

## Basicranial architecture and relative brain size of Sts 5 (*Australopithecus africanus*) and other Plio-Pleistocene hominids

Fred Spoor

Evolutionary Anatomy Unit, Department of Anatomy and Developmental Biology, University College London, University Street, London WC1E 6JJ, UK (e-mail: ucgafrs@ucl.ac.uk).

*The cranial base has long been recognised as a complex morphological region where major structural changes have occurred during hominid evolution. Here the relationship between relative brain size and basicranial shape in modern humans, fossil hominids, Sts 5 in particular, and other primates is investigated. The results reveal that basicranial shape is well correlated with relative brain size among non-hominid primates, supporting the notion that brain size is a prime factor underlying basicranial morphology. Whereas Sts 5 and modern humans largely follow the non-hominid trends, three other hominid crania (KNM-WT 17000, OH 5 and Sangiran 17) show stronger basicranial flexion and a more inferiorly-facing foramen magnum than predicted for their brain size. This suggests that during hominid evolution a factor related to obligatory bipedalism supplemented the overall effect of relative brain size on these aspects of the cranial base.*

The *Australopithecus africanus* specimen Sts 5 from Sterkfontein Member 4 has one of the best-preserved cranial bases currently known in the fossil record of Plio-Pleistocene hominids. Thus this fossil is crucial to our understanding of the major structural changes of this complex morphological region during hominid evolution. Two important aspects of the basicranium that distinguish modern humans from other extant primates are the orientation of the temporal petrous pyramids and the degree of mid-line sagittal flexion. The human basioccipital has a more inclined orientation relative to the anterior cranial base, shown as a high degree of basicranial flexion, and the foramen magnum faces more inferiorly. The petrous pyramids are more coronally orientated and, like the basioccipital, their posterior surface is more inclined relative to the orientation of the anterior cranial base. Consequently, the human posterior cranial fossa is much wider and deeper than in other primates, which seems predominantly related to the large human brain. However, as has been extensively reviewed elsewhere,<sup>1-3</sup> other factors underlying this

unique morphology have been proposed, including body posture, masticatory biomechanics and nasopharyngeal demands.

A study investigating alternative hypotheses explaining interspecific differences in the degree of basicranial flexion has found that among extant non-human primates the degree of flexion is positively correlated with brain size relative to basicranial length.<sup>3</sup> This observation appears to corroborate the hypothesis that the highly flexed human basicranium predominantly results from the combination of a large brain and a relatively short cranial base.<sup>1</sup> In a follow-up study, Ross and Henneberg<sup>4</sup> showed that the basicranium of Sts 5 has the flexion predicted by the trend among non-human primates for its relative brain size, whereas that of modern humans is less flexed than predicted. Moreover, the basicranial flexion in Sts 5 was found to be not significantly different from that in modern humans. The latter conclusion is surprising because, both endo- and exocranially, the cranial base of Sts 5 clearly has a less flexed appearance than that of modern humans.<sup>5-9</sup>

In the present study the relationship between relative brain size and basicranial shape in non-human primates, modern humans and fossil hominids, Sts 5 in particular, is further investigated by considering aspects such as petrous pyramid and foramen magnum orientations, and seeks to verify Ross and Henneberg's conclusions by using an alternative method of quantifying basicranial flexion.

### Materials and methods

Basicranial measurements were taken from computed tomography (CT) scans of 42 specimens of 17 extant non-human primate species, 48 modern human crania of diverse geographic origin, and the Sts 5 *A. africanus* cranium (Table 1; see ref. 10 for full information on the extant specimens). Moreover, estimates of the measurements for the hominid fossils OH 5 (*A. boisei*), KNM-WT 17000 (*A. boisei/aethiopicus*) and Sangiran 17 (*Homo erectus*), not taken from the actual specimens, were included in the analyses to obtain an impression of the basicranial

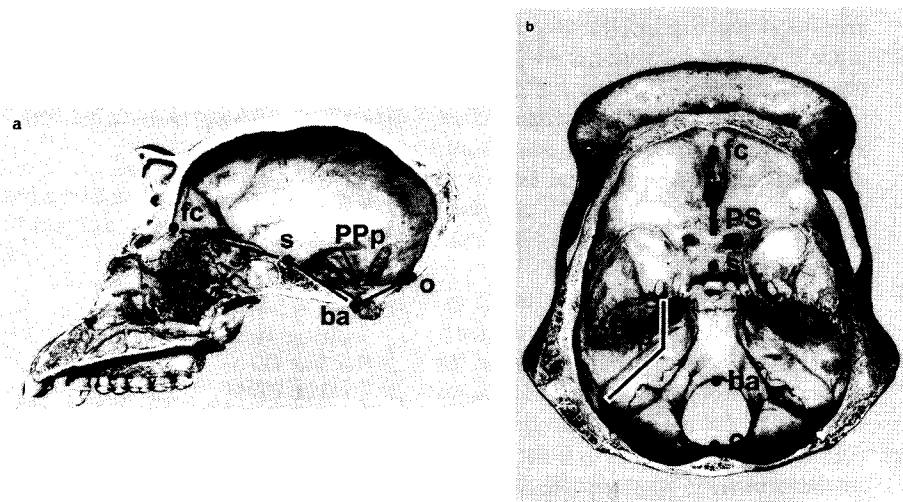


Fig. 1. *a*, Medial view of a midsagittally sectioned cranium of *Pan troglodytes*, showing the landmarks opisthion (o), basion (ba), sella (s) and foramen caecum (fc), and the orientation of the posterior petrosal surface (PPp). The angles of o-ba, ba-s and PPp to s-fc, listed in Table 1, are the ones that open antero-inferiorly. *b*, Superior view of the internal surface of the cranial base of *P. troglodytes*, showing the orientation of the posterior petrosal surface (PPip) to the sagittal plane, the landmarks given in (*a*), and the planum sphenoidum (PS).

morphology in hominid species other than *A. africanus*. Those of OH 5 were obtained from CT scans of a Wenner Gren cast and from a mid-sagittal craniogram,<sup>11</sup> those of Sangiran 17 from CT scans of a high-quality cast prepared at the Geological Research and Development Centre, Bandung, Indonesia, and those of KNM-WT 17000 from an endocast prepared by A. Walker and housed in the Division of Palaeontology of the National Museums of Kenya. The casts of OH 5 and Sangiran 17 are housed in the Nationaal Natuurhistorisch Museum, Leiden, The Netherlands.

The CT scans were made with an exposure of 480 mAs at 120 kVp tube voltage, and a slice thickness of 1.5 mm, using a Philips Tomoscan 310/350 scanner. Midsagittal CT scans were used to measure the orientations of the lines sella (s) to foramen caecum (fc), basion (ba) to sella, and opisthion (o) to basion, representing the orientations of the anterior cranial base, the basioccipital, and the foramen magnum, respectively (Fig. 1a). The orientations of the posterior petrosal surface were measured both from a parasagittal CT scan and a transverse CT scan. These are measurements Ppp (Fig. 1a) and PPip (Fig. 1b), respectively (see ref. 12 for exact definitions). All measurements were taken to the nearest degree. In KNM-WT 17000 opisthion is absent, and the foramen magnum orientation is based on a reconstruction.<sup>13</sup> In Sangiran 17 point sella was estimated.

The four angles considered in relation to relative brain size are those between the anterior cranial base and the basioccipital (ba-s-fc), the foramen magnum (o-ba to s-fc) and the posterior petrosal surface (PPp to s-fc), shown in Fig. 1a, and the angle of

the posterior petrosal surface (PPip) to the sagittal plane, shown in Fig. 1b. For angles concerning the petrous pyramids of the hominid fossils, the average values of the two sides were used, whereas only one of the petrous pyramids was assessed in each of the extant specimens.

Relative brain size, based on the definition of the Index of Relative Encephalization 1,<sup>3</sup> is calculated as the cube root of brain volume divided by basicranial length (the distance basion to sella plus sella to foramen caecum: ba-s + s-fc). Brain volumes of extant primates were calculated from brain mass values kindly provided by R.D. Martin (see ref. 14 for mass-volume conversion), except that of *Hylobates pileatus*.<sup>15</sup> Endocranial volumes were obtained from the literature for *Pan paniscus*,<sup>16</sup> Sangiran 17,<sup>17</sup> KNM-WT 17000,<sup>18</sup> Sts 5 and OH 5.<sup>19</sup>

The statistical significance of differences between the basicranial angles of the individual hominid fossils and the mean values for the human sample was assessed using *t*-tests. The relationships between the basicranial angles and the relative brain size among non-hominid primate species were investigated by calculating the product-moment correlation coefficient (*r*) and testing its significance using a *t*-test. Reduced major axis (RMA) regression equations calculated for the non-hominid primate sample were used to predict basicranial angles for modern humans and the hominid fossils on the basis of their relative brain size. *T*-tests were employed to investigate the significance of the differences between these predicted values and the actual values.<sup>20</sup> In all significance tests a level of *P* < 0.05 was used to reject the null hypothesis.

Table 1. The basicranial angles in degrees and the relative brain size of extant primates and four hominid fossils, giving the number of specimens investigated (*n*), as well as the mean and standard deviation (s.d.) for species represented by multiple specimens. The angles and brain size as defined in the text and Fig. 1. Statistical significance of differences between the values obtained for the fossils and the modern humans means is indicated by \* (*P* < 0.05), \*\* (*P* < 0.01) and \*\*\* (*P* < 0.001).

	<i>n</i>	ba-s-fc		o-ba to s-fc		PPp to s-fc		PPip to sagittal		Relative brain size
		Mean	s.d.	Mean	s.d.	Mean	s.d.	Mean	s.d.	
<i>Homo sapiens</i>	48	137	4.9	7	6.4	116	7.0	125	4.4	1.17
Sangiran 17		129		-4		109		132		1.02
OH 5		135		6		110		133		0.98
WT 17000		156***		25**		130*		135*		0.88
Sts 5		147*		27**		121		136*		1.00
<i>Pan paniscus</i>	6	148	9.0	29	8.4	136	8.9	137	7.3	0.95
<i>Pan troglodytes</i>	7	154	3.6	30	6.0	139	8.0	132	5.2	0.95
<i>Gorilla gorilla</i>	5	154	3.6	37	11.1	133	8.3	138	6.7	0.90
<i>Pongo pygmeus</i>	6	159	6.4	36	8.1	140	3.1	146	4.1	0.93
<i>Hylobates symphalangus</i>	2	173	0.1	46	4.6	155	3.1	148	0.7	0.78
<i>H. moloch</i>	1	170		46		147		144		0.84
<i>H. pileatus</i>	1	166		44		162		138		0.92
<i>Macaca fascicularis</i>	2	173	0.6	41	0.0	139	8.8	151	1.4	0.84
<i>Nasalis larvatus</i>	1	170		40		134		160		0.76
<i>Papio ursinus</i>	1	152		38		143		161		0.90
<i>Theropithecus gelada</i>	1	156		43		135		159		0.75
<i>Mandrillus sphinx</i>	1	162		40		132		167		0.75
<i>Lagothrix lagothricha</i>	1	175		45		147		163		0.81
<i>Alouatta seniculus</i>	1	185		70		144		169		0.57
<i>Saimiri sciureus</i>	1	169		45		153		167		0.81
<i>Propithecus diadema</i>	1	185		73		149		181		0.57
<i>Indri indri</i>	1	173		57		144		172		0.65

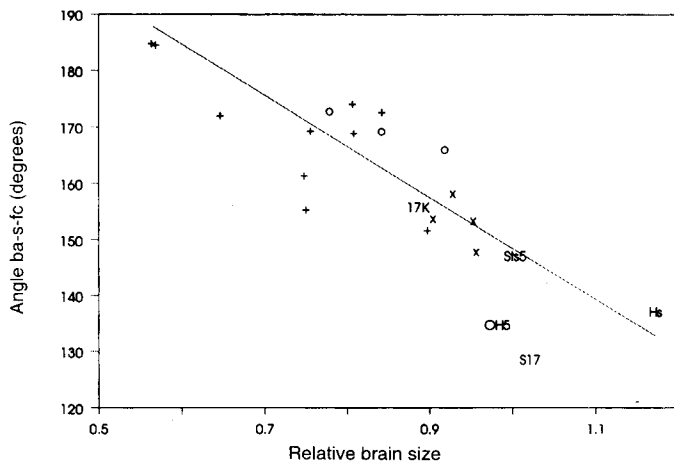


Fig. 2. Bivariate plot of relative brain size (cube root of brain volume/basicranial length  $ba-s + s-fc$ ) and the angle of basicranial flexion ( $ba-s-fc$ ). Hs, *Homo sapiens*; 17K, KNM-WT 17000; S17, Sangiran 17; x, great apes; o, hylobatids; +, non-hominoid primates. The reduced major axis (RMA) for the non-hominid primates is given.

## Results

The angular measurements and the relative brain volumes of the extant and fossil species are listed in Table 1. The mean values of the basicranial angles for modern humans and the chimpanzee species closely correspond to values reported for much larger samples ( $134^\circ$  for 339 modern human specimens,<sup>21</sup>  $152^\circ$  for 42 specimens of *P. troglodytes*, and  $146^\circ$  for 59 specimens of *P. paniscus*<sup>22</sup>). This suggests that for these three species, crucial in the analysis of hominid fossils, the samples used here are likely to be representative.

The angles of Sts 5 are very close to the mean values of *P. paniscus*, with the exception of the orientation of the posterior petrosal surface to the anterior cranial base (Table 1: PPp to  $s-fc$ ), which is intermediate between great ape and modern human mean values. All four angles of KNM-WT 17000 are significantly different from those in modern humans and close to great ape mean values. The angles obtained for OH 5 and Sangiran 17 are not significantly different from those of modern humans, although the orientation of the petrosal surface to the sagittal plane is closest to the mean for *P. troglodytes*.

Bivariate comparisons among the non-hominid primates show a highly significant negative correlation between relative brain

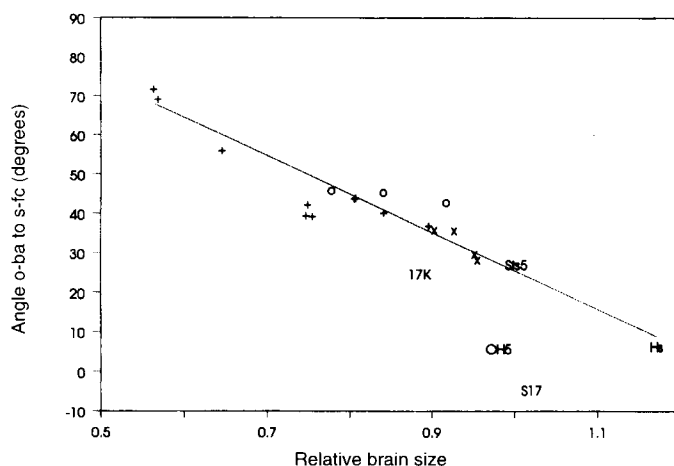


Fig. 3. Bivariate plot of relative brain size and the angle between the foramen magnum and the anterior cranial base ( $o-ba$  to  $s-fc$ ). Legend as in Fig. 2.

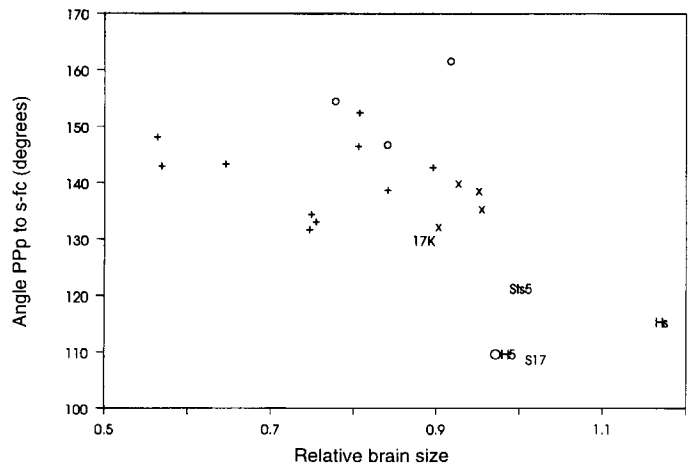


Fig. 4. Bivariate plot of relative brain size and the angle between the posterior petrosal surface and the anterior cranial base (PPp to  $s-fc$ ). Legend as in Fig. 2.

size and the basicranial angles except the orientation of the posterior petrosal surface to the anterior cranial base (Table 2). Hence, a relatively large brain size corresponds with a more inclined basioccipital (a more flexed cranial base), a more inferiorly facing foramen magnum, and more coronally orientated petrous pyramids (Figs 2-5).

When comparing the angles obtained for modern humans and the fossil hominids with the values predicted by RMA regression equations for the non-hominid primates, the following results were found. The angles between the basioccipital and the anterior cranial base ( $ba-s-fc$ ) of modern humans, Sts 5 and KNM-WT 17000 are not different from the predicted values, whereas those of OH 5 and Sangiran 17 are significantly smaller (Fig. 2). The angle between the foramen magnum and the anterior base ( $o-ba$  to  $s-fc$ ) in modern humans and Sts 5 corresponds with the predicted values, and in KNM-WT 17000, OH 5 and Sangiran 17 is significantly smaller (Fig. 3). The angle between the posterior petrosal surface and the sagittal plane is not different from the predicted value in Sts 5, OH 5 and Sangiran 17, is smaller in KNM-WT 17000, and larger in modern humans (Fig. 5). Hence, given their relative brain size modern humans are characterised by petrous pyramids that are less coronally-orientated than predicted, Sts 5 completely follows the trends observed for non-hominid primates, KNM-WT 17000 has a more inferiorly-facing

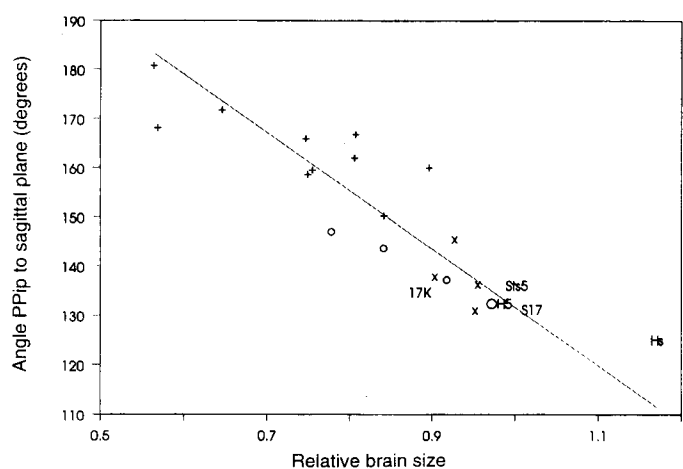


Fig. 5. Bivariate plot of relative brain size and the angle between the posterior petrosal surface (PPip) and the sagittal plane. Legend as in Fig. 2.

Table 2. Correlation coefficients ( $r$ ) between relative brain size and four basicranial angles, calculated for the non-hominid primate sample. For the bivariate comparisons with a significant correlation coefficient ( $P < 0.001$ ) the slope and intercept of the reduced major axis regression line is given. The angles and brain size are as defined in the text and Fig. 1.

	$r$	Slope	Intercept
ba-s-fc	-0.786	-91.0	239.2
o-ba to s-fc	-0.909	-97.4	122.9
PPp to s-fc	-0.075		
PPip to sagittal	-0.850	-118.2	249.9

foramen magnum, and more coronally-orientated petrous pyramids than predicted, and both OH 5 and Sangiran 17 have a more flexed cranial base and inferiorly facing foramen magnum than predicted.

### Discussion

The results of this study reveal highly significant correlations between relative brain size and three major aspects of basicranial shape among non-hominid primates, and support the notion that brain size is a prime factor underlying basicranial morphology. That humans closely follow the trends among non-hominid primates corroborates the hypothesis that their highly flexed cranial base and inferiorly facing foramen magnum are predominantly the result of the combination of a large brain size and a relatively short basicranium.<sup>1</sup> It also gives support to the hypothesis that large brain size accounts for the coronally-orientated petrous pyramids in modern humans, although this study did not specifically assess cerebellar expansion, the factor specifically proposed.<sup>2</sup> However, the petrous orientation in humans is not as coronal as predicted by the non-hominid trend (Fig. 5). Perhaps constraints of cranial architecture limit the degree of petrous reorientation possible, and a maximum has been reached in modern humans. It has been argued that more coronally orientated petrous pyramids are a direct consequence of increased basicranial flexion,<sup>7</sup> rather than of relatively large brain size. However, this is not supported by the present results because the partial correlation coefficient between the two angles, with relative brain size held constant (ba-s-fc and PPip to sagittal plane;  $r = -0.145$ ) is not significant.

The angle that does not significantly correlate with relative brain size is the orientation of the posterior petrosal surface to the anterior cranial base. Thus, forces of increased relative brain size that do result in deflection of the basioccipital among non-hominid primates apparently do not have an equivalent effect on the more lateral parts of the posterior cranial fossa.

The basicranial shape of Sts 5, as represented by the angles investigated here, are closest to those of *Pan paniscus*. This confirms analyses comparing basioccipital and foramen magnum orientations to the palate<sup>23</sup> and the vestibular reference plane<sup>10</sup> rather than to the anterior cranial base, and is in agreement with studies concluding that its external petrous orientation and its external and internal basicranial flexion are close to those in *Pan*.<sup>8,9</sup>

Whereas Sts 5 follows the relationships between relative brain size and basicranial shape found among non-hominid primates, the foramen magnum is more inferiorly positioned in KNM-WT 17000, OH 5 and Sangiran 17 than predicted for their brain size, and in the last two specimens the basicranium is also more flexed

than predicted. Hence, the evidence from these three specimens strongly indicates that other factors than relative brain size influence their basicranial shape. The factor likely shared by *A. boisei* and *H. erectus*, and associated with reorientation of the basioccipital and the foramen magnum,<sup>7</sup> is their commitment to obligatory bipedalism.<sup>24,25</sup> In these hominids a postural/locomotor factor may have supplemented the overall effect of relative brain size observed among non-hominid primates, this to accommodate a more vertically orientated vertebral column, spinal cord and brainstem relative to the anterior cranial base and face, and perhaps to bring the foramen magnum closer to the centre of mass of the head.<sup>7</sup> It is intriguing that both OH 5 and Sangiran 17 have strongly vertically inclined posterior petrosal surfaces (Table 1). Hence, in the possibly locomotor-induced process of basicranial changes these surfaces do follow the reorientation of the basioccipital, whereas they did not in the brain size-related changes among non-hominids.

Assuming that *H. erectus* is ancestral to modern humans, an important implication of Sangiran 17's strong divergence from the non-hominid trends for basioccipital and foramen magnum orientation is that it is mere coincidence that modern humans appear to follow these trends. Thus, the seeming conformity appears to be the consequence of post-*Homo erectus* increase in relative brain size, without change of basioccipital or foramen magnum orientation.

The *Pan*-like basicranium of Sts 5 lacks the reorientated basioccipital and foramen magnum possibly associated with obligatory bipedalism. This can be seen as support for studies of the postcranial skeleton and the organ of balance which propose that *A. africanus* was a facultative rather than obligatory biped.<sup>26-32</sup> More relatively complete specimens of this species will be required to establish whether the cranial base of Sts 5 is typical for its species or represents an extreme in the range of variation, as has been suggested.<sup>33</sup>

KNM-WT 17000 is known for its remarkably unflexed cranial base in combination with rather coronally orientated petrous pyramids.<sup>2,13,18</sup> This basicranial flexion is as predicted by the non-hominid trend for its relative brain size, unlike the stronger flexion of the later East African robust australopithecine OH 5. The external petrous orientation of KNM-WT 17000<sup>34</sup> is indeed more coronal than has been reported for *A. africanus*, though less so than for later *A. boisei* specimens.<sup>33</sup> Its internal petrous orientation, on the other hand, is close to either australopithecine as well as the great apes, and less coronal than in modern humans (Table 1). However, when its relative brain size is taken into account it is actually somewhat more coronal than predicted (Fig. 5). Among extant primates the internal petrous orientation is correlated with basicranial width and intercondylar distance relative to basicranial length,<sup>10</sup> although less so than to relative brain size. Hence, the possibility that the petrous orientation in KNM-WT 17000 reflects its marked basicranial widening, perhaps in relation to the 'hyper robust' masticatory apparatus, deserves further investigation.

The results obtained in this study confirm the previously reported correlation between relative brain size and basicranial flexion among non-hominid primate species,<sup>3</sup> and corroborate Ross and Henneberg's finding that the degree of basicranial flexion shown by Sts 5 follows this trend.<sup>4</sup> However, they disagree with the latter study's conclusions that modern humans clearly diverge from the trend by having a less flexed cranial base than predicted, that the flexion of Sts 5 and modern humans is not significantly different, and that the limit of biologically possible flexion is reached in *A. africanus*. The likely cause for these dis-

parities is the different definitions used to quantify the orientation of the anterior cranial base. Whereas this study employs the line sella to foramen caecum, Ross and Henneberg use the planum sphenoidale. The latter was not used here because it concerns a very short, unrepresentative segment of the anterior cranial base (Fig. 1b). Moreover, its landmarks are difficult to establish in some non-hominid primates, the great apes in particular, because the planum has a bulging, curved shape from the optic chiasma to the posterior border of the cribriform plate. The line sella to foramen caecum represents the full stretch of the anterior cranial base, because the latter landmark, situated in the fronto-ethmoid suture, developmentally represents its supero-anterior margin.<sup>35</sup> Owing to the superior position of the orbits relative to the nasal cavity, foramen caecum in the great apes is situated at the anterior margin of an olfactory pit, but this does not render it less biologically relevant.

This paper and previous studies<sup>3,4</sup> demonstrate the great potential of unravelling the factors and mechanisms underlying complex cranial morphology by assessing overall relationships among a wide range of primate species. In particular the basicranial morphologies of KNM-WT 17000, OH 5 and Sangiran 17 clearly demonstrate that different aspects, such as the orientations of the basioccipital, the petrous pyramids or the foramen magnum, should be considered independently.<sup>8</sup> Each may be influenced by multiple structural demands from, for example, brain development, locomotor behaviour and perhaps masticatory adaptation.

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