The cranial base of *Australopithecus afarensis*: new insights from the female skull

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Cranial base morphology differs among hominoids in ways that are usually attributed to some combination of an enlarged brain, retracted face and upright locomotion in humans. The human foramen magnum is anteriorly inclined and, with the occipital condyles, is forwardly located on a broad, short and flexed basicranium; the petrous elements are coronally rotated; the glenoid region is topographically complex; the nuchal lines are low; and the nuchal plane is horizontal. *Australopithecus afarensis* (3.7–3.0 Ma) is the earliest known species of the australopith grade in which the adult cranial base can be assessed comprehensively. This region of the adult skull was known from fragments in the 1970s, but renewed fieldwork beginning in the 1990s at the Hadar site, Ethiopia (3.4–3.0 Ma), recovered two nearly complete crania and major portions of a third, each associated with a mandible. These new specimens confirm that in small-brained, bipedal *Australopithecus* the foramen magnum and occipital condyles were anteriorly sited, as in humans, but without the foramen's forward inclination. In the large male A.L. 444-2 this is associated with a short basal axis, a bilateral expansion of the base, and an inferiorly rotated, flexed occipital squama—all derived characters shared by later australopiths and humans. However, in A.L. 822-1 (a female) a more primitive morphology is present: although the foramen and condyles reside anteriorly on a short base, the nuchal lines are very high, the nuchal plane is very steep, and the base is as relatively narrow centrally. A.L. 822-1 illuminates fragmentary specimens in the 1970s Hadar collection that hint at aspects of this primitive suite, suggesting that it is a common pattern in the *A. afarensis* hypodigm. We explore the implications of these specimens for sexual dimorphism and evolutionary scenarios of functional integration in the hominin cranial base.

Keywords: *Australopithecus*; cranial base; bipedality

1. INTRODUCTION

As the critical intersection of the locomotor, neural and masticatory systems, the cranial base is a frequently consulted source for insight into the evolution of the human head in phylogenetic and functional–adaptive contexts. A great deal of experimental and comparative research on extant primates has been conducted to elucidate the relative influence of each of these systems on cranial base form (e.g. Lieberman *et al.* 2000), but the fossil record—especially its earlier segments—is less often studied because of small samples, poor preservation, and/or inaccessible endocranial spaces. Yet, the ultimate test of hypotheses regarding the conjunction of structural innovations and their purported functions in an adaptive context is the relative timing of their first appearances in taxa potentially ancestral (or at least sister) to the extant taxa targeted by most of this research. Therefore, it is important to glean as much information as possible from the available fossil remains.

The 3.7–3.0 Myr old hominin species *Australopithecus afarensis* is usually considered to be the plesiomorphic ('primitive', African apeline) sister taxon to subsequent australopiths and the genus *Homo* (e.g. Kimbel *et al.* 2004; Strait & Grine 2004). Relative to these successor taxa, the skull and dentition of *A. afarensis* is characterized by numerous primitive features, many of which are part of, or at least influenced by, the masticatory system (see Kimbel & Delezenne 2009, for a recent review). The cranial base was spottily represented in the initial (1970s) hypodigm of the species; a single partial calvaria of an adult male individual from A.L. 333 (*ca* 3.2 Ma) was the principal source of information until the first complete adult skull of the species was recovered in 1992 (A.L. 444-2, a large adult male, *ca* 3 Ma). These specimens showed that, in contrast to the primitive morphology of the temporal bone (e.g. low-relief mandibular fossa, tubular tympanic element, highly inflated squama, asterionic notch sutural pattern, etc.), the calvaria is derived in its anteriorly positioned foramen magnum and occipital condyles on a short, broad cranial base—features shared with modern humans.

The female calvaria of *A. afarensis* was until recently known only from fragments of the calotte, and while

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these hinted at several morphological differences from the larger (male) skulls, particularly in aspects of occipital squama form, interpreting this morphology in the context of the entire skull was not possible. Fieldwork in the 2000s rectified this with the recovery of a nearly complete skull of a small, probably female individual, A.L. 822-1. This specimen adds information on variation in *A. afarensis* cranial base form, casts previously known fragmentary remains of small (female) individuals of this species in a new light,

Figure 1. The reconstructed A.L. 822-1 skull, oblique view. Approximately 45% natural size.

and reveals an apparently unique (in the extant African hominoid context) pattern of sexual dimorphism in the australopith cranial base. Our more comprehensive description of the A.L. 822-1 skull is in preparation, but here we focus on the cranial base of this specimen and its substantive role in illuminating these issues.

2. THE A.L. 822-1 SKULL

The skull A.L. 822-1 was found by the late Dato Adan, an Afar member of the Hadar Research Project, during the 2000 field season. It was recovered from the surface of sediments of the Hadar Formation's KH-1 sub-member and is estimated to be approximately 3.1 Ma (C. Campisano 2009, personal communication). It is the third adult individual from Hadar to preserve both the mandible and cranium (A.L. 444-2, KH-2 sub-member, *ca* 3 Ma and A.L. 417-1, SH-3 sub-member, *ca* 3.3 Ma, are the other two).

The specimen was recovered in approximately 200 fragments, which have been cleaned, reconstructed and reassembled to constitute most of an adult skull with almost all of the dentition (figure 1). The reconstruction of the original specimen reveals remnant distortion, owing to both warping and crushing, in (i) the failure of the palatal and calvarial midlines to align, (ii) the temporal bones' placement on different coronal planes, and (iii) some bilateral compression of both palatal and mandibular arches (figure 2). We describe in detail this deformation and the steps taken to correct it in our comprehensive comparative study currently in preparation. The data and analyses presented here are based on our final restoration using casts of the original fossil.

The A.L. 822-1 skull presents numerous characteristics diagnostic of *A. afarensis* (see Johanson *et al.* 1978; White *et al.* 1981, 1993, 2000; Rak 1983;

Figure 2. Pattern of distortion in the A.L. 822-1 reconstruction. (a) Basal view. Note the asymmetric positions of the temporal bones, resulting from deformation of the (anatomical) left side. (b) Superior view. Note the offset of the face in relation to the calvarial midline. Red line denotes anatomical midline.

Figure 3. Box-plot metrical profile of A.L. 822-1. Data for A.L. 822-1 shown in Hadar *A. afarensis* sample distribution. Bold vertical line indicates value for A.L. 822-1; rectangle defines the 25th and 75th quartiles; diamond defines the mean and 95% CI; short vertical line within rectangle defines the median.

Figure 4. Lateral view of A.L. 822-1 'final' restoration (cast), showing the superiorly extended position of the nuchal lines as expressed by W. E. Le Gros Clark's nuchal area height index: maximum height of nuchal lines (upper horizontal line) above Frankfurt Horizontal (lower horizontal line) as a percentage of maximum cranial vault height above FH (vertical line).

Kimbel *et al.* 1984, 1994, 2004; Kimbel & Delezenne 2009). These include:

- strongly prognathic, biconvex maxillary subnasal surface,
- narrow midface (nasal aperture and interorbital block),
- mild sagittal convexity of the low frontal squama,
- medial to lateral supraorbital thickness gradient,
- posteriorly convergent temporal lines,
- steeply inclined nuchal plane,
- low upper scale (la-i) and long lower scale (i-o) of occipital squama,

Figure 5. Hadar cranium A.L. 444-2. Note the low position of the compound temporal/nuchal crest (arrow), which approximates the biasterion line, a phylogenetically derived condition of other mature males of *A. afarensis*. Approximately 50% natural size.

- sharply angled articular surface of the occipital condyle,
- flattened, horizontally oriented tympanic elements,
- hollowed lateral surface of the mandibular corpus (beneath the premolars) with high ramal root and narrow extramolar sulcus,
- marked topographic step down from mesial P_3 to the distal- P_3 to M_3 occlusal platform.

The A.L. 822-1 skull is most probably that of a female. Its overall cranial dimensions are small, closely approximating those of the very small though incomplete Hadar adult calvaria A.L. 162-128 (Kimbel *et al.* 1982). The mastoid process is much smaller than the mastoids of male crania such as A.L. 333-45, A.L. 333-84 and A.L. 444-2. Consistent with its small external dimensions, our preliminary estimate of endocranial volume (using mustard seed) is 385 cc, which is similar to that estimated for A.L. 162-28 (375–400 cc) and smaller than the estimates

Table 1. Nuchal area height index in hominoids. Negative value indicates nuchal area height is below Frankfurt Horizontal. Comparative data from Kimbel *et al.* (2004).

taxon/specimen	nuchal area height index (%)
<i>Australopithecus afarensis</i>	
A.L. 444-2	13
A.L. 333-45 (recon.)	12
A.L. 822-1	23
<i>Australopithecus africanus</i>	
Sts. 5	10
<i>Australopithecus boisei</i>	
OH 5	11
KNM-ER 406	7
KNM-ER 13 750	-3
KNM-ER 732	12
<i>Australopithecus aethiopicus</i>	
KNM-WT 17 000	14
<i>Homo sapiens</i> ($n = 10$)	-2
<i>Pan troglodytes</i> male ($n = 10$)	51
<i>Pan troglodytes</i> female ($n = 10$)	47
<i>Gorilla gorilla</i> male ($n = 10$)	108
<i>Gorilla gorilla</i> female ($n = 10$)	67

for clearly male crania A.L. 333-45 (*ca* 485 cc) and A.L. 444-2 (*ca* 550 cc; Holloway & Yuan 2004). As shown in figure 3, the condyle of the A.L. 822-1 mandible is the second smallest in mediolateral diameter among six Hadar condyles, and its maxillary canine breadth falls near the top of the smallest quartile in the Hadar sample distribution ($n = 12$). Other aspects of A.L. 822-1 cranial morphology consistent with female status are discussed below.

3. THE CRANIAL BASE OF A.L. 822-1

(a) Nuchal area height and morphology of the occipital bone

In the 1940s W. E. Le Gros Clark argued that the small, horizontally oriented nuchal plane of the occipital bone of South African australopith crania was compatible only with a humanlike poise of the head on the cervical vertebral column (Le Gros Clark 1947, p. 309; 1950, p. 241–243). He devised the ‘nuchal area height index’ to express the much smaller degree to which the insertion area of the neck muscles extended superiorly (relative to the Frankfurt horizontal (FH) baseline) as a percentage of maximum calvarial height in fossil and living hominins as compared with the great apes. In the African great apes the height of the nuchal area constitutes (on average) approximately 50 per cent of the calvarial height in both male and female chimpanzees and 67 per cent in female gorillas (in male gorillas the index is more than 100 per cent because the superior extension of the enormous compound temporal/nuchal crest actually surpasses maximum vault height). Among the australopiths, in contrast, the percentage averages only about 10 per cent (with a total range of -3% to +14%, $n = 10$), which is much closer to what is observed in modern humans (average = -2%, i.e. nuchal plane height is slightly below the FH; see table 1).

Two large (presumptive male) *A. afarensis* crania have nuchal area height index values slightly higher than the australopith average of 10 per cent (A.L. 333-45, in which FH is based on the ‘composite reconstruction’ of Kimbel *et al.* 1984, 13%; A.L. 444-2, 12%). For A.L. 822-1, however, the value is *ca* 23 per cent, about 9 per cent higher than for any other measurable, undistorted australopith cranium and about midway between chimpanzee and human means (figure 4). The relatively high index value is consistent with the visibly steep nuchal plane in A.L. 822-1, which faces posteroinferiorly at *ca* 67° to the FH. (The usual way of expressing nuchal plane steepness is the inclination of the inion–opisthion chord relative to FH; for A.L. 822-1, this angle is 42°. However, when the foramen magnum is anteriorly located—as it is in all australopiths (see below)—the inion–opisthion chord angle can understate the steepness of the more lateral surfaces on which the mass of the nuchal muscles insert.)

The superiorly extensive, steeply angled nuchal plane of A.L. 822-1 illuminates the morphology of other less complete *A. afarensis* crania. In *A. afarensis* partial calvariae A.L. 162-28 and KNM-ER 2602, the nuchal plane is steep and the superior nuchal lines highly arched; the transition between nuchal and occipital planes across the superior nuchal lines is smooth and convex; and the nuchal plane consists of bilateral, posterolaterally directed plates that merge at a median topographic peak (Kimbel *et al.* 1984, 2004; Kimbel 1988). While neither fossil can be oriented precisely on FH, their anatomical similarity to A.L. 822-1 is remarkable. Both specimens are small presumptive females that bear compound temporal/nuchal crests; although A.L. 822-1 does not, the temporal lines sweep laterally towards the asteria within a few millimetres of the highly arched superior nuchal lines. Except for the relatively low nuchal area height index value, the overall morphological pattern of these female specimens is extremely primitive.

Figure 5 depicts the large, male *A. afarensis* cranium A.L. 444-2 in posterior view. Asterion in hominins usually lies close to the FH and the low position of the superior nuchal line relative to the biasterion line is indicated in the figure. We draw attention to the distinction between Hadar crania that have high nuchal lines and steep nuchal planes (A.L. 822-1, A.L. 162-28 and A.L. 439-1; the A.L. 288-1a, ‘Lucy’, occipital, too incomplete to orient with precision, bears these same hallmarks), and those in which the nuchal lines are lower (closer to the biasterion line) and the nuchal plane much more horizontal (A.L. 333-45, A.L. 444-2), as in most later hominins. With one exception, this difference divides the sample by size, which we take to indicate sex, with males showing the more derived morphology. The exception is A.L. 439-1, a very large male occipital (comparable in size to that of A.L. 444-2). Although this specimen bears massive compound temporal/nuchal (T/N) crests that extend on each side from the middle of the nuchal line laterally to asterion, it is not fully mature judging from the open lambdoidal suture. The same morphology is replicated in yet another even more

fragmentary Hadar occipital, A.L. 444-1 (from the same locality as the complete, old adult A.L. 444-2 skull); this specimen, which consists of two non-articulating squamous fragments that span the boundary between nuchal and occipital planes on opposite sides, is from a large, thick-vaulted cranium and bears a weak compound T/N crest. The relatively feeble expression of the compound crest, together with the completely patent and 'puffy' lambdoidal sutural surface, argues for a younger subadult growth stage of this apparently male individual compared with A.L. 439-1. As in A.L. 439-1, however, the nuchal plane is very steep, facing more posteriorly than inferiorly, even making allowance for errors in orientation of the fragments. These two relatively young, large male individuals present a significant contrast with older adult males as represented by A.L. 333-45 and A.L. 444-2.

The expanded sample of Hadar skulls permits the identification of a cross-sectional ontogenetic transformation of male occipital morphology (from young to old, A.L. 444-1 → 439-1 → 333-45 → 444-2). This transformation entails increasing horizontality of the nuchal plane, which results in greater flexion of the occipital squama on the sagittal plane; increasing topographic flattening of the nuchal plane; lowering of the nuchal crest, and related to these shifts, an alteration of the compound T/N crest from a posterosuperior extension of the nuchal plane to an inferior projection of the occipital plane (see Kimbel *et al.* 2004, for comparative observations and data). We do not, based on presently available evidence, see the same transformation in female individuals of *A. afarensis*. All four specimens from which relevant information can be extracted are mature (A.L. 162-28, A.L. 822-1 and KNM-ER 2602, probably A.L. 288-1a) and these clearly demonstrate the symplesiomorphic pattern associated with young males of the species. This similarity partly explains (along with an expansive posterior temporalis) why compound T/N crests are so common in the smaller crania of this species (Kimbel *et al.* 2004).

(b) Position and orientation of the foramen magnum

The margins of the foramen magnum in A.L. 822-1 are preserved on two fragments: one extends from the basioccipital posterolaterally to include the right occipital condyle and adjacent jugular process; the other is a strip of nuchal plane bearing a short (14 mm) segment of the margin just anterolateral to opisthion (although this fragment does not connect to the main portion of the occipital squama, external morphology constrains its placement to within a few mm). Between these two pieces we can estimate the size and position of the foramen within a narrow error range (± 2 mm).

In *A. afarensis*, as in all australopith species, the foramen magnum, and with it the occipital condyles, resides in an anterior position on the cranial base. Typically, this is assessed through indices expressing the anteroposterior position of basion (ba) or opisthion (o) in relation to cranial length. We use Weidenreich's (1943) index relating the position of opisthion to the

Table 2. Position and orientation of foramen magnum. Index calculated as the projected length opisthion–opisthocranion/projected length glabella–opisthocranion. Negative value for foramen orientation indicates anteroinferior orientation.

taxon/specimen	FM position index (%)	FM orientation (°)
<i>Australopithecus afarensis</i>		
A.L. 444-2	24	16
A.L. 333-45 (recon.)	19	—
A.L. 822-1	23	14
<i>Australopithecus africanus</i>		
Sts. 5	19	20
<i>Australopithecus boisei</i>		
OH 5	24	7
KNM-ER 406	18	13
KNM-ER 13 750	20	—
<i>Australopithecus aethiopicus</i>		
KNM-WT 17 000	21	—
<i>Homo sapiens</i> ($n = 10$)	31	–8
<i>Pan troglodytes</i> male ($n = 10$)	12	18
<i>Pan troglodytes</i> female ($n = 10$)	14	20
<i>Gorilla gorilla</i> male ($n = 10$)	7	27
<i>Gorilla gorilla</i> female ($n = 10$)	13	30

horizontal projected length of the calvaria (g–op).¹ In our sample of African great apes, the mean index value ranges between 7 per cent (male gorillas, with their massive compound crests) and 14 per cent (female chimpanzees). In humans the more anterior position of opisthion is conveyed by the much higher mean index value in our sample of 31 per cent (range = 28–34%). Individual australopith values vary between 18 and 24 per cent, with the two *A. afarensis* specimens (A.L. 444-2 = 24%, A.L. 822-1 = 23%) falling at the high end of this range (table 2). Weidenreich's reported values for Asian *Homo erectus* crania yields an average of about 26 per cent (range = 24–28%).

The importance of these data on foramen magnum position among fossil hominins is that neither hypothesized postural/locomotor differences (i.e. between the australopiths and *H. erectus*) nor absolute brain-size differences (with *H. erectus* having endocranial volumes 1.5 to 2.0 times larger than australopith values) has a large impact on the position of the foramen on the cranial base. Rather, the major difference is between the quadrupedal apes and the bipedal hominins. However, a different division applies to the data on foramen magnum orientation (ba–o line relative to FH). In humans the foramen is forwardly inclined (i.e. the plane of the foramen faces anteroinferiorly) whereas in the great apes it is posteriorly inclined (posteroinferior orientation). In *A. afarensis* the reconstructed angle of the ba–o line is *ca* 14° in A.L. 822-1 and *ca* 16° in A.L. 444-2, values that lie within the range for other australopith crania. The australopith range (table 2) is well below the range for our sample of modern humans (the mean value for which is *ca* –8°; again, the foramen faces anteroinferiorly) but overlaps the low end of the range for

Table 3. Measures of basi-occipital length.

taxon/specimen	basi-occip. length (mm)	basi-occip. lg/biorbital br * 100
<i>Australopithecus afarensis</i>		
A.L. 444-2	20	21
A.L. 822-1	22	23
A.L. 417-1	19	24
<i>Australopithecus africanus</i>		
Sts. 5	25	29
MLD 37/38	21	—
Stw 187	17	—
<i>Australopithecus boisei</i>		
OH 5	20	20
KNM-ER 406	25	24
KNM-ER 407	21	—
<i>Australopithecus aethiopicus</i>		
KNM-WT 17 000	25	27
<i>Homo sapiens</i> (n = 10)	21	22
<i>Pan troglodytes</i> male (n = 10)	28	29
<i>Pan troglodytes</i> female (n = 10)	26	28
<i>Gorilla gorilla</i> male (n = 10)	37	33
<i>Gorilla gorilla</i> female (n = 10)	29	30

Table 4. Cranial base breadth in hominoids.

taxon/specimen	bi-entoglenoid br (mm)	bi-entogl. br/ biorbital br * 100
<i>Australopithecus afarensis</i>		
A.L. 444-2	80	84
A.L. 333-45 (recon.)	78	89
A.L. 822-1	57	62
<i>Australopithecus africanus</i>		
Sts. 5	65	76
MLD 37/38	62	—
<i>Australopithecus boisei</i>		
OH 5	89	84
KNM-ER 406	85	89
KNM-ER 13 750	86	80
KNM-ER 23 000	80	—
KNM-ER 407	65	—
<i>Australopithecus aethiopicus</i>		
KNM-WT 17 000	80	85
<i>Homo sapiens</i> (n = 10)	74	77
<i>Pan troglodytes</i> male (n = 10)	61	67
<i>Pan troglodytes</i> female (n = 10)	59	65
<i>Gorilla gorilla</i> male (n = 10)	72	63
<i>Gorilla gorilla</i> female (n = 10)	64	64

chimpanzees (mean = ca 19°; gorilla means are about 50% higher; see Kimbel *et al.* 2004, for details). Thus, in contrast to the data on foramen magnum position, which align *A. afarensis* and other australopiths with modern humans, the data on orientation of the foramen situate the australopiths in an intermediate

Figure 6. Schematic of relative cranial base breadth in hominoids. Dashed vertical lines represent the biorbital breadth of A.L. 822-1, to which all specimens are size-adjusted. MSP, midsagittal plane; be, terminus of bi-entoglenoid breadth; bt, terminus of bi-articular tubercle breadth; bz, terminus of bizygomatic breadth. Heavy red line defines the breadth of the articular eminence. Note in A.L. 822-1, chimpanzees (males, n = 10) and gorillas (females, n = 10) the close approximation of the entoglenoid processes, expressing a narrow central cranial base.

position between modern apes and humans, but closer to the former (chimpanzees, specifically).

Whereas the anterior shift of basion and opisthion accounts for the forward location of the foramen magnum in australopiths and modern humans, the relative vertical positions of these landmarks (beneath the FH, for example) explain the differences in orientation of the foramen (Kimbel *et al.* 2004). Because the vertical position of basion is similar in apes and humans, differences in foramen orientation reduce to differences in the vertical position of opisthion. In humans, uniquely, opisthion sits much further below FH than basion (the foramen opens anteroinferiorly), which can be explained as a consequence of overall expansion and rotation of the occipital squama with encephalization (e.g. Weidenreich 1941; Biegert 1957). In the small-brained *A. afarensis*, although the foramen magnum is far forward on the base, opisthion is elevated relative to basion and so the plane of the foramen inclines posteriorly, more similar to what is observed in the apes.

Occipital morphology in *A. afarensis* is consistent with these signs of affinity from the foramen magnum. As discussed above, the orientation of the nuchal plane, the height of the nuchal muscles' insertion area, and the degree of sagittal flexion of the occipital squama range from symplesiomorphic (ape-like) to more derived, but taken as a package convey an intermediate position on the hominoid occipital bone morphocline. At the derived end of the morphocline occipitals approach a quasi-human form in their relatively horizontal nuchal plane, low nuchal area height index and strongly flexed squama, but they do not show the strongly rotated squama that in modern humans confines the maximum height of the nuchal area below the FH (on average) and drops opisthion

Figure 7. Bivariate plot of palate breadth and cranial base (bi-entoglenoid) breadth in hominoids. Light brown data points, male gorilla; dark brown, female gorilla; light blue, male chimpanzee; X, *Australopithecus afarensis*; +, *A. africanus*; Z, *A. boisei*.

very far below basion, introducing a negative angle to the foramen's orientation. It bears noting that the *position* of the foramen magnum, which is relatively anterior in *A. afarensis* and close to the condition in modern humans, is not linked to this impressive range of variation in occipital bone morphology.

(c) Length and breadth of the cranial base

Along with the anterior position of the foramen magnum, the shortened external length of the cranial base is a derived feature in A.L. 822-1 shared with modern humans. This can be judged from the length of the basi-occipital fragment associated with this fossil (22 mm) as well as that attributed to another Hadar specimen, A.L. 417-1 (19 mm), which essentially match the mean for modern humans both absolutely and relative to biorbital breadth (table 3). A shortened external base can be inferred for specimens of *A. afarensis* in which the basi-occipital is missing, such as the large (male) crania A.L. 333-45 and A.L. 444-2, from the anteroposterior distance between the carotid foramen and foramen ovale (which roughly approximates basi-occipital length) or the length of the petrous elements (which frame the basi-occipital area), both of which are shorter than in gorillas and chimpanzees.

Most other early hominins share the shortened external anterior cranial base with *A. afarensis* (table 3). Dean & Wood (1982), however, showed that the *A. africanus* base is unusual in its somewhat elongated anteroposterior dimensions compared with other australopithecids and early *Homo*. Specimen Sts 5 indeed has absolutely and relatively long basi-occipital and petrous elements compared with other hominins (table 1), but it is the only *A. africanus* cranium in which these dimensions can be judged relative to a non-calvarial size standard (such as biorbital breadth or palatal length). In absolute terms the basi-occipital of MLD 37/38 and Stw 187 are as short as those of *A. afarensis*, so it is unclear whether Sts 5 is typical of *A. africanus*.

Relative to body size and skull size the modern human cranial base is short, but also wide, whereas the great apes exhibit the opposite proportions.² Tobias (1967) noted that the mandibular fossa is equally wide (mediolaterally) in gorillas and OH 5 (the type specimen of *Australopithecus boisei*), but only in the latter does the fossa project laterally far beyond the calvarial wall to anchor the temporal root of the flaring zygomatic arch. In gorillas, he found, the mandibular fossae, in spite of their great breadth, are actually closer together on the cranial base and so do not project nearly as far from the calvarial wall. This difference is depicted graphically in figure 6,

Table 5. Palate dimensions in fossil hominins. Palate depth is the midline height of the palatine process of the maxilla above the inner alveolar margin at M2. Palate breadth is the width across the internal alveolar crests at mid-M2. Palate length is the direct distance between orale and staphylion (reconstructed in some specimens). Relative palatal breadth (Palatal Index) is calculated as palate breadth/palate length $\times 100$.

taxon/specimen	palate depth	palate breadth	palate length	palatal index
<i>Australopithecus afarensis</i>				
A.L. 58-22	—	27.0	—	—
A.L. 199-1	11.0	32.0	54.0	59.3
A.L. 200-1a	8.5	33.5	65.0	51.5
A.L. 417-1d	14.0	28.5	58.0	49.1
A.L. 427-1	11.0	32.0	—	—
A.L. 442-1	—	25.0	—	—
A.L. 444-2	12.0	41.0	75.0	54.7
A.L. 486-1	11.2	33.0	—	—
A.L. 822-1	14.0	31.0	63.0	49.2
<i>Australopithecus africanus</i>				
Sts. 5	18.0	35.7	65.3	54.7
Sts. 53	—	32.0	54.0	59.3
Stw. 73	14.5	30.0	58.0	51.7
<i>Australopithecus robustus</i>				
SK 12	12.8	32.0	—	—
SK 46	12.2	35.0	—	—
SK 48	15.5	—	—	—
SK 79	13.5	—	—	—
SKW 11	15.0	34.6	60.0	57.7
<i>Australopithecus boisei</i>				
KNM-ER 405	22.0	38.0	75.0	50.7
KNM-ER 406	20.0	37.4	70.0	53.4
OH 5	21.0	38.2	79.1	48.3
KNM-CH 1	—	40.8	72.0	56.7

where it can be seen that many other australopiths resemble the morphology Tobias (1967) described for OH 5. A notable exception is A.L. 822-1, which, in relative terms (note that all specimens in the figure are scaled to the biorbital breadth of this Hadar cranium), has a very narrow cranial base. As measured across the entoglenoid processes (the reconstructed positions of which are validated by the bicondylar breadth of the specimen's mandible), the cranial base of A.L. 822-1 is as narrow as average for our sample of female gorillas, and narrower than in any other of the figured australopith specimens, including Sts 5 and the A.L. 444-2 cranium of *A. afarensis*, in which the mandibular fossae are spread far apart on the base.

Another Hadar specimen, A.L. 58-22, appears similar to A.L. 822-1 in its narrow cranial base. This specimen is a craniofacial fragment with part of the right posterior maxilla, sphenoid and temporal bone; the vomer establishes the midline (Kimbel *et al.* 1982). As with A.L. 822-1, the bi-entoglenoid distance (60 mm) is small compared with the larger Hadar crania, by at least 20 mm (table 4). This absolute difference may reflect sexual dimorphism in cranial base dimensions in *A. afarensis*, as both of these Hadar specimens also have abbreviated mandibular fossa

breadths compared with clearly male crania (A.L. 333-45, A.L. 444-2). Biorbital breadth is not available for A.L. 58-22, but another way to assess the relative width of the central cranial base is by a simple index expressing the bi-entoglenoid distance as a percentage of the bi-articular tubercle distance. When this is done, it can be seen that in spite of small fossa breadths (which would increase the index), the bi-entoglenoid distance is relatively small in these two specimens (*ca* 48%), compared with the larger Hadar crania (*ca* 55%) and other early hominins, including *A. africanus* (*ca* 54%, $n = 2$).

(d) *The cranial base and palate shape*

In their diagnosis of *A. afarensis*, Johanson *et al.* (1978, p. 6) listed as a distinguishing feature of the adult cranium 'palate shallow, especially anteriorly; dental arcade long, narrow and straight-sided'. Subsequent discovery and analysis have confirmed this symplesiomorphic feature set of the *A. afarensis* palate (Kimbel *et al.* 2004). However, two specimens found since 1990 extend the range of variation in this species' palatal form. In both A.L. 417-1 and A.L. 822-1 the palate is both very narrow and very deep: internal palate depth (both 14 mm at M²) is the greatest among seven measureable Hadar specimens, while relative palate breadth (internal breadth at M²/length $\times 100 = ca$ 49%) is the lowest among five Hadar specimens and, indeed, among 11 of 12 australopith specimens in our sample overall (table 5).

The very narrow palate of the smaller Hadar crania is potentially related to the narrow cranial base in these *A. afarensis* individuals. Recall that the base (measured between the entoglenoid processes) of A.L. 822-1 is as relatively narrow as in gorillas. Cranial base width cannot be measured for A.L. 417-1, but in A.L. 58-22, which (as described in the previous section) has a cranial base width approximately as small as that of A.L. 822-1, estimated palate breadth (*ca* 27 mm, at M²) is the second smallest in the *A. afarensis* sample (palate length for A.L. 58-22 cannot be estimated). The relationship between the narrowness of the palate and the narrowness of the cranial base would appear to hold, albeit on limited available evidence.

This relationship is explored further in the context of African great ape comparative data in figure 7. Among the apes there is a strong correlation ($r^2 = 0.52$, $p < 0.0001$) between absolute values of palate breadth and bi-entoglenoid breadth, which appears largely to be a function of strong size-dimorphism in gorillas (figure 7). Using size-standardized variables (with biorbital breadth as the standard), the correlation is much weaker (because male gorillas no longer stand out; $r^2 = 0.14$, $p < 0.017$). However, in both cases the smaller *A. afarensis* individuals are the most apelike of the small fossil hominin sample in their combination of narrow palates and narrow cranial bases, with *A. boisei* and even *A. africanus* specimens highly divergent (indeed, humanlike, though humans were not included in our analysis) in their broader cranial bases.

Of considerable interest is the position of A.L. 444-2, the large male *A. afarensis* skull. Compared

with the smaller specimens, it has a much broader cranial base for its palate breadth than predicted by either great ape regression, which hints at an unusual—but perhaps not exceptional—pattern of sexual dimorphism in *A. afarensis*. Note that there are no small *A. boisei* specimens in the sample for which both palate and cranial base breadths can be measured (only OH 5 and KNM-ER 406 preserve both dimensions). However, the bi-entoglenoid breadth of KNM-ER 407, considered by consensus a female *A. boisei* calvaria, is less than 10 mm wider than that of the two *A. afarensis* females (see *y*-axis in figure 7), and if we grant this individual a palate breadth somewhere between, say, those of A.L. 822-1 and Sts 5 (*ca* 31–36 mm), then the presumptive female-to-male trend in the cranial base versus palate breadth relationship for *A. boisei* would be very similar to that of *A. afarensis*. That is, compared with extant African apes (and other anthropoid species; M. Spencer 2010, personal communication), males have a *much* wider cranial base for their palate width than females (see also the suggestive position of other large *A. boisei* and *A. aethiopicus* specimens on the *y*-axis of figure 7). (Unfortunately, the fossil record does not permit us to extract any more information from the size-standardized data.) This suggests a unique pattern of cranial sexual dimorphism among australopith species.

4. DISCUSSION

The A.L. 822-1 skull focuses attention on several aspects of adult cranial base morphology that were not previously well understood for *A. afarensis*.

First, this Hadar specimen presents a particularly primitive basicranial profile. Its relatively narrow cranial base, high nuchal lines, and correspondingly steep nuchal plane are more similar to African great ape conditions compared with other australopiths so far known. While other more fragmentary *A. afarensis* specimens hint at relatively generalized occipital form, A.L. 822-1 places this morphology within the context of the entire skull for the first time.

Second, A.L. 822-1 points to a pattern of cranial sexual dimorphism neither recognized previously among the australopiths nor encountered among extant hominoids. The apelike cranial base proportions and nuchal area form are already presented in derived conditions in larger *A. afarensis* specimens usually considered to be males (A.L. 333-45, A.L. 444-2). In these crania the basicranium is wider (absolutely and size-standardized) and the position of the nuchal lines approximates FH, with a horizontal nuchal plane, differences that raise the question of whether species-level taxonomic distinction between the two morphs is warranted. Two further points argue otherwise. First, the combination of high nuchal lines and a steep nuchal plane in two large, immature occipital specimens (A.L. 439-1, A.L. 444-1) suggests that this dimorphism in the Hadar cranial sample has an ontogenetic basis, with young males ‘passing through’ the final adult form of the smaller females to reach mature male (and more derived) morphology. Second, the adult cranial

sample of *A. boisei* hints at the same pattern of cranial base breadth dimorphism, while the occipital of the L338y-6 calotte (Shungura Formation, Member E), interpreted by Rak & Howell (1978) as a immature male of this species, has a very steep nuchal plane, as is also observed in the young Hadar males. These observations convince us that the variation in Hadar occipital and cranial base form, though phylogenetically informative, is intraspecific. A similar case has previously been made for the polymorphic lower third premolar in *A. afarensis* (Kimbel *et al.* 2004, 2006).

Finally, the expanded cranial sample of *A. afarensis* highlights the strongly mosaic nature of basicranial evolution in the hominin clade. Evolutionary changes in the cranial base and occipital squama that are thought to unite early hominins with modern humans (and which, for example, have raised suspicions of pervasive homoplasy in the crania of robust australopiths and *Homo*), were still not completed by the time of *A. afarensis*, *ca* 3.5–3.0 Ma. Thus, although an anteriorly located foramen magnum and a short basioccipital segment are shared with extant humans, the narrow cranial base, posteriorly inclined foramen magnum, high nuchal lines and concomitantly steep nuchal plane, are apelike characteristics that are inferred to have been commonly, though not universally, expressed in this taxon.

Upright posture and a large brain are the most commonly invoked influences on the cranial base morphology of modern humans (see Lieberman *et al.* 2000, for a review). According to Le Gros Clark (1947), Robinson (1958) and Olson (1981), among others, the descent of the nuchal musculature and the rotation of the nuchal plane to a horizontal position beneath the brain case mirrors the adoption of upright posture and bipedal locomotion in the hominin clade. Biegert (1957; also Weidenreich 1941), in contrast, argued that the architectural remodelling of the hominin posterior calvaria was a by-product of cerebral expansion, which introduced a strongly flexed basicranial axis and a ‘rolling up’ of the braincase that impelled the foramen magnum and occipital condyles forward. After casting doubt on the oft-proposed correlation among foramen magnum orientation, occipital condyle position and mode of locomotion in primates, Biegert (1963) pointed to the horizontal nuchal plane and anterior foramen magnum of *A. africanus* (Sts 5) as evidence of an initial phase of encephalization in hominin evolution. Robinson (1958), citing the case of the ‘short-faced squirrel monkey’ (*Saimiri*), noted that the orientation of the nuchal plane (steep) and the position of the occipital condyles and foramen magnum on the cranial base (anterior) are not necessarily related, which recalls the situation in *A. afarensis*. The review by Lieberman *et al.* (2000) concluded that the orientation of the foramen magnum (as distinct from its anteroposterior position) is unrelated to the posture of the head on the vertebral column but, with cranial base flexion, is primarily a reflection of brain size relative to cranial base length.

The skulls of *A. afarensis* bear on these issues. This species is demonstrably an upright biped with a mean

endocranial volume (*ca* 450 cc) slightly larger than that of *Pan troglodytes*, to which, among the living hominoid taxa, it is probably closest in body size. The marked variation in the height of the nuchal muscle insertions and angulation of the nuchal plane in *A. afarensis* would seem to negate a major role for upright locomotion in dictating morphological variation in this region of the hominin skull. One caveat is that we do not have a good idea about how the head was held on the cervical vertebral column in *Australopithecus*; while the anterior position of the occipital condyles suggests a head posture more similar to that of modern humans than apes, the slightly posterior orientation of the foramen magnum, the strongly angled atlanto-occipital articular surfaces (on A.L. 333-45, A.L. 822-1, and the A.L. 333-83 first cervical vertebra), and the long, straight and robust spine of the lower cervical vertebra (C6, A.L. 333-106), may be signs of a mechanical environment dissimilar to that of the modern human craniovertebral interface. We do not know the extent of cervical lordosis in these early hominins, but it would not surprise us to find a less lordotic cervical column in *A. afarensis* than in modern humans.

Obviously, whether measured absolutely or relative to estimated body mass, brain size in *A. afarensis* is much closer to that of apes than modern humans. This indicates that the humanlike anterior position of the foramen magnum is largely, if not entirely, unrelated to overall brain size. Perhaps, though, *relative* neocortical (cerebral) expansion is responsible for the forward migration of the foramen. In this context, the (by now) clear evidence of a relatively posterior position of the lunule sulcus on earliest australopithecine brain endocasts (Holloway *et al.* 2004) can be seen as a sign of relative cerebral expansion, which, posteriorly, is manifested as a bulging of the occipital poles over the cerebellar lobes, and, perhaps, a forward 'rotation' of the cranial base (similar to what Biegert 1963 hypothesized). In the *A. afarensis* brain endocast the absolute and relative size of the cerebellar lobes (and especially their anteroposterior length) is much smaller than in African great apes, in which the cerebral and cerebellar lobes protrude subequally (Holloway & Yuan 2004). However, it is unclear to what extent the form of the braincase beneath the *tentorium cerebelli* would be affected morphogenetically by enlargement of the cerebrum posteriorly; this is an area in need of further research.

The ape-sized brain of *A. afarensis* rests on a base with a much shorter basi-occipital segment than in any great ape. As shown by Lieberman *et al.* (2000; see also Spoor 1997; McCarthy 2001), brain size relative to cranial base length explains a fairly large amount (but not all) of the observed variation in cranial base angle across a wide spectrum of anthropoid primates. We do not know the exact length of the anterior cranial base (sella turcica to foramen caecum) in *A. afarensis*, but evidence from fragmentary specimens (i.e. A.L. 58-22, A.L. 417-1) and the demonstrably short segment between basion and the rear of the palate indicate a total cranial base length less than an ape of comparable brain size. (The index of relative encephalization 1, which expresses

the cube root of endocranial volume as a percentage of cranial base length [ba-sella + sella-fc], is roughly 0.94 in A.L. 822-1, which is smaller than values for fossil and extant *Homo* but in the zone of overlap for the small sample of australopithecines and extant apes measured from CT scans by Spoor 1997.) Similarly, we can only estimate the (internal) flexion of the cranial base in *A. afarensis*, using the preserved morphology of A.L. 822-1 (which includes a marked superior deflection of the external basioccipital surface at basion) with support from the other more fragmentary specimens mentioned above; for A.L. 822-1 the angle (ba-se/se-fc; CBA1 of Lieberman *et al.* 2000) is approximately $142^\circ (\pm 5^\circ)$, which is some 15–20° more flexion than great ape species' means and close to the modern human mean. This Hadar skull has a more highly flexed cranial base than extant African apes of similar relative brain size (details in preparation; see also Spoor 1997; Lieberman *et al.* 2000, for comparative data).

Although the influence of body posture on primate cranial base form has been discounted by recent research (see Lieberman *et al.* 2000), we see the anterior position of the foramen magnum and occipital condyles as the *major* cranial base distinction between *Australopithecus* and *Homo*, on one hand, and the great apes on the other. The fact that this distinction maps onto primary locomotor differences speaks to upright posture in hominins as an important factor in the positional shifts of these cranial base structures. In our view (see also Spoor 1997; Kirk & Russo 2010), the adoption of upright posture (though not necessarily striding bipedal locomotion *per se*) in hominins led to a forward migration of the foramen magnum/occipital condyles and a shortened cranial base.³ The combination of a small, ape-sized brain on a relatively short base introduced the flexion of the basicranial axis. Thus, despite their small brains, the anterior position of the foramen magnum (basion) in *Australopithecus* was associated with the relatively short, flexed cranial base typical of modern humans by *ca* 3 Ma (figure 8). Subsequent changes in the orientation of the foramen magnum (anteroinferior-facing) in the *Homo* clade are probably linked to an increase in endocranial volume and the consequent descent of opisthion beneath the braincase, as discussed above (see Kimbel *et al.* 2004 for details). The introduction of the cervical vertebral lordosis may also play a role in this change, but the fossil record is currently mute on the timing of the initial appearance of this innovation.

If we consider the potential link between cranial base configuration and facial orientation (e.g. Ross & Ravosa 1993; Lieberman *et al.* 2000), the short, flexed base may account for the relatively vertical midfacial segment in *A. afarensis*, which creates an overall less prognathic facial profile than in chimpanzees and gorillas (Kimbel *et al.* 2004: fig. 3.24, where midfacial prognathism is measured as the angle between a line connecting nasion or sellion to nasospinale and the FH). In the great apes pronounced midfacial prognathism—a dorsal deflection of the nasion-nasospinale segment in relation to a weakly flexed cranial base—results in an airorhynch facial configuration. The contrasting klinorhynch condition is a

Figure 8. Midsagittal craniograms of A.L. 822-1, female gorilla, and modern human, showing cranial base and midfacial angles. A.L. 822-1 anterior cranial base (sella-foramen caecum) reconstructed with additional information from A.L. 417-1 and A.L. 58-22. See text for discussion.

hallmark of the human facial skeleton already manifested, at least incipiently, in *A. afarensis* (figure 8). The prognathic maxilla, with its strongly inclined nasoalveolar clivus, would not be expected to be impacted as directly by cranial base form, and this remains the most apelike aspect of the *A. afarensis* face.

5. CONCLUSIONS

The A.L. 822-1 specimen, providing the first view of the complete small, presumptively female skull of

A. afarensis, reveals a particularly generalized pattern of morphology in occipital squama and cranial base. With superiorly extended nuchal lines, a concomitantly steep nuchal plane, and a narrow cranial base, this skull is notably more apelike than other australopith crania, including those of larger, clearly male, individuals of this species, which share derived states of these characters with subsequent australopith species and *Homo*. It throws into sharp relief the morphology of previously known fragmentary cranial specimens from the Hadar site, demonstrating that the generalized pattern is probably common in small (female) individuals of this species. Qualitative data on a cross-sectional cranial growth series contained within the Hadar sample suggest that some of the variation in *A. afarensis* is indeed intraspecific because young adult males resemble mature females more than they do older males in their generalized occipital form.

Although the inference is limited by the few data available, these observations suggest for *A. afarensis* a pattern of cranial sexual dimorphism unknown among extant hominoids, with adult males characterized by relatively wider cranial bases and more horizontal nuchal muscle origin surfaces than females. At least for the cranial base width, this dimorphism may apply to *A. boisei* as well; no other australopith taxon currently permits comparison.

Morphological variation in the cranial base of *A. afarensis* is consistent with a mosaic pattern of evolutionary change in this region of the skull. Early australopiths were upright bipeds with small brains. The anterior position of the foramen magnum and occipital condyles on a short (though not necessarily broad), flexed cranial base—a derived character complex linked plausibly to upright posture—is unrelated to substantial variation in the morphology of the nuchal region of the calvaria, which is often thought to mirror postural differences. In species potentially descendant from *A. afarensis* the nuchal region became more uniformly humanlike in form and orientation, the functional basis for which remains poorly understood. A derived, relatively upright midfacial profile, which likewise ties *A. afarensis* to later australopiths and *Homo*, may be related to these cranial base modifications and thus, indirectly, to upright posture itself.

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ENDNOTES

¹Weidenreich chose opisthion rather than basion for this purpose probably because none of the *Homo erectus* crania he described preserves the anterior margin of the foramen magnum.

²Here, cranial base length is taken as the combined length of the segments basion to sella turcica to foramen caecum. Width of the base is measured between the summits of the entoglenoid processes.

³As noted by Schultz (1955), in ontogenetic context the hominin foramen magnum does not migrate anteriorly; from the relatively

anterior position common to all juvenile hominoids, the foramen fails to shift posteriorly with growth of the cranium, as it does in all great apes.

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