, for example, are beginning to yield results that could be applied to anthropological problems. Because of the explosion of knowledge becoming available, developmental biological applications to anthropological questions will increase markedly in the coming years.

Current Issues and Directions

Issues still plaguing our understanding of australopithecines today involve interpreting the temporal, geographic, and taxonomic variability of the australopithecine fossil sample and understanding the significance of morphological features we see in these fossils. Especially important is the interpretation of the many primitive, apelike characters of the australopithecine skeletons, because it is extremely difficult to discern whether these characters were maintained by stabilizing selection or were primitive holdovers of no current selective value. Discovering ever earlier hominins, reconstructing evolutionary history using data from Miocene apes, and employing new techniques for understanding genetic and epigenetic influences on morphology will be key to sorting out what this morphology tells us about the pattern of selection that produced and shaped our lineage.

STUDIES OF HUMAN ORIGINS AND THE AMERICAN ANTHROPOLOGIST

The revelations brought by the acceptance of *Australopithecus* into human evolutionary history and the modern synthesis not only affected studies of hominin origins, it affected the field of anthropology as a whole. Although understanding hominin origins is the first step toward understanding anthropology, it has not occupied a central position in the *American Anthropologist* (AA). In 1910, only two articles and two book reviews appeared in AA. In 1925, there were reviews of five books on human evolution, but

no articles appeared in the 1920s or 1930s. In the 1940s, there were only three articles dealing with the origin of races and Neandertals, but none on early hominins. Beginning in the 1950s, there were three articles directly discussing early hominin evolution: Washburn's seminal "*Australopithecines: The Hunters or the Hunted?*" (1957), Garn and Lewis's "Tooth-Size, Body-Size, and 'Giant' Fossil Man" (1958), and Raymond Dart's "The Minimal Bone-Breccia Content of Makapansgat and the Australopithecine Predatory Habitat" (1958). There were several on natural selection and humans. The 1960s provided the greatest number of papers on early hominin evolution. There were a dozen articles specifically on early hominin evolution, many of which were influential, several more on Neandertals and later human evolution, several on primate behavior including locomotion, a small handful on taxonomy, and even a special issue on the Paleolithic. This number declined thereafter, with only two early articles on the early hominin fossil record in the seventies, six in the eighties, and none in the nineties, although there were still book reviews and other brief comments occasionally, and a handful of articles on later human evolution or primate behavioral ecology that are relevant to early hominin research.

There are probably several reasons for this light coverage of human origins in AA, in addition to the interdisciplinary nature of anthropology. The popularity of Hrdlička's *American Journal of Physical Anthropology (AJPA)* drew most articles on human origins and, more recently, the *Journal of Human Evolution* and *Evolutionary Anthropology* have attracted these types of articles. Another factor was that, especially early in the past century, many prominent human origins researchers were anatomists by training and by trade, such as Dart, Broom, Dubois, Keith, and Henry Fairfield Osborn, and thus were unlikely to publish in anthropological journals. In addition, most scholars of human origins were European, largely because of geographic proximity to the fossils. There were notable exceptions like Osborn, Ameghino, Miller, MacCurdy, and Ernest Hooton, but these scholars were fewer in number than their primarily European counterparts elsewhere. A lack of ready access to relevant fossil materials or direct interaction with European colleagues contributed to a majority of Europeans being at the forefront of the field early on. Hrdlička may have been the first U.S. anthropologist to travel overseas to study the known hominin fossils, and it was on this trip that Dubois convinced him of the relevance of *Pithecanthropus* and Neandertals to human evolution, and the concept of change over time within human evolution. Le Gros Clark, a European, was the first non-African to travel to South Africa to see the *Australopithecus* fossils (Bowler 1986).

By the 1950s, there were many more physical anthropologists trained and working in this country. The 1950 Cold Spring Harbor Symposium brought the modern synthesis of biology to physical anthropology and began the current trend to view humans as evolved organisms shaped

by selection, led by Washburn, Brace, William Howells, and many others. In addition, according to Alan Walker, transatlantic travel became easier, enabling U.S. researchers easier access to original fossil material and interaction with European colleagues (personal communication, March 2002).

Simply having these other venues available or background of researcher is not the only reason for the lack of publications in AA. As it does today, AA has always stressed sociocultural anthropology more heavily than other subdisciplines. The apparent deep division between cultural and biological anthropology was set up during the first half of the century, before there was a recognition that humans are products of an evolutionary past. Prior to this, studies of human behavior did not consider the effects of the evolved mind on our behaviors, because there was no widespread recognition of this important aspect of our minds.

Even over the latter part of the 20th century, integrating human biology and the evolved mind into many cultural studies has been difficult. Although today there is broad recognition that human behavior is a product of our minds, and our minds are the product of natural selection, there is still much work to be done integrating these approaches. The field of cultural anthropology often seems divorced from our basic biology as humans, and with such a perspective human evolutionary studies may not seem important, especially studies of our deepest past. Yet to understand our cultural capacities and human abilities with any accuracy, we must consider the process of selection that shaped our lineage. At each step of the way we must understand the stage from which we were evolving and what types of selection were shaping our ancestors. Only this approach will reveal why we are what we are and can do what we do. On that note, modern humans provide a necessary venue to test hypotheses about our evolution.

During recent decades, anthropology has begun to change into more of a question-oriented rather than subfield-oriented discipline, however. Excellent examples of this are bioarcheology, ethnoarcheology, and human behavioral ecology. With the growing recognition that anthropological questions require many perspectives and approaches to be answered adequately, perhaps more integration of the traditional subfields is beginning to, and will continue to, occur in order to make progress in understanding ourselves as a species. Not only is our evolutionary history pivotal for understanding the mind and behavior, anthropology is also the study of humans, and humans are more than just our cultural behavior. Studying the biology and evolution of our lineage is equally central as studying culture to understanding humans as a species.

SUMMARY AND CONCLUSION

What we know today about human origins is entirely different from what we thought we knew 100 years ago. We realize that our earliest ancestors did not share many of

our most distinctive features such as intelligence, language, or complex culture. We know chimpanzees are our closest living relatives. Tool use and hunting no longer distinguish hominins from apes, nor does intraspecific cultural variability (or at least intraspecific variability in learned traditions). We know that the original hominins arose from a great apelike creature five to seven million years ago. It appears that the initial major adaptive shift of hominins, which may not even have occurred yet at this branching point, was a shift to habitual bipedality, a dietary change, and altered social behavior. We know that these changes preceded significant stone tool manufacture by almost two million years, and encephalization for at least 2.5 million years, and that encephalization and tool manufacture are not necessary correlates. We know that the hominin family tree is bushy, as with other lineages of mammals, and that hominins were a diverse group of species through much of our evolutionary history.

We also know much more about phylogenetic reconstruction, primate behavioral ecology, and links between anatomy and behavior and among different aspects of behavior such as diet, locomotion, and social structure that we can use to develop and test hypotheses about early hominin behavior. We are becoming more sophisticated in reading the signals given by bone morphology and recognizing influences of genetics, ontogeny, and behavior. Thus, we are now in a position to move to ever more detailed questions. Instead of simply counting features of *Australopithecus* as "apelike" or "humanlike," balancing them and proposing a locomotor repertoire in the middle, we can assess the polarity of these traits to reconstruct the vector of evolutionary change. This is possible now with our more extensive fossil record allowing us to more accurately hypothesize about hominoid phylogeny and to incorporate the growing diversity of Miocene apes into this phylogeny to even more accurately reconstruct the behavioral and anatomical traits of the last common ancestor.

The acceptance of *Australopithecus* as early hominins combined with the modern synthesis of biology set us up on the basic course of our investigations we follow today, studying hominins as products of evolution by natural selection. Before this realization became widespread in anthropology, many aspects of cultural and biological anthropology appeared to have little relevance to each other. Even though there is general awareness that the two are integrally related, this gap between cultural and biological anthropology established prior to this has been hard to bridge. Slowly, however, things are beginning to change as anthropology continues to reinvent itself as a question-oriented discipline and the traditional divisions between subfields become less clear.

The remarkable developments in biology and technology in recent years are opening up new avenues of research in which to test our ideas and refine our knowledge. The future of paleoanthropology, as with all branches of anthropology, will be ever more integrative. As the past 100 years has shown, anthropology benefits from ad-

vances in fact and theory in other disciplines, and we can maximize our understanding of humans through interdisciplinary work (Goodenough 2002). This is not to say that these insights are not inherently anthropological. In contrast, it is the insights into understanding human evolution that these discoveries have given us that make them fundamentally anthropological in nature. It is in the ability to integrate information and theoretical approaches from a variety of disciplines with those from our own, and in our reliance on a breadth of knowledge to understand humans that makes anthropology unique. When we do not read and consider the breadth of approaches to understanding humans, we lose the nature of our discipline and our ability to accurately understand ourselves. Our questions, not our methods, make us anthropologists.

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NOTES

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1. *Hominin* is used to refer to all taxa more closely related to humans than to *Pan*, and includes *Ardipithecus*, *Orrorin*, *Sahelanthropus*, *Kenyanthropus*, *Australopithecus*, *Paranthropus*, and *Homo*. This term is preferred to *hominid*, which technically should refer to the clade including *Pan* and hominins.

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