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ORIENTATION OF THE FORAMEN MAGNUM IN LATE MIOCENE TO EXTANT AFRICAN APES AND HOMINIDS

ABSTRACT: *The postcranial skeleton of the Late Miocene hominoid Sahelanthropus tchadensis is unknown; because of this the possibility of bipedal posture and locomotion has been based on cranial features, an interpretation that has not been accepted by all paleoanthropologists. Part of the evidence includes the orientation of the foramen magnum relative to the orbital plane (FM-OP angle), an acute angle being said to characterise more pronograde postures such as that of the chimpanzee, and more obtuse angles to characterise orthograde humans, australopithecines and Sahelanthropus. This paper examines the soundness of the FM-OP evidence used to infer the likelihood of bipedal posture in Sahelanthropus.*

KEY WORDS: *Hominoids – Foramen magnum plane (FM) – Orbital plane (OP) – FM-OP angle – Occlusal plane – Miocene to recent – Bipedal posture*

INTRODUCTION

Zollikofer *et al.* (2005: 758, fig. 4) employed the relationship between the plane of the foramen magnum and the orbital plane (FM-OP angle) to infer that "as a quadruped" *Sahelanthropus* "would require an unusually extended angle of the neck relative to the plane of the foramen magnum", an inference reinforced by Brunet and Allemand (2005: 37) who, on the basis of the FM-OP angle, wrote that "the probability that *Sahelanthropus tchadensis* was a biped is greater than that it was not" (present author's translation from the French).

Zollikofer *et al.* (2005) reported that FM-OP angle in *Pan troglodytes* is $63.7^{\circ} \pm 6.2^{\circ}$, $n=20$, and in humans $103.2^{\circ} \pm 6.9^{\circ}$, $n=23$. In their figure 4, the authors illustrated the two planes superimposed on the skulls of a) a human, b) a chimpanzee, c) *Australopithecus africanus* (Sts 5) and d) *Sahelanthropus tchadensis*. Brunet and Allemand (2005: p. 38) published the same figure and reported that the chimpanzee FM-OP "is acute, of the order of 65° ".

Measurement of the FM-OP angle in the figure reveals that the human one is 97° , that of the chimpanzee is 57° , that of the australopithecine, 81° and that of *Sahelanthropus*, 96° . Out of the four species illustrated, the FM line intercepts the dentition in two, and only in the chimpanzee is the FM line below the dentition. The OP in three of the species intercepts the molar row (in chimpanzee the intercept is M1/, in *Sahelanthropus* it is the junction between M1/–M2/, and in the australopithecine it is about M2/), humans being the exception with the OP intercepting the premolar row at P3/.

The human FM-OP angle illustrated (97°) is close to the lowest value measured in humans (96.3° according to Zollikofer *et al.* 2005) and the chimpanzee FM-OP illustrated (57°) is more acute than the most acute angle given in the text (57.5°) and well below the mean (63.7°) given by these authors or the value (ca 65°) estimated by Brunet and Allemand (2005). Because of the latter inconsistency, the present author decided to measure the FM-OP angle in chimpanzees, gorillas and some humans and to compare them with the values published for

Sahelanthropus and other hominoids. This paper presents the results of this analysis and discusses the implications for bipedal posture in *Sahelanthropus*.

MATERIAL AND METHODS

The skulls of 21 chimpanzees (10 male, 11 female), 30 gorillas (19 male, 11 female) and 2 humans (1 unrecorded sex, 1 female) (*Table 1*) were photographed using a digital camera in lateral view with a straight edge positioned in contact with opisthion and basion (*Figure 1*). The resultant images were treated using Photoshop to eliminate unwanted elements of the image such as the background. A line was drawn precisely along the edge of the ruler that was in contact with opisthion and basion, and the image of the ruler was then *eliminated* (*Figures 2, 3, 4*). This procedure gives an accurate estimate of the FM plane ($\pm 0.25^\circ$), opisthion and basion being precise cranial landmarks located in the sagittal plane.

The OP is inherently a less accurate plane to measure on account of the lack of precise landmarks. Zollikofer *et al.* (2005) and Brunet and Allemand (2005) did not provide details of how they measured the orientation of the OP, but judging from the illustrations it was obtained by drawing a vertical line in the middle of the orbit extending from the anterodorsal margin of the orbit to the antero-ventral edge of the orbit immediately beneath the former point. There are four main difficulties with this measurement, the first being that the left and right sides of the same skull may be different (in fact each orbit has its own OP). The second, and a more serious difficulty is that the upper and lower margins of the orbits are curved dorsoventrally (strongly) and mediolaterally (gently), and thus it is difficult to define precise points for consistent measurements between individuals or successive measurements in the same individual, and thus of obtaining reliable results for the orientation of the orbital plane itself. I estimate that the uncertainty in defining the margins of the orbit results in an error margin of $3\text{--}5^\circ$. The third difficulty is that the orbits are not in the sagittal plane, and thus the FM line and the OP lines are offset from each other, intersecting each other outside the points used to define the OP. The fourth difficulty relates to the images of the skulls obtained, a slight difference in position of the camera introducing a small difference in apparent orientation of the OP. To minimise the effect, images were taken such that the orbits were in the same plane as each other and the camera was positioned so as to be near the intersection of the FM and OP planes (error margin in OP estimated to be $\pm 1^\circ$). Thus, with the method used, the FM plane can be accurately defined (error margin $\pm 0.25^\circ$) whereas the OP less so (error margin $\pm 4\text{--}6^\circ$).

The OP was drawn onto the digital images so obtained, and the angle between the FM-OP measured using a protractor.

The FM-OP angles published by Zollikofer *et al.* (2005)

of chimpanzees ($63.7^\circ \pm 6.2^\circ$) and humans ($103.2^\circ \pm 6.9^\circ$) are markedly divergent, with no overlap even if the maximal error margins are applied. The error margins introduce a relatively minor degree of uncertainty (noise) into the analysis but do not completely invalidate the approach.

RESULTS

Chimpanzee foramen magnum

In the chimpanzee skulls examined (*Table 1*) the FM line intersects the occlusal plane in 20 individuals, and in only one individual (1952.144, male) does it lie below the tooth row (i.e. the FM intersects the occlusal plane behind the M3/). In chimpanzees the orientation of the FM line is extremely variable, in some individuals the line extends anteriorly to the level of the incisors, in others it intersects the molar row (*Figure 2*).

Chimpanzee orbital plane

In chimpanzees the orbital plane (OP) intercepts the M1/ in 16 individuals, the M2/ in 4 individuals, and in only one individual (1952.144, male) does it intercept the M3/.

Chimpanzee FM-OP angle

The most acute chimpanzee FM-OP angle measured was 60° , the least acute 78° , mean 69° . Males ($60^\circ\text{--}76^\circ$) tend to have a more acute FM-OP than females ($64^\circ\text{--}78^\circ$) but there is a great deal of overlap between the sexes in the sample analysed.

Gorilla foramen magnum

As with the chimpanzee skulls, in most gorillas examined (*Table 1*), the FM line intercepts the occlusal plane, with only four individuals (all males) having the line below the tooth row (ie intersecting the occlusal plane behind the



FIGURE 1. Method of determining the orientation of the foramen magnum plane (FM). A straight edge is laid in contact with basion and opisthion, this line defining the FM plane which is at right angles to the sagittal plane. Specimen KC3 female *Gorilla*.

TABLE 1. Specimens examined for obtaining the FM-OP angle (all specimens are housed at the Muséum National d'Histoire Naturelle, Paris). Individuals marked with an asterisk * are those published in figure 4 of Zollikofer *et al.* (2005).

Specimen	Genus	Sex	FM intersection with occlusal plane	OP intersection with toothrow	FM-OP angle
1940.467	<i>Pan</i>	Female	At incisors	Middle of M1/	72°
1941.151	<i>Pan</i>	Male	At M1/	Middle of M1/	60°
1952.144	<i>Pan</i>	Male	Behind toothrow	At M3/	74°
1956.67	<i>Pan</i>	Female	At canine	Front of M1/	68°
A13924	<i>Pan</i>	Male	At M2/	Middle of M1/	62°
1940.377	<i>Pan</i>	Male	At canine	Front of M1/	69°
A519	<i>Pan</i>	Female	At incisors	Rear of M1/	75°
1898.178 (A11612)	<i>Pan</i>	?Female	At incisors	Rear of M1/	78°
A12769	<i>Pan</i>	Male	At canine	Middle of M1/	70°
1910.126	<i>Pan</i>	Male	At incisors	Front of M2/	76°
1930.81	<i>Pan</i>	Female	At incisors	Middle of M1/	67°
1974.72	<i>Pan</i>	Female	At M2/	Rear of M1/	65°
1923.2497	<i>Pan</i>	Female	At canine	Middle of M2/	69°
1899.111	<i>Pan</i>	Male	At canine	Front of M2/	70°
1899.129	<i>Pan</i>	?Male	At M2/	Rear of M1/	69°
1899.17	<i>Pan</i>	Male	At P3/	Middle of M1/	63°
1920.135	<i>Pan</i>	Female	At canine	At M1/	71°
1939.507	<i>Pan</i>	Female	At M1/	Front of M1/	64°
Libongi	<i>Pan</i>	Male	At canine	Front of M1	64°
Mbadi	<i>Pan</i>	Male	At incisors	Middle of M1/	77°
A 983	<i>Pan</i>	Male	At M2/	Rear of M2	67°
A10663	<i>Gorilla</i>	Male	At P4/	Rear of M1/	63°
1877.759	<i>Gorilla</i>	Female	At P3/	Rear of M1/	71°
1940.393	<i>Gorilla</i>	Male	At M2/	Rear of M1/	58°
1887.1148	<i>Gorilla</i>	Male	Behind toothrow	Rear of M1/	49°
1909.358	<i>Gorilla</i>	Female	At P3/	Front of M1/	64°
1940.373	<i>Gorilla</i>	Female	At P4/	Middle of M1/	66°
1884.708	<i>Gorilla</i>	Male	At M2/	Rear of M2/	59°
1885.482	<i>Gorilla</i>	Male	At M3/	Front of M1/	49°
A9772	<i>Gorilla</i>	Female	At incisors	Rear of M1/	75°
PVA107	<i>Gorilla</i>	?	Behind toothrow	Rear M1/	59°
1927.176	<i>Gorilla</i>	Male	At M2/	Rear of M1/	59°
1971.203	<i>Gorilla</i>	Male	Behind toothrow	Rear of M1/	42°
Spot277	<i>Gorilla</i>	Male	At M2/	Middle of M1/	62°
1866.121	<i>Gorilla</i>	Male	At canine	Rear of M1/	66°
1940.372	<i>Gorilla</i>	Male	At M2/	Middle of M1/	59°
1924.385	<i>Gorilla</i>	Male	At canine	Front of M1/	65°
1940.398	<i>Gorilla</i>	Male	At M2/	Rear of M1/	58°
1921.161	<i>Gorilla</i>	Female	At incisors	Middle of M1/	71°
1977.44	<i>Gorilla</i>	Male	At incisors	Middle of M1/	67°
1940.396	<i>Gorilla</i>	Male	Behind toothrow	Middle of M2/	50°
1986.441	<i>Gorilla</i>	Male	At canine	Rear of M2/	72°
1911.352	<i>Gorilla</i>	Female	At canine	Front of M2/	71°
1940.376	<i>Gorilla</i>	Female	At canine	Middle of M1/	70°
1978.6	<i>Gorilla</i>	Female	At incisors	Front of M1/	70°
1978.5	<i>Gorilla</i>	Female	At incisors	Front of M1/	74°
1978.4	<i>Gorilla</i>	Female	At canine	Front of M1/	65°
1978.3	<i>Gorilla</i>	Male	At M1/	Front of M2/	59°
PVA113	<i>Gorilla</i>	Male	At M3/	Front of M2/	52°
899.16	<i>Gorilla</i>	Male	At canine	Rear of M1/	66°
KC3	<i>Gorilla</i>	Female	At P3/	Middle of M1/	59°
1932.154	<i>Homo</i>	Female	Behind foramen magnum	At P3/	100°
PVA 1	<i>Homo</i>	?	Behind foramen magnum	At P4/	105°
None*	<i>Homo</i>	?	Behind foramen magnum	At P3/	97°
TM 266-01-60-1*	<i>Sahelanthropus</i>	?	Behind foramen magnum	Front of M2/	96°
Sts 5*	<i>Australopithecus</i>	?	At about canine	About M2/	81°
None*	<i>Pan</i>	?	Behind toothrow	Front of M1/	57°

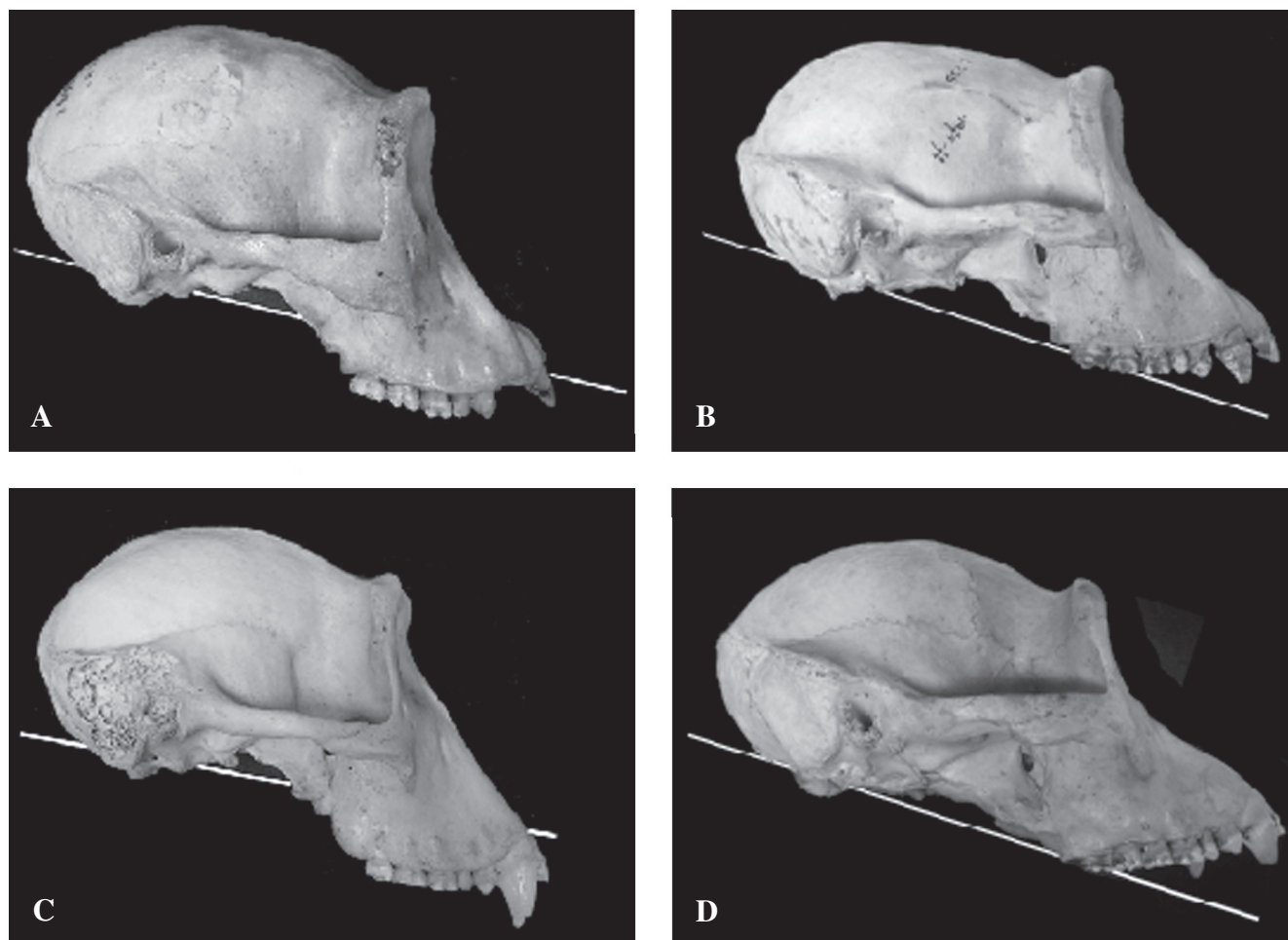


FIGURE 2. Examples of the FM plane in extant chimpanzees showing part of the range of variation. Note that in most specimens the FM plane intersects the toothrow. A – 1898.178 female; B – 1974.72, female; C – 1910.126 male; D – A 13924 male.

M3/). In some females the FM line is obtuse enough to intercept the incisors (*Figure 3*).

Gorilla orbital plane

The orbital plane intercepts the M1/ in the majority of gorilla individuals (23) or is anterior to it (at the front of M1/ in 7 females). It intersects M2/ in 6 individuals. Thus the orbital plane of the gorilla has much the same relation to the tooth row as it does in chimpanzees.

Gorilla FM-OP angle

The most acute gorilla FM-OP angle measured was 42° (2 males) and the least acute was 75° (a female), the mean being 63.5°. Males (42°–72°, mean 57°) tend to have more acute FM-OP angles than females (59°–75°, mean 67°) but there is overlap between the sexes. Aged males have more acute FM-OP angles than young males, and it is evident that this angle changes ontogenetically.

Human foramen magnum

In both of the humans measured (*Table 1*) the FM line was well above the dentition, intersecting the nasal cavity. This is considerably more elevated anteriorly than in any

of the chimpanzees and gorillas. The relationship with the occlusal plane is thus diametrically opposite to that of chimpanzees and gorillas (*Figure 4*), the intersection of the FM plane occurring posterior to the foramen magnum rather than anterior to it as in chimpanzees and gorillas.

Human orbital plane

The orbital plane in both humans examined intersected the premolars.

Human FM-OP angle

The two humans in the sample have FM-OP angles of 100° and 105°.

COMPARISONS

Foramen magnum orientation

In chimpanzees and gorillas, the plane of the foramen magnum, as defined by basion and opisthion, generally intersects the occlusal plane somewhere along the tooth row, the few specimens that intersect this plane behind the M3/ all being males (1 chimpanzee out of 20 examined, and

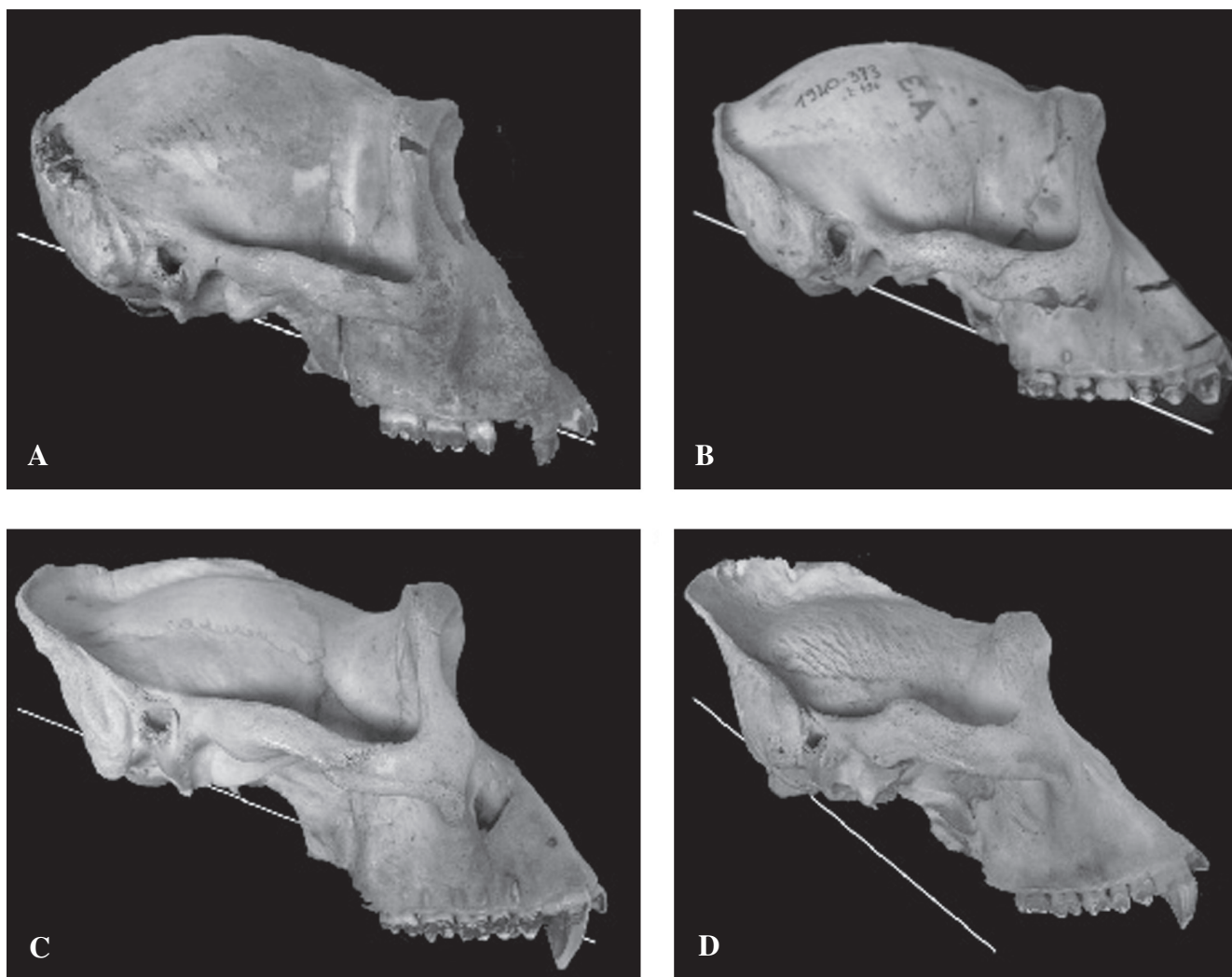


FIGURE 3. Examples of the FM plane in extant gorillas showing part of the range of variation. Males tend to have steeper FM planes than females, but note that in most individuals the FM plane intersects the tooththrow. A – 1978.6 female; B – 1910.373 female; C – 1924.385 male; D – 1971.203 male.

4 out of 31 gorillas included in the study). The specimens in which the FM plane falls below the tooththrow are all fully adult to aged males, young males being more like females in the values obtained. From this it is inferred that the relationship between the FM plane and the maxilla changes ontogenetically, the inclination of the FM increasing with age relative to the occlusal plane, especially in gorillas (Delattre, Fenart 1960). It is also evident that there is a great deal of individual variation in the orientation of this plane, reflecting individual differences in the angle at which the splanchnocranium is hafted onto the neurocranium.

In humans the FM plane in the two specimens examined lies above the tooththrow (including the roots), intersecting the nasal cavity anteriorly and the occlusal plane well behind the foramen magnum (Figure 4). In the individual illustrated by Zollikofer *et al.* (2005) the FM intersects the apices of the molar roots, and thus appears to be an extreme variant among humans, a conclusion confirmed by the values published by the authors.

The FM plane in *Sahelanthropus* as reconstructed by Zollikofer *et al.* (2005), lies above the roots of the tooththrow including the apex of the canine, which is extremely elongated within a hominid context, and it intersects the nasal cavity anteriorly and the occlusal plane well behind the foramen magnum as in humans.

The FM plane of the australopithecine illustrated by Zollikofer *et al.* (2005) is inclined at such an angle that it intersects the tooththrow low down, much lower than in the *Sahelanthropus* reconstruction and close to the condition in *Gorilla* and *Pan*.

The published FM plane of *Sahelanthropus* relative to the occlusal plane is more elevated than it is in australopithecines, chimpanzees and gorillas, and falls well within the range of variation of humans.

The orbital plane

The orbital plane of chimpanzees and gorillas generally intersects the M1/, with a few individuals intersecting the

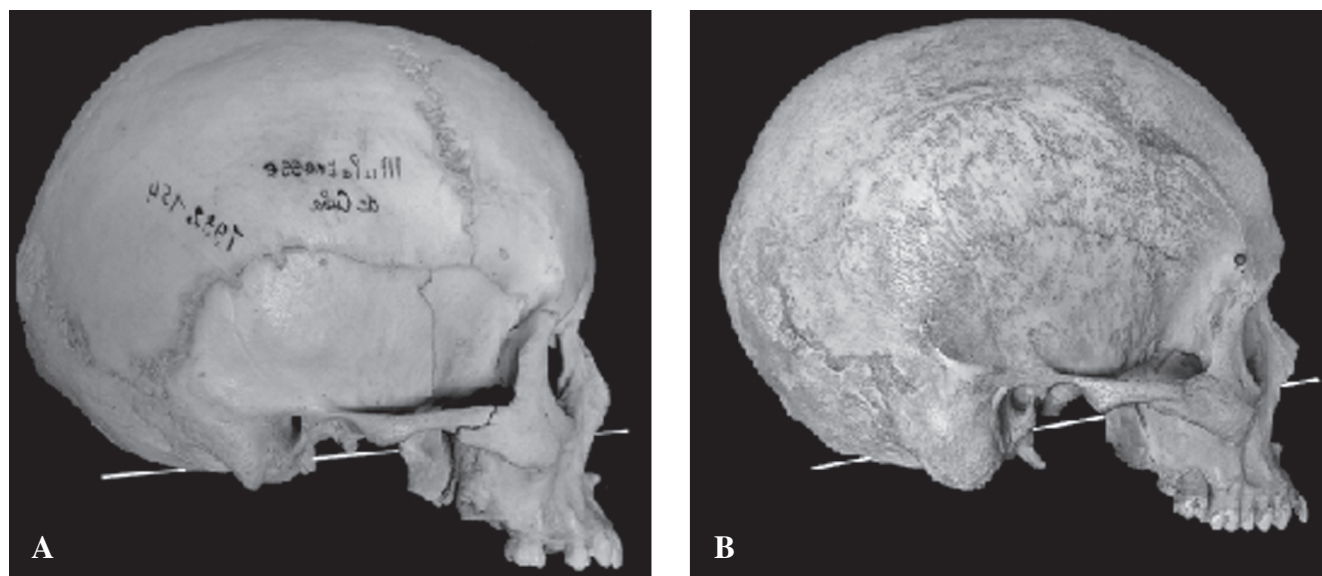


FIGURE 4. Examples of the FM plane in humans. Note that the plane does not intersect the toothrow. A – 1932.152 female (reversed); B – PVA 1, unrecorded sex.

M2/ behind or the contact between M1/ and P4/ anteriorly. In none of the chimpanzees examined did the OP intersect the premolars, although in some female gorillas the plane intersected the contact between the P4/ and M1/.

In humans, the OP intersects the premolars, usually the P3/ (Zollikofer *et al.* 2005) (Figure 4).

In the reconstruction of *Sahelanthropus*, the OP intersects the M2/, which is posterior to the mean position in chimpanzees and gorillas, although it falls within the range of variation of these species. Thus the intersection of the OP and the tooththrow of *Sahelanthropus* is markedly different from the situation in humans.

In *Australopithecus*, the OP published by Zollikofer *et al.* (2005) intersects the tooththrow far back, probably about the level of M2/ (the teeth are missing in Sts 5).

Thus, if the OP of *Sahelanthropus* is correctly positioned in the reconstruction, then its orientation is more like that of chimpanzees and gorillas than that of humans.

FM-OP angle

The FM-OP angle reflects the position and orientation of two planes. In the reconstructed cranium of *Sahelanthropus*, the FM plane falls well within the range of variation of humans, whereas the OP falls into the lower part of the range of variation of gorillas and chimpanzees, well outside the range of variation of humans. As a consequence, the angle between these planes, as published by Zollikofer *et al.* (2005), falls close to the human range of variation, and well above that of gorillas, chimps and australopithecines.

In *Australopithecus*, both the FM and OP published by Zollikofer *et al.* (2005) fall within the range of variation of gorillas and chimpanzees, although the angle between them is slightly outside the range of variation of the African apes.

The chimpanzee FM-OP angle (57°) illustrated by Zollikofer *et al.* (2005) and Brunet and Allemand (2005) is more acute than any of the specimens examined in this study, and is smaller than the most acute angle (57.5°) listed by Zollikofer *et al.* (2005) in their text. It is 8° more acute than the value published by Brunet and Allemand (2005).

The chimpanzee FM-OP measurements in this study range from $60^\circ - 78^\circ$ (mean 69°) which is uniformly less acute than the range of variation published by Zollikofer *et al.* (2005 – $63.7 \pm 6.2^\circ$). These differences are possibly related to ways of measuring the OP, taking into account the estimated error margin of $4-6^\circ$. The chimpanzee individual illustrated by these authors falls beyond their own estimate of the range of variation of the FM-OP angle in chimpanzees, a result confirmed by this study. In particular, the orientation of the FM plane in the illustration appears to be too steeply inclined anteriorly, the line representing the plane passing well below the tooth row. Out of the 20 chimpanzees examined during the present study, only one individual showed an FM line below the tooth row, all the others intersecting the occlusal plane, some as high as the incisors. It is thus concluded that the chimpanzee FM-OP angle illustrated by Zollikofer *et al.* (2005) exaggerates the acuteness of the FM-OP angle and thus magnifies the apparent difference between chimpanzees on the one hand and the other hominoids illustrated by them on the other. Examination of the image suggests the possibility that basion has been misidentified.

The FM-OP angle of *Australopithecus africanus* (Sts 5) measured directly from the illustration published by Zollikofer *et al.* (2005) is 81° . This is only 3° more obtuse than the highest value for the chimpanzee examined in this study and 11.1° greater than the most obtuse FM-OP measurement that Zollikofer *et al.* (2005) provided in the

text (69.9°). In *Australopithecus* the FM plane intersects the toothrow in much the same way as in chimpanzees and gorillas, and it is likely that the range of variation of the FM-OP in australopithecines is about the same order of magnitude as it is in extant African apes. It is not known precisely what the range of variation in australopithecines is, but the chances are that Sts 5 has neither the most acute nor the most obtuse FM-OP angle among the subfamily. It is thus possible that there is overlap between the FM-OP angle of chimpanzees and australopithecines. It is also possible that there is overlap between the FM-OP angle of female gorillas and australopithecines, the most obtuse gorilla FM-OP angle determined in this study (75°) being only 6° less than the estimated angle in *A. africanus*.

DISCUSSION AND CONCLUSIONS

It is generally agreed that australopithecines were bipedal, whereas chimpanzees and gorillas are quadrupedal, albeit with the ability to stand and move on two feet for short periods and short distances. Australopithecines show skeletal morphology that reflects their bipedal stance and locomotion, whereas chimpanzees and gorillas do not. The fact that the FM-OP angles of chimpanzees and gorillas are close to those of australopithecines, with the possibility of overlap between the ranges of variation, indicates that this angle does not provide a clear idea of locomotor or postural potential, at least for these groups.

Humans in contrast possess a considerably more obtuse FM-OP than either australopithecines or African apes ($103.2 \pm 6.9^\circ$ according to Zollikofer *et al.* 2005). There is no overlap between the ranges of variation of chimpanzees and gorillas on the one hand (maximum 78°) and humans (minimum 96.3°) on the other. The FM-OP value for *Sahelanthropus* is estimated to be 96° by Zollikofer *et al.* (2005), which, if correctly determined, would imply that it is just below the range of variation of humans.

Given the observation that the FM plane of the reconstructed *Sahelanthropus* falls within the range of variation of humans, whereas its OP falls well outside the human range, it is pertinent to ask whether the value of the FM-OP angle illustrated by Zollikofer *et al.* (2005) is reliable. The proximity of values between the FM-OP of humans and *Sahelanthropus* has been used to infer the strong possibility of bipedal posture in the genus (Brunet, Allemand 2005). If the angle is correctly determined, and if the FM-OP angle reflects posture and locomotor repertoire as claimed, then it is difficult to evade the conclusion that *Sahelanthropus* was likely to have been better adapted for bipedal posture than australopithecines were, as the FM-OP of *Australopithecus* is significantly more acute (81°) than that of *Sahelanthropus* (96°), and is only marginally more obtuse than that of chimpanzees (most obtuse angle is 78°). However, since the OP of *Sahelanthropus* is quite unlike that of humans, it is legitimate to ask whether its FM plane has been accurately reconstructed.

The original specimen of *Sahelanthropus tchadensis* is crushed and warped (Brunet *et al.* 2002), making any direct measurement of the foramen magnum and orbital planes, as well as the relationship between them, impossible. For this reason, Zollikofer *et al.* (2005) based their measurements on a virtual reconstruction of the skull. The basicranium was particularly badly damaged, with the foramen magnum fractured into two, one part with basion, the other with opisthion (Brunet *et al.* 2002). Furthermore, the relationships between the basicranium on the one hand and the rest of the neurocranium and splanchnocranium on the other were heavily distorted, with displacement of fragments in three dimensions, as well as rotation and translation of the various pieces relative to each other. There could even be some plastic deformation, although this is not immediately apparent from the published images. Given that the basicranium is far removed from the splanchnocranium (taking into account size differences, the distance between the foramen magnum and the rear of the tooth rows is as great in *Sahelanthropus* as it is in gorillas), then the possibility of obtaining an erroneous relationship between the foramen magnum and the orbits is rather high.

With crania oriented in the Frankfurt horizontal, the dorsal profile of the skulls of chimpanzees, gorillas, australopithecines and humans show a rise in the profile of the braincase behind the orbits. In the virtual reconstruction of *Sahelanthropus* this part of the cranium is almost flat, suggesting that the neurocranium may be hafted onto the splanchnocranium at too horizontal an angle. If this is so, then all the posterior elements of the neurocranium may have been rotated ventrally with respect to their life position (i.e. in right lateral view, counterclockwise rotation of the neurocranium relative to the splanchnocranium). There are several breaks in the neurocranium about which rotation could have taken place. Removal of this rotation would make the nuchal area steeper and would make the plane of the foramen magnum more acute relative to the orbital plane. A change in angle of the FM plane of only 5° would result in a value of the FM-OP angle of ca 89°, a change of 10° would result in an angle of ca 84°, not very different from the maximal figure for chimpanzees and gorillas.

Given the uncertainties of working with crushed and distorted fossils, and considering the ape-like orientation and position of the orbital plane in *Sahelanthropus*, the presence of a fully human-like FM plane in it is surprising. Because, if *Sahelanthropus* is a hominid which gave rise to humans via australopithecines, as envisaged by Brunet *et al.* (2002), Zollikofer *et al.* (2005) and Brunet and Allemand (2005), then the FM plane would change from human-like in *S. tchadensis* to ape-like in *Australopithecus* and back to human-like in the genus *Homo*, at the same time that its OP remained ape-like until the human stage was reached.

In view of these contradictions it is considered that the FM plane of *Sahelanthropus* has been incorrectly estimated by Zollikofer *et al.* (2005). In the author's view, the FM of *Sahelanthropus* would probably have intersected the

tooththrow as in chimpanzees, gorillas and australopithecines, and if so, then its FM-OP angle would have been appreciably more acute than the reconstructed figure published by Zollikofer *et al.* (2005). As a consequence it is considered premature to deduce bipedal posture and locomotion for *Sahelanthropus* on the basis of its reconstructed FM-OP angle. This conclusion reinforces that of Wolpoff *et al.* (2002) that *Sahelanthropus tchadensis* was not a hominid in the strict sense of the term.

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