Morphological affinities of the *Sahelanthropus tchadensis* (Late Miocene hominid from Chad) cranium

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The recent reconstruction of the *Sahelanthropus tchadensis* cranium (TM 266-01-60-1) provides an opportunity to examine in detail differences in cranial shape between this earliest-known hominid, African apes, and other hominid taxa. Here we compare the reconstruction of TM 266-01-60-1 with crania of African apes, humans, and several Pliocene hominids. The results not only confirm that TM 266-01-60-1 is a hominid but also reveal a unique mosaic of characters. The TM 266-01-60-1 reconstruction shares many primitive features with chimpanzees but overall is most similar to *Australopithecus*, particularly in the basicranium. However, TM 266-01-60-1 is distinctive in having the combination of a short subnasal region associated with a vertical upper face that projects substantially in front of the neurocranium. Further research is needed to determine the evolutionary relationships between *Sahelanthropus* and the known Miocene and Pliocene hominids.

geometric morphometric | 3D reconstruction | *Homo* | *Australopithecus* | African apes

Discoveries in Chad by the Mission Paleoanthropologique Franco-Tchadienne from the Late Miocene Toros-Menalla 266 fossiliferous locality (≈7 million years ago) have substantially added to our understanding of early human evolution in Africa (1–3). Among the material recovered is a nearly complete cranium (TM 266-01-60-1) assigned to a new hominid‖ species *Sahelanthropus tchadensis* (1). Despite its relative completeness, the TM 266-01-60-1 specimen exhibits partial distortion from fracturing, displacement, and plastic deformation. The hypothesis that TM 266-01-60-1 is an ape (4–6) has been once again refuted by the recent virtual reconstruction (2), which confirms the presence of many hominid features in *S. tchadensis* and indicates that it was likely some kind of biped. However, questions remain about the species' systematic relationship to extant apes, other known Late Miocene hominids, and later hominids from the Pliocene. Although we do not believe it yet possible to resolve reliably the phylogenetic position of *S. tchadensis* and other early hominids, a first step is to consider in what ways the TM 266-01-60-1 cranium shares primitive features with extant apes and derived features with various known hominids. Thus, we assess here the morphological similarities and differences of the reconstructed TM 266-01-60-1 cranium with ape and other hominid taxa by using geometric morphometric methods (7, 8) along with comparative quantitative data on variables that reflect key similarities and differences in hominid craniofacial morphology.

Our analysis uses the maximum number of three-dimensional landmarks we could reliably obtain from the reconstruction of TM 266-01-60-1 (2) (see Table 2, which is published as supporting information on the PNAS web site). Landmark coordinates (26 facial, 11 neurocranial, and 15 basicranial) were acquired by using a Microscribe digitizer on a stereolithographic replica of the virtual reconstruction. The landmarks were also digitized on

cross-sectional ontogenetic samples of *Pan troglodytes* ($n = 40$), *Gorilla gorilla* ($n = 41$), and *Homo sapiens* ($n = 24$) (see Table 3, which is published as supporting information on the PNAS web site). In addition, we digitized as many of the same landmarks as possible on a sample of available relatively complete fossil hominid crania: the stereolithograhic replica of AL 444-2 (*Australopithecus afarensis*) (9); CT scans of Sts 5 and Sts 71 (*Australopithecus africanus*) and KNM-ER 1813 (*Homo habilis*); and a cast of OH 5 (*Paranthropus boisei*). Rigorously, it has to be noted that the restorations, reconstructions, and/or deformations associated with some fossil hominid crania (e.g., AL 444-2, OH5, and Sts 71) are potential sources of bias because the changes represent approximations, even if they are accurate, of the proper morphology.

To compare overall cranial shape in TM 266-01-60-1 with that of other taxa, we first performed a principal components analysis of shape by using the maximum shared set of 29 cranial landmarks (see Table 4, which is published as supporting information on the PNAS web site) for TM 266-01-60-1, the above fossil sample, and pooled-sex samples of adult *P. troglodytes*, *G. gorilla*, and *H. sapiens* crania following a generalized least squares (GLS) superimposition using MORPHOLOGIKA software (10) (Fig. 1*A*). The first principal component (PC1), which accounts for 78% of total variance, quantifies shape changes that primarily describe facial length and projection, the relative anteroposterior position of the foramen magnum and mandibular fossae, and the length and height of the cranial vault. This component discriminates humans, early hominids, and great apes, and it places TM 266-01-60-1 within the shape space occupied by the australopiths. Compared with *Pan* and *Gorilla*, TM 266-01-60-1 has a more vertical face with a relatively anteroposteriorly shorter rostrum, and a posterior cranial base** in a more anterior position. The second principal component (PC2), which explains only 5% of the variance, separates TM 266-01-60-1, AL 444-2 (*A. afarensis*), OH 5 (*P. boisei*), and Sts 5 (*A. africanus*) from other crania in the analysis. PC2 quantifies shape changes that primarily describe the midsagittal contour of the neurocranium and the relative height and projection of the upper face.

To quantify the allometric differences between TM 266-01-60-1 and other taxa, Fig. 1*B* graphs the first principal component
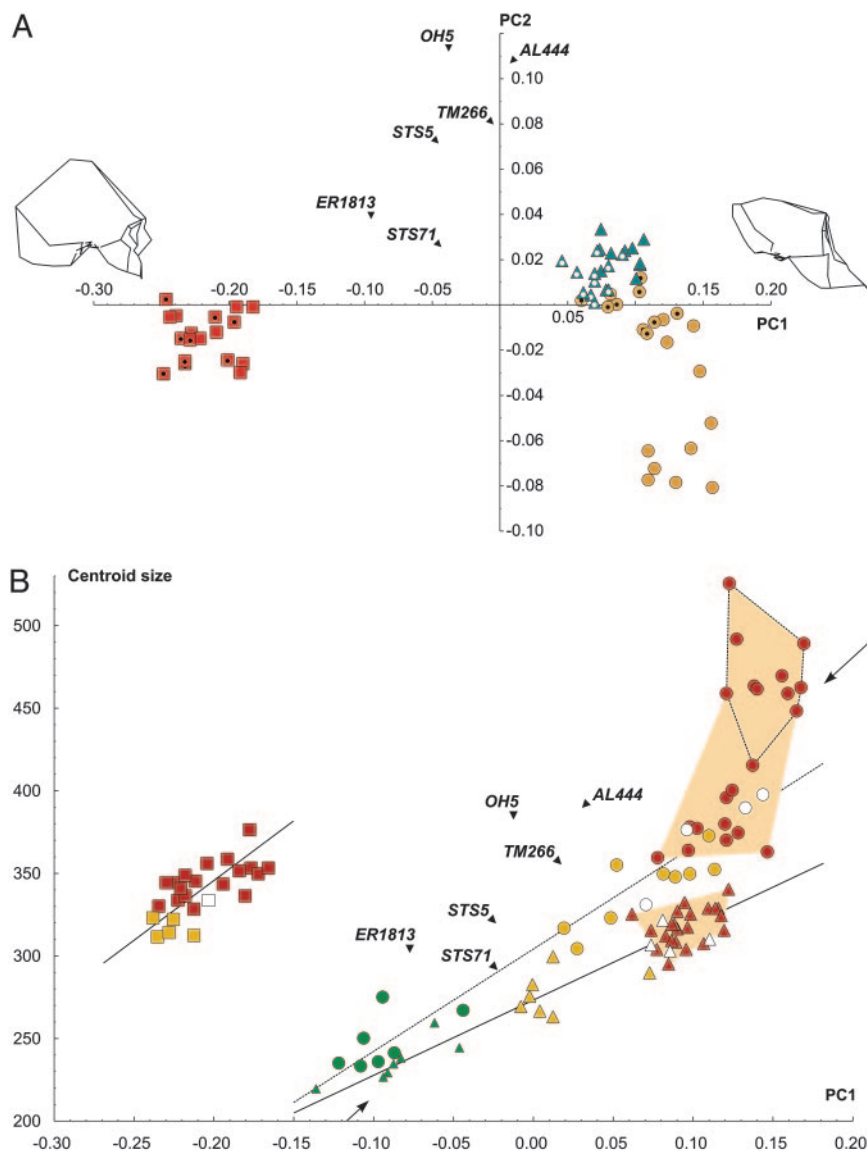

Fig. 1. *S. tchadensis* cranial reconstruction and comparative fossil hominid/African ape morphology. (*A*) PC1 (78% of variance) versus PC2 (5% of variance) of adult *P. troglodytes* (triangles), *G. gorilla* (circles), *H. sapiens* (squares), and various hominids including TM 266-01-60-1. The wire-framed crania (lateral view) indicate pattern and magnitude of shape change associated with PC1. Dotted symbols indicate females. (*B*) PC1 (74% of variance) vs. centroid size of cross-sectional ontogenetic samples of *H. sapiens* (squares), *P. troglodytes* (triangles), *G. gorilla* (circles), and various hominids including TM 266-01-60-1. Red symbols indicate adults, white symbols indicate subadults, orange symbols indicate juveniles, and green symbols indicate infants. The shaded areas encompass adult *P. troglodytes* and *G. gorilla*, with male adult *G. gorilla* in the area within the dashed line. For *G. gorilla*, the dashed line is the female reduced major axis regression; arrows indicate the reduced major axis regression line when males are included.

of shape variation following a GLS superimposition of the same 29 landmark configurations against centroid size in an expanded sample that includes juvenile apes and humans (see Tables 3 and 4). The shape changes described by PC1, which explains 74% of the variance, are essentially the same as PC1 in Fig. 1*A*. TM 266-01-60-1 falls within the same range of values on PC1 as the other adult hominids, but well above the ontogenetic allometries (calculated by reduced major axis regression) between size and shape for the African apes. This result suggests that, like other hominids, TM 266-01-60-1 is paedomorphic for PC1, primarily because of its shorter rostrum and its projected upper face relative to overall cranial size.

To explore further the key morphological similarities and differences between TM 266-01-60-1, African apes, and other hominid taxa for which sufficient data are available, we compared in lateral view the TM 266-01-60-1 reconstruction with *G.*

gorilla (consensus adult), *P. troglodytes* (consensus adult), AL 444-2 (*A. afarensis*), Sts 5 (*A. africanus*), and KNM-ER 1813 (*H. habili*s). Each comparison, shown in Fig. 2, was computed by using a GLS superimposition of the maximum possible set of landmarks. In terms of cranial vault shape, TM 266-01-60-1 resembles *P. troglodytes* and *G. gorilla* in having a low, long superior contour of the neurocranium, particularly anterior to the apex of the vault. The nuchal plane in TM 266-01-60-1, however, is relatively long, flat, and rotated toward the horizontal as in *A. africanus* and *A. afarensis* (11). Relative facial height (from nasion to prosthion) in TM 266-01-60-1 is similar to that of AL 444-2 and Sts 5 (respectively, *A. afarensis* and *A. africanus*) and KNM-ER 1813 (*H. habilis*) but shorter than that in *G. gorilla* and *P. troglodytes*.

The GLS superimposition in Fig. 2 also suggests that TM 266-01-60-1 exhibits some possibly derived differences from crania

Table 1. Cranial features of *S. tchadensis* compared with African apes and representative hominids

Features	Sex	*G. gorilla*	*P. troglodytes*	TM 266-01-60-1	*A. afarensis*	*A. africanus*	*A. boisei*	*H. habilis*	*H. sapiens*
a. Nasoalveolar angle	M	34 ± 6 (9)	39 ± 6 (9)	50	41 (39–42) (9)	48 (37–57) (9)	83 (78–88) (9)	47 (9)	90 ± 10 (9)
	F	43 ± 7 (9)	45 ± 5 (9)						
b. Subnasal height	MF	31.7 ± 6.3	32.3 ± 4.5	21.5	29.3 (25.0–33.0) (23)	27.7 (24.0–32.3) (23)	41.5	22.5 (22.0–23.0) (23)	19.1 ± 3.5
b′. Subnasal height std.	MF	25.7 ± 3.8	31.2 ± 3.6	ca19.1	26.3	29.0 (27.5–30.5)	33.3	25.3	17.3 ± 2.9
c. Index of palate protrusion	M	71 ± 5 (9)	68 ± 6 (9)	ca47	57 (55–59) (9)	54 (43–68) (9)	43 (35–53) (9)	40 (9)	15 ± 8 (9)
	F	63 ± 4 (9)	67 ± 5 (9)						
d. UI2 root relative to nasal aperture	MF	In line/medial	Lateral	In line	Lateral (24)	Medial (24)	Medial (24)	Medial	Medial
e. Nasal aperture margin	MF	Var., large C	Var., large C	Dull, small C	Sharp, small C (9)	Dull, small C (9)	Dull, small C (9)	Sharp evert., small C (9)	Sharp evert., small C (9)
f. Nasal aperture position	MF	Well Below	Below	In line	Below	Below	Below	In line	Above
g. Ant. zygomatic root position	MF	M^1–M^2	M^1–M^2	M^1	M^1	P^4–M^1 (24)	P^3P^4 (24)	P^4M^1	P^4–M^1
h. Interorbital breadth	M	32 ± 3 (9)	20 ± 2 (9)	23	18 (16–19) (9)	22 (19–27) (9)	28 (27–31) (9)	(17)	26 ± 2 (9)
	F	21 ± 2 (9)	24 ± 2 (9)						
h′. Interorbital breadth std.	MF	17.4 ± 3.0	19.9 ± 2.3	20.4	17.2	19.1 (19.1–19.2)	24.2	(17.8)	24.2 ± 1.0
i. Orbital shape	M	0.9 ± 0.1 (9)	0.9 ± 0.1 (9)	1.07	0.98 (9)	0.97 (0.94–1.00) (9)	1.00 (9)	1.03	0.9 ± 0.07 (9)
	F	1.0 ± 0.03 (9)	0.9 ± 0.1 (9)						
j. Rel. upper facial projection	MF	62.8 ± 1.4	64.4 ± 2.1	72.0	64.1	66.6 (64.8–68.3)	70.7	74.8	93.3 ± 5.8
k. Facial mask index	F	1.38 ± 0.06 (9)	1.23 ± 0.05 (9)	ca1.19	1.52 (1.49–1.54) (9)	1.40 (1.39–1.41) (9)	1.58 (1.44–1.67) (9)	—	1.18 ± 0.04 (9)
	M	1.39 ± 0.04 (9)	1.14 ± 0.03 (9)						
l. Torus thickness std.	MF	9.0 ± 0.9	8.4 ± 1.0	12.2	8.2	7.0 (6.4–7.6)	9.3	6.4	4.3 ± 0.6
m. UI2/UC diastema	MF	Present	Present	Absent	Common (24)	Absent (24)	Absent (24)	Absent	Absent

of *Australopithecus* and African apes, notably in the upper face (including the orbital superstructures, glabella and nasion), which projects substantially in front of the neurocranium. Upper facial projection in the TM 266 cranium most likely accounts for its long and flat frontal squama and its elongated supraorbital torus (12, 13). In addition, the *Sahelanthropus* face has a relatively short premaxilla with no diastema and reduced subnasal prognathism compared not only to *Pan* and *Gorilla* but also to some cranial representatives of *Australopithecus* (e.g., AL 444-2). Subnasal prognathism, partly a function of premaxilla length, varies within *Australopithecus* (9, 14), but no known crania attributed to *A. afarensis* or *A. africanus* show evidence of the association of a shortened rostrum with a substantial projection of the upper face relative to neurocranium seen in TM 266-01-60-1. Aspects of the overall structure of the TM 266-01-60-1 face (i.e., projecting upper face and reduced subnasal prognathism) resemble the configuration seen in KNM-ER 1813 (*H. habilis*) (Fig. 2*F*). However, further research is necessary to determine the structural bases of this apparent similarity. For instance, TM 266-01-60-1 contrasts with KNM-ER 1813 in its frontal squama morphology, which is flat, long and low, possibly because of its small endocranial capacity relative to the length and flexure of the cranial base (15). The TM 266 cranium also has a distinctive midfacial conformation with an anteroinferiorly sloping midfacial contour in the midsagittal plane (see ref. 2, Fig. 2).

To clarify the similarities and differences between the reconstructed *S. tchadensis* cranium and other hominid crania, Table 1 summarizes some of the features that TM 266-01-60-1 shares with African apes, and those it shares with a selected sample of several Pliocene hominid representatives (all of which are at least 3 million years younger). We currently lack sufficient data to compare the overall cranial morphology of TM 266-01-60-1 with specimens close in age such as *Ardipithecus* (16–19), and there are no cranial remains attributed to *Orrorin* (20).

Table 1 indicates that, as might be expected for a Late Miocene hominid (21), TM 266-01-60-1 shares many apparently primitive features with *Pan* and *Gorilla*, particularly in the palate and regions of the cranial vault other than the nuchal plane (e.g., Table 1, n, o, and w). TM 266-01-60-1 also has an estimated endocranial volume of 360–370 ml (2), which is the smallest yet documented for an adult hominid but within the chimpanzee range (22).

The TM 266-01-60-1 reconstruction exhibits several widely recognized hominid synapomorphies, including a long, flat nuchal plane that is more horizontally oriented than in African apes (*contra* ref. 4); a shortened basioccipital; and a more anteriorly positioned foramen magnum (1) (e.g., Table 1, t, x, and y). In addition, as discussed in Brunet *et al.* (1, 6, 30), the dentition of TM 266-01-60-1 and referred specimens resembles those of *Ardipithecus* and later hominids compared with *Pan* in several respects such as reduced canines, a C/P$_3$ nonhoning complex, and postcanine teeth with thicker enamel. TM 266-01-60-1 also shares several derived cranial features with later hominids, especially in the posterior cranial vault and the cranial base (e.g., Table 1, r, s, t, v, and z). However, as noted above, some aspects of the overall facial structure of TM 266-01-60-1 are unlike those of any known published *Australopithecus,* in-

Guy *et al.*

Table 1. (continued)

Features	Sex	*G. gorilla*	*P. troglodytes*	TM 266-01-60-1	*A. afarensis*	*A. africanus*	*A. boisei*	*H. habilis*	*H. sapiens*
n. Ant. palate depth	MF	Shallow	Shallow	Shallow	Shallow (24)	Variable (24)	Deep (24)	Deep (24)	Deep (24)
o. Palate shape	M	0.7 ± 0.03 (9)	0.9 ± 0.05 (9)	ca0.81	1.02	1.01	1.05	1.07	1.3 ± 0.06 (9)
	F	0.8 ± 0.05 (9)	0.9 ± 0.05 (9)		(0.91–1.15) (9)	(0.94–1.09) (9)	(1.03–1.08) (9)	(1.05–1.10) (9)	
p. Postorbital constriction	MF	56.5 ± 5.5	67.4 ± 3.8	59.1	61.6	62.5 (62.4–62.6)	57.6	66.0	87.2 ± 3.1
q. Sagittal crest in male	—	Present	Rare	Absent	Present (24)	Rare (24)	Present (24)	Absent	Absent
r. Orbital angle	MF	20.0 ± 11.2	17.0 ± 6.1	63.0	60.0	50.5	54.7	—	69.7 ± 7.4
s. Foramen magnum orientation	MF	44.4 ± 9.2	47.1 ± 4.3	32.1	20	32	38.2	—	33.5 ± 4.4
t. Nuchal plane orientation	M	—	67 ± 7 (9)	36.0	25 (9)	40 (9)	16 (9)	30	25 ± 6 (9)
	F	79 ± 10 (9)	71 ± 8 (9)						
u. Nuchal plane length std.	MF	58.1 ± 7.5	43.5 ± 3.2	40.7	39.0	39.7 (34.1–45.4)	33.2	44.1	47.3 ± 5.5
v. Nuchal crest orientation	—	Superior	Superior-horizontal	Inferior	Inferior	—	Inferior	—	—
w. Vault shape	MF	90.9 ± 2.9	85.4 ± 2.5	86.7	72.8	73.7 (72.9–74.5)	—	73.8	59.8 ± 2.8
x. Foramen magnum position	M	7 ± 2 (9)	12 ± 3 (9)	22	24 (9)	20 (19–21) (9)	21 (18–24) (9)	25 (9)	31 ± 2 (9)
	F	13 ± 4 (9)	14 ± 2 (9)						
y. Basioccipital length	M	37 ± 2 (9)	28 ± 3 (9)	ca22.2	20 (20–19) (9)	21 (17–25) (9)	22 (20–25) (9)	—	21 ± 1 (9)
	F	29 ± 2 (9)	26 ± 2 (9)						
z. Petrous orientation	MF	72 ± 5 (25)	69 ± 5 (25)	61	59 (53–64) (9)	66 (60–65) (9)	47 (44–50) (9)	46 (9)	46 ± 6 (25)
ev. Cranial capacity	M	537.4 ± 64.0 (26)	406.5 ± 50.5 (26)	360–370	500 (26)	485 (475–500) (27)	530 (522–700) (27, 29)	510 (500–510) (27, 29)	1424.5 ± 95.2 (26)
						428 (370–520) (27, 28)			
					ca550 (9)	515 (513–625) (27, 28)			

Measurements are in mm (mean ± SD, range values for fossil hominids, when available, are in parenthesis) except for cranial capacity in ml. (See Table 5, which is published as supporting information on the PNAS web site, for definitions of the measurements used.) M, male; F, female; MF, pooled-sex data; Ant., anterior; Rel., relative; std., data standardized by geometric mean *100 of glabella-external occipital protuberance, biporionic breadth, glabella-prosthion, biorbital breadth. Var., variable; evert, everted; —, no data.

cluding AL 444-2 (*A. afarensis*). Several of these features, such as subnasal height, palatal protrusion, and relative upper facial projection (Table 1, b, c, and j), may be derived differently than those in *Australopithecus*. Others are probably either primitive or convergent with *Homo*. For example, the upper and middle portions of the face in TM 266-01-60-1 are similar in width, as in *Pan* and *Homo*, but unlike the hexagonal-shaped configuration in *Australopithecus*, in which the midface is wider than the upper face because of masticatory-related expansion of the zygomatic region (Table 1, k) (9).

The mosaic of primitive and derived features in TM 266-01-60-1 poses some interesting questions about early hominid systematics. A preliminary study, derived from the three-dimensional cranial shape data (31), suggests that *S. tchadensis* groups phenetically with later hominids rather than *Pan* but is not overall more similar to any other, more derived hominid species (Fig. 3). This affinity stems from the many basicranial and neurocranial similarities discussed above and is supported by previous results derived from more classical data (32). However, further research is needed to determine the evolutionary relationship between *Sahelanthropus* and known Miocene and Pliocene hominids. First, we currently lack sufficient cranial data to include other key taxa such as *Ardipithecus* (16–19), *Orrorin* (20), and *Australopithecus bahrelghazali* (3) in a comprehensive anal-

ysis. Second, we do not yet understand the developmental bases of most cranial features that allow us to define independent characters known to be phylogenetically informative (33–36), and it has sometimes proven difficult to derive robust, reliable phylogenetic relationships from morphological data (31, 32). As suggested above, a reasonable possibility is that *Sahelanthropus* is part of a clade of primitive hominids that is ancestral to all later genera, including *Australopithecus* and *Homo*. Other members of this clade potentially include *Ardipithecus* and *Orrorin*, but further research is necessary to test the hypothesis. Derived features that support this phylogenetic hypothesis include the many basicranial and neurocranial similarities between TM 266-01-60-1 and *Australopithecus* (see Table 1, r–t, v, and x–z), along with the additional derived features of the vault, palate, and expanded brain shared exclusively by *Australopithecus* and *Homo* (see Table 1, d, n, o, w, and ecv).

However, the picture is more complicated and less easy to resolve. Critical answers will probably come from detailed study of the upper Miocene hominids biogeography. Hence, although *Ardipithecus* and *Orrorin* are both known from eastern Africa (respectively, Ethiopia and Kenya), *Sahelanthropus* is known from central Africa (Chad), 2,500 km west of the Rift Valley. This pattern raises intriguing questions about hominid phylogeny with, for instance, potamophile mammals (Anthracotheriid and Hippopota-
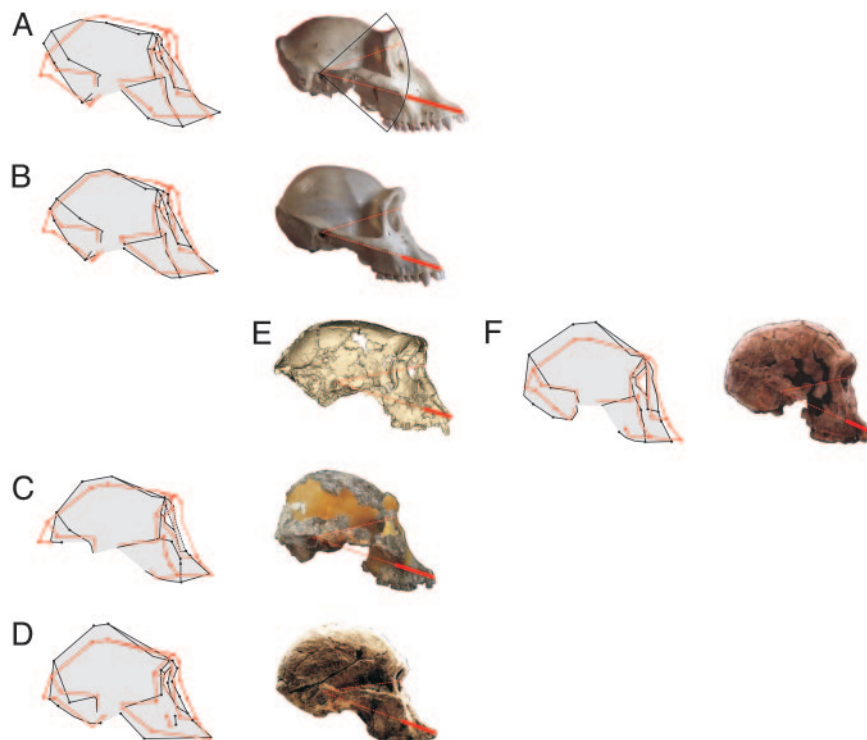
ANTHROPOLOGY

Fig. 2. GLS superimposition (left column), lateral view, of TM 266-01-60-1 with female adult consensus of *G. gorilla* (*A*), pooled-sex adult consensus *P. troglodytes* (*B*), AL 444-2 (*A. afarensis*) (*C*), Sts 5 (*A. africanus*) (*D*), and KNM-ER 1813 (*H. habilis*) (*F*). TM 266-01-60-1 configuration of landmarks is figured in red. Dots indicate location of main cranial landmarks deviations. Each comparison is associated to lateral view (right column) of *G. gorilla* (female) cranium (*A*), *P. troglodytes* cranium (*B*), AL 444-2 (*A. afarensis*) (*C*), Sts 5 (*A. africanus*) (*D*), virtual reconstruction of the TM 266-01-60-1 cranium (*E*), and KNM-ER 1813 (*H. habilis*) (*F*). Inferior and superior dashed line, respectively, correspond to alveolare–porion and nasion–porion; the solid line is alveolare–porion minus nasion–porion distance (see Table 1 for data on relative facial projection).

mid) attesting, around 7 million years ago, to faunal exchanges between Libya and Chad but not with eastern Africa (37).

Although *Sahelanthropus tchadensis* is clearly a hominid, its complex mosaic of features poses some interesting systematic questions about early hominid evolution that can be resolved only with more data of four types. First, more information is needed to compare *Orrorin*, *Ardipithecus*, and *Sahelanthropus* in detail. Sec-
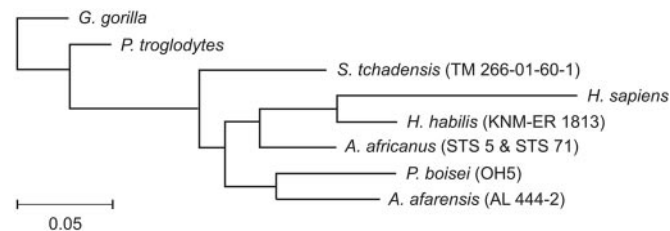
ond, additional hominid fossil material is needed from Late Miocene deposits in different parts of Africa. Third, we need a better understanding of the developmental and functional bases of cranial morphology that are necessary to hypothesize phylogenetically informative characters. Fourth, we particularly need a better understanding of the vertebrate and hominid biogeographical relationships through Africa during the upper Miocene.

Fig. 3. Phenetic analysis of affinities between *S. tchadensis* (TM 266-01-60-1), living apes, and representative hominids generated from three-dimensional cranial shape data. Raw data consist of Euclidean distances calculated from Procrustes coordinates of each taxon in the overall generalized Procrustes analysis. Mean Procrustes coordinates have been used for *G. gorilla* (pooled sex), *P. troglodytes* (pooled sex), *H. sapiens* (pooled sex), and *A. africanus* (Sts 5 and Sts 71). Taxa were clustered by using the neighbor-joining method (31).

1. Brunet, M., Guy, F., Pilbeam, D., Mackaye, H. T., Likius, A., Ahounta, D., Beauvilain, A., Blondel, C., Bocherens, H., Boisserie, J.-R., *et al.* (2002) *Nature* **418**, 145–151.
2. Zollikofer, C. P. E., Ponce de León, M. S., Lieberman, D. E., Guy, F., Pilbeam, D., Likius, A., Mackaye, H. T., Vignaud, P. & Brunet, M. (2005) *Nature* **434,** 754–759.
3. Brunet, M., Beauvillain, A., Coppens, Y., Heintz, E., Moutaye, A. H. E. & Pilbeam, D. (1995) *Nature* **378,** 273–274.
4. Wolpoff, M. H., Senut, B., Pickford, M. & Hawks, J. (2002) *Nature* **419,** 581–582.
5. Senut, B. (2004) in *Miscelanea en Homenaje a Emiliano Aguirre*, eds. Baquedano, E. & Rubio, S. (Museo Arqueológico de la Comunidad de Madrid, Madrid), Vol. 3.

6. Brunet, M. (2002) *Nature* **419,** 582.
7. Bookstein, F. L. (1991) *Morphometric Tools for Landmark Data: Geometry and Biology* (Cambridge Univ. Press, London).
8. Dryden, I. L. & Mardia, K. V. (1998) *Statistical Shape Analysis* (Wiley, Chichester, U.K.).
9. Kimbel, W. H., Rak, Y. & Johanson, D. C. (2004) *The Skull of Australopithecus afarensis* (Oxford Univ. Press, New York).
10. O'Higgins, P. & Jones, N. (1999) *MORPHOLOGIKA: Tools for Shape Analysis* (University College, London), available at www.york.ac.uk/res/fme/resources/software.htm.
11. Kimbel, W. H., White, T. D. & Johanson, D. C. (1984) *Am. J. Phys. Anthropol.* **64,** 337–388.
12. Bilsborough, A. & Wood, B. A. (1988) *Am. J. Phys. Anthropol.* **76,** 61–86.
13. Lieberman, D. E. (2000) in *Development, Growth and Evolution: Implications for the Study of Hominid Skeletal Evolution*, eds. O'Higgins, P. & Cohn, M. (Academic, London), pp. 85–122.
14. Kimbel, W. H., Johanson, D. C. & Coppens, Y. (1982) *Am. J. Phys. Anthropol.* **57,** 453–499.
15. Lieberman, D. E., Ross, C. F. & Ravosa, M. J. (2000) *Yearb. Phys. Anthropol.* **31,** 117–169.
16. White, T. D., Suwa, G. & Asfaw, B. (1994) *Nature* **371,** 306–312.
17. White, T. D., Suwa, G. & Asfaw, B. (1995) *Nature* **375,** 88.
18. Haile-Selassie, Y. (2001) *Nature* **412,** 178–181.
19. Haile-Selassie, Y., Suwa, G. & White, T. D. (2004) *Science* **303,** 1503–1505.
20. Senut, B., Pickford, M., Gommery, D., Mein, P. & Cheboi, K. (2001) *C. R. Acad. Sci. Paris* **332,** 137–144.
21. Pilbeam, D. (1996) *Mol. Phylogenet. Evol.* **5,** 155–168.
22. Tobias, P. V. (1971) *The Brain in Hominid Evolution* (Columbia Univ. Press, New York).
23. Kimbel, W. H., Johanson, D. C. & Rak, Y. (1997) *Am. J. Phys. Anthropol.* **103,** 235–262.
24. Asfaw, B. (1999) *Science* **284,** 629–635.
25. Dean, M. C. & Wood, B. A. (1981) *Am. J. Phys. Anthropol.* **54,** 63–71.
26. Kappelman, J. (1996) *J. Hum. Evol.* **30,** 243–276.
27. De Miguel, C. & Henneberg, M. (2001) *Homo* **52,** 2–56.
28. Conroy, G. C., Weber, G. W., Seidler, H., Tobias, P. V., Kane, A. & Brundsen, B. (1998) *Science* **280,** 1730–1731.
29. Elton, S. (2001) *J. Hum. Evol.* **41,** 1–27.
30. Brunet, M., Guy, F., Pilbeam, D., Lieberman, D. E., Likius, A., Mackaye, H. T., Ponce de León, M. S., Zollikofer, C. P. E. & Vignaud, P. (2005) *Nature* **434,** 752–754.
31. Lockwood, C. A., Kimbel, W. H. & Lynch, J. M. (2004) *Proc. Natl. Acad. Sci. USA* **101,** 4356–4360.
32. Strait, D. S & Grine, F. E. (2004) *J. Hum. Evol.* **47,** 399–452.
33. Lieberman, D. E., Pilbeam, D. R. & Wood, B. A. (1996) *J. Hum. Evol.* **30,** 97–120.
34. Collard, M. & Wood, B. (2000) *Proc. Natl. Acad. Sci. USA* **97,** 5003–5006.
35. Lieberman, D. E. (1999) *Evol. Anthropol.* **7,** 142–151.
36. McCollum, M. A. (1999) *Science* **284,** 301–305.
37. Vignaud, P., Duringer, P., Mackaye, H. T., Likius, A., Blondel, C., Boisserie, J.-R., de Bonis, L., Eisenmann, V., Geraads, D., Guy, F., *et al.* (2002) *Nature* **418**, 152–155.

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