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Accessibility
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 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.

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 basioccipital) 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 stereolithographic 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 MORPHOLOGIIKA software (10) (Fig. 1A). The first principal component (PC1), which accounts for 73% of total variance, quantifies shape changes that primarily describe cranial shape external to the braincase (e.g., face and vault). The second principal component (PC2) quantifies shape changes that primarily describe shape changes associated with the braincase (e.g., orientation 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. 1B graphs the first principal component

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Abbreviations: GLS, generalized least squares; PC1 and PC2, first and second principal components.

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†The term hominid is used here for convenience to denote all taxa that are closer to humans than chimpanzees and does not connote any taxonomic scheme; similarly, australopithicus is used as a generic term sensu lato to refer to all Pliocene hominid taxa that do not belong to the genera Ardiapithecus and Homo.

**Posterior cranial base is defined as the portion of the cranial base posterior to the division between pre- and postchordal portions of the sphenoid.

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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. 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. habilis). 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. africanaus 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
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* and 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 hominin (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 p). TM 266-01-60-1 also has an estimated endcranial 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 z). 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 cranial also has a distinctive midfacial configuration 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).
groups phenetically with later hominids rather than dimensional cranial shape data (31), suggests that 60-1 poses some interesting questions about early hominid zygomatic region (Table 1, k) (9).

Upper face because of masticatory-related expansion of the 

Australopithecus bahrelghazali and other key taxa such as 

in a comprehensive analysis. 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 Oreoros, but further research is necessary to test the hypothesis. Derived features that support this phylogenetic hypothesis include 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), Oreoros (20), and Australopithecus bahrelghazali (3) in a comprehensive analysis.

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. chadensis 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), Oreoros (20), and Australopithecus bahrelghazali (3) in a comprehensive analysis. 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 Oreoros, but further research is necessary to test the hypothesis. Derived features that support this phylogenetic hypothesis include 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), Oreoros (20), and Australopithecus bahrelghazali (3) in a comprehensive analysis. 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 Oreoros, but further research is necessary to test the hypothesis. Derived features that support this phylogenetic hypothesis include 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), Oreoros (20), and Australopithecus bahrelghazali (3) in a comprehensive analysis.
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. Second, 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.

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