

An Ape or the Ape: Is the Toumaï Cranium TM 266 a Hominid?

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ABSTRACT

The Toumaï cranium TM 266 is the first known from any Late Miocene African hominoid clade, and is one of the best preserved crania of any Miocene hominoid. Since its publication there has been debate in the scientific literature and discussion in the popular press over the assertion that this cranium is significant because it is the earliest known hominid¹. The basis of the hominid assessment rests on two interpretations of the anatomy: a hominid-like, small, flat-wearing canine; and, cranial features reflecting an upright stance and bipedal locomotion. In fact, it is widely reported that the specimen is an upright hominid biped (Haile-Selassie et al., 2004; Kimbel, 2004; Lieberman, 2002), although this is yet to be verified by independent observations and study. The history of paleoanthropology may be relevant to this assessment, because there have been similar claims for other extinct primate species. Here, we evaluate the hypothesis that *Sahelanthropus* (the genus TM 266 is attributed to) is a hominid by examining features of the canine and of the cranial base that are said to reflect canine reduction and change of function, and upright posture and bipedal locomotion. These are hominid autapomorphies and their presence or absence in late Miocene hominoids has fundamental importance for identifying the hominid clade.

INTRODUCTION

The *Sahelanthropus tchadensis* (TM 266) cranium has been described in its original (Brunet et al., 2002) and reconstructed (Zollikofer et al., 2005) forms, and interpreted as a hominid (Begun, 2004; Brunet et al., 2002; Guy et al., 2006), even as the same hominid species as *Ardipithecus kadabba* (Haile-Selassie et al., 2004). The basis of the hominid assessment rests on two interpretations of the anatomy—a hominid-like small, flat-wearing canine, and cranial features reflecting an upright stance and bipedal locomotion. It was widely reported that the specimen is an upright hominid biped (Haile-Selassie et al., 2004; Kimbel, 2004; Lieberman, 2002), although this is yet to be verified by independent observations and study. The history of paleoanthropology may be relevant to this assessment, because there have been similar claims for other extinct primate species.

Canine characteristics play an important role in the assessment of *Sahelanthropus* as a hominid and this role has been widely recognized since Darwin's modeling of hominid origins. While the search for hominid origins has not been restricted to the Miocene (Schultz, 1936; Simons, 1964), there is a significant and influential 20th century his-

tory of mistaking Miocene ape dentitions for hominid ones. Best known is *Ramapithecus* (Lewis, 1934), and there is a record of misinterpretation as hominids for *Gigantopithecus*, *Oreopithecus*, and others. *Ramapithecus*, together with *Kenyapithecus*, was initially described as resembling hominids in combining a foreshortened face, small, low canine, and parabolic dental arcade (Aguirre, 1972, 1975; Pilbeam, 1966; Simons, 1969). Later, a powerful masticatory apparatus was added to this depiction (Kay, 1981). Whether or not any or all of these characterizations were a valid interpretation of the remains, they constituted a case that was once used to incorrectly place *Ramapithecus* within the hominids (Genet-Varcin, 1969; Greenfield, 1979, 1980; Hrdlička, 1955; Pickford, 1985; Wolpoff, 1982). This case was based on the then dominant Darwinian paradigm of hominid origins and adaptive divergence, hypothesizing the coevolution of four interrelated changes (Jolly, 1973; Tuttle, 1974): terrestrial bipedalism, canine reduction and functional change, tool use, and the change from traditions to culture for passing information across generations. As Pilbeam (1966, p. 3) put it:

Ramapithecus punjabicus is completely hominid in known parts—anterior teeth are small and the rostrum is reduced. Canines therefore could not have been utilized in agonistic display behavior and group defense; presumably, weapon use was established by this time. ... The evidence, admittedly circumstantial at present, suggests a primate perhaps already bipedal and fully terrestrial.

Pilbeam's reasoning was explicitly Darwinian, reflecting the adaptive link between canine reduction, tool use, and bipedalism that Darwin (1871) had proposed. The Darwinian model was widely accepted when this was written.

There is a similar context for understanding the claim of bipedalism for the TM 266 cranium, and there is also historical precedent for this claim. In his 1951 paper questioning the place of the australopithecines in human evolution, "An ape or the ape?" Sir Solly Zuckerman drew the wrong conclusion about the posture and locomotion of *Australopithecus*, and consequently about its phylogeny, because he misunderstood the functional significance of the nuchal area. Zuckerman claimed that *Australopithecus* was an ape because he mistook the cranial anatomy of a biped for that of a quadruped (Robinson, 1954a, b). We remain concerned about the potential for accurately inferring posture and locomotion from cranial features, and develop this topic further here.

The Toumaï cranium TM 266 has the potential to inform this issue. This enigmatic Miocene species mixes characteristics of some australopithecines and some portions of the *Homo* clade such as "*Homo erectus*." Yet, the hominid interpretation was not without objection (Wood, 2002) because TM 266 has also been described as a hominoid ape (Cela-Conde & Ayala, 2003; Wolpoff et al., 2002). The ape interpretation could mean that *Sahelanthropus* was uniquely ancestral to a living ape, or that the species was an extinct related lineage that diverged before the hominids, or that it is close to or actually the last common ancestor of hominids and chimpanzees. If any of the alternative phylogenies is correct, the description of "ape" would be valid. The common ancestor of *Homo* and any ape species is traditionally and currently described as an ape.

That man is derived from a form which ... can be properly called an 'anthropoid ape' is a statement which no longer admits doubt (Le Gros Clark, 1934).

Today ... we recognize ... that the last common ancestor of apes and hominins was a great ape but not necessarily like any particular modern species (Ward, 2003, p. 75).

If the hypothesis that *Sahelanthropus* is a hominid is rejected, it must therefore be categorized as an ape, as described above. Here, we examine the basis for the null hypothesis that there is no phylogenetic difference between *Sahelanthropus* and hominids: can the contention that TM 266 is a hominid be rejected? We consider the two pillars of support for this hypothesis, the evidence of canine anatomy and function, and the cranial evidence supporting the interpretation of upright posture and obligate bipedalism, and consider the constraints provided by molecular diver-

gence date estimates.

Our comparisons are based on the published descriptions, dimensions and photographs of the TM 266 cranium and its computer reconstruction, and on first-hand observations of the other apes and hominids.

AGE AND SEX

AGE

Age assessment of TM 266 is based on the unworn M³ (Brunet et al., 2002). If we use a chimpanzee mean gingival eruption schedule (compiled from a number of sources by Reid et al., 1998) and assuming an occlusal eruption lag of a half to one year (data from humans), we estimate an age at death of more or less 11 years. The development of the cranial superstructures, including the supraorbital torus, is consistent with this age (Leigh and Shea, 1996).

SEX

Supraorbital torus

Our discussion must begin with an assessment of the age and sex of the cranium, because these inform the issue of how hominid-like characteristics may be evaluated. The original assessment of sex was based on the vertical thickness of the supraorbital torus, reported as 18.2 mm (Brunet et al., 2002, figure 3). We noted (Wolpoff et al., 2002) that at this size, the structure exceeds the height of any extant ape or australopithecine supraorbital (Brunet et al., 2002, Figure 3) and could only be matched within the *Homo erectus* sample. The supraorbital height has been reduced in reconstruction and is now 16 mm (Zollikofer et al., 2005, supplementary data). This places it within the range of both male and female gorillas (Figure 1, after Brunet et al., 2002, Figure 3), but still outside the range of any australopithecine species or the range of chimpanzees. This is an unusually large structure for a head so small (Guy et al., 2006).

Because *Sahelanthropus* is not thought to be an immediate ancestor of *Homo erectus*, its similar supraorbital size does not reflect phylogeny, but it might reflect sex, and it is widely assumed to do so. We further examine this possibility. TM 266 is not a gorilla or a chimpanzee; the question is which of these species, if either, the sexual dimorphism of the *Sahelanthropus* supraorbital resembles.

If *Sahelanthropus* has a chimpanzee-like pattern of sexual dimorphism, the amount of overlap between male and female ranges for chimpanzee supraorbital torus thickness is so great that it would be impossible to establish sex from supraorbital torus thickness (see Figure 1). One scientist suggested, "if this is the female, I'd hate to see the male." But if *Sahelanthropus* followed a chimpanzee pattern of sexual dimorphism, this would be hyperbole because we could expect that in many cases the male is similar to the female.

If *Sahelanthropus* follows a gorilla-like pattern of sexual dimorphism, male and female ranges overlap less (see Figure 1), but still overlap so greatly that the size of the TM 266 structure is not diagnostic for sex unless it is particu-

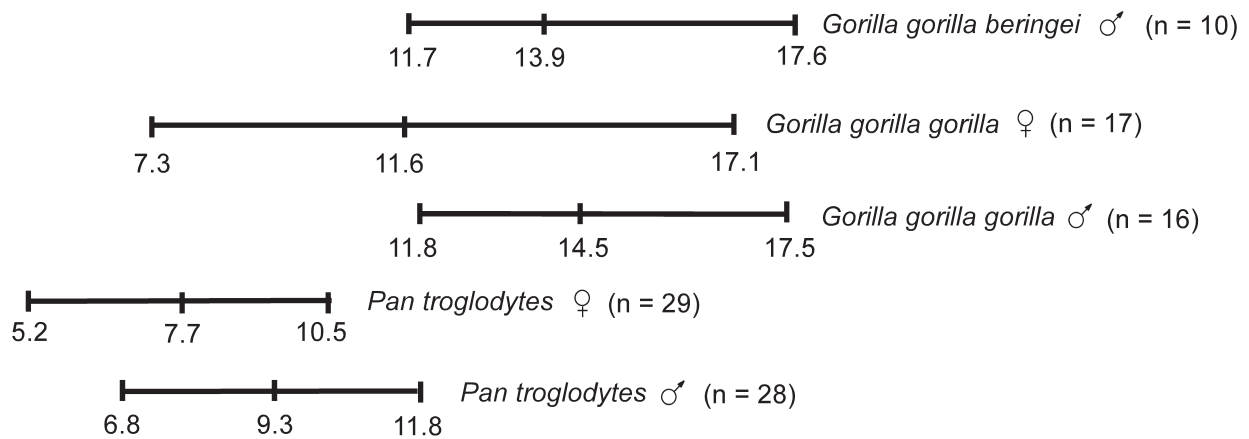


Figure 1. Variation in vertical thickness of the supraorbital torus, comparing samples of the African apes by sex (after Brunet et al., 2002, Figure 3).

larly small. In the Figure 1 data from Brunet and colleagues (2002), the *Gorilla gorilla* male (n=16) minimum is almost exactly at the female (n=17) mean, and the male and female maxima are only 0.4 mm apart. The male gorilla range lies almost entirely within the female gorilla range. For these apes the thicker supraorbitals overlap so that a thick supraorbital torus is not specifically or uniquely characteristic of males.

The vertical thickness of the supraorbital torus, especially if it is large, is not diagnostic for sex within either African ape model. In both African ape species, male and female supraorbitals of the same thickness are expected in the larger part of the size range. If TM 266 was a female, and we do not specify whether it was or was not, the supraorbital torus of the corresponding male could easily be the same size.

Canine size

The canine is a potentially independent source for sex determination, because the canine is the most dimorphic of all the teeth in primates. There is a single maxillary right canine and a left canine root preserved for TM 266. Brunet and colleagues (2002) describe its key features as its small size, mesiodistal elongation and blunt shape. Other comments from the Nature description addressing its shape include “non-incisiform” (Brunet et al., 2002, p. 146), or “less incisiform than *Ardipithecus*” (p. 146), or “not chimp-like” (p. 146), or not diamond shaped. It was said there is a “low distal shoulder” (p. 146), even “lower than *Ardipithecus*,” ... “suggesting an earlier evolutionary stage” (p. 150). However, the original crown shape is difficult to ascertain because of a vertical break in the crown and because of (what is described as) its “extensive apical wear.”

In fact, canine crown size for TM 266 is not exceptionally small for a Miocene ape (Figure 2) and also may not be convincingly diagnostic for sex assessment. Only the breadth can be reliably measured and compared with the dimensions of other teeth because of the vertical break. Among the medium sized Miocene apes, the TM 266 canine breadth is between specimens generally regarded as male

and female (Figure 3; Kelley, 1995), and within the range of variation of both. Scaling for relative canine size is limited to molars, the only postcanine teeth preserved. Breadth ratios are only possible with the third molar because there is no first molar breadth and the breadth given for the second molar is just an estimate and is suspect². However, the third molar is the most variable, and so we examined the ratio of

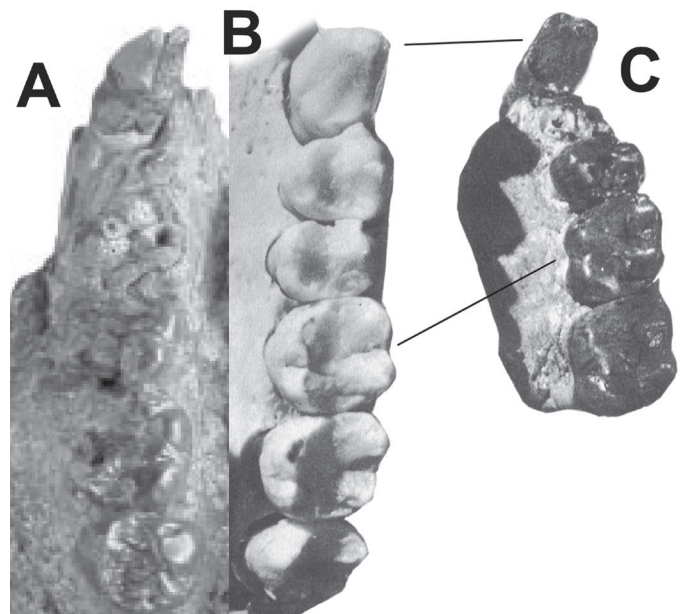


Figure 2. Kenyapithecus maxilla FT 1271 (C) compared with a female bonobo maxilla (B, after Simons, 1969) and the TM 266 palate (A, after Brunet et al., 2002). The TM 266 palate is scaled to the size of the bonobo. Note the reduced canine of the Fort Ternan ape, compared with TM 266 and this small bonobo canine. Compared with the second molar, the Kenyapithecus canine is relatively narrower than the TM 266 canine, but there is a general similarity in molar morphology and canine size between the three specimens that helps show links between TM 266 and Miocene apes that involve canine features that are interpreted as hominid. In our opinion, neither TM 266 nor the Miocene apes with small canines are hominids.

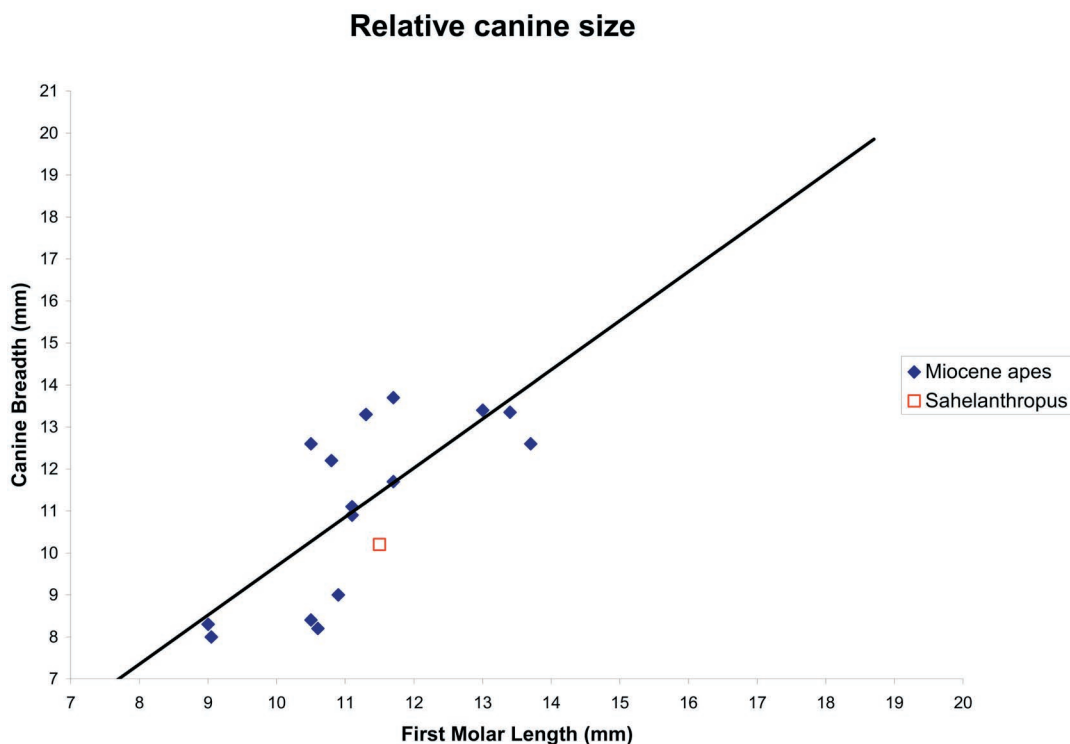


Figure 3. Bivariate plot of canine breadth and M1 length in Miocene apes and TM 266. The linear regression line is defined by the Miocene ape data without TM 266. Note that the individuals with canines smaller than TM 266 (y axis) are Rudabanya RUD-12, Fort Ternan FT-45/46, RUD-15, Haritalyangar D-299/300, and Sinap AS95-500. Most or all of these (depending on author) are considered females. The specimens with larger canines are all regarded as males: Sivapithecus, Ouranopithecus, and Ankarapithecus specimens GSP-9977, 11704 and 15000; YPM-13823; Ravin RPL-775; GSI D-1; GSP-16075; Ravin RPL-228, XIR-1; Sinap MTA-2125. TM 266 canine size falls between male and female Miocene ape distributions; it is large for a female, and small for a male. Assuming that male and female size ranges overlap, as they do for other hominoids, this makes sex determination from the canine uncertain.

the breadth of the canine to the length of the first molar (Figure 3). This may not be the optimum ratio for assessing relative canine size, but we believe it is the most useful one for this particular specimen. Each of these dimensions is midway in the Miocene hominoid distributions, as is their ratio. Deviation from the Miocene ape regression line (see Figure 3) shows the canine is relatively small, but not more so than many other of the Miocene ape canines. The teeth closest in size to TM 266 are the *Sivapithecus* male GSP 9977, and the Sinap *Ankarapithecus* female AS95-500.

Neither the absolute value for canine breadth nor its relative size provides an unambiguous indication of sex. We conclude from the supraorbital and canine comparisons that sex cannot be reliably determined for this single cranium from a new, unknown taxon.

HOMINID FEATURE 1: CANINE WEAR

PATTERN OF WEAR

The blunted apical canine wear of the TM 266 tooth (see Figure 2) is one of the features said to support the hominid assessment. The TM 266 maxillary right canine has significant apical wear, and a transversely oriented distal wear facet (Brunet, 2002; Brunet et al., 2002, p. 151) that is described as a “steep, narrow distal wear strip reaching basally” (p. 150)

that exposes dentin. The TM 266 maxillary canine crown originally must have extended below the adjacent teeth to account for its distal wear which goes almost to the crown’s base, where it wore distally against a projecting P3 cusp even as occlusal wear blunted the apex of the crown.

To varying extents, a number of Miocene ape canines evince wear surfaces with a similar pattern (Figure 4). It is known in males and females of *Ugandapithecus*, *Afropithecus*, *Nacholapithecus*, *Kenyapithecus*, *Ouranopithecus*, *Ankarapithecus*, *Oreopithecus*, and *Sivapithecus*. All these forms also show apical wear of the canine crowns, and poorly developed C-P₃ honing complexes, as reported in TM 266. In some of the above mentioned ape fossils, such as *Gigantopithecus* and *Ouranopithecus*, taking age differences into account, the resemblance to the TM 266 condition is especially marked.

The wear on the canine of the *Gigantopithecus* 1 mandible (Figure 5) is most similar to the TM 266 condition, although the *Gigantopithecus* postcanine teeth are at a later stage of wear, this individual having died later in life. In this *Gigantopithecus* mandible, there is flat apical wear, significantly truncating the tooth, while the distal facet extends toward the base of the tooth and is oriented transversely, just as is described for TM 266. Much less worn lower canines of *Gigantopithecus* (Figure 6) suggest the original height of this



Figure 4. *Ouranopithecus maxilla XIR-1*, a worn maxillary dentition with canines showing a combination of blunted apical wear and transverse wear across the distal surface. This is an older version of the wear combination described for TM 266 (Brunet, 2002; Brunet et al., 2002).

canine crown was probably low, and less worn teeth show the beginning of this wear pattern, with both apical and honing wear facets that eventually become blunting.

It might be that adjudged on the canine wear pattern evidence alone that TM 266 could be regarded as a hominid, just as *Gigantopithecus*, whose expression of apical canine wear is extreme for a Miocene ape, once was. But the explanation for the wear characteristics of *Gigantopithecus* canines and, we expect, for the size and wear characteristics of the TM 266 canine, are better sought in the common basis for what is obviously a homoplasy: an adaptation for powerful mastication (Jolly, 1973). Greenfield (1998) observes that tip blunting of maxillary canines results from edge-to-edge occlusion with the mandibular canine and puncture crushing. Because canine crown height reduction is associated with powerful mastication (Jolly, 1970, 1973), both of these causal explanations are compatible with the wear pattern on the TM 266 canine. However, the unusual magnitude of the wear (see below) suggests that puncture crushing may play the more important role for this primate.

MAGNITUDE OF WEAR

The magnitude of TM 266 apical canine wear is exceptional, given the almost-adult age estimate. While wear on ca-

nine crown tips is much more common in primate females than it is in males of the same species (Greenfield, 1998), wear of the magnitude found in TM 266 is greater than usual in young apes of either sex (see Figure 2), although

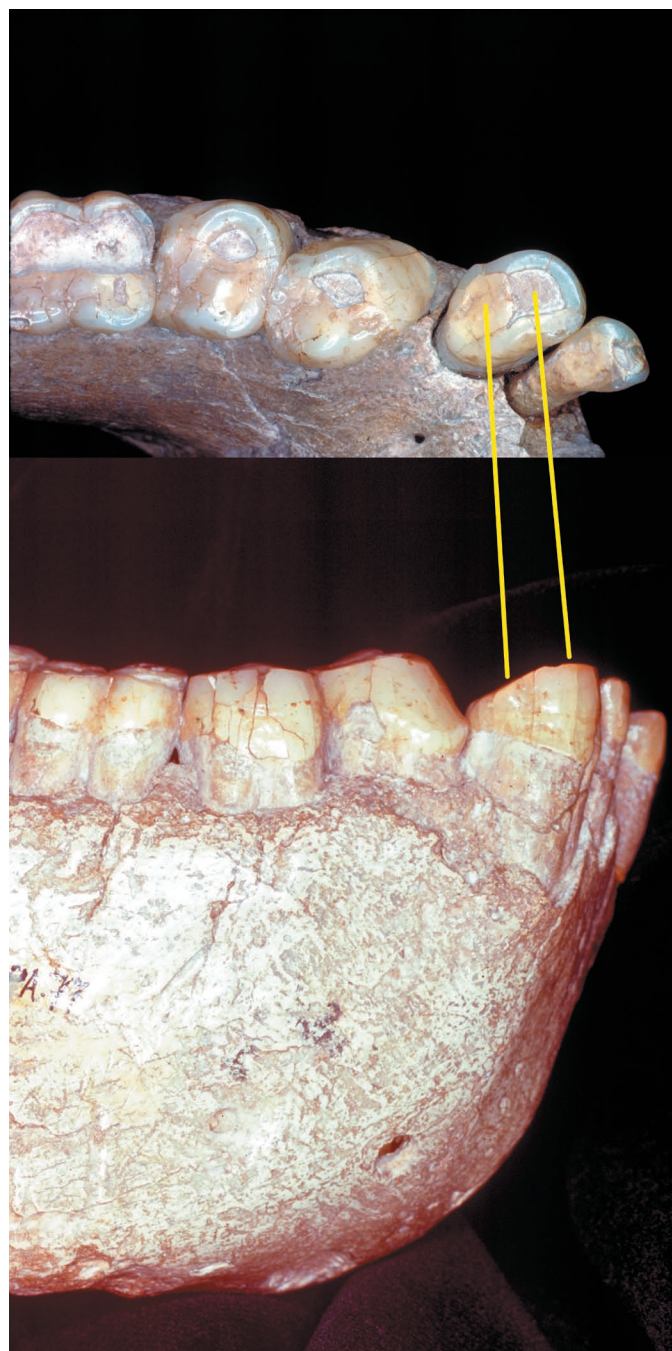


Figure 5. *Gigantopithecus mandible 1* in occlusal (image reversed) and lateral views, showing the teeth between the first molar and the lateral incisor. The canine wear is similar to that of TM 266. Note that the top of the mandibular canine is worn flat, and the distal edge is transversely worn. Dental wear has proceeded further than in *Toumaï*—the *Gigantopithecus* specimen died at an older age—but the wear pattern is quite clearly the same. These surfaces are marked in occlusal and lateral views. The form of a lightly worn *Gigantopithecus* lower canine is shown in Figure 6.

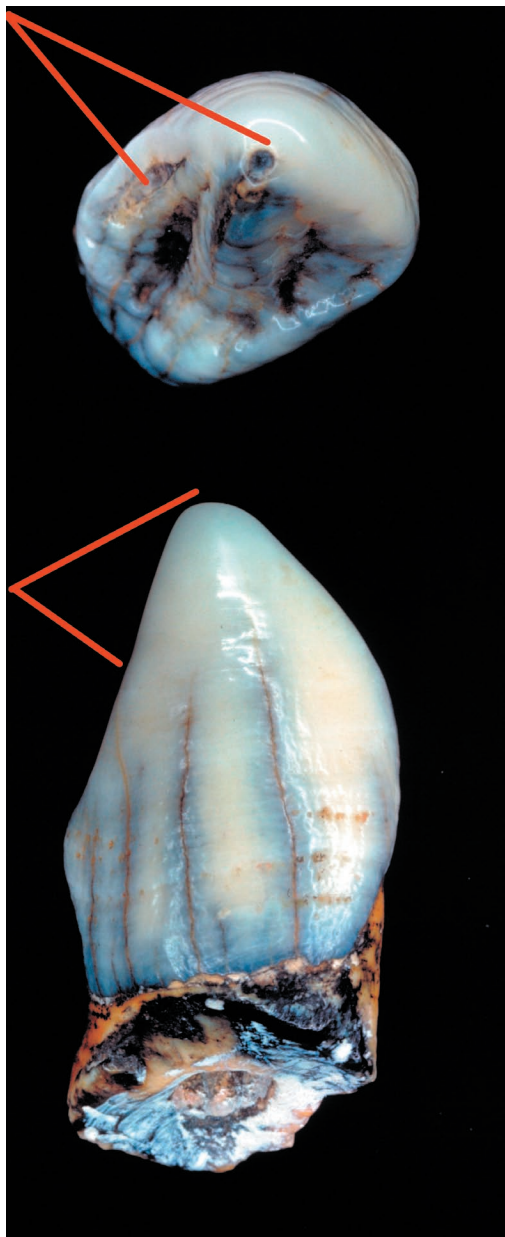


Figure 6. Lightly worn *Gigantopithecus* canine C-9, in labial (below) and occlusal views, showing a distal honing facet (marked in both views) extending part of the way down the tooth, as well as slight apical wear. We see this as an earlier stage of the wear pattern found in the *Gigantopithecus* 1 mandible (Figure 5) and the TM 266 canine (Figure 2). Many Miocene apes also show this combination of blunted and shearing canine wear.

it is common in old ones. Again turning to the chimpanzee model and estimating occlusal eruption from gingival data, the maxillary canine attains occlusal eruption at about 9.5 years for males and 8 years for females (estimated from data in Conroy and Mahoney, 1991). Given the 11 year old maximum age estimate, this gives 1.5 years for the canine to wear significantly if TM 266 is male, and 3 years if it is female. This relative wear on the tooth is said to support a hominid assessment, but it may not because the difference between canine and third molar eruption in *early* hominids

is no more than a year or two greater than it is in apes. In fact, the unusual magnitude of age specific canine wear for TM 266 does not clearly support either taxonomic assessment but instead suggests a masticatory cause that is compatible with the explanation for canine tip blunting discussed above.

HOMINID FEATURE 2: UPRIGHT STANCE AND BIPEDALISM

Obligate bipedalism is the most significant autapomorphy describing the hominid clade (Caspari, 2002; Dart, 1925; Lovejoy et al., 2002; Senut, 2003; White et al., 1994; and many others). Without description of postcranial remains that could be associated with the TM 266 cranium, any assessment of posture and locomotion is bound to be uncertain, and Brunet and colleagues wrote (2002, p. 150): “there is not yet sufficient information to infer reliably whether *Sahelanthropus* was a habitual biped.” They further asserted: “however, such an inference would not be unreasonable given the skull’s other basicranial and facial similarities to later fossil hominids that were clearly bipedal.” This is not an unexpected inference, given their contention that TM 266 is a hominid, and it is not the first time that bipedalism has been inferred for a putative Miocene hominid. But is the inference valid?

We review the three key observations that inform issues of posture, and thereby locomotion. These are the characteristics consistently advanced to support the argument that the TM 266 cranium reflects the consequences of upright posture and bipedal locomotion.

NUCHAL PLANE AND INION POSITION

TM 266 (Figure 7) is described as combining a vault the size of a chimpanzee with a much larger, flattened, gorilla-shaped nuchal plane (Brunet et al., 2002), a contention supported by the cranial capacity and nuchal plane length dimensions Brunet and colleagues provided. At the superior center of the nuchal crest there is a hominid-like development of a *tuberculum linearum*. The gorilla-like form might be taken to show a special relationship with gorillas, the hominid-like *tuberculum linearum* might be taken to show a special relationship with hominids. However, we interpret these biomechanically and contend that the form and features of the nuchal plane provide insight into posture and the relation of the head to the spine by reflecting the size and orientation of the neck musculature.

The TM 266 nuchal plane (Figures 7, 8 and 9) is both long and flat, with a strong *tuberculum linearum* at its most superior aspect that forms an inion-like prominence. The unreconstructed angle of the nuchal plane to the Frankfurt Horizontal is approximately 55° (Wolpoff et al., 2002) and the reconstructed value is 36° (Zollikofer et al., 2005).

Nuchal plane length (inion-opisthion) is a key aspect of this nuchal area. The nuchal plane is described as “relatively longer than in *Pan* [and] *Gorilla* ... and with crests as large as those in *Gorilla* implying the presence of relatively large superficial neck muscles” (Brunet et al., 2002:150), and it extends to the top of the posterior aspect of the vault.

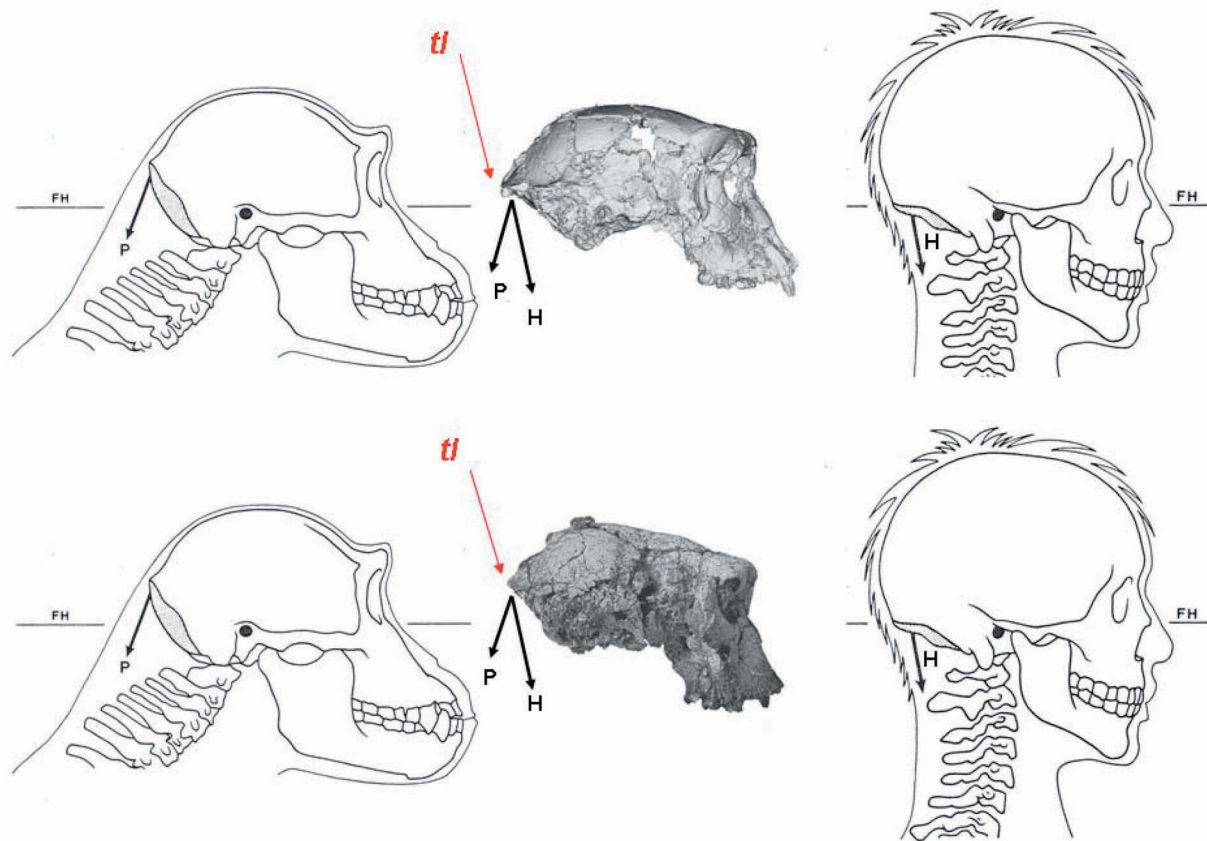


Figure 7. The TM 266 reconstruction (above) and unreconstructed cranium (below) compared with a human (r) and chimpanzee (l) in Frankfurt Horizontal orientation, after Jaanusson (1987), Brunet and colleagues (2002), and Zollikofer and colleagues (2005). The three are shown to the same approximate size and are not to scale. The tuberculum linearum (tl) is marked, as is the approximate line of action of the nuchal muscles for chimpanzee neck position (P) and human neck position (H). The human neck position for TM 266 creates a disadvantageous and unlikely vector for the nuchal muscles because of their deviation from and angle more perpendicular to the nuchal plane.

In fact, the published length of the nuchal plane exceeds all early hominid crania (Figure 10 y axis), in spite of the cranial capacity of the vault which is less than any of the australopithecine crania. For a relative length determination, we compared the nuchal plane length to the cube root of cranial capacity since an accurate measure of cranial length is not possible (Figure 10). Using the cube root rather than the actual capacity estimate puts the two variables in the same units. The comparisons show the TM 266 nuchal plane is relatively longer than in any australopithecine, including the largest-vaulted specimens.

The length, breadth, and many details of the nuchal plane are ape-like and not hominid-like (see Figures 7 and 9), even when comparison is made with the australopithecine with the most posterior foramen magnum position. One expects from these data that the neck muscles have a somewhat different role in TM 266 than in hominids, even hominids with small heads, and that this role is more like the role they play in apes (see Figures 7 and 8). The long, angled nuchal region of TM 266 results in maximum displacement of the nuchal crest in flexion, but extension would be inefficient from this position if the neck were in a human-like configuration. To a lesser but still significant

extent, this would be true for extension of the head with the head in a horizontal position. Neither the canines nor incisors are significantly expanded, which could provide an alternative explanation for at least some aspects of the combination of size, angulation, and position in the nuchal muscle attachment area of TM 266. We contend that these features are a direct reflection of the position and angulation of the neck, and thereby of posture and locomotion.

In addition, the presence of a significant tuberculum linearum at the center of the superior nuchal line denotes a strong development of the ligamentum nuchae, which gives rise to additional muscles involved in neck function and upper limb support. Added to the elongated, angled, and expanded nuchal plane, compared to the hominid condition, this structure reflects an unusually powerful neck and is not an obvious indication of upright stance.

The nuchal plane extends above the Frankfurt Horizontal to the top of the low vault (see Figure 7). This is in dramatic contrast to all known hominids, where the top of the nuchal plane is invariably at or very close to the Frankfurt Horizontal. In their description of the AL 444-2 cranium, Kimbel and colleagues (2004, p. 34) write:

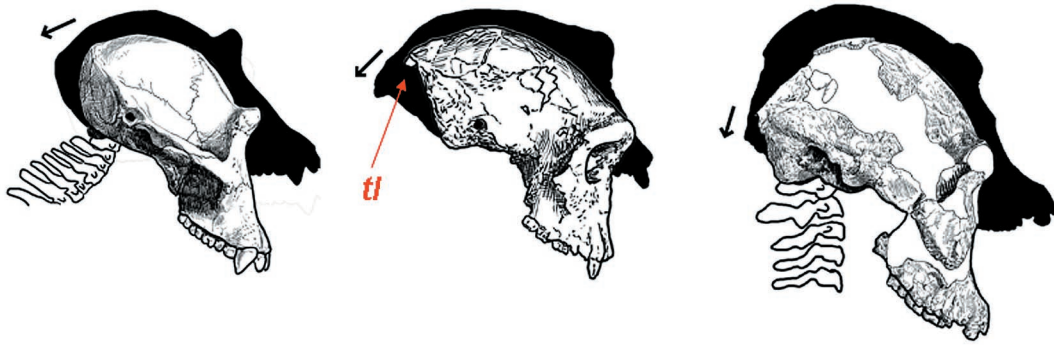


Figure 8. Chimpanzee (l), TM 266 (c), AL 444-2 (r), shown to the same size and each with 30 degree flexion of the cranium about the occipital condyles (invisible behind mastoid region in TM 266 and AL 444-2). The arrow represents the displacement direction at the inion position (tuberculum linearum (tl) for TM 266). The nuchal plane in AL 444-2 is short and the inion is low, approximately at the level of the supramastoid crest. This orientation gives the nuchal muscles a maximally vertical component of force, as reflected by the vector, and the inion displacement is minimum in flexion. All early hominid crania have short nuchal planes with low inion positions because the nuchal musculature originates on a vertical spine and trunk. This results in a low nuchal area height index in hominids. The long nuchal plane and high inion position in TM 266 and the chimpanzee add a significantly posterior component to the nuchal force, and there is a maximum inion displacement in flexion, allowing effective extension with a posteriorly sloping cervical spine and trunk. This angle is less inclined in TM 266 than in the chimpanzee, and the nuchal crest is inferiorly lipped in compensation, reflecting the consequences of high nuchal muscle force and a well-developed ligamentum nuchale.

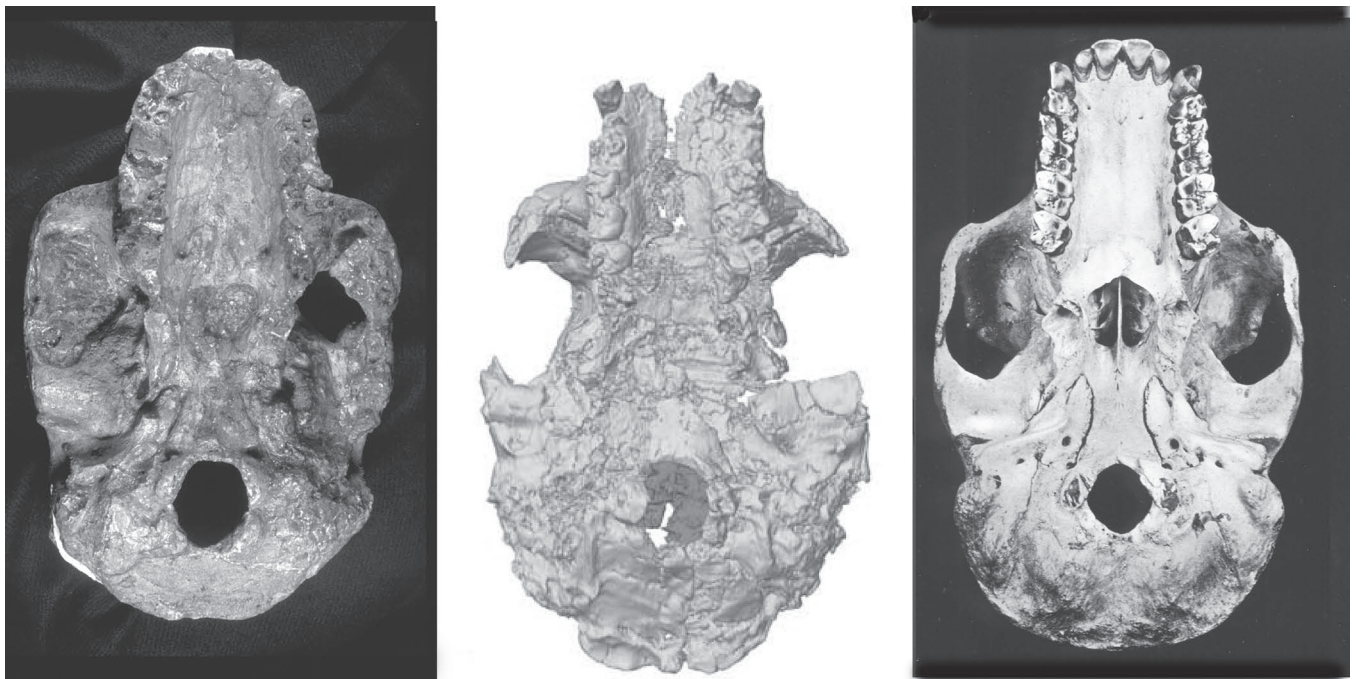


Figure 9. Cranial bases of the reconstructed TM 266 vault (center, after Zollikofer et al., 2005), compared with STS 5, the australopithecine with the most posterior foramen magnum position (left), and a female gorilla from the Senckenberg collection (right, after Elliot, 1913, plate XXXIII). The three are shown to the same approximate size, although the 181 mm base of STS 5 (prosthion-opisthocranion dimension) is markedly smaller than the 211 mm long TM 266 base. By scaling these bases to the same size and exactly matching the anterior foramen magnum (basion) positions, there are also similar positions for canine and third molar, the glenoid and posterior of the temporal fossae. Proportional differences in the nuchal region are evident. The nuchal plane is by far the shortest in the hominid, while longest in TM 266. Adding to the TM 266 length is the visible lipping of the nuchal crest and the significant tuberculum linearum development. The discernable foramina and canals are positioned as in the gorilla, but the expanded TM 266 glenoid fossa and articular eminence is similar to a robust australopithecine. In most basal features the TM 266 base resembles the gorilla and contrasts with this and all other australopithecines. The point is not that the TM 266 cranial base is like all female gorillas, but the surprise is that it should be like any female gorilla (or other ape) given the expectation of adaptations to obligate bipedalism if it is a hominid.

Relative Nuchal Plane Length

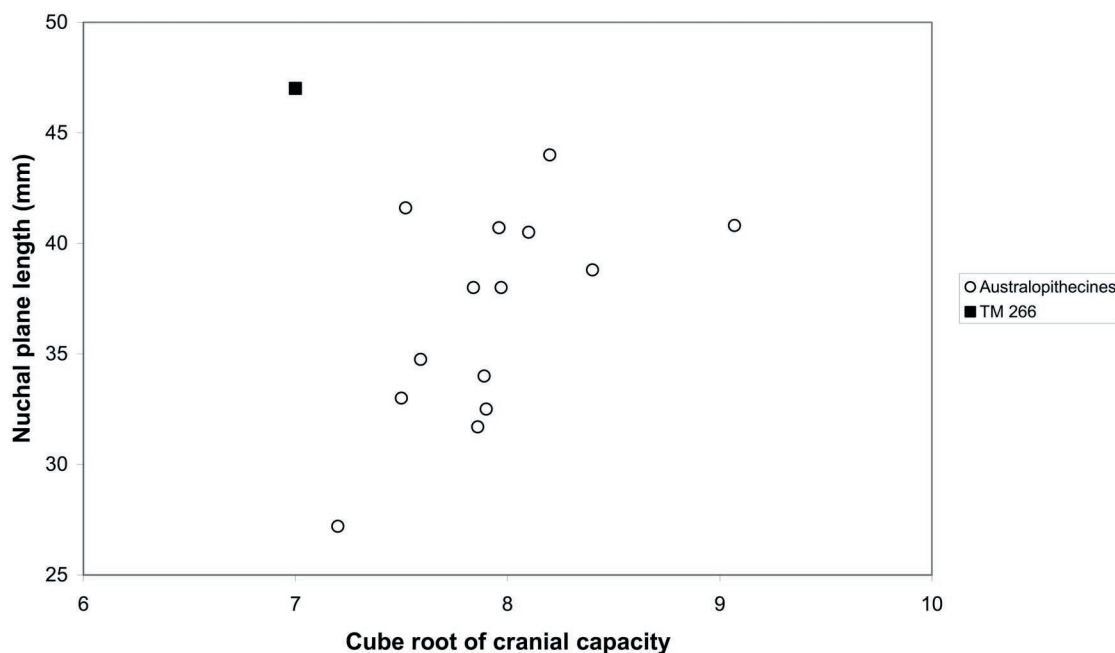


Figure 10. Relative length of the nuchal plane in australopithecines (including habilines) and TM 266: inion-opisthion (mm) plotted against the cube root of cranial capacity (in $cc^{1/3}$). Data are presented for (in order of capacity – x axis size) AL 288-1 (estimated cranial capacity from AL 162-1), Omo L-338, STS 71, MLD 37, AL 333-45, STS 5, ER 23000, ER 407, ER 1813, ER 406, OH 5, AL 444-2, OH 24, and ER 1470. TM 266 has a very long nuchal plane in absolute dimensions and relative to the size of the vault. In this comparison between TM 266 and the small-brained hominids, TM 266 is quite unlike these or any other hominids. Nuchal plane length for TM 266 is from Brunet et al. (2002), other lengths were measured by the authors.

As in other hominins, but in contrast to the African apes, inion in A.L. 444-2 is low, close to the FH [Frankfurt Horizontal] This value is similar to that of other early hominins, in which inion is always in the vicinity of the FH.

Kimbel and colleagues, and others, describe this condition with the nuchal area height index (Le Gros Clark, 1950). This measure was devised to show the height of the most superior aspect of the nuchal line above the Frankfurt Horizontal as a size-independent ratio with the absolute height of the cranium above the Frankfurt Horizontal. Le Gros Clark developed it to show structural differences between australopithecines and apes that reflected posture, and thereby to demonstrate that *Australopithecus* was a hominid genus.

We report here (Table 1) the value of the index using inion. Inion values are often lower than the nuchal height index using the most superior aspect of the nuchal line (see Kimbel et al, 2004: Table 3.6), but this is the index we can determine for TM 266, and so it is the one we must use to maintain homology. The unreconstructed nuchal area height index for TM 266 is about 50, and the reconstructed value is much lower, 23. Small as it is, the reconstructed value is almost 65% larger than the maximum relative height for any early hominid, while this reconstructed value overlaps with the chimpanzee and bonobo ranges as observed in small samples. We believe that Le Gros Clark was correct in his interpretation of this index, and that Kimbel and col-

leagues were correct in their assessment of the hominid position for inion close to the Frankfurt Horizontal, as the data in Table 1 confirm. The TM 266 nuchal area height index from inion reflects its ape-like posture and locomotion.

THE FORAMEN MAGNUM-ORBITAL PLANE ANGLE
Zollikofer and colleagues (2005) argue that posture can be assessed by examining the relation between the orbital plane (defined by the line connecting the upper and lower orbital margins as projected onto the sagittal plane) and the line connecting the anterior-posterior of the foramen magnum in the sagittal plane. The intersection of these two lines forms an angle that is said to reflect the orientation of the head on the neck. The contention is that primates tend to move with their orbital planes approximately orthogonal to the ground (Strait and Ross, 1999), and that the angle of the foramen magnum reflects the orientation of the first cervical vertebrae because the superior cervicals are orthogonal to this plane (Zollikofer and colleagues wrote that flexion and extension at the atlanto-occipital joint is no more than 10°). These two constraints combine to explain the observation of different angles between orbital and foramen magnum planes in *Pan* and *Homo*. Zollikofer and colleagues report the mean angles to be $64 \pm 6^\circ$ for *Pan* and $103 \pm 7^\circ$ for *Homo*.

The TM 266 reconstruction is published with a foramen magnum-orbital plane angle of 95° , we estimate the angle

TABLE 1. NUCHAL AREA HEIGHT INDEX (LE GROS CLARK, 1950): the maximum height ofinion above the Frankfurt Horizontal as a ratio to the maximum cranial height above the Frankfurt Horizontal (not including the sagittal crest, when present). Data are from Kimbel and colleagues (2004) and (Tobias, 1967, 1991). In the Tobias data some values may be larger than the index from inion because they are calculated from the highest point on the superior nuchal line.

	Nuchal Area Height Index from inion	$\pm\sigma$ range
<i>Human means</i>		
English	0	-6 - +6
Australian	3	-5 - +12
West African	5	-1 - +10
<i>Australopithecine individuals</i>		
ER 1813	-8	
OH 5	-5	
ER 13750	-3	
ER 23000	-2	
ER 406	0	
MLD 37/38	1	
STS 5	4	
AL 444-2	6	
ER 732	6	
AL 333 reconstruction	8	
OH 24	11	
WT 17000	14	
TM 266		
unreconstructed	50	
reconstructed	23	
<i>Ape minima</i>		
Bonobo	21	
Chimpanzee	23	
Orangutan	35	
Gorilla	44	
<i>Ape means</i>		
Chimpanzee female	36	23-50
Chimpanzee male	40	37-69
Gorilla female	67	56-82
Gorilla male	108	101-114

on the unreconstructed cranium to be between 70° and 87°. The more open angle of the reconstruction is interpreted to mean: “the probability that *Sahelanthropus tchadensis* was a biped is greater than that it was not” (Brunet and Allmand, 2005: 37).

Why would this indicator of posture be so different from the other postural indicators? One possibility is that supraorbital projection might be a significant component of the orbital plane angle: increasing projection would in-

crease the angle. Another concerns curvature in the cervical portion of the spine. The difference between straight (chimpanzee) and negative (human) neck curvature (see Figure 7) creates a divergence between the foramen magnum angle and the angle of the neck that makes the neck angulation prediction uncertain without knowledge of the cervical spine curvature. However, the most significant problem is in the ranges and means for the species most closely related to TM 266.

Chimpanzee Foramen Magnum - Orbital Angle

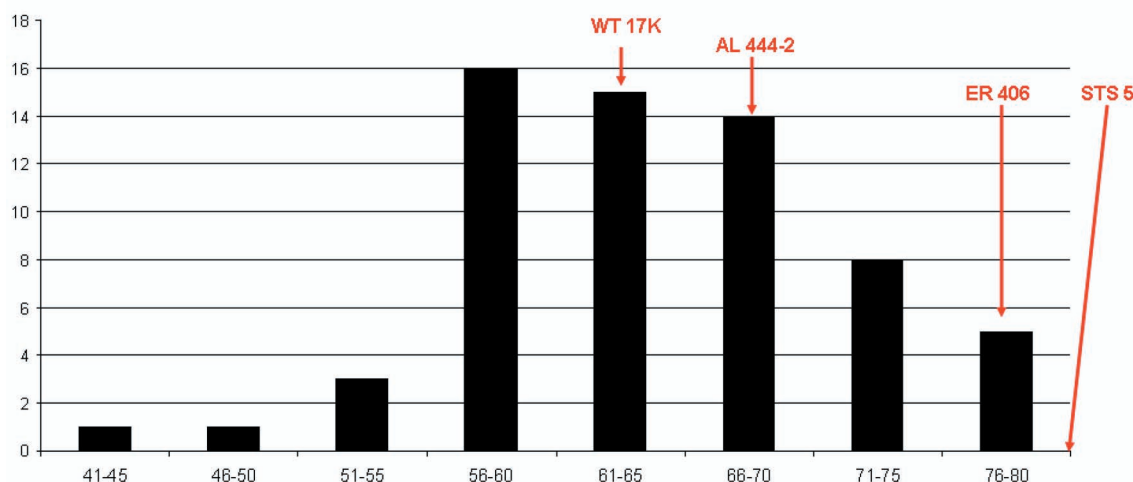


Figure 11. Foramen magnum – orbital plane angle for 63 chimpanzees and four australopithecine crania. This is the angle between the anterior-posterior plane of the foramen magnum and the vertical plane of the orbit at midorbit, between the superior and inferior margins. Chimpanzee data were merged from studies by two of us (J.H. and M.P. (Pickford, 2005)), based on different chimpanzee collections. Zollikofer and colleagues (2005) published the figure for STS 5 from which the angle can be determined, a microscribe was used to determine the data for angle calculation of a WT 17K cast, and ER 406 and AL 444-2 were determined from foramen magnum angle data published by Kimbel and colleagues (2002), and orbit angle data determined from published figures and casts. It is not reasonable to conclude that this angle provides information about posture and locomotion for these hominoid primates since their posture and locomotion are different while the foramen magnum-orbital plane angles cannot be distinguished.

The distribution of chimpanzee foramen magnum-orbital plane angles for 63 specimens is shown in Figure 11, and four australopithecines (the hominids closest in time) are plotted with them. The australopithecines range from 64° to 81° and fall almost completely within the chimpanzee range. These australopithecines are completely outside the human range. However, the australopithecine posture and locomotion is like humans in that it involves upright stance and obligate bipedalism, and is quite unlike chimpanzees. The near-identity of chimpanzee and australopithecine foramen magnum-orbital plane angles does not reflect their significant differences in posture and locomotion.

And if the foramen magnum-orbital plane angle *did* reflect posture and locomotion, we would conclude that the australopithecines were quadrupedal, but their putative ancestor, *Sahelanthropus*, was an obligate biped (Pickford, 2005). This interpretation is contradicted by all known australopithecine postcranial data.

We deduce from this comparison that the foramen magnum – orbit plane angle does not distinguish the posture and locomotion of australopithecines and chimpanzees, and therefore it cannot be expected to address the posture and locomotion of a species said to be close to the last common ancestor of australopithecines and chimpanzees.

TM 266 POSTURE AND LOCOMOTION

The TM 266 cranial rear and posterior portion of the cranial base, including the size, shape, and orientation, of the nuchal plane, are compatible with a chimpanzee pattern of locomotion. The nuchal plane is exceptionally long, and even with the greatly reduced nuchal angle of the reconstruc-

tion, its most posterior extent is markedly above the Frankfurt Horizontal. The prominence of the nuchal muscles, so important in head balance and loading, and shoulder movements, is enhanced by the significant development of the *tuberculum linearum*. The point is not that the TM 266 cranial rear and posterior portion of the cranial base was unlike hominids because the region *looks like apes*, but that TM 266 had a posture that is not upright because the region *reflects nuchal functions similar to those of apes*.

The foramen magnum - orbit plane angle does not directly address posture or locomotion in these hominoid primates (contra Zollikofer et al., 2005). Without a key postcranial element such as a pelvis or femur, none of these data provide compelling evidence for upright posture or obligate bipedal locomotion, and the various details of the nuchal plane argue against it. This functional implication has a phylogenetic consequence—by itself it is sufficient to disprove the phylogenetic hypothesis that TM 266 was a hominid.

ONE LAST HOMINID PROBLEM: THE DIVERGENCE DATE

The search for the earliest hominids is approaching a chronological limit: the date of the human-chimpanzee divergence as inferred from genetic evidence. While it is always possible that *Sahelanthropus* is young enough to be later than the last common ancestor of humans and chimpanzees, as is now widely but inexplicably assumed, there is no particular reason to think so. Although the genetic evidence has not quite reached the point claimed by Sarich as early as 1971: “one no longer has the option of consider-

ing a fossil specimen older than about eight million years a hominid *no matter what it looks like*" (1971, p. 76, italics in original), very ancient claims that a fossil is a "phylogenetic hominid" must now meet close scrutiny in the absence of strong morphological evidence.

The best current genetic estimates places the time of genetic isolation between humans and chimpanzees at about 5 myr. Yang (2002) determined a divergence time of 5.2 million years ago, with a 95% confidence interval from 4.6 to 6.1 million years. Kumar and colleagues (2005) calculated a 5.0 myr divergence with a 95% confidence interval of 4.4–5.9 myr based on synonymous mutations in 167 genes (55,008 codons) and the assumption of 23.8 myr for the ape-Old World monkey divergence (see Goodman et al., 1998).

The earliest known hominids with a well-developed postcranial adaptation to obligate bipedalism were discovered by a team including two of us (M.P., B.S.), dated to around 6 million years ago (Pickford et al., 2002; Senut et al., 2001), and others are almost as old (Haile-Selassie, 2001; Haile-Selassie et al., 2004). The uniquely hominid bipedal adaptations of *Orrorin* (Galik et al., 2004) and *Ardipithecus*³ (Haile-Selassie, 2001) shows that bipedality had been established. At this time the fossil record places a firm lower limit on the isolation time between the two lineages at 6 million years. The fossil and genetic divergence estimates thus overlap, if just barely.

The first *Sahelanthropus* date estimate range of 6–7 myr (Brunet et al., 2002) also seemed to just overlap with these genetic and other fossil-based divergence determinations, but all subsequent publications have placed the minimum date for *Sahelanthropus* substantially earlier, at approximately 7 myr (Brunet et al., 2005; Guy et al., 2006; Zollikofer et al., 2005). This is a million years older than the maximum of the likely genetic estimate of divergence times, and also the earliest postcranial evidence of hominid bipedalism.

Have we reached the point at which fossil and genetic evidence agrees upon the age of the earliest hominid? Certainly there is an error term in any genetic estimate of human-chimpanzee isolation time that is large and itself uncertain. The largest source of error is the estimation of substitution rates in each of the lineages compared (they may not be the same), which itself depends both upon accurate knowledge of other divergences from the fossil record and upon sufficient genetic information to evaluate the amount of variation in substitution rates among genetic loci. The lower limit of the ape-Old World monkey divergence is well established, but the upper limit is less clear. Thus, additional information from the fossil record remains important to allow genetics to test the likelihood that earlier hominids may have existed. But with respect to the human-chimpanzee divergence, evidence about it must provide a strong morphological indication of hominid affinities to push back existing genetic estimates. TM 266 does not meet this expectation.

DISCUSSION AND CONCLUSIONS

The TM 266 skull is the first known from any Late Miocene African hominoid clade, and is one of the best preserved

crania of any Miocene ape. The temporal placement of *Sahelanthropus* is compatible with indications that the ancestral condition for hominid dental evolution was more like known Miocene apes than like chimpanzees. For these reasons and others, the TM 266 cranium provides an important record of the evolution of late Miocene hominoids, and if it does not witness the divergence of the hominid clade, it does provide important information that helps us better understand this divergence.

Sahelanthropus was an ape living in an environment later abandoned by apes but subsequently inhabited by australopithecine species. Both TM 266 and the later australopithecines reflect the masticatory adaptations of earlier Miocene apes, and differ from later African apes in many of these adaptations. This creates the potential for significant homoplasies, and combined with the consequences of a limited fossil record, makes assessment of phylogeny problematic. Yet, it is a highly significant discovery; both because it evidences a unique pattern of homoplasy, and perhaps mostly because of the insight it might give for understanding the ancestral condition before the hominid-chimpanzee split.

Several commentators, including those addressing this specimen, have framed the importance of fossil discoveries as a way to uncover the phylogenetic diversity of early hominids, such as the supposed dispute about whether early hominids had a "tidy" or "bushy" evolutionary history (Wood, 2002). Such forays into metabiology are almost purely rhetorical, since even strong advocates of the position that most hominid species are fictitious (White, 2003) accept the existence of several early hominid species and even genera (e.g. White et al., 1994). The rhetoric also misses the point, since the significant information provided by *Sahelanthropus* does not address the shape of the phylogeny—after all, even Brunet and colleagues (2002), in describing the specimen as a hominid, rely implicitly on an antiquated rectilinearist interpretation of hominid canine evolution.

Instead, the remains have a significant power to inform about the polarity of early hominid characters. After the demise of *Ramapithecus* as a hominid (Greenfield, 1980), it became widely accepted that the powerful masticatory apparatus of many Miocene apes was the ancestral dentognathic condition for the earliest hominids (Wolpoff, 1982) and that the small low, female canines may have provided the basis for hominid canine reduction (Greenfield, 1996). Then the *Ardipithecus* remains confounded this issue with support for an opposing, and much older, interpretation of the ancestral condition, because it presented an early manifestation of dentognathic features that were described as chimpanzee-like (Haile-Selassie, 2001; White et al., 1994). The *Orrorin* discovery (Senut et al., 2001) is incompatible with the interpretation that the primitive dentognathic condition for hominids is more like living chimpanzees than like Miocene apes, but this leaves us in a quandary because White (cited in Wong, 2003) and Haile-Selassie and colleagues (2004) propose there is but a single hominid lineage prior to 4 million years ago which would include *Orrorin*

and *Ardipithecus* together, and not without relevance also includes *Sahelanthropus*.

Metric and morphological variation within available small samples of late Miocene teeth attributed to *A. kadabba*, *O. tugenensis*, and *S. tchadensis*, is no greater than that 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 (Haile-Selassie et al., 2004: 1505).

In fact, there may be dental similarities between TM 266 and the *Ardipithecus* remains, the former is too poorly illustrated and the latter not well enough published for us to address this possibility, although the comments above speak for themselves. Of most relevance to us is the comparison of occipitals. The nuchal plane in *Ardipithecus ramidus* ARA-VP-1/500 is very short and broad as it is in known bipedal australopithecine crania. TM 266 has a narrow and very long nuchal plane. In the end, we think this testimony of analysis further demonstrates what the fossils clearly show, the fact that the existing early hominid samples are far too small, incomplete, and closely related to allow a phylogenetic resolution of the issue of the ancestral condition for hominids.

So every discovery counts. *Sahelanthropus* may be an early member of the gorilla clade, as two of us (B.S., M.P.) have suggested, or it may be closely related to the chimpanzee clade, or to the human-chimpanzee common ancestor (Wood, 2002), or perhaps most likely a member of an extinct closely related clade. In any of these cases, *Sahelanthropus* tends to confirm the notion (Wolpoff, 1982) that the ancestral condition for hominids, and for extant African apes, is much more like the Miocene ape condition than like living chimpanzees. Only if it turns out that *Sahelanthropus* represents a more distantly related hominoid lineage would it fail to be informative about the ancestral condition for these lineages, and address the issue of whether the chimpanzee is a reasonable model for this last common ancestor.

TM 266 is a young specimen of indeterminate sex. Its canines are large for a Miocene ape female and small for a Miocene ape male, in absolute and relative dimensions. Canine wear is apical and transversely distal, a condition found in many other Miocene ape specimens, but it is possible that the TM 266 canine is more heavily worn than most other Miocene canines of similar dental age. Unlike australopithecines, the evidence indicates that TM 266 *did not* habitually hold its head in an upright position over the spine and thus lacked this significant obligate bipedal adaptation. By itself this contrasts with all known hominids, and even in the absence of postcranial remains this anatomy is sufficient to exclude *Sahelanthropus* from the hominid clade as we currently understand it, an exclusion compatible with genetic estimates of the chimpanzee/hominid divergence. It is this exclusion, and not any combination of synapomorphies, which demonstrates that TM 266 was an ape.

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ENDNOTES

- ¹ "Hominid" rather than "hominin" (or other term) is used here because, like the word "ape," hominid has a clear referent even though neither "hominid" nor "ape" is a valid taxonomic term. "Ape" no longer refers to a monophyletic group. The human clade is a monophyletic group, but in our view it would be foolhardy to use any vernacular term for this group that is specifically tied to the level of taxonomic assessment for the human clade (Cela-Conde et al., 2000) when it is still unclear whether this clade must be incorporated within a single genus (Goodman et al., 1998; Curnoe & Thorne, 2003; Wildman et al., 2003), subfamily (Mann & Weiss, 1996), or family (Tattersall & Schwartz, 2000).
- ² The reported second molar breadth is reconstructed, and a number of problematic results flow from basing ratios on its estimated size, since these invariably "show" TM 266 to be an outlier in every comparative distribution. Most convincing is the fact that while the breadth estimate of 12.8 mm reported for the second molar is less than the measured breadth of the third molar, 14.9 mm, visual inspection of the illustrated base of the skull shows that before it was broken the second molar must have been broader than the third (Figure 2, and Brunet et al., 2002, Figure 1d). We do not use M2 breadth in any of our analyses.
- ³ One of us [B.S.] does not consider the evidence of bipedalism in *Ardipithecus kadabba* to be convincing.

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