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The Hominid Status of *Sahelanthropus tchadensis* and *Orrorin tugenensis*

Introduction

Since the time when Charles Darwin first proposed that humans were descended from an ape-like ancestor, anthropologists have been searching for the oldest members of the human lineage. While this has often entailed the hunt for older and older fossil material, a large part of this search has also been concerned with defining exactly what falls into the human family tree. At the present, this has led to a plethora of terminology (hominid, hominin, hominine) that is often used interchangeably to describe the same material. For the purposes of this paper, a strict definition of the term 'hominid' will be used, which includes only those taxa that are directly part of the human lineage and excludes *Pan*. Within the strict definition, there are two distinct classes of evidence that are considered when calling something a hominid. These two types of data are morphological and genetic.

The morphological basis for terming a fossil a hominid essentially rests on its dentition and the skeletal evidence that would show that it was a biped. Dental evidence has long been used to try to determine evolutionary relationships both because of the prevalence of teeth in the fossil record and because of the marked differences between human dentition and that of chimpanzees, specifically in the human reduction of the canine and the loss of the C/P₃ honing complex. The number of fossil teeth known to anthropologists makes it an interesting cladistic exercise to look at the characters of the dentition of modern humans and try to work backwards to the morphology that characterized human ancestors at the point at which they split from the ancestors of chimpanzees, though this does not provide definite answers as to what the ancestral condition was or to the tempo or mode of evolution. The use of dental evidence of canine reduction to predict the second hallmark of a morphological hominid, bipedalism, is also an idea that is rooted in the literature of human evolution thanks to Darwin (1871), though the scientific basis for this link has been mostly discarded in favor of viewing dental reduction as relating to mastication rather than weapon use. Though it has now been uncoupled from canine reduction, bipedalism remains one of the stronger pieces of evidence for giving a fossil hominid status. Bipedalism is important in that it is what obviously differentiates humans and their prospective ancestors from chimpanzees, their closest relatives. It is a trait that anthropologists expect to see far back in the human lineage, as it potentially represents the functional adaptation that characterized the split from the ancestors of chimpanzees.

The genetic basis for considering something a hominid is much less clear than the morphological basis. This is related to the assumptions inherent in the use of the molecular clock and the differing available dates for the split between humans and chimpanzees, as well as to the disparities between the morphological evidence and these dates. One of the main assumptions in the molecular clock is that there is a constant rate at which neutral genetic differences accumulate following a divergence. This allows genetic differences to be paired with a divergence date known from the fossil record in order to calculate the divergence times for other groups. The logic in the use of the molecular clock seems somewhat circular, as it uses

fossil dates to calibrate the clock, which is then used to date other fossils, assuming that that lineage accumulates mutations at the same rate. In the case of the human/chimpanzee divergence, these issues are reflected in the fact that different researchers obtain different dates for the divergence. These dates range from 3.5-4.0 million years ago or less in some cases (Wall 2003) to up to 4.98-7.02 million years ago in other studies (Kumar *et al* 2005). If the younger dates were used, then it would appear that the australopithecines are potentially the earliest definitely identifiable ancestors of humans. If the older dates are used, then there is room for older potential hominids in the human family tree. In looking at the fossil evidence with the genetics, the disparity between the two should be resolved by the careful consideration of the fossil morphology. A fossil that is dated to before the genetic divergence (based on whichever dates one chooses) would have to show exceptionally strong evidence of hominid traits in order to be considered one. All of the genetic dates are actually estimates with confidence ranges and cannot be taken as absolute, and the clock is calibrated using fossil morphology, after all. Based on the issues with the molecular clock and the genetic divergence times, this paper will be focused on the morphology of the fossil taxa than their genetic dates.

The purpose of this study is to examine the hominid status of *Sahelanthropus tchadensis* and *Orrorin tugenensis*. Both of these taxa have been called the earliest hominid and it is obviously impossible for both of them to occupy this position. They are from different fossil localities, though may have overlapped in time. *S. tchadensis* is known from teeth, several mandibles, and a cranium, while *O. tugenensis* is known from teeth, three partial femora, a distal humerus, and a proximal manual phalanx. If either were to be identified as the earliest hominid, it would give researchers important clues to the chimpanzee/human divergence, as well as the primitive morphology for the human clade. The motivation for this study is to consider the controversies that currently exist in the debate over the oldest hominid, and to determine if either of them can be considered hominids based on what is known about their morphology. In looking at this question, the additional issues of whether they are actually separate taxa will be addressed, as well as their potential overlap in time, a condition that could thoroughly discount one or more of the taxa as human ancestors. The hominid status of these taxa will be determined through a comparative approach to their morphology, specifically with regard to their dental characters and traits that could reflect bipedalism.

Sahelanthropus tchadensis

Background

The fossil specimens known of *Sahelanthropus tchadensis* all originate from a single area, the Toros-Menalla locality (sites 247, 266, 292), in the Djurab Desert of Chad. This site has been dated to older than 5.3 million years using biochronology (Vignaud *et al* 2002). The biochronological dating of the site is based on the degree of faunal evolution present relative to the fauna at sites of known age. The upper and lower third molars of the suid *Nyanzachoerus syrticus* are similar to those present in the Lothagam Nawata Formation, which has been estimated to be between 7.4 and 5.2 million years in age (Vignaud *et al* 2002). This age estimate is also supported by members of Anthracotheriidae, Proboscidea, Equidae, and Bovidae found at the site (Vignaud *et al* 2002). The proboscideans in particular show a co-occurrence of two types that are also found in the Lukeino Formation of Kenya, which has been dated to approximately 6 million years, though the fossils from Toros-Menalla show more primitive

characters, suggesting an older age (Vignaud *et al* 2002). This indicates an age of closer to 7.4 million year may be the best estimate; older than the *Orrorin* remains, and substantially older than estimates of genetic divergence discussed above

The faunal remains from Toros-Menalla, in addition to being used for dating, are also important in reconstructing the paleoecology of the site. The fossils present suggest that it was a mosaic environment, consisting of open grassland, wooded savanna, fresh water, and some gallery forest (Vignaud *et al* 2002).

Fossil Material

The original *S. tchadensis* find consisted of a fairly complete cranium and partial mandible, as well as several isolated teeth (Brunet *et al* 2002), with a later find adding two more partial mandibles with some associated dentition and an upper third premolar crown (Brunet *et al* 2005) to the known material for this taxon.

Dental Remains

The dental material for the taxon includes both isolated teeth and teeth associated with the skull and mandibles. The isolated teeth are a right upper third molar, a right upper central incisor, a right lower canine, and a right upper third premolar. The teeth that were found in association with the skull are all upper teeth and include a right canine, right first molar, right second molar, right third molar, and a left first molar. The teeth that have been found in association with the various partial mandibles are a series from the fourth premolar to the third molar, a left first molar, a left second molar, a right first molar, a left canine, and a partially preserved group from the third premolar to the first molar.

The central incisor is relatively small, with distinct marginal ridges and multiple tubercles on the lingual fossa (Brunet *et al* 2002). The presence of multiple tubercles differentiates *S. tchadensis* from *Orrorin tugenensis* (Brunet *et al* 2002). The upper canine is also relatively small for a presumed male of the species (an assumption the authors base on the thickness of the browridge and mandibular corpus), with extensive apical wear on both upper and lower canines (Brunet *et al* 2002). It is unclear from the description of the original fossil material whether the mandible Brunet *et al* (2002) use as evidence of a relatively small canine was found in association with the cranium. There is no lower canine- third premolar diastema, which contributes to the idea that the taxon possessed a non-honing canine, as does the apical wear (Brunet *et al* 2002). The lack of a diastema differentiates *S. tchadensis* from extant great apes. All of the known premolars possess two roots, which is the presumed primitive condition for the hominid clade, and seems to support the claim of the lack of a honing canine complex, as there is a small contact facet on the lower third premolar that indicates the lack of a diastema (Brunet *et al* 2005). The molars have low, rounded cusps, with bulging lingual faces, and an enamel thickness between *Pan* and *Australopithecus* (Brunet *et al* 2002). No doubt the discoverers of the specimen consider this a piece of evidence for its place at the base of the hominid clade. The size of the cheek teeth falls into the lower end of the range of tooth sizes found in *Australopithecus afarensis* (Brunet *et al* 2002). The most important aspect of the dentition, from the standpoint of conveying hominid status, is the lack of a honing canine, which presents as part of a suite of derived dental features pointed out by the authors (Brunet *et al* 2005). They consider *S. tchadensis* a hominid based on these derived features: the lack of a diastema between the lower canines and third premolars; long-rooted and small-crowned canines; a lower canine

crown with a large distal tubercle; an intermediate enamel thickness; and the occlusal morphology of the postcanine dentition (Brunet *et al* 2005).

Cranial Remains

The relatively complete (though distorted) cranium of *S. tchadensis* is an important piece of the fossil record, as it records dentition and can suggest the mode of locomotion used by the taxon. It also shows other features that can be used to support a claim of hominid status, in addition to its dental traits and possible bipedalism. Brunet *et al* (2002) describe the cranium as a mosaic of primitive and derived features, some indicative of bipedalism. As the focus of this paper is on dentition and bipedalism as hominid traits, the majority of the discussion on the cranium will concern the characters that potentially show bipedalism.

The cranium (called Toumai) has an orthognatic face with weak subnasal prognathism and a small braincase with quite a bit of postorbital constriction (Brunet *et al* 2002). It has a strong, continuous supraorbital torus, with no supraorbital sulcus behind it (Brunet *et al* 2002). Toumai also possesses a large nuchal crest, with a long and flat nuchal plane, and a large, anteriorly positioned foramen magnum (Brunet *et al* 2002). The angle of the petrous pyramid appears to be primitive (Brunet *et al* 2002). Brunet *et al* (2002) consider the anterior positioning of the foramen magnum, the flatness of the face, and the morphology of the supraorbital torus to be derived features. In a comparative study by Guy *et al* (2005), the authors determined that the specimen had the following hominid synapomorphies: a long, flat, and horizontal nuchal plane; a shortened basicranium; and an anterior foramen magnum. They consider the orthognatic face to be a case of convergence, rather than homology (Guy *et al* 2005). The features that they identify as hominid synapomorphies are those which are important in determining bipedalism. Also important in the bipedalism debate is the Zollikofer *et al* (2005) virtual reconstruction of the cranium, which they believe shows that Toumai was both a hominid and a biped. The reconstruction shows an orthognatic face, anterior foramen magnum, and a long, flat, horizontal nuchal plane, as in Guy *et al*'s (2005) study. Zollikofer *et al* (2005) reconstructed the cranium by making a high-resolution CT scan of it, then removing the matrix digitally and using two established protocols to create their virtual reconstruction. They then evaluated the reconstruction using three independent tests. The first test looked at the fit between the face and the neurobasicranium, which were reconstructed separately (Zollikofer *et al* 2005). The second test assessed the virtual reconstruction against an anatomical constraint that was not used in the reconstruction, dealing with the angle between the posterior maxillary plane and the neutral horizontal axis of the orbits (Zollikofer *et al* 2005). The third test dealt with the shape variability of the cranium, creating a series of landmarks on the reconstruction which were then tested for fit against a sample of African ape and hominid skulls by seeing how much change was necessary to fit the Toumai cranial landmarks to the landmarks on the sample skulls (Zollikofer *et al* 2005). To fit the reconstruction to the African ape landmarks would have required overlapping pieces of the skull and creating discontinuity between anatomical features, which demonstrated that the cranial morphology of Toumai could not be made to fit the size/shape space of African apes, but could be fit to the crania of Pliocene hominids (Zollikofer *et al* 2005). They also oriented the foramen magnum using the angle of the junction between the first cervical vertebra and the occipital condyles and the orbital plane and claimed that this clearly showed the head was upright on the vertebral column, making the specimen an upright biped (Zollikofer *et al* 2005).

Issues

There are five major issues concerning the *S. tchadensis* remains. These are the virtual reconstruction (as previously addressed), the lack of postcranial remains, the existence of only one cranium of this taxon known thus far, the distortion of the skull, and the way its hominid status has been claimed. As the virtual reconstruction has already been discussed, the first issue under consideration is the lack of postcranial remains. While the conclusion of any analysis of the fossil record is that more material would help to clarify things, in this case its lack truly does hinder the claim for hominid status. Postcranial remains, particularly those of the pelvis, leg, or foot, would help to settle the issue of whether Toumai walked upright. In that same vein, it would be nice to have another even partial cranium of *S. tchadensis*, to be able to more fully understand its morphology and the variation within a species, both at the individual and the sex level. Another cranium would certainly shed more light on the relative size of the canine and whether all members of the taxon lacked a honing complex. The distortion of the currently known cranium is also something of an issue, despite Zollikofer *et al*'s (2005) claim that it is not too badly distorted. It is possible for the distortion of a fossil to render certain features impossible to measure, as well as give it an appearance that it did not have in life, which can in turn affect its reconstruction. The final issue also plagues nearly all claims of the discovery of the earliest hominid. For a researcher, wanting to believe that something is the earliest hominid makes them more prone to try to prove this. It also tends to make them look more critically at competing claims than at their own, which, while it can lead to new insights, tends to make them even more staunch in the defense of their own claim, rather than open to new ideas.

Orrorin tugenensis

Background

The fossil remains of *Orrorin tugenensis* were discovered in several members of the Lukeino Formation of Kenya. These remains have been dated using K-Ar dating techniques as well as magnetostratigraphy and biochronology. The radioisotopic dating of lavas from above and below the Lukeino Formation, as well as the dating of crystals from within the sediments of the Formation give an age of approximately 6 million years (Pickford and Senut 2001). In a later study, K-Ar dating and the results of magnetostratigraphic dating also show that the Lukeino Formation was deposited between 6 and 5.7 million years ago, with the hominid remains concentrating around 5.9-5.8 million years ago (Sawada *et al* 2002). The age of the Lukeino Formation was also assessed based on its faunal remains, which later supplied the biochronological matches for the dating of *Sahelanthropus tchadensis*, with the fauna suggesting an age of approximately 6 million years (Pickford and Senut 2001; Senut *et al* 2001). Based on the faunal remains, it is suggested that the paleoenvironment of *O. tugenensis* appears to have likely been open woodland interspersed with more heavily wooded areas, inferred from the presence of *Colobus* (Pickford and Senut 2001). However, based on the sediments, others have suggested that the species “lived in or near the flood plain that bordered Palaeolake Lukeino” (Sawada *et al* 2002). The two conclusions are not necessarily incompatible, as a lakeshore area would have been a watering hole for many species, explaining their presence in the fossil record.

Fossil Material

The known fossil material for *O. tugenensis* consists of isolated teeth, two partial mandibles with associated dentition, three partial femora (two left and one right), a proximal manual phalanx, and a partial humeral shaft (Senut *et al* 2001).

Dental Remains

The dental remains of *O. tugenensis* include: a lower molar, an upper central incisor, a lower fourth premolar, an upper right canine, a lower left second molar, a lower right third molar, a lower left third molar, an upper left third molar, and an upper right third molar (Senut *et al* 2001). The unspecified lower molar was collected by Martin Pickford in 1974 at the Cheboit locality and has been the subject of much debate concerning its affinity to the taxon (Senut *et al* 2001). As a result, it will not be discussed in this paper.

The upper central incisor is large and not shoveled, as well as being only lightly worn (Senut *et al* 2001). It appears to have thick enamel (Senut *et al* 2001), like the *Homo* condition, with thin enamel being the condition in *Pan* (Smith *et al* 2008). It is relatively large mesio-distally, though smaller than the australopithecine condition and fairly equal in size to those of *Ardipithecus ramidus*, with a sloping lingual surface like that found in *Pan* (Senut *et al* 2001). The upper canine is of great interest, as it can show whether the taxon in question had a canine/lower third premolar honing complex, the reduction of which is a hallmark of later hominids. In *O. tugenensis*, the upper right canine is short, with a shallow, narrow vertical mesial groove, such as is common in Miocene and extant apes, though not present in the australopithecines or *Homo* (Senut *et al* 2001). The canine has a pointed apex and is “almost sectorial,” like the canines of female chimpanzees (Senut *et al* 2001). The upper third molars are small and almost triangular in outline, unlike the very trapezoidal upper third molars of *Australopithecus afarensis* (Senut *et al* 2001). The crown is low and the roots are long, and the pattern of occlusal wrinkling is not as strongly marked as in the australopithecines (Senut *et al* 2001). The lower fourth premolar has an oblique crown and is oval-shaped (mesio-distally compressed) in occlusal outline, with two offset roots (Senut *et al* 2001). The distal fovea is large, which is a feature present in both extant and fossil apes (Senut *et al* 2001). The preserved lower molars are small and rectangular, as in *Homo*, with enamel thicknesses comparable to those of other hominids, though not *Ar. ramidus* (Senut *et al* 2001). There is no cingulum present on the molars (Senut *et al* 2001), the absence of which is thought to be a derived feature, as they are present in Miocene apes and *Pan*.

Femoral Remains

While the dentition of a specimen can suggest hominid affinities, demonstrating bipedalism in fossil remains is a more obvious way to try to establish hominid status. As bipedalism is one of the main functional differences that separates humans from chimpanzees, it is assumed that it is also what separated the ancestors of those two species. In attempting to show that a fossil was bipedal, the femur is a particularly useful bone to have, as it preserves distinct anatomical markers of this behavior. Other postcrania can be helpful in making a case for bipedalism (and will be discussed later), but femoral morphology tends to be strong evidence.

Included in the *O. tugenensis* remains are three partial femora. The most complete of these is BAR 1002'00, a left femur, which preserves the femoral head, proximal femoral morphology (excluding the greater trochanter), and about half of the shaft. The second proximal left femur lacks the femoral head and the greater trochanter, while the right femur is even more fragmentary. While BAR 1002'00 has been the primary focus of the bipedalism analyses done

on *O. tugenensis*, Pickford *et al* (2002) point out that the three fragments are similar to each other in morphology, though not in size and robusticity.

As bipedalism is considered an important hominid trait, several studies have been done on the femoral morphology of *O. tugenensis*, comparing it to various hominids as well as apes. These studies make it simple to assess which traits are primitive and which seem derived for the taxon. According to Pickford *et al* (2002), there are a great many characters that are hominid-like in the *O. tugenensis* femur. The first of these characters is the femoral tubercle, which they say blends into the greater trochanter proximo-medially, and resembles the femora of other hominids, though not those of Miocene or African apes (Pickford *et al* 2002). The intertrochanteric line is clearly visible though not in high relief, a feature that is absent in extant and Miocene apes, but present in some australopithecines (Pickford *et al* 2002). The femoral neck is elongated compared to those of African apes and Miocene hominoids and relatively more similar in length to those of hominids (Pickford *et al* 2002). In conjunction with a broad proximal shaft, this feature seems to indicate differences in hip morphology related to gait in australopithecines and *O. tugenensis* (Richmond and Jungers 2008). The internal morphology of the femoral neck is also of interest in the bipedalism debate. Low resolution computerized tomography scans of the neck appear to show that the cortical bone is thinner superiorly and thicker inferiorly, as it is in hominids (Galik *et al* 2004). Extant African apes have roughly equal cortical bone distribution around the whole of the femoral neck. While the greater trochanter is missing, the shape and depth of the superior notch appear to be of the hominid type, as does the trochanteric fossa, rather than like the living or fossil ape type (Pickford *et al* 2002). Both the swelling of the gluteal tuberosity and the angle of the intertrochanteric crest appear to be similar to the australopithecine condition (Pickford *et al* 2002). One of the features that argues most strongly for bipedalism is the clearly visible obturator externus groove, which is produced by the full extension of the femur in frequent bipedalism and is a consequence of Haversian remodeling on the bone (Pickford *et al* 2002). This feature is generally absent in apes, as they do not spend enough time walking bipedally. Also, the femoral shaft is platymeric, which is the hominid condition, not the ape condition (Pickford *et al* 2002).

In addition to these hominid-like characters, there are two potential autapomorphies in the femur, as well as traits that Pickford *et al* (2002) consider to be “human-like,” as opposed to australopithecine-like. The first of the potential autapomorphies is the position of the lesser trochanter. In *O. tugenensis* it is medially salient, while in australopithecines and extant humans it is generally posteriorly projecting (Pickford *et al* 2002). The second potential autapomorphy is a saddle-shaped depression on the intertrochanteric crest that appears in all three of the fragmentary femora, but not in other hominids (Pickford *et al* 2002). It is possible that these autapomorphies are related to its mode of bipedalism, perhaps indicating that it differed from the bipedalism practiced by australopithecines and modern humans. This is particularly plausible in the case of the lesser trochanter position, as it serves as the insertion for the iliopsoas muscle, an important hip flexor. Despite its antiquity, Pickford *et al* (2002) also make a case that several of the characters of the femur are more like *Homo* than the australopithecines, though a number of their statements have been contested. The potential issues that result from this will be discussed later in the paper. The first feature they choose to focus on is the size of the femoral head relative to the shaft diameter, saying that it is relatively much larger than what is seen in australopithecines and apes, and approaches the human condition (Pickford *et al* 2002). In a later study, this is rejected based on the idea that the difference in relative head size between *O. tugenensis* and the australopithecines is “within the expected level of intraspecific variation”

(Richmond and Jungers 2008). Pickford *et al* (2002) also point out that the spiral line at the base of the lesser trochanter looks like it does in humans and not as it does in australopithecines, though it lacks a human-like *linea aspera*. Additionally, they state that the digital fossa looks human-like, not australopithecine-like, and suggest that the slightly pronounced appearance of the hypotrochanteric fossa may be a precursor to the more voluminous fossa that modern humans possess (Pickford *et al* 2002).

Other Postcranial Remains

In addition to the dental and femoral remains, a few other postcranial remains have been found from *O. tugenensis*, including a partial right distal humerus and a proximal manual phalanx. While these are not bones that are directly involved in the debate over the fossil's hominid status, they still provide some clues as to the behavior and adaptation of the taxon. The humerus consists of a partial distal shaft and end. The most prominent feature of the humerus is a vertical brachioradialis crest, of the type seen in chimpanzees and *A. afarensis* (Senut *et al* 2001). This would appear to show some arboreal adaptation, though its specific nature cannot be determined, if both chimpanzees and *A. afarensis* evince it. Chimpanzees engage in a variety of climbing behaviors, while the arboreal adaptations of *A. afarensis* are still being debated, as it was certainly a biped. A reasonable conclusion to draw from this adaptation is that it appears to have been able to climb if necessary, especially given that estimates of its size make it of comparable weight to adult chimpanzees (Nakatsukasa *et al* 2007), though it was likely more habitually bipedal. The other postcranial remain, the proximal manual phalanx, has been described as curved and similar to those of chimpanzees and *A. afarensis* (Senut *et al* 2001), showing the same affinities as the humerus for possibly grasping and climbing adaptations. Based on these two bones, it would seem as though the upper limb of *O. tugenensis* was at least somewhat arboreally adapted, in contrast to the bipedal lower limb. This does not necessarily provide evidence that it was not a hominid, as *A. afarensis* is a fairly undisputed hominid with similar adaptations.

Issues

Despite its bipedalism being a good piece of evidence for potential hominid status, there are still lingering issues concerning the fossil material itself, and its evolution and phylogeny. The issues concerning the fossils are their associations with each other and the repair that has been done on the BAR 1002'00 femur. The issues of evolution and phylogeny are its arboreal and bipedal adaptations, and the conclusions Senut *et al* (2001) have drawn regarding its place in the hominid lineage.

The first issue that has been raised is that of the associations of the *O. tugenensis* fossils to each other. Some of the teeth that have been ascribed to the taxon were found isolated in different parts of the fossil locality. For this reason, it is possible to suggest that they may not belong to the same taxon as the femur. The Miocene produced an abundance of ape fossils of different types and it is possible that these teeth could belong to another Miocene ape, rather than a hominid. Another issue of the fossil material comes from the publication of Galik *et al* (2004), which claims that the cortical bone of the BAR 1002'00 femur neck might be thinner superiorly and thicker inferiorly, as it is in bipeds. It seems that the femur was originally broken into two pieces at the femoral neck and was glued back together without doing direct measurements on the relative thicknesses of the cortical bone at the break. Additionally, there have been some questions regarding the quality of the CT scans that have been published and the lack of

conventional x-rays done on the specimen, as well as whether the CT scans actually show a biped-like distribution of cortical bone (White 2006). The most obvious solution to this issue would be to either unglue the specimen and directly measure the cortical bone, or to take high resolution scans that would resolve the controversy. At this time, neither of these things has been done, leaving a very important piece of biomechanical evidence for bipedalism unsubstantiated.

The evolutionary and phylogenetic issues of *O. tugenensis* are not likely to be so easily resolved as questions concerning the bones themselves. The first of these is the arboreal adaptation the postcranial remains of the upper limbs show. Combined with the bipedal lower limbs and estimates of body size, it seems as though these things could suggest an arboreal ancestry for the human clade, especially given that some australopithecines have a similar pattern of adaptation, with the traits of the upper limb as a primitive retention. There is a fair amount of support for the idea of a climbing ancestor to later bipeds, primarily based on the “climbing/suspensory features retained in modern humans and shared with great apes, a variety of biomechanical similarities between human bipedalism and vertical climbing in great apes, and numerous climbing features retained in early hominin fossils” (Richmond *et al* 2001). The adaptations to bipedalism that the femora show are different in some ways from the suite of characters that the australopithecines show, though it clusters with them in morphometric analyses (Richmond and Jungers 2008). Given both the upper limb and lower limb similarities between the two, the possibilities exist that *O. tugenensis* could have been an ancestor to the australopithecines or that this is an example of convergent evolution in a Miocene ape. This issue will likely remain unresolved until more fossil remains have been found. The question of phylogeny is further complicated by the conclusions of Senut *et al* (2001), who believe that the derived characters of *O. tugenensis* and the similarities between the fossil taxon and modern humans suggest that it is the direct ancestor of *H. sapiens* and the australopithecines are not part of that lineage. It is generally believed in the field that the australopithecines are definite hominids and the ancestors of *H. sapiens*, due to the studies that have been done on the available fossil remains, many more of which exist for the australopithecines than for *O. tugenensis*. Basing a claim that involves a major paradigm shift on a single, incomplete set of remains is not well supported. Additionally, if one has an unpopular theory about the relationship between two species, it seems possible that one would look for features that would substantiated this claim, rather than having a purely objective outlook. The removal of the australopithecines as human ancestors also leaves a large time-gap between the time of *O. tugenensis* and the rise of *Homo*. For these reasons, considering *O. tugenensis* the ancestor of *Homo* to the exclusion of the australopithecines does not seem parsimonious at this time.

Discussion

In attempting to determine hominid status for *S. tchadensis* and *O. tugenensis*, it is necessary to compare and evaluate the evidence for the two, as they represent competing claims for the oldest known hominid. This evidence can be broken down into the broad categories of dental characters and the traits that are supportive of bipedalism in the two taxa. Any discussion of the status of the two taxa should also include at least a mention of their potential time overlap and its implications.

Dental Characters

The dental morphology of *S. tchadensis* appears to be the dentition of a hominid. The lack of a honing canine is fairly compelling, in that it is a synapomorphy of the hominid clade, though it is interesting that it does not appear to be a transitional morphology. If the taxon is truly at the base of the hominid line, should it not retain more primitive features? It is especially interesting in light of its intermediate enamel thickness. Another question that could be raised concerns the published sex of the cranium, which the authors call likely male, based on its browridge and the thickness of the mandibular corpus (Brunet *et al* 2002). If the specimen is male, that would certainly make the lack of a honing canine significant, however, the thickness of the mandibular corpus can be functionally related to increasing the power of the masticatory apparatus, as in robust australopithecines. This might also correlate with the extensive canine wear, as certain other Miocene apes such as *Gigantopithecus* show this same pattern and lack of honing complex (Wolpoff *et al* 2006). If the specimen were a female ape such as *Ramapithecus*, it might also explain the lack of a honing complex (Wolpoff *et al* 2002). Additionally, Wolpoff *et al* (2002) argue that the size of the canine falls within the range of extant chimpanzees, which goes against Brunet *et al* (2002) describing it as a small canine. The studies tend to focus on the canine without thoroughly comparing the other teeth to those of extant and fossil apes, in terms of primitive and derived features. While the lack of a canine honing complex can suggest hominid status, it is by no means beyond question.

In *O. tugenensis*, for the most part, the teeth appear to be fairly primitive in morphology. This is essentially what would be expected in a hominid that has only recently diverged from its common ancestor with chimpanzees. The primitive traits that appear are generally shared with both extant and Miocene apes. This could indicate either its position at the base of the hominid clade or its inclusion in an ape clade. The potentially derived exceptions to an overall primitive morphology are the enamel thickness, the small size of the teeth, the slight reduction in the canine/premolar honing complex, and the lack of a cingulum on the molars. The authors also compare the size of the molars to those of *Homo* and use this (along with the enamel data) to make a claim that these are the primitive conditions for the human lineage and are retained in *Homo*, displacing the australopithecines as human ancestors (Senut *et al* 2001). While it is possible that small, thick enameled teeth are the primitive condition, it is premature to assume that this means the australopithecines should be removed from the family tree, as tooth size varies based on a variety of factors. The reduction of the canine/premolar honing complex is described as “almost sectorial” and similar to that of female chimpanzees. Without crania or pelvises from this taxon, determining the sex of the individual who produced this canine is impossible. It seems logical to suggest that perhaps the canine in question belonged to a female ape, rather than a hominid, who would not have shown a complete canine/premolar honing complex even if one were present in the males of her species. Finally, the lack of a cingulum on the molars, while it is a feature derived relative to apes, does not necessarily mean that the owner of the teeth was a hominid. The absence of a cingulum could be an autapomorphy of the species rather than an indicator of hominid status. In considering the dentition as a whole, it is fairly ape-like. There is no definite indicator in the teeth alone that should convey hominid status on the taxon.

Evidence of Bipedalism

Despite the various authors making a case for the hominid status and bipedalism of *S. tchadensis*, there are a few questions still unanswered and some who do not agree with their claims. An initial question about the Zollikofer *et al* (2005) reconstruction concerns their

method of reconstruction. While a virtual reconstruction may be a useful tool, doing an actual reconstruction may result in a different morphological outcome. In doing a virtual reconstruction, as in manual reconstruction, some amount of bias may creep in, as the one doing the reconstruction has a preconceived idea about how the specimen should look. Those who reconstructed the skull were also quite adamant in their claims that there is no other way to reconstruct Toumai. Their reconstruction includes a long, flat, horizontal nuchal plane. The original description of the specimen talks about it having a large nuchal crest. A large nuchal crest and long nuchal plane would seem to indicate large neck muscles, as cresting is produced by strong muscle forces acting on the skeleton and a long nuchal plane would provide a large muscle attachment area. Very strong nuchal muscles would be needed to counterbalance the weight of a projecting face, but Toumai has an orthognatic face (Wolpoff *et al* 2006). They also attempted to prove bipedalism through the orientation of the skull using the angles between features. Wolpoff *et al* (2006) take exception to this, saying that the analysis fails to take into account the projection of the supraorbital torus and the potential curvature of the cervical spine, in addition to the fact that chimpanzees and australopithecines have the same angles demonstrated in Toumai. While Toumai looks fairly hominid-like dentally, the case for its bipedalism is not as strong.

The femoral neck morphology may support the idea that *O. tugenensis* was a habitual biped, though better CT imaging of the cross section of the femoral neck is needed to make this a truly compelling case. The absence of a linea aspera does occur in some australopithecines, however (Richmond and Jungers 2008). The proximo-distal femoral shaft curvature appears to be anteriorly convex, as is seen in humans, not apes, and the pilaster also has a human-like, rather than *Pan*-like, appearance (Pickford *et al* 2002). This does not necessarily mean that it had the same type of bipedalism as an australopithecine or a modern human, as it does not have the same suite of characters that either of these hominids possess. Pickford *et al* (2002) believe that it is a very modern human-like femur morphologically, but Richmond and Jungers (2008) say that it clusters with the australopithecines in statistical and morphometric analyses. If the initial study compared the *O. tugenensis* femora to that of the *Australopithecus afarensis* Lucy (AL 288-1), then it is possible that some of the differences between the two can be attributed to size. The Lucy femur, compared to other *A. afarensis* remains, comes from a particularly small individual. Their contention that it looks very modern raises some questions about why they would be comparing a 6 million-year-old femur to one of an anatomically modern *H. sapiens*. It is obvious that they are trying to make a case for *O. tugenensis* as a human ancestor, but it is unlikely that the same morphology could endure without adaptation for 6 million years. Complete, modern-like femoral morphology does not seem like a good candidate for the primitive condition of the human lineage, particularly without other material to support it. It is likely that *O. tugenensis* was some kind of a biped, though without a more complete skeleton, it seems premature to think that it is definitely a hominid.

Dating

In addition to the unresolved issues of primitive versus derived dental morphology and the relative merits of each of the arguments for bipedalism, there is also the question of dating. *S. tchadensis* has been dated to between 7.4 and 5.2 million years in age, most likely slightly older than 6 million years, based on biochronology (Vignaud *et al* 2002). *O. tugenensis* has been dated to approximately 6 million years (Pickford and Senut 2001) using radioisotopic dating of lava flows, and to around 5.9 to 5.8 million years using K-Ar dating and magnetostratigraphic

dating (Sawada *et al* 2002). These dates are sufficiently older than the genetic divergence estimates to suggest extraordinary morphological evidence might be required to establish hominids at this age.

It is worth noting that the comparative biochronological data used to date *S. tchadensis* came from the same fossil locality as the *O. tugenensis* remains, suggesting (at the very least) a certain amount of consistency between the two sets of dates. What is also worth noting is that, given margins of error, there is potential time overlap between the two taxa. If this is the case, there are three possibilities for their claims of hominid status: that neither are hominids (which is independent of their overlap and may be the case anyway), that only one can truly be a hominid, or that both are hominids, because they are the same. To add to the last possibility, the only fossil remains in which the two taxa overlap are teeth, and there is some question of the association of the *O. tugenensis* teeth to the femora. Given the evidence and their derived traits, there is nothing that would make it absolutely impossible for both taxa to actually be the same taxon, as stated by Haile-Selassie *et al* (2004) in the following quote: “metric and morphological variation within available small samples of late Miocene teeth attributed to *A. kadabba*, *O. tugenensis*, and *S. tchadensis* is no greater in degree than that seen within extant ape genera...we question the interpretation that these taxa represent three separate genera or even lineages. Given the limited data currently available, it is possible that all of these remains represent specific or subspecific variation within a single genus.” Ultimately, more fossils are necessary before any of this can be said with any certainty.

Conclusions

Based on the comparisons that have been made, it seems that at this time, neither of the taxa under consideration can be definitively termed hominids, though neither can be entirely ruled out either. In the case of *S. tchadensis*, an argument that is sufficiently convincing has not been made for its bipedalism, and without postcranial remains, no totally convincing confirmation of this claim can be made. While it does lack a honing canine, this could be explained by convergence, as this condition is also seen in some Miocene apes, especially females. Without firm evidence of bipedalism in addition to the reduction in the canine complex, nothing definitive can be said about the hominid status of this taxon at this time. In the case of *O. tugenensis*, the fossil remains appear to show a biped with a fairly ape-like dentition, including a canine that did not seem to be fully honing. The combination of bipedalism with a slightly derived, still fairly primitive dentition seems to be a better fit for hominid status than *S. tchadensis*, though it is also by no means a certainty. It is possible that the bipedal locomotion of *O. tugenensis* could be the result of convergence or arboreal bipedality, though some studies have shown that the femoral morphology clusters with that of australopithecines. At this time, the claim that *O. tugenensis* is a hominid is better supported than the claim for *S. tchadensis*, though this does not necessarily mean that it is a hominid. More fossil evidence is needed before these issues can be resolved and perhaps a more objective outlook as well. While the motivation to find the oldest member of the human lineage is a potent driving force, it is not necessarily the only important unknown in paleoanthropology.

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