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A Critical Analysis of Hominin Morphology: The Partial Skeleton of Ardipithecus ramidus

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The Partial Skeleton of *Ardipithecus Ramidus*

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Introduction

In 1994 a new species of *Australopithecus* was described that was purported to be the new stem hominin[1] and the ancestor of the then widely recognized stem hominin, *Australopithecus afarensis* (White, Suwa, and Asfaw 1994). Mostly a collection of dental and mandibular fragments, accompanied by a portion of the basicranium, the newly minted *Australopithecus ramidus* was dated to 4.4 Ma, and, thus, became the oldest australopithecine on record (White, Suwa, and Asfaw 1994). The hominin status of *Au. ramidus*, or rather its bipedality, was inferred from its morphological similarity to *Au. afarensis* and the inferior orientation of the foramen magnum (White, Suwa, and Asfaw 1994). As *Au. afarensis* was already established as an obligate biped[2], it was suggested that *Au. ramidus* was likely a bipedal hominin (White, Suwa, and Asfaw 1994). However, it was clear that the new species not only preceded *Au. afarensis* chronologically, but that it also displayed a more primitive morphology. *Au. ramidus* lacked the postcanine megadontia[3] of *Australopithecus*, had thinner molar enamel, and had more ape-like canines, which resulted in the naming of a new specific taxon to distinguish this material from known australopithecines (White, Suwa, and Asfaw 1994).

Shortly thereafter, a corrigendum reassigned this material to a new genus, and the "root" australopithecine became the "root ground ape" *Ardipithecus ramidus* (White, Suwa, and Asfaw 1994, 1995). There was little justification of this taxonomic revision in the corrigendum, and no new material was described, other than a brief mention of a recovered partial skeleton (White, Suwa, and Asfaw 1995). It could only be assumed that this taxonomic revision implied that the new material must have been morphologically and adaptively distinct from *Australopithecus*. Paleoanthropologists eagerly awaited the description of the partial skeleton, especially with the implications arising from the new genus, but the wait for the publication would be a protracted one.

It was not until 2009 that the aforementioned partial skeleton was described in a publication. Bestowed with the appellation "Ardi", in perhaps a conscious attempt to capture the notoriety of the famous Lucy skeleton, the partial skeleton ARA-VP-6/500 contained more skeletal elements than Lucy, but was plagued by extreme fragmentation and horrendous presservation (White *et al.* 2009). This was given as the main reason for the delay in publication (White *et al.* 2009). A series of eleven articles described the new *Ar. ramidus* material and these descriptions relied heavily on virtual reconstructions of the fragmentary fossils using micro-CT technology. A critical analysis of the virtual reconstructions is necessary, as the morphological inferences found among the descriptions are only as solid as the quality of the reconstructions and one's confidence in them.

From the virtual reconstructions, it was inferred by the authors that *Ar. ramidus* was a hominin, a facultative biped[4], and was most likely ancestral to *Australopithecus* (White *et al.* 2009). These conclusions were identical to those already postulated in the original 1994 descriptions based on only a few skeletal elements, and perhaps that was to be expected (White, Suwa, and Asfaw 1994). What was surprising was the extremely primitive morphology of *Ar. ramidus* relative to *Australopithecus* (White *et al.* 2009). In spite of claims to facultative

terrestrial bipedalism, *Ar. ramidus* retained a completely divergent hallux[5] (White *et al.* 2009). Its primitive foot and hand morphology suggested that it retained a substantial arboreal component in its locomotive repertoire (White *et al.* 2009). There were no adaptations for knuckle-walking, vertical climbing, or suspension to be found in the skeleton, and this suggested *Ar. ramidus* was a palmigrade clamberer, a generalized form of arboreal hominid locomotion (White *et al.* 2009).

Their claims for a hominin status rested most notably on the derived characteristics of the pelvis and foot that supposedly enabled *Ar. ramidus* to walk bipedally, and the derived characteristics of a vestigial canine/premolar complex (White *et al.* 2009). The honing complex[6] was significantly reduced from that of extant and extinct hominids, yet was primitive relative to *Australopithecus* (White *et al.* 2009). As a corollary to the canine reduction, it was suggested that *Ar. ramidus* lacked significant body-size dimorphism, with Ardi herself weighing in at a hefty 50 kg, compared to the diminutive Lucy's 30 kg estimate (White *et al.* 2009). The lack of sexual dimorphism was a surprising claim, as *Au. afarensis* as well as all other extant and extinct hominids are, to varying degrees, sexually dimorphic in both canines and body size (Plavcan 2001).

It was also suggested that *Ar. ramidus* differs from the extant hominines in exhibiting primitive hominid characteristics. This implies that the extant hominines are, in fact, highly derived in the morphology of their pelvis and limbs, and have acquired their unique adaptations to vertical climbing and knuckle-walking convergently and only after the *Pan* and the *Gorilla* ancestors diverged from the LCA (White *et al.* 2009). The lack of a honing complex combined with body-size monomorphism and the novel locomotor repertoire suggested that,

behaviourally, *Ar. ramidus* was unlike the extant hominids, and consequently, the discovery of *Ar. ramidus* questions their value as referential models for the LCA (White *et al.* 2009). The analysis of *Ar. ramidus* suggested instead that the LCA was, in fact, a generalized arboreal clambering ape (White *et al.* 2009).

In summary, *Ar. ramidus* was seen to be far more primitive than *Au. afarensis* and yet derived enough relative to the hominids for it to be a considered a hominin (White *et al.* 2009). It supposedly resembled the morphology of the LCA more than any other taxa with known postcranial elements (White *et al.* 2009). Yet, it was strongly inferred that *Ar. ramidus* was both ancestral to *Australopithecus* and morphologically similar to *Sahelanthropus,* and that it could be easily accommodated into a linear account of hominin evolution (Lovejoy *et al.* 2009c; White *et al.* 2009). However, as many of these claims question the conventional wisdom of hominin evolution and in light of proposed alternative theoretical scenarios of hominin evolution, the *Ar. ramidus* material requires a detailed examination. The level of confidence in the virtual reconstructions is crucial to any interpretations of *Ar. ramidus*. The inferences made about *Ar. ramidus* are largely based on these reconstructions, and these interpretations are only valid if the reconstructions are sound. Finally, any interpretations of *Ar. ramidus* need to be placed within the context of what is known about other penecontemporaneous hominin and hominine taxa, as well as within competing theoretical approaches to hominin evolution. In an attempt to minimize bias and avoid presupposing any particular hypothesis in regards to *Ar. ramidus*, the morphology of this taxon will be compared to all relevant hominin and hominine taxa. Only then will conclusions

of its phylogenetic positioning and related inferences be offered.

Dentition

The dental elements are by far the best preserved and most numerous elements recovered for *Ar. ramidus* and were examined in detail (Suwa *et al.* 2009b). The most significant hominin characteristic of the *Ar. ramidus* dentition is the reduction of the canines, particularly in crown height, relative to extant and extinct hominines (Suwa *et al.* 2009b). There were no statistically significant differences between the inferred male and female canines in size or shape in the recovered sample, or in other words, the canines were monomorphic and could not be confidently split into two sexually dimorphic clusters (Suwa *et al.* 2009b). In this regard *Ar. ramidus* was said to fit the hominin pattern (Suwa *et al.* 2009b). The sample size of 21 canines was claimed to be statistically large enough so that it assured that males are represented in the *Ar. ramidus* sample, which is not the case for either *Sahelanthropus* or *Orrorin* (Brunet *et al.* 2002a; Senut *et al.* 2001; Suwa *et al.* 2009b).

The overall size of the canines in *Ar. ramidus* are similar to that of female chimpanzees, but they differ significantly in their shape—they are diamond-like, rather than dagger-like in *Pan* or other hominines (Suwa *et al.* 2009b). There is no evidence of a functional canine/premolar honing complex in *Ar. ramidus*, but there are vestiges of a diastema[7] (Suwa *et al.* 2009b). The canines are, thus, further derived in the hominin direction from those of *Ardipithecus kadabba,* which are significantly more dagger-like in shape and still show evidence of a diastema and distal edge honing (Haile-Selassie, Suwa, and White 2004; Suwa *et al.* 2009b). The canines of *Ar. ramidus* do express some distal edge wear, as the crowns are not fully reduced, and therefore, they are still primitive relative to *Australopithecus*, in which only the largest specimens show traces of distal edge wear (Kimbel and Delezene 2009; Suwa *et al.* 2009b). Thus, *Ar. ramidus* is depicted as evidence of a linear transition in the reduction of the honing complex from *Ar. kadabba* through to *Australopithecus* (Suwa *et al.* 2009b).

Molar enamel thickness in *Ar. ramidus* was found to be intermediate between the thin enamel of both *Dryopithecus* and extant hominines, and the thick enamel of *Australopithecus* (Suwa *et al.* 2009b). Again, it was implied that *Ar. ramidus* fits within a linear progression in the increase of molar enamel thickness from the Miocene hominines to *Australopithecus* (Suwa *et al.* 2009b). The postcanine dentition is primitive in size, however, and does not display any sign of the megadontia inherent in *Australopithecus* (Suwa *et al.* 2009b). The postcanine dentition was also found to be monomorphic in size and supported the claim that there was limited sexual dimorphism present in *Ar. ramidus* (Suwa *et al.* 2009b). In general, however, there seems to be only a limited amount of sexual dimorphism in hominin and hominine postcanine dentition (Plavcan 2001). Molars are less dimorphic in hominins and hominines than they are in the other anthropoids, and it is harder to infer the sex of a specimen based on the postcanine dentition in these taxa (Plavcan 2001).

It was, rather, the canines that played a major role in the assessment of the Ardi partial skeleton as that of a female and the determination of the degree of sexual dimorphism present in *Ar. ramidus* (Suwa *et al.* 2009b; White *et al.* 2009). The canines of Ardi were the second smallest out of thirteen known canines, and this was interpreted to suggest that Ardi was likely a female (Suwa *et al.* 2009b; White *et al.* 2009). However, as previously mentioned, Ardi had a large body mass for an early hominin. Based on a

sample of recovered humeri, Ardi's was either the second or third largest of the eight known elements (White *et al.* 2009). Thus, Ardi was a large animal and yet a female, and this resulted in the claim that *Ar. ramidus* was a monomorphic species (White *et al.* 2009). However, as mentioned above, the canines could not be separated into two statistically distinctive clusters, and it is possible that Ardi was a male with small canines. It has to be determined whether it is more parsimonious that *Ar. ramidus* was a departure from the Miocene hominine and *Australopithecus* pattern of sexual dimorphism, or that Ardi was, in fact, a male with small canine teeth, keeping in mind that small is only a relative term. Hominine and especially hominin canines are also less sexually dimorphic than in other anthropoids (Begun 2009; Kimbel and Delezene 2009).

Skull

The skull of *Ar. ramidus* exceeded the pelvis in terms of its incompleteness, distortion and fragmentation (Suwa *et al.* 2009a). The cranial vault was compressed to such an extent that the cranial height of the recovered fossil elements measured only 35 mm (Suwa *et al.* 2009a). Like the pelvis, the skull was also the focus of a major virtual reconstruction; luckily, the recovered facial elements and the supraorbital torus did not suffer extensive post deposition distortion (Suwa *et al.* 2009a). Interpreting the morphology of *Ar. ramidus* is handicapped by the limited number of images of the original fossil elements accompanying the published descriptions. The authors of these papers rely on the images from the virtual reconstructions, which are based on heavily manipulated micro-CT scans, for the basis for their morphological analyses (Suwa *et al.* 2009a). This fact should be kept in mind throughout discussions of *Ar. ramidus* as the skeletal elements, rendered as complete and

intact computer generated images, bear little resemblance to the original fossils.

To complete the cranial reconstruction, the temporo-occipital region from the original published *Ar. ramidus* material (White, Suwa, and Asfaw 1994) was rescaled to fit the newly described *Ar. ramidus* skull (Suwa *et al.* 2009a). The resultant virtual reconstruction depicts *Ar. ramidus* with a very hominin-like degree of reduction in facial prognathism, a foramen magnum clearly inferior on the cranial base accompanied by a short basicranial length, and a hominine-like cranial capacity (Suwa *et al.* 2009a). These morphological similarities to *Sahelanthropus tchadensis* are repeatedly stressed, and it is ultimately concluded that the skull validates the hominin status of *S. tchadensis* as they share a similar constellation of derived characteristics (Suwa *et al.* 2009a).

Pelvis

The importance of the pelvic and femoral morphology in interpreting the hominin status of *Ar. ramidus* cannot be overstated. Lovejoy and colleagues (2009d) see derived features in these elements that indicate *Ar. ramidus* was a facultative biped, capable of effective bipedal walking. Like other skeletal elements, the pelvis was said to display a mosaic constellation of traits (Lovejoy *et al.* 2009d). The ischium was large, robust and ape-like, while the ilium was short inferiorly-superiorly, like those in later hominins adapted to obligate bipedalism (Lovejoy *et al.* 2009d). The ilium also featured an anterior inferior iliac spine, a bipedal hominin trait that is not present in extant hominines (Lovejoy *et al.* 2009d).

However, these claims are open to interpretation due to the poor preservation and fragmentary nature of the recovered pelvic elements. The pelvis of *Ar. ramidus* is represented by two extremely fragmentary and badly distorted os coxae, and

unfortunately, no sacrum was recovered (Lovejoy *et al.* 2009d). To say the pelvis was heavily reconstructed would be an understatement. Claims for the presence of a greater sciatic notch and a forward curvature or flaring of the iliac blade, both bipedal characteristic, are not at all discernable in the images of the original left os coxae (Lovejoy *et al.* 2009d). The pelvic elements are not presented in normal anatomical positions, but rather are photographed at unusual angles which obscure the reader's interpretations of certain pelvic features, such as the reported greater sciatic notch (Lovejoy *et al.* 2009d). It would have been helpful to have a completely lateral view included to allow for study of the acetabulum, the projection of the anterior inferior iliac spine, and the aforementioned greater sciatic notch.

Major portions of the iliac crest appear to be missing from the wing of the ilium, and this makes it hard to determine the vertical height of the ilium; the ilium may be higher inferiorly-superiorly than the fossil would indicate. However, the reconstruction seems to imply that the majority of the pelvis is there, as the reconstruction is equal in vertical height to the fossil pelvis (Lovejoy *et al.* 2009d). Also, the blade of the fossil ilium is extremely flat and lacking in any hominin-like curvature and is very hominine-like in this regard. Lovejoy and colleagues (2009d) conclude that this is due to taphonomic processes, and their reconstructed os coxae turned out to be very different morpho-logically than the recovered fossil, as it is far more hominin-like in appearance.

Also presented as hominin-like is the sacrum that is said to be wider mediolaterally than the narrow sacra of extant hominids (Lovejoy *et al.* 2009d). However, no sacrum was ever recovered, and their reconstructed sacrum is purely hypothetical (Lovejoy *et al.* 2009d). The breadth of the sacrum was estimated based on the angle of the articulation of the pubic symphysis; assuming they can articulate the two halves of the pubic symphysis properly, the resulting alignment of the os coxae should reveal the sacral width. But the pubic symphysis is also fragmentary and distorted, and the reconstructed pubis symphysis also differs in morphology from that of the original fossil (Lovejoy *et al.* 2009d).

Thus, the validity of the reconstructed sacrum can be called into question, and as a result, the shape of the entire pelvic girdle. Where the recon-struction differs from the fossils, it differs towards the hominin direction. It should also be noted that this reconstruction is still far less hominin-like than that of *Au. afarensis* (Lovejoy *et al.* 2009d). The ilium is most likely shorter in inferior-superior length than that of a hominine but the ischium and pubis are more akin to those of hominines. The morphology of the sacrum and the presence of either a greater sciatic notch or any anterior curvature of the iliac blades are debatable based on the fossil evidence presented at this point. The pelvis is, therefore, primitive relative to *Au. afarensis* and appears to be only partially derived in the hominin direction.

It is interesting to note that, while a complete tibia was recovered for *Ar. ramidus*, as it is clearly visible in the photograph of Ardi's skeletal elements, no description of the tibia was included in the analysis of the skeleton (David Begun, personal communication, 2010; White *et al.* 2009a). This is surprising as the morphology of the tibia is highly informative in discerning bipedality, as was the case in the description of the proximal tibia of *Australopithecus anamensis* (Leakey *et al.* 1995). In *Au. anamensis* the medial and lateral condyles of the tibia were approximately equal in size, lengthened anteriorly-posteriorly, and concave in shape,

similar to those found in bipedal hominins and unlike the smaller convex condyles found in extant quadrupedal hominids (Leakey *et al.* 1995). As the move towards obligate bipedalism required the re-distribution of body-mass through two legs rather than four, the remodelling of the knee joint is thought to be highly diagnostic of bipedalism, and the *Au. anamensis* tibia is regarded as the earliest uncontested evidence of bipedalism in the fossil record (Harrison 2010; Leakey *et al.* 1995; Richmond, Begun, and Strait 2001). One can only speculate why the tibia of *Ar. ramidus* was not similarly subjected to such an analysis.

Hands and feet

Where as the skull and pelvis of *Ar. ramidus* were both highly fragmented and distorted, a major boon was the recovery of intact hand and foot elements, bones that are not often recovered but are valuable assets in assessing the phylogeny and locomotion of *Ar. ramidus* (White *et al.* 2009). The hand morphology is superficially that of a generalized arboreal hominid and does not show any specific adaptations to knuckle-walking or suspension (Lovejoy *et al.* 2009b). Superficially, the hand is long and features curved phalanges, but the pollex[8] is larger and more robust than that of *Pan*; the metacarpals are shorter and lack the ridges and grooves that provide stability in the knuckle-walking *Pan* and *Gorilla* (Lovejoy *et al.* 2009b). The hand is primitive relative to *Australopithecus*, which had shorter phalanges relative to the hallux, but it must be noted that *Au. afarensis* also retained arboreal characteristics in the hand; it was not until the emergence of *Homo* that the hand became significantly restructured (Tocheri *et al.* 2008).

It should also be noted that extant hominid hand morphology is generalized and highly adaptable to various forms of locomotion and grasping, and this might be its greatest adaptive advantage (Tocheri *et al.* 2008). The overall postcranial morphology of *Ar. ramidus* and the hand, in particular, is said to rule out the knuckle-walking hypothesis as the form of locomotion in the LCA (Lovejoy *et al.* 2009b, 2009c; White *et al.* 2009). It is highly doubtful that *Ar. ramidus* was a knuckle-walker, but it needs to be established that *Ar. ramidus* is indeed a hominin for this information to invalidate the knuckle-walking hypothesis. Also, it is possible that all vestiges of knuckle-walking might have been lost by this time in hominin evolution, although I find this to be unlikely given the amount of time available (perhaps less than one million years based on the youngest molecular divergence dates) (Harrison 2010; Patterson *et al.* 2006; Richmond, Begun, and Strait 2001). Complicating the knuckle-walking hypo-thesis is the suggestion that the appearance of knuckle-walking adaptations in the hand are a result of plastic remodelling of the bone, and are not genetically derived adaptations (Tocheri *et al.* 2008). As such, the degree of remodelling depends upon the weight of the animal, and the degree to which knuckle-walking was employed as a form of locomotion (Tocheri *et al.* 2008). *Pan paniscus* hand bones can show no signs of diagnostic knuckle-walking traits in their bone anatomy, and, thus, knuckle-walking may have been employed by early hominins without evidence showing up in the fossil record (Begun 1993; Shea and Inouye 1993). This is only mentioned to show the difficulties in trying to infer behaviour from fossilized morphology.

Enough major foot elements were also recovered to clearly demonstrate that *Ar. ramidus* had a divergent hallux, another primitive characteristic that appears to be lacking in the more derived *Au. afarensis* (Lovejoy *et al.* 2009a). The divergent hallux,

in concert with the robust pollex, would suggest that *Ar. ramidus* operated as an arboreal clamberer, using the hands and feet to grasp branches securely (Lovejoy *et al.* 2009a; Lovejoy *et al.* 2009b). However, despite the clearly divergent and primitive hallux, it was claimed that the foot of *Ar. ramidus* was unlike that found in any hominine in that the second pedal digit was adapted to provide stability when travelling bipedally and it lacked the flexibility of the *Pan* foot that enables the chimpanzee to excel at vertical climbing (Lovejoy *et al.* 2009a). Thus, the foot of *Ar. ramidus* is claimed to be both primitive in its ability to climb, yet derived enough to allow it to walk bipedally (Lovejoy *et al.* 2009a). It is difficult to make comparisons with the foot of *Ar. ramidus* to other hominins or hominines as this combination of adaptations is unlike any described previously. The feet of both *Pan* and *Homo* would be considered derived relative to *Ar. ramidus* but in different directions (Lovejoy *et al.* 2009a, 2009c). There have yet to be any publications critiquing the interpretations of the *Ar. ramidus* foot. However, the foot appears to be superficially very primitive in morphology as does the hand previously described. In combination, the hands and feet suggest that an interpretation of the foot as an adaptation to arboreal clambering seems to be on a more solid footing than does the additional inference that the foot was equally capable of facultative bipedalism.

Ardipithecus *and the hominines*

One issue of concern regarding the descriptions of *Ar. ramidus* is a lack of comparison of this material to known fossil hominines and hominids. This is partly understandable as one obstacle in obtaining a consensus in hominin evolutionary studies has always been the dearth of known hominine fossils, both contemporaneous and ancestral to known fossil hominins (Bernor 2007). As a result, *Pan* is most often used as a referent to hypothesize the morphologies and behaviours of the LCA, especially those synapomorphies[9] that are shared by *Pan* and *Gorilla*, as the principle of parsimony suggests that these traits would be present in the LCA (Begun 2007; Richmond, Begun, and Strait 2001). However, it must be remembered that both of these lineages have been evolving since they diverged from the LCA, and traits that are assumed to be homologous may in fact represent homoplasies (White *et al.* 2009). Thus, the discovery of fossils of panins and those hominines ancestral to the LCA are of utmost importance to constructing evolutionary relationships and in addressing whether traits are in fact homologies or homoplasies.

The specific morphology of the LCA needs to be indentified if questions of hominin evolution are to be resolved satisfactorily. The extant hominines may be highly derived morphologically, thus obfuscating the morphology of the LCA. Most Middle or Late Miocene hominids display one or more hominin characteristics, such as thick molar enamel, reduction of canines and reduced facial prognathism – characteristics that are absent from extant hominines. This complicates the picture of what are primitive characteristics for the LCA (Begun 2002, 2007). Furthermore, if questions of hominin evolution are to be resolved, future research needs to be directed at the discovery of these hominines as few fossils currently exist. In the meantime, *Ar. ramidus* can only be compared to the few hominine taxa presently known, and it should be kept in mind that any tentative conclusions may be open to major revisions following future discoveries.

There is a large gap in the fossil record between the last known African and European hominids at roughly 10 Ma and

the emergence of the first purported hominin at 7 Ma (Bernor, 2007). There is still a question as to whether or not these Middle Miocene African hominids gave rise to the LCA, or whether a Middle Miocene European hominid returned to Africa to spawn the LCA (Begun 2009; Harrison 2010). Until very recently, no African hominids were known from this window, which formed the basis of the European origin hypothesis (Begun 2002, 2009). If they were not found in Africa, it implied that they must have come from elsewhere (Begun 1994).

Dryopithecus had often been postulated as a generalized hominid that may have given rise to the hominines, as it shares primitive characteristics with extant hominids, such as a suspensory form of locomotion. It does lack the derived characteristics of the Asian hominids (the pongines), traits which would have excluded *Dryopithecus* as being a possible ancestor to the African hominines (Begun 1994, 2009). While molecular genetics have solidified the *Homo-Pan* clade (Patterson *et al.* 2006), fossil analyses of *Dryopithecus*, compared to both *Pan* and fossil hominins, suggest that *Dryopithecus* cannot be ruled out as a possible ancestor to this clade (Begun 1992, 1994). *Dryopithecus* may instead be a sister taxon of an unknown Late Miocene European hominid that returned to Africa to spawn the hominines (Begun 2002). Other Late Miocene European forms include the possibly facultative biped, *Oreopithecus* (Begun 2002, 2007). However, evidence for bipedality in *Oreopithecus* is even less certain than it is for *Ar. ramidus*, and it is more likely that *Oreopithecus* was a suspensory ape, with an autapomorphic[10] dentition (Begun 2002, 2007). *Ouranopithecus* has also been suggested as a possible LCA for the hominins, as it is the best known late Miocene form, with dentition morphologically similar to extant hominines, including the recently discovered *Nakalipithecus* (Begun 2007; Senut 2007). However, *Ouranopithecus* differs from *Dryopithecus* and extant hominines in having derived characteristics shared with hominins, including molar enamel that approaches *Australopithecus* in thickness along with a similar adaptation to heavy mastication (Begun 2007; Senut 2007). The similarities between *Ouranopithecus* and *Nakalipithecus*, both chronologically and morphologically may, in fact, support the hypothesis that a European hominid moved into Africa to give rise to the hominines. There have been major mammalian dispersal events throughout the Tertiary Period, and just because extant forms are found in certain locales today, it does not necessarily mean that their ancestors must have originated in the same place (Begun 2009).

The Eurasian origin hypothesis may be challenged by newly described African hominids. Note that I have been referring to both the African and European forms as hominids, as only those hominids of the lineage that gave rise to the LCA can properly be described as hominines, and the issue to which lineage represents the hominines remains unresolved (Harrison 2010). The first of these African fossil hominids, *Chororapithecus*, was described in 2007 and is represented by a number of individual teeth dating to 10 Ma from East Africa (Suwa *et al.* 2007). The molars of *Chororapithecus* were said to be similar in size and morphology to those of *Gorilla*, and the new taxa was forwarded as a possible gorilla ancestor (Suwa *et al.* 2007). Later in the same year, *Nakalipithecus* was also published represented by a right partial mandible and individual tooth fragments; this new taxa was also dated to 10 Ma (Kunimatsu *et al.* 2007). *Nakalipithecus* was interpreted as being ancestral to extant hominines, the molars supposedly being similar in morphology to extant hominines

in both size and enamel thickness (Kunimatsu *et al.* 2007). The only other African hominid known from this period, and again only from dental remains, is *Samburupithecus*, but this taxa presents morphologies that are distinct from extant apes, and *Samburupithecus* may be too derived to be ancestral to extant hominids (Kunimatsu *et al.* 2007). Unfortunately, in the case of *Nakalipithecus*, the occlusal surfaces of the molar teeth are badly damaged, thus rendering any phylogenetic[11] comparisons problematic (Kunimatsu *et al.* 2007).

While these discoveries show that there were indeed a few hominids present in Africa between 10 Ma to 7 Ma, the small hypodigms[12] and the poor quality of the specimens makes any phylogenetic comparisons to earlier hominids and later hominins contentious. Here, it should be noted that the dearth of hominine fossils in Africa may amount to an absence of evidence, rather than an evidence of absence, as known fossil hominid and hominin sites represent an area equal to only 0.1% of the African continent (Bernor 2007). Since searches for fossil hominins have historically received more attention from palaeontologists than those for fossil hominids, and since hominins and hominids likely occupied different ecological niches, it is highly likely that fossil African hominids are out there waiting to be found. The recently discovered hominins of Chad (Brunet *et al.* 1995, 2001) lend credence to this alternative hypothesis of hominine origins, and thus far, researchers may have been looking in the wrong places.

Ardipithecus *and* Sahelanthropus tchadensis

After a gap of roughly three million years in the African hominid fossil record comes the purported hominin *Sahelanthropus tchadensis*. *S. tchadensis*

was a surprise, not only for its early date of 7 Ma and interesting mosaic of primitive and derived characteristics, but more so for where it was discovered—in Chad, more than 2,500 km west of the East African fossil hotspots (Brunet *et al.* 2002a). Some have argued that *S. tchadensis* must have predated the divergence time of the LCA, and as such, it is unlikely to be a hominin (Wolpoff *et al.* 2002). However, according to molecular studies, there may have been a period of hybridization occurring between these soon to be separate lineages, which would suggest that fossils presenting different constellations of mosaic traits should be expected (Patterson *et al.* 2006). Both *S. tchadensis* and *Ar. ramidus* are compatible with this prediction.

Despite predating *Ar. ramidus* by over two million years, S. *tchadensis* is the only other skull available for comparison until *Au. afarensis* made an appearance, and a detailed comparison is necessary. The braincase of *S. tchadensis* is primitive and hominine-like in its cranial capacity, while the face is highly derived and hominin-like (Brunet *et al.* 2002a). It lacks the facial prognathism of extant hominines, and all known canines are reduced in crown size and present with apical wear (Brunet *et al.* 2002a, 2005). There is no functional canine/premolar honing complex in known specimens, and the canines only show a slight degree of distal edge wear (Brunet *et al.* 2002a, 2005). Both skulls feature short basicranial lengths and inferiorly located positions of the foramen magnum (Suwa *et al.* 2009a). Taken together, they are indicative of bipedalism to the degree that this trait can be inferred from cranial material alone (Suwa *et al.* 2009a; Zollikofer *et al.* 2005). *S. tchadensis* shares all these derived hominin-like characteristics with the virtual reconstruction of *Ar. ramidus*. *S. tchadensis* was also the subject of a CT-based virtual reconstruction

(Zollikofer *et al.* 2005), but the fossil skull of *S. tchadensis* was 95% complete to begin with and did not suffer major distortion; thus, the confidence in its reconstruction greatly exceeds that of the *Ar. ramidus* reconstruction.

There are significant differences in the two skulls, as should be expected in fossils that are greatly separated geographically and temporally. The robust supra-orbital torus of *S. tchadensis* is unique among extant hominines and early hominins and clearly separates it from *Ar. ramidus* (Brunet *et al.* 2002a; Suwa *et al.* 2009a). *S. tchadensis* also lacks the supraorbital sulcus present in *Ar. ramidus* (Suwa *et al.* 2009a; Zollikofer *et al.* 2005). While both crania have similar cranial capacities, as mentioned above, *Ar. ramidus* has a braincase that is superficially similar to that of *Au. afarensis,* while *S. tchadensis* has a braincase that is long and low and distinct from those of early hominins and extant hominines (Kimbel and Delezene 2009; Suwa *et al.* 2009a; Zollikofer *et al.* 2005). The occipital region projects posteriorly, resulting in an oblong or angular occipital region when viewed laterally. *S. tchadensis* also features heavy nuchal cresting, again unlike that of *Ar. ramidus* (Brunet *et al.* 2002a, 2002b). The *S. tchadensis* skull may express more robusticity as it is a male specimen, while the *Ar. ramidus* skull is supposedly a female (Brunet at al. 2002a; Suwa *et al.* 2009a). Like the possibility that Ardi may, in fact, be male, it was suggested that the skull of *S. tchadensis* is that of a female hominine rather than a male hominin (Wolpoff *et al.* 2002). However, if the lack of facial prognathism and canine reduction is attributed to *S. tchadensis* as being a female hominine, one is left to explain the robusticity of the occipital torus and nuchal cresting. As a result, this interpretation appears to be a less parsimonious

explanation (Brunet *et al.* 2002b; Wolpoff *et al.* 2002).

In the description of the skull of *Ar. ramidus,* the hominin characteristics it shared with *S. tchadensis* were trumpeted to the degree that it was claimed that *Ar. ramidus* validated the hominin status of *S. tchadensis* (Suwa *et al.* 2009a). It had been suggested previously that the plethora of early hominin taxa may not belong in separate genera, and that when further evidence is discovered, these genera may have to be revised; perhaps they might all be sunk into *Ardipithecus* (White *et al.* 2006). It is unsurprising in hindsight that the similarities to hominins and *Ar. ramidus* would be stressed in a comparison of these two taxa. Of course, since 2.5 million-years and 2,500 km separate the two fossils, it stretches credulity that a simple case of anagenetic evolution can be assumed, especially in light of the number of morphological differences between the two taxa.

Ardipithecus *and* Orrorin tugenensis

Discovered just prior to *S. tchadensis* and dating to 6 Ma, *Orrorin tugenensis* is the next oldest of the purported first hominins, and the fossil material described increases morphological diversity of these early taxa (Senut *et al.* 2001). The hypodigm for *O. tugenensis* includes mandibular and maxillary fragments, numerous teeth, and, most significantly, postcranial elements including the BAR 1002'00 femur (Senut *et al.* 2001). The canines of *O. tugenensis* are very similar to those found in female *Pan* and are the most primitive of any of the purported first hominins (Senut 2007). They are dagger-like in morphology and display vestiges of a canine/premolar honing complex and an accompanying diastema (Senut *et al.* 2001; Senut 2007). While the postcanine teeth were smaller in size than those of *Australopithecus*, they displayed thick molar enamel similar to those of later

hominins (Senut *et al.* 2001). *O. tugenensis,* thus, presented a dental morphology that was expected in a transitional form (Senut *et al.* 2001). The biggest surprise surrounding *O. tugenensis*, and what suggested that this taxa was a hominin, was the morphology of the BAR 1002'00 femur (Senut *et al.* 2001). The femur was described as not only being that of a biped, but of a biped with a fully modern bipedal gait that had lost all of its arboreal adaptations (Senut *et al.* 2001). Since *O. tugenensis* was suggested to be more modern in femoral morphology than *Australopithecus*, which *Orrorin* preceded in time, its discoverers concluded that *O. tugenensis* was directly ancestral to the genus *Homo*, and that the genus *Australopithecus* lay on an evolutionary side branch (Senut *et al.* 2001).

The highly derived *Homo*-like morphology of the femur rested on an analysis of the gross morphology of the bone and an examination of the cortical bone thickness of the femoral neck (Galik *et al.* 2004). In extant hominines, cortical bone thickness is symmetrical around the circumference of the femoral neck, a response to the variability in loading stresses placed upon the neck due to their arboreal adaptations (Galik *et al.* 2004). In bipeds, the stress pattern is less varied, and, thus, cortical bone thickness is asymmetrical; a biped should theoretically be identifiable based on the pattern of cortical bone thickness (Galik *et al.* 2004). *O. tugenensis* was found to match the pattern of *Homo*, both in internal and external bone morphology (Galik *et al.* 2004). Critics were quick to point out that the resolution of the CT scans was so poor that no confidence could be placed on any conclusions based on the internal morphology (Ohman, Lovejoy, and White 2005). As encountered previously with *Ar. ramidus,* the use of new technologies does not necessarily provide easy solutions for palaeontologists. It should

also be noted that the critics of Galik *et al.* (2004) included the describers of *Ar. ramidus*, and as such, they were not likely to agree with a conclusion that shunted this lineage to an evolutionary side branch (Ohman, Lovejoy, and White 2005). In a similar vein, it was the describers of *O. tugenensis* that were involved in the most vocal opposition to the hominin status of *S. tchadensis*, as it usurped their position as the discoverers of the oldest hominin (Wolpoff *et al.* 2002).

The status of the BAR 1002'00 femur was revisited in a later analysis that would both validate its status as a biped, while at the same time concluding that the external morphology of the *O. tugenensis* femur is indistinguishable from that of *Australopithecus* (Richmond and Jungers 2008). The femur was compared anatomically to those of *Pan*, *Australopithecus* and *Homo*. It found that the femur was least similar to *Pan* and did not fall within the range of *Homo* variation (Richmond and Jungers 2008). This study both vindicated *O. tugenensis* as a biped, while simultaneously invalidating the notion that *O. tugenensis* was a separate lineage from *Australopithecus* that would have given rise to *Homo* through the hypothetical taxa *Praeanthropus* (Richmond and Jungers 2008; Senut 2007). Parsimony would suggest that early bipeds would have an *Australopithecus*-like femur, and yet would be more primitive dentally. *O. tugenensis* fit within this hypothesis.

However, the description of the new *Ar. ramidus* material affects the interpretation of the *O. tugenensis* material, increases the morphological variation present in early hominins and complicates the constructions of phylogenetic relationships. While the postcanine teeth of *O. tugenensis* are more primitive than *Australopithecus* in lacking the megadontia of that genus, they appear to be derived

relative to the much younger *Ar. ramidus* (Begun 2004; Senut 2007). *O. tugenensis* shows the first signs of molar enamel thickening and increase in molar size prior to *Australopithecus* (Begun 2004; Senut 2007). *Ar. ramidus* and *S. tchadensis* are more alike in postcanine dentition than either is to *O. tugenensis* (Brunet *et al.* 2005; Suwa *et al.* 2009b). To further complicate matters, while the postcanine teeth in *O. tugenensis* are more derived in the hominin direction than those of *S. tchadensis*, the canines appear to be more primitive; they display not only vestiges of a honing complex and diastema but also retain some of the dagger-like morphology of *Pan* (Senut *et al.* 2001; Brunet *et al.* 2005). While *O. tugenensis* also has an *Australopithecus*-like femur at 6 Ma, the 4.4 Ma *Ar. ramidus* has the postcranial morphology of an arboreal hominine (Richmond and Jungers 2008). Unfortunately, while femoral fragments of *Ar. ramidus* have been recovered, they lacked the proximal end that would enable a direct comparison to *O. tugenensis* (Lovejoy *et al.* 2009d).

Ardipithecus ramidus *and* Ardipithecus kadabba

The last of the purported first hominins, *Ardipithecus kadabba*, underwent a process of taxonomic revision similar to *Ar. ramidus*. *Ardipithecus ramidus kadabba* was originally described as a subspecies of *Ar. ramidus*, a rather odd decision in that the fossil material predated *Ar. ramidus* by 1.2 Ma and featured significant morphological differences to the later specimens (Haile-Selassie 2001). A fairly fragmentary collection of teeth and arm bones, along with a single toe phalanx were recovered from multiple locations and spanned a time range of 5.8 to 5.2 Ma (Haile-Selassie 2001). These finds extended the genus back in time to a point where *Ardipithecus*

became a player in the first hominin sweepstakes, and the hesitancy to name a new species may have, in part, been influenced by a desire to return *Ar. ramidus* to prominence in hominin discussions. Even more influential may be the theoretical approaches of the discoverer, who clearly sees anagenetic processes operating in early hominin evolution (Haile-Selassie, Suwa, and White 2004).

Just as *Au. ramidus* was reassigned to a new genera, the *Ar. ramidus kadabba* material was eventually elevated to the species level as *Ar. kadabba* along with the description of an expanded hypodigm (Haile-Selassie, Suwa, and White 2004). *Ar. kadabba* has canine teeth that are more primitive and *Pan*-like than *Ar. ramidus*, with higher canine crowns and a more dagger-like morphology, as well as remnants of a canine/premolar complex and its accompanying diastema (Haile-Selassie 2001; Haile-Selassie, Suwa, and White 2004). The *Ar. kadabba* canines are most similar to the penecontemporaneous, *O. tugenensis*, although they are relatively more incisiform in morphology (Begun 2004; Haile-Selassie, Suwa, and White 2004; Senut 2007). The postcanine dentition of *Ar. kadabba* differs from *O. tugenensis* in having thinner molar enamel, even thinner than that found in *Ar. ramidus* (Begun 2004; Haile-Selassie, Suwa, and White 2004; Senut 2007).

As mentioned previously, *O. tugenensis* shows signs of postcanine enamel thickening and molar enlargement that is not present in *Ar. ramidus* or the earlier *Ar. kadabba* (Haile-Selassie, Suwa, and White 2004; Senut 2007). The postcanine dentition of *Ar. kadabba* is most similar to *Ar. ramidus*, although *Ar. kadabba* may be more primitive in having slightly thinner enamel and slightly more pronounced molar cusps (Haile-Selassie, Suwa, and White 2004; Suwa *et al.* 2009b).

However, the question remains as to whether thin enamel is actually the primitive condition for the LCA. The recovered toe phalanx was said to be evidence in support of *Ar. kadabba* being a bipedal hominin, in concert with its supposed affiliation with *Ar. ramidus* (Haile-Selassie 2001). However, while the phalanx was recovered in roughly contemporaneous deposits, it was found some distance from other *Ar. kadabba* specimens (Haile-Selassie 2001). As such, it is possible it might not even belong to this taxon, and interpreting bipedalism from a single phalanx strains credulity.

The discovery of *Ar. kadabba* certainly increases the morphological variation present in early hominins, especially when it is recognized as a species in its own right. The original notion that the hominin fossil record had reached a level of fidelity that one could begin to identify subspecies should never have been taken seriously. *Ar. kadabba* is most likely the species ancestral to *Ar. ramidus* as it appears to be primitive in all respects (Haile-Selassie, Suwa, and White 2004; White *et al.* 2006). The primitive nature of *Ar. ramidus* and doubts as to whether it is the ancestor of *Australopithecus* or not, has led to a questioning of its hominin status (Harrison 2010). That being the case, the hominin status of the even more primitive *Ar. kadabba* must be more uncertain in light of the new *Ar. ramidus* material. We now turn to the hypothesized decedents of *Ar. ramidus* to address these issues.

Ardipithecus *and* Australopithecus

Ar. ramidus was originally assigned to the genus *Australopithecus*, and was thought to be a primitive form of this genus, and, ultimately, the stem australopithecine (White, Suwa, and Asfaw 1994). Now that more is known about both *Ar. ramidus* and *Australopithecus,* the evolutionary relationships of these taxa should be re-examined.

Canine reduction, postcanine megadontia, thick enamel, and unambiguous evidence of bipedalism in both the lower limbs and pelvis are all synapomorphies of the genus *Australopithecus* (Kimbel and Delezene 2009). All of these undisputed early hominin characteristics are either absent or ambiguous in *Ardipithecus*.

Au. anamensis

The *Ar. ramidus* material was originally compared to *Au. afarensis*, the stem hominin of the day (White, Suwa, and Asfaw 1994). Since that time, an older and more primitive species of *Australopithecus* has been discovered (Leakey *et al.* 1995). *Au. anamensis* pushed the genus back to 4 Ma, and, as it is either primitive or similar morphologically to *Au. afarensis*, *Au. anamensis* is an excellent candidate to be the ancestor of *Au. afarensis* (Kimbel and Delezene 2009; Leakey *et al.* 1995; White *et al.* 2006). The morphology, geography and chronology of these two species overlap to such a degree that there that is some question as to whether *Au. anamensis* should be treated as a distinct taxon, or whether it represents the early morphology of a chronospecies of *Au. afarensis* (Haile-Selassie *et al.* 2010). The original description of *Au. anamensis* listed diagnostic characteristics that separated it from *Au. afarensis* (Leakey *et al.* 1995). These included smaller and, thus, more primitive postcanine dentition, larger canine teeth, and a sharp recession of the anterior/inferior region of the mandible, all characteristics that distinguished *Au. anamensis* from the type specimen of *Au. afarensis* (Leakey *et al.* 1995; Kimbel and Delezene 2009). However, comparing the holotypes of species is no longer an adequate methodology to assigning specimens to taxa; rather, the entire hypodigm needs to be taken into consideration (Haile-Selassie *et al.* 2010). It

is here that the rich hypodigm of *Au. afarensis* can shed light on hominin evolution in a way individual fossils cannot (Kimbel and Delezene 2009).

Au. afarensis

More is known about the taxa *Au. afarensis* than any other early hominin, and for the first time in paleoanthropology, we can now study the evolution within a particular lineage (Kimbel and Delezene 2009). As mentioned above, the holotypes for these two taxa are morphologically distinctive, but these distinctions become blurred when the two hypodigms are compared in full (Haile-Selassie *et al.* 2010). *Au. afarensis* is now known to be a morphologically variable and sexually di-morphic species, with early specimens displaying morphologies more similar to that of *Au. anamensis* than they are to the larger and more robust specimens of *Au. afarensis* from later time periods (Kimbel and Delezene 2009). With the expansion of the *Au. anamensis* hypodigm, even more morphological and geographical variation has been uncovered, and it is now suggested that these two taxa may represent the same species (Haile-Selassie *et al.* 2010). There now appears to be a lack of diagnostically derived characteristics that would clearly separate *Au. afarensis* from *Au. anamensis* (Haile-Selassie *et al.* 2010). It may be the case that a speciation event did occur, and it should be recalled that a daughter species would look very similar to the parent species. As a result, increasing numbers of fossils may actually cloud the picture, as a fine-grained analysis could capture so much small scale evolutionary change that the speciation event could be lost in the clutter.

However, the transition from *Au. anamensis* to *Au. afarensis* presents by far the best evidence of anagenetic evolution in the hominin fossil record (Haile-Selassie *et al.* 2010). Small evolutionary changes are

traced from 4.0 Ma to 3.0 Ma, in enough detail that there seems to be no evidence of a sudden transition from one form to another (Kimbel and Delezene 2009). Contrast this scenario with the claim that *Ar. ramidus* evolved into *Au. anamensis* between 4.4 Ma and 4.0 Ma (Lovejoy *et al.* 2009c; White *et al.* 2009). Major evolutionary changes in almost all skeletal elements of *Ar. ramidus* would be required in a short period of time, and there is no known fossil evidence to support this transition. For example, there is no hint of the evolution of the australopithecine megadontia and thick molar enamel in *Ar. ramidus*, which would have been indicative of a major ecological shift and would likely have required a significant amount of time to evolve. There should be *in situ* evidence of this transition in East Africa if *Ar. ramidus* was truly ancestral to *Australopithecus*. When you also consider the slow pace of evolutionary change in the *Ardipithecus* linage from 5.8 Ma to 4.4 Ma, it is surprising that there would be an unprecedented shift in morphology from *Ardipithecus* to *Australopithecus* in a small amount of time. This undermines the claim that *Ar. ramidus* was the ancestor of the genus *Australopithecus*.

Conclusions and phylogenetic interpretations

Only when *Ar. ramidus* is analyzed in the context of other early fossil hominins can conclusions be reached in reference to its phylogenetic placement and the pattern that early hominin evolution has followed. To reiterate, the fragmentary nature of the *Ar. ramidus* skeleton casts doubt on the quality of the virtual reconstructions of the skull and pelvis in particular, and, thus, interpretations based on these reconstructions may be subject to revision. Still, elements of the skeleton provide valuable insights into early hominine

morphology. As *Ar. ramidus* is primitive to *Australopithecus* in all major respects, it cannot be excluded as a potential ancestor on these grounds (Lovejoy *et al.* 2009c; White *et al.* 2009). However, since the two taxa were only separated by 400 Ka, it is unlikely that *Ar. ramidus* was, in fact, ancestral to *Australopithecus* (Harrison 2010). In addition, *Ar. ramidus* may lack synapomorphies with *Australopithecus* - those shared derived traits that are crucial in establishing phylogenetic relationships. The pelvis is described as one major synapomorphy, but based on the condition of the fossils and the reliance on the virtual reconstruction, this claim is easily disputed.

The other major synapomorphy *Ar. ramidus* shared with *Australopithecus* is the reduction of the canine teeth. Much has been written on the reduction of the canine in hominin evolution, and clearly, later hominins have reduced canines and the absence of a canine/premolar complex (Haile-Selassie, Suwa, and White 2004; White *et al.* 2006). However, the reduction of the canines may be of limited value in sorting out the phylogenies of early hominins. It is true that there appears to be a trend towards canine reduction from the Late Miocene through to, and continuing within, the genus *Australopithecus* (Haile-Selassie, Suwa, and White 2004; White *et al.* 2006). But this evolution of the canine is most likely akin to the expansion of cranial capacities in the *Homo* lineage, or the changing enamel thicknesses of hominids during the Miocene. It is clear encephalization was a trend occurring over time in *Homo*, but it is of limited value in establishing evolutionary relationships between taxa, or in defining a taxon, just as enamel thickness as a trait viewed in isolation is of little phylogenetic value. Examining the reduction of canines in isolation biases the analysis towards a linear interpretation of hominin evolution (Haile-Selassie, Suwa,

and White 2004; White *et al.* 2006). This anagenetic interpretation of canine evolution is belied by *O. tugenensis*, and *Ar. kadabba*, which had more prominent canines and honing complexes than did the earlier *S. tchadensis* (Brunet *et al.* 2005; Senut *et al.* 2001).

Thick molar enamel and an increase in the size of the postcanine dentition is another hominin synapomorphy that has been used to sort out phylogenetic relationships (Kimbel and Delezene 2009; White *et al.* 2009). Thick molar enamel is a shared hominin characteristic, and time and again it has been inferred that intermediate enamel thickness was the intermediate condition in hominin evolution (Begun 2004). However, many of the often ignored Miocene apes also had thick molar enamel, and the thin enamel of extant apes may be the derived and not the primitive condition (Begun 2007). Here too with the postcanine teeth, there does not appear to be evidence of a linear trend over time. It is *O. tugenensis* that again does not fit the pattern, but this time by being derived in postcanine anatomy relative to later hominins (Begun 2004; Senut 2007). If one is still hoping to find evidence of anagenetic evolution in the early hominin fossil record, disregarding *O. tugenensis*, there appear to be similarities between *S. tchadensis* and *Ar. ramidus* in the skull and dentition (Suwa *et al.* 2009a, 2009b). Indeed, this claim has been made, and the similarities between the two taxa have been stressed, suggesting that these early hominins may belong to the same taxa (White *et al.* 2006). However, while dentally similar and sharing similarities of the basicranium, the skulls of these two taxa are morphologically and geographically distinctive (Suwa *et al.* 2009a, 2009b; Zollikofer *et al.* 2005).

If one is looking for similarities and shared characteristics in early hominin taxa, one will surely find them. All of these early

hominins, or contemporary hominines for that matter, will have to be similar in morphology to the LCA (Harrison 2010; Patterson *et al.* 2006). Most relevant to assessing phylogenetic relationships and determining hominin status are the synapomorphies and autapomorphies. Taking this into consideration, even based on the limited hominin evidence available, there is a considerable amount of morphological and geographic variation present in known taxa (Begun 2004). This variation is most visible when all hominin taxa are submitted to a detailed comparative analysis as this paper has attempted to do.

Ar. ramidus is best interpreted as a unique species in its own right, rather than attempting to accommodate it within preconceived notions as to how hominin evolution should operate. The very primitive morphology of *Ar. ramidus* validates the removal of the hypodigm from *Australopithecus*. It could qualify as a phylogenetic hominin based on the derived nature of the canine teeth, the inferior location of the foramen magnum and the short basicranium. *S. tchadensis* is considered to be a hominin based on similar evidence (Zollikofer *et al.* 2005). That does not imply that either form was truly bipedal. If hominins are defined phylogenetically as any taxa on the human lineage following the divergence with the LCA, the earliest hominins may not necessarily have been bipedal (Harrison 2010). In fact, the postcranial material of *Ar. ramidus* is most indicative of an arboreal animal, rather than a terrestrial biped. If it is a hominin, it could best be described as "a damned odd one" (Ian Tattersall, personal communication, 2010). As such, it is highly likely its assessment as a hominin could be revised based on future fossil discoveries. It is also likely that some of the 'missing' fossil hominines, perhaps including *Ar. ramidus*, may have been misidentified as hominins.

Even if this is the case, rather than being a disappointment, *Ar. ramidus* would be an equally valuable discovery, indicating the large amounts of morphological variation present in both early hominin and hominine morphologies.

This study of the *Ar. ramidus* partial skeleton concludes that, rather than fitting nicely into an anagenetic pattern of early hominin evolution, the unique morphology of *Ar. ramidus* and indeed the unique morphologies of the limited purported hominin taxa known, are best described by a cladogenetic pattern of evolution. More hominin taxa are likely to be forthcoming, and the focus of future research should be finding fossil panins and other hominines, as well as addressing the question of the origin of the African hominines. Searches for fossils should be expanded away from Eastern Africa, as it is very unlikely that all the major evolutionary events in hominin evolution would have occurred there. Rather than fill in a missing gap in the hominin lineage, *Ar. ramidus* has most likely provided yet another branch in what is most likely a bushy family tree.

Acknowledgments

Notes

[1]1 This paper follows a taxonomy that places all the great apes, humans, and their combined ancestors in the family *Hominidae*. This is in line with recent taxonomic practices based on categorizing taxa exclusively on evolutionary relationships (Harrison

2010). Thus, all of these taxa will be referred to as hominids. The African great apes, humans, and their combined ancestors are assigned to the subfamily *Homininae* and will be referred to as hominines (Harrison 2010). Humans and their ancestors, or those taxa found on the branch leading to human after the divergence point with the last common ancestor (LCA) are assigned to the tribe *Hominini* and will be referred to as hominins (Harrison 2010). These are the taxa that have been traditionally referred to as hominids. The chimpanzees and their ancestors, or those taxa found on the opposing branch after the divergence point with the LCA are assigned to the tribe *Panini* and will be referred to as panins (Harrison 2010). While the renaming of hominids as hominins, and simultaneously expanding the definition of hominid to be more inclusive might be confusing, it is becoming more common in paleoanthropology, and has the benefit of recognizing phylogenetic relationships in the nomenclature, and thus should become the standard practice in the discipline.

2 obligate biped: An animal adapted to full-time bipedal locomotion. An obligate biped could still maintain an arboreal component in its behavioural repertoire but would no longer employ a quadrupedal form of locomotion.

3 postcanine megadontia: A significant enlargement of the premolars and molars and typified by the genus *Australopithecus*.

4 facultative biped: A quadruped capable of sustained bipedal locomotion for a significant period of time as part of its normal behavioural repertoire.

5 hallux: The first pedal digit (the big toe).

6 honing complex: An association between the upper canine and lower first premolar where a projecting upper canine is sharpened or honed against the front of the lower first premolar. Honing complexes are present in extant hominids but missing in known hominins who lack large projecting canines.

7 diastema: A space in the tooth row that accommodates a large projecting canine tooth. Diastemata are present in extant hominids but missing in known hominins who lack large projecting canines.

8 pollex: The first manual digit (the thumb).

9 synapomorphy: A shared derived character present in one or more taxa and their last common ancestor but not present in the previous common ancestor.

10 autapomorphy: A unique derived character that evolved for the first time in a particular taxon but is not present in sister taxa or in their shared last common ancestor.

11 phylogenetics: The study of evolutionary relationships among a group of organisms.

12 hypodigm: All of the known material of a taxon.

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