

A new hominid from the Upper Miocene of Chad, Central Africa

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The search for the earliest fossil evidence of the human lineage has been concentrated in East Africa. Here we report the discovery of six hominid specimens from Chad, central Africa, 2,500 km from the East African Rift Valley. The fossils include a nearly complete cranium and fragmentary lower jaws. The associated fauna suggest the fossils are between 6 and 7 million years old. The fossils display a unique mosaic of primitive and derived characters, and constitute a new genus and species of hominid. The distance from the Rift Valley, and the great antiquity of the fossils, suggest that the earliest members of the hominid clade were more widely distributed than has been thought, and that the divergence between the human and chimpanzee lineages was earlier than indicated by most molecular studies.

From their initial description in 1925¹ until 1995, hominids from the Pliocene (5.3–1.6 million years, Myr) and late Upper Miocene (~7.5–5.3 Myr) were known only from southern and eastern Africa. This distribution led some authors to postulate an East African origin for the hominid clade (where the term 'hominid' refers to any member of that group more closely related to extant humans than to the extant chimpanzee, *Pan*)^{2,3}. The focus on East Africa has been especially strong in the past decade, with the description of several new forms from Kenya and Ethiopia, including *Kenyanthropus platyops* (3.5 Myr; ref. 4); *Australopithecus anamensis* (3.9–4.1 Myr; ref. 5); *Ardipithecus ramidus ramidus* (4.4 Myr; ref. 6); *Ardipithecus ramidus kadabba* (5.2–5.8 Myr; ref. 7) and *Orrorin tugenensis* (~6 Myr; refs 8, 9). The discoveries of *A. ramidus ramidus*, *A. r. kadabba* and *O. tugenensis* have extended the human lineage well back into the Miocene. However, the discovery of *Australopithecus bahrelghazali* in Chad, central Africa^{10,11}, demonstrated a considerably wider geographic range for early hominids than conventionally expected.

Since 2001, the Mission Paléoanthropologique Franco-Tchadienne (MPFT), a scientific collaboration between Poitiers University, Ndjamena University and Centre National d'Appui à la Recherche (CNAR) (Ndjaména), has recovered hominid specimens, including a nearly complete cranium, from a single locality (TM 266) in the Toros-Menalla fossiliferous area of the Djurab Desert of northern Chad (Table 1). The constitution of the associated fauna suggests that the fossils are older than material dated at 6 Myr from Lukeino, Kenya^{8,9}. Preliminary comparison with the fauna from the Nawata formation at Lothagam, Kenya^{12,13}, suggests that the fossils are from

the Late Miocene, between 6 and 7 Myr old. All six recovered specimens are assigned to a new taxon that is, at present, the oldest known member of the hominid clade.

Systematic palaeontology

Order Primates L., 1758

Suborder Anthropeoidea Mivart, 1864

Superfamily Hominoidea Gray, 1825

Family Hominidae Gray, 1825

Sahelanthropus gen. nov.

Etymology. The generic name refers to the Sahel, the region of Africa bordering the southern Sahara in which the fossils were found.

Generic description. Cranium (probably male) with an orthognathic face showing weak subnasal prognathism, a small ape-size braincase, a long and narrow basicranium, and characterized by the following morphology: the upper part of the face wide relative to a mediolaterally narrow and anteroposteriorly short lower face; a large canine fossa; a small and narrow U-shaped dental arch; orbits separated by a very wide interorbital pillar and crowned with a large, thick and continuous supraorbital torus; a flat frontal squama with no supratoral sulcus but with a marked postorbital constriction; a small, posteriorly located sagittal crest and a large nuchal crest (at least, in presumed males); a flat and relatively long nuchal plane with a large external occipital crest; a large mastoid process; small occipital condyles; a short, anteriorly narrow basioccipital; the long axis of the petrous temporal bone oriented roughly 30° relative to

the sagittal plane; the biporion line touching the basion; a round external auditory porus; a broad glenoid cavity with a large post-glenoid process; a robust and superoinferiorly short mandibular corpus associated with a wide extramolar sulcus; a large, anteriorly opening mental foramen centred beneath lower teeth P₄–M₁, below midcorpus height; relatively small incisors; distinct marginal ridges and multiple tubercles on the lingual fossa of upper I¹; small (presumed male) upper canines longer mesiodistally than buccolingually; upper and lower canines with extensive apical wear; no lower c–P₃ diastema; upper and lower premolars with two roots; molars with low rounded cusps and bulbous lingual faces, M³ triangular and M₃ rounded distally; enamel thickness of cheek teeth intermediate between *Pan* and *Australopithecus*.

Differential diagnosis. *Sahelanthropus* is distinct from all living great apes in the following respects: relatively smaller canines with apical wear, the lower showing a full occlusion above the well-developed distal tubercle, probably correlated with a non-honing C–P₃ complex (P₃ still unknown).

Sahelanthropus is distinguished as a hominid from large living and known fossil hominoid genera in the following respects: from *Pongo* by a non-concave lateral facial profile, a wider interorbital pillar, superoinferiorly short subnasal height, an anteroposteriorly short face, robust supraorbital morphology, and many dental characters (described below); from *Gorilla* by smaller size, a narrower and less prognathic lower face, no supratoral sulcus, and smaller canines and lower-cusped cheek teeth; from *Pan* by an anteroposteriorly shorter face, a thicker and more continuous supraorbital torus with no supratoral sulcus, a relatively longer braincase and narrower basicranium with a flat nuchal plane and a large external occipital crest, and cheek teeth with thicker enamel; from *Samburupithecus*¹⁴ by a more anteriorly and higher-placed zygomatic process of the maxilla, smaller cheek teeth with lower cusps and without lingual cingula, and smaller upper premolars and M³; from *Ouranopithecus*¹⁵ by smaller size, a superoinferiorly, anteroposteriorly and mediolaterally shorter face, relatively thicker continuous supraorbital torus, markedly smaller but mesiodistally longer canines, apical wear and large distal tubercle in lower canines, and thinner postcanine enamel; from *Sivapithecus*¹⁶ by a superoinferiorly and anteroposteriorly shorter face with non-concave lateral profile, a wider interorbital pillar, smaller canines with apical wear, and thinner cheek-teeth enamel; from *Dryopithecus*¹⁷ by a less prognathic lower face with a wider interorbital pillar, larger supraorbital torus, and thicker postcanine enamel.

Sahelanthropus is also distinct from all known hominid genera in the following respects: from *Homo* by a small endocranial capacity (preliminary estimated range 320–380 cm³) associated with a long flat nuchal plane, a longer truncated triangle-shaped basioccipital, a flat frontal squama behind a robust continuous and undivided supraorbital torus, a large central upper incisor, and non-incisiform canines; from *Paranthropus*¹⁸ by a convex facial profile that is less

mediolaterally wide with a much smaller malar region, no frontal trigone, the frontal squama with no hollow posterior to glabella, a smaller, longer and narrower braincase, the zygomatic process of the maxilla positioned more posterior relative to the tooth row, and markedly smaller cheek teeth; from *Australopithecus*^{19–21} by a less prognathic lower face (nasospinale–prosthion length shorter at least in presumed males) with a smaller malar (infraorbital) region and a larger, more continuous supraorbital torus, a relatively more elongate braincase, a relatively long, flat nuchal plane with a large external occipital crest, non-incisiform and mesiodistally long canines, and thinner cheek-teeth enamel; from *Kenyanthropus*⁴ by a narrower, more convex face, and a narrower braincase with more marked postorbital constriction and a larger nuchal crest; from *Ardipithecus*^{6,7} by upper I¹ with distinctive lingual topography characterized by extensive development of the crests and cingulum; less incisiform upper canines not diamond shaped with a low distal shoulder and a mesiodistal long axis, bucco-lingually narrower lower canines with stronger distal tubercle, and P₄ with two roots; from *Orrorin*⁸ by upper I¹ with multiple tubercles on the lingual fossa, and non-chimp-like upper canines with extensive apical wear.

Type species. *Sahelanthropus tchadensis* sp. nov.

Etymology. In recognition that all specimens were recovered in Chad.
Holotype. TM 266-01-060-1, a nearly complete cranium with the following: on the right—I² alveolus, C (distal part), P³–P⁴ roots, fragmentary M¹ and M², M³; and on the left—I² alveolus, C–P⁴ roots, fragmentary M¹–M³ (Fig. 1 and Tables 1–5). Found by D.A. on 19 July 2001.

After study, the holotype and paratype series will be housed in the Département de Conservation des Collections, Centre National d'Appui à la Recherche (CNAR) in Ndjaména, Chad. The holotype has been dubbed 'Toumaï'; in the Goran language spoken in the Djurab Desert, this name is given to babies born just before the dry season, and means 'hope of life'.

Paratypes. See Table 1 for a list of paratypes, and Fig. 2 for illustrations.

Locality. Toros-Menalla locality TM 266, a single quarry of about 5,000 m², 16° 14' 30"–16° 15' 30" N, 17° 28' 30"–17° 30' 00" E (western Djurab Desert, northern Chad).

Horizon. All hominid specimens were found in the Toros-Menalla anthracotheriid unit (AU) and come from a perilacustrine sandstone¹². The associated fauna is biochronologically¹² older than fossils from Lukeino, Kenya (~6 Myr; refs 8, 9), and more closely resembles material from the Nawata formation at Lothagam, Kenya, which is radio-isotopically dated to 5.2–7.4 Myr (ref. 13). Biochronological studies are still underway and TM 266 fauna can be tentatively dated between 6 and 7 Myr (ref. 12).

Diagnosis. Same as for genus.

Preservation

All specimens are relatively well preserved, but almost the entire

Table 1 Specimens of *Sahelanthropus tchadensis* gen. et sp. nov.

| Specimen number | Collected | Element | Discoverer | Dental dimensions (mm) |
|-------------------------------------|-----------|--|------------|--|
| TM 266-01-060-1 (holotype) (Fig. 1) | 2001 | Cranium | D.A. | RC, BL = 10.2; RM ¹ , MD = 10.9; RM ² , MD = 13.0, BL = (12.8); RM ³ , MD = 10.8, BL = 14.9; LM ¹ , MD = 11.5 |
| TM 266-01-060-2 | 2001 | Symphyseal fragment with I and C alveoli | Group | RM ³ , MD = 10.7, BL = 12.7 |
| TM 266-01-447 | 2001 | | Group | |
| TM 266-01-448 (Fig. 2a) | 2001 | | Group | |
| TM 266-02-154-1 (Fig. 2b, c) | 2002 | | D.A. | |
| | | Right mandible, (P ₃) P ₄ –M ₃ | | RI ¹ , MD = (13.3), BL = 8.9 RP ₄ , MD = 8.0; RM ₁ , MD = 11.0, BL = 11.9; RM ₂ , MD = 12.5; RM ₃ , MD = 13.3, BL = 12.2 Rc, MD = 11.0, BL = 8.5 |
| TM 266-02-154-2 (Fig. 2d, e) | 2002 | Right c | D.A. | |

Fossil hominids recovered from Toros-Menalla between July 2001 and February 2002. BL, buccolingual; L, left; MD, mesiodistal; R, right. Parentheses indicate estimated measurements—(P₃) indicates that only the roots are known.

cranium has been flattened dorsoventrally and the entire right side is depressed. The cranium exhibits broken but undistorted bone units and matrix-filled cracks (Fig. 1). Estimated measurements are given from a preliminary three-dimensional reconstruction. It will soon be possible to use computer tomography (CT) scans to generate a definitive three-dimensional reconstruction and stereo-lithographic casts.

Comparative observations

Cranial comparisons of comparably aged hominids are limited to a fragmentary basicranium and temporal bone: ARA-VP1/500 and ARA-VP1/125 (ref. 6) from 4.4 Myr *Ardipithecus ramidus ramidus*.

The next-oldest maxillary and cranial specimens are younger: KNM-KP-29283 (*A. anamensis*^{5,20}), KNM-WT40000 (*Kenyanthropus platyops*⁴), and *A. afarensis* specimens, which include the well-preserved AL 444-2 (ref. 21). The most notable anatomical features of the *S. tchadensis* cranium for comparative purposes are to be found in the face, which shows a mosaic of primitive and derived features. The face (Fig. 1a) is tall with a massive brow ridge, yet the mid-face is short (in the superoinferior dimension) and less prognathic than in *Pan* or *Australopithecus* (Table 3). This unusual combination of features is in turn associated with a relatively long braincase, comparable in size to those of extant apes (Fig. 1b, c). Preliminary comparisons with *Pan* suggest an endocranial volume

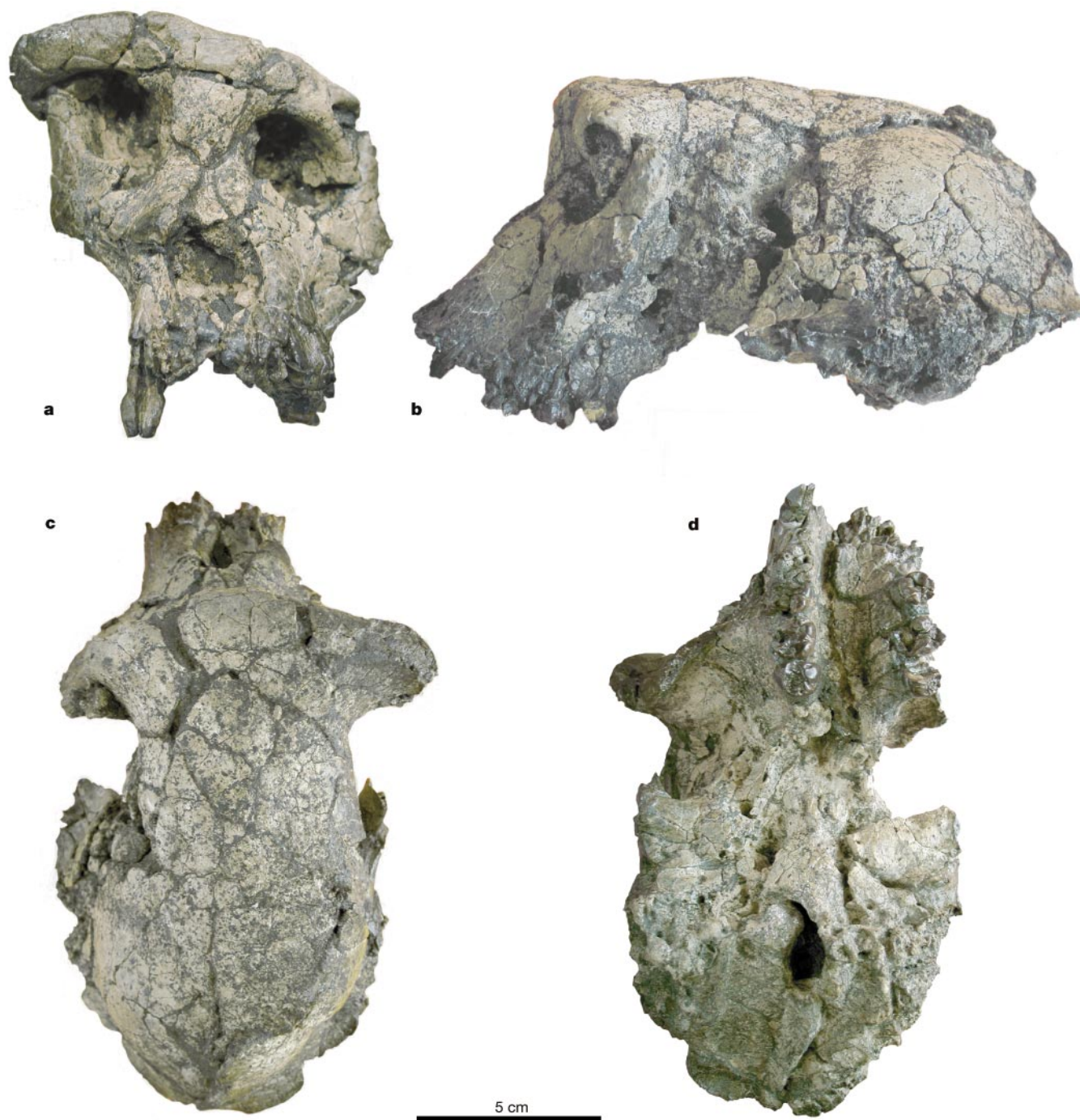


Figure 1 Cranium of *Sahelanthropus tchadensis* gen. et sp. nov. holotype (TM 266-01-060-1). **a**, Facial view. **b**, Lateral view. **c**, Dorsal view. **d**, Basal view.

of 320–380 cm³.

Although the *Sahelanthropus* cranium is considerably smaller than that of a modern male *Gorilla*, its supraorbital torus is relatively and absolutely thicker. This is probably a sexually dimorphic character (see Fig. 3), presumably reflecting strong sexual selection. If this is a male, then the combination of a massive

brow ridge with small canines suggests that canine size was probably not strongly sexually dimorphic. The interorbital pillar is wide (Fig. 1a). The zygomatic process of the maxilla emerges above the mesial margin of M¹ and is therefore more posterior relative to the cheek teeth than in *Australopithecus*^{19–21} and *Paranthropus*¹⁸. The infraorbital plane (from the lower orbital margin to the inferior

Table 2 Comparative dental measurements

| | | Mesiodistal | | | | | Buccolingual | | | | |
|--|--|-------------|--------|--------|--------|------|--------------|--------|--------|--------|------|
| | | <i>n</i> | Min. | Max. | Mean | s.d. | <i>n</i> | Min. | Max. | Mean | s.d. |
| Upper dentition | | | | | | | | | | | |
| I ¹ | <i>S. tchadensis</i> | 1 | – | – | (13.3) | – | 1 | – | – | 8.9 | – |
| | <i>O. tugenensis</i> ⁸ | 1 | – | – | (10.0) | – | 1 | – | – | 8.7 | – |
| | <i>A. r. ramidus</i> ⁶ | 1 | – | – | (10.0) | – | 2 | 7.5 | 8.2 | – | – |
| | <i>A. anamensis</i> ²⁰ | 3 | 10.5 | 12.4 | 11.3 | 1.0 | 3 | 8.2 | 9.3 | 8.8 | 0.6 |
| | <i>A. afarensis</i> ⁶ | 3 | 10.8 | 11.8 | 11.2 | 0.6 | 5 | 7.1 | 8.6 | 8.2 | 0.6 |
| <i>P. t. troglodytes</i> ²⁶ | 14 | – | – | 12.2 | 0.8 | 14 | – | – | 9.4 | 0.8 | |
| C | <i>S. tchadensis</i> | – | – | – | – | – | 1 | – | – | 10.2 | – |
| | <i>O. tugenensis</i> ⁸ | 1 | – | – | 11.0 | – | 1 | – | – | 9.3 | – |
| | <i>A. r. ramidus</i> ⁶ | 2 | (11.2) | 11.5 | – | – | 2 | 11.1 | 11.7 | – | – |
| | <i>A. anamensis</i> ²⁰ | 2 | (10.6) | 11.7 | – | – | 2 | 10.2 | 11.2 | – | – |
| | <i>A. afarensis</i> ⁶ | 9 | 8.9 | 11.6 | 10.0 | 0.8 | 10 | 9.3 | 12.5 | 10.9 | 1.1 |
| <i>P. t. troglodytes</i> ²⁶ | 15 | – | – | 15.6 | 2.1 | 15 | – | – | 11.3 | 1.37 | |
| M ¹ | <i>S. tchadensis</i> | 2 | (10.9) | (11.5) | – | – | – | – | – | – | – |
| | <i>A. r. kadabba</i> ⁷ | 1 | – | – | (10.6) | – | 1 | – | – | 12.1 | – |
| | <i>A. anamensis</i> ²⁰ | 7 | 10.3 | 12.9 | 11.7 | 0.8 | 6 | 11.7 | 14.1 | 13.0 | 0.9 |
| | <i>A. afarensis</i> ²⁶ | 14 | 10.5 | 13.8 | 12.2 | 1.0 | 12 | 12.0 | 15.0 | 13.4 | 0.9 |
| <i>P. t. troglodytes</i> ²⁶ | 14 | – | – | 10.5 | 0.5 | 14 | – | – | 11.3 | 0.6 | |
| M ² | <i>S. tchadensis</i> | 1 | – | – | 13.0 | – | 1 | – | – | (12.8) | – |
| | <i>A. r. ramidus</i> ⁶ | 2 | (11.8) | 11.8 | – | – | 2 | (14.1) | (15.0) | – | – |
| | <i>A. anamensis</i> ²⁰ | 6 | 10.9 | 14.2 | 12.5 | 1.2 | 6 | 13.2 | 16.3 | 14.8 | 1.0 |
| | <i>A. afarensis</i> ⁶ | 5 | 12.1 | 13.5 | 12.8 | 0.5 | 6 | 13.4 | 15.1 | 14.7 | 0.6 |
| <i>P. t. troglodytes</i> ²⁶ | 16 | – | – | 10.7 | 0.6 | 16 | – | – | 11.7 | 0.8 | |
| M ³ | <i>S. tchadensis</i> | 2 | 10.7 | 10.8 | – | – | 2 | 12.7 | 14.9 | – | – |
| | <i>O. tugenensis</i> ⁸ | 2 | 10.2 | 10.3 | – | – | 2 | 12.9 | 13.1 | – | – |
| | <i>A. r. kadabba</i> ⁷ | 1 | – | – | 10.9 | – | 1 | – | – | 12.2 | – |
| | <i>A. r. ramidus</i> ⁶ | 1 | – | – | 10.2 | – | 1 | – | – | 12.3 | – |
| | <i>A. anamensis</i> ²⁰ | 7 | 11.1 | 15.7 | 12.4 | 1.6 | 5 | 13.0 | 14.7 | 13.8 | 0.6 |
| | <i>A. afarensis</i> ⁶ | 8 | 10.5 | 14.3 | 11.9 | 1.4 | 8 | 13.0 | 15.5 | 13.8 | 1.0 |
| | <i>P. t. troglodytes</i> ²⁶ | 16 | – | – | 9.9 | 0.6 | 16 | – | – | 10.8 | 1.0 |
| Lower dentition | | | | | | | | | | | |
| c | <i>S. tchadensis</i> | 1 | – | – | 11.0 | – | 1 | – | – | 8.5 | – |
| | <i>A. r. kadabba</i> ⁷ | 2 | 10.8 | 11.2 | – | – | 2 | 7.8 | 7.8 | – | – |
| | <i>A. r. ramidus</i> ⁶ | – | – | – | – | – | 1 | – | – | 11.0 | – |
| | <i>A. anamensis</i> ²⁰ | 7 | 6.6 | 10.4 | 9.0 | 1.3 | 6 | 9.2 | 11.4 | 10.2 | 1.0 |
| | <i>A. afarensis</i> ²⁷ | 11 | 7.5 | 11.7 | 8.9 | 1.2 | 13 | 8.8 | 12.4 | 10.4 | 1.1 |
| <i>P. t. troglodytes</i> ²⁶ | 15 | – | – | 14.0 | 1.5 | 15 | – | – | 11.4 | 1.4 | |
| P ₄ | <i>S. tchadensis</i> | 1 | – | – | 8.0 | – | – | – | – | – | – |
| | <i>O. tugenensis</i> ⁸ | 1 | – | – | (8.0) | – | 1 | – | – | (9.0) | – |
| | <i>A. r. kadabba</i> ⁷ | 1 | – | – | (8.1) | – | 1 | – | – | 10.0 | – |
| | <i>A. r. ramidus</i> ⁶ | 2 | 7.5 | 8.9 | – | – | 2 | (9.9) | (11.5) | – | – |
| | <i>A. anamensis</i> ²⁰ | 8 | 7.4 | 9.8 | 8.8 | 1.0 | 9 | 9.6 | 11.9 | 10.7 | 0.8 |
| | <i>A. afarensis</i> ⁶ | 15 | 7.7 | 11.1 | 9.7 | 1.0 | 14 | 9.8 | 12.8 | 10.9 | 0.8 |
| <i>P. t. troglodytes</i> ²⁶ | 15 | – | – | 8.1 | 0.6 | 16 | – | – | 8.8 | 0.8 | |
| M ₁ | <i>S. tchadensis</i> | 1 | – | – | 11.0 | – | 1 | – | – | 11.9 | – |
| | <i>A. r. ramidus</i> ⁶ | 2 | 11.0 | 11.1 | – | – | 2 | (10.2) | 10.3 | – | – |
| | <i>A. anamensis</i> ²⁰ | 11 | 11.5 | 13.8 | 12.6 | 0.9 | 12 | 10.5 | 14.8 | 12.1 | 1.3 |
| | <i>A. afarensis</i> ⁶ | 17 | 11.2 | 14.0 | 13.0 | 0.6 | 16 | 11.0 | 13.9 | 12.6 | 0.8 |
| <i>P. t. troglodytes</i> ²⁶ | 15 | – | – | 10.7 | 0.4 | 15 | – | – | 9.2 | 0.6 | |
| M ₂ | <i>S. tchadensis</i> | 1 | – | – | 12.5 | – | – | – | – | – | – |
| | <i>O. tugenensis</i> ⁸ | 1 | – | – | (11.5) | – | 1 | – | – | (11.8) | – |
| | <i>A. r. kadabba</i> ⁷ | 1 | – | – | (12.7) | – | 1 | – | – | 11.8 | – |
| | <i>A. r. ramidus</i> ⁶ | 1 | – | – | (13.0) | – | 1 | – | – | 11.9 | – |
| | <i>A. anamensis</i> ²⁰ | 8 | 13.0 | 15.9 | 14.1 | 1.4 | 11 | 12.3 | 15.1 | 13.5 | 0.9 |
| <i>A. afarensis</i> ⁶ | 23 | 12.4 | 16.2 | 14.3 | 1.0 | 22 | 12.1 | 15.2 | 13.5 | 0.9 | |
| <i>P. t. troglodytes</i> ²⁶ | 15 | – | – | 11.3 | 0.5 | 15 | – | – | 10.6 | 0.9 | |
| M ₃ | <i>S. tchadensis</i> | 1 | – | – | 13.3 | – | 1 | – | – | 12.2 | – |
| | <i>O. tugenensis</i> ⁸ | 2 | (12.3) | (12.4) | – | – | 2 | 10.4 | 11.2 | – | – |
| | <i>A. r. kadabba</i> ⁷ | 1 | – | – | 13.3 | – | – | – | – | – | – |
| | <i>A. r. ramidus</i> ⁶ | 1 | – | – | 12.7 | – | 1 | – | – | 11.0 | – |
| | <i>A. anamensis</i> ²⁰ | 6 | 13.7 | 17.0 | 14.6 | 1.2 | 6 | 11.9 | 13.4 | 12.8 | 0.7 |
| | <i>A. afarensis</i> ⁶ | 14 | 13.7 | 16.3 | 14.8 | 0.8 | 14 | 12.1 | 14.9 | 13.3 | 0.8 |
| <i>P. t. troglodytes</i> ²⁶ | 16 | – | – | 11.0 | 0.6 | 16 | – | – | 9.6 | 0.8 | |

Parentheses indicate estimated measurements.

Table 3 Hominid alveolar height measurements

| Taxon | Alveolar height (mm) |
|---|----------------------|
| <i>S. tchadensis</i> (TM 266-01-060-1) | (22) |
| <i>A. afarensis</i> ²¹ (AL 417-1, AL 444-2) | 30, 33 |
| <i>A. africanus</i> ²⁸ (mean and range, <i>n</i> = 11) | 25.7 (21.1–30.0) |
| <i>P. boisei</i> ²⁸ | 42.2 |
| <i>H. habilis</i> ²⁸ (KNM-ER 1470, KNM-ER 1813) | 31.0, 25.0 |

Alveolar height from nasospinale to prosthion. Parentheses indicate estimated measurements from a preliminary three-dimensional reconstruction.

malar margin) is similar to that of *Pan* and differs from both *Gorilla* and larger *Australopithecus*, in which this region is absolutely and relatively taller. The canine fossa is similar to that in AL 444-2 (ref. 21) and there is no diastema between the alveoli of I² and C in the Chadian specimen. There is no supratoral sulcus. Between the temporal lines, the frontal squama is slightly depressed but not like the frontal trigone usually seen in *P. boisei*¹⁸. The temporal lines converge behind the coronal suture as in crested *Pan*, whereas their junction is more anterior than generally seen in some large *A. afarensis* (for example, AL 444-2; ref. 21). The sagittal crest is a little larger posteriorly than in either AL 444-2 (ref. 21) or KNM-WT 40000 (ref. 4). The compound temporal–nuchal crest is marked as in KNM-ER 1805 (ref. 22) and much larger than in the male *A. afarensis* AL 444-2 (ref. 21), suggesting a relatively large posterior temporalis muscle. The postorbital breadth (Fig. 1c) is absolutely smaller than the *Pan*–*Gorilla* average, and similar to that in AL 444-2 and AL 417-1 (ref. 21) (Table 5).

The basicranium (Fig. 1d) has small occipital condyles associated with an apparently large foramen magnum. Despite damage, the

Table 4 Cranio-facial measurements of *S. tchadensis*

| Cranio-facial features | Size (mm) |
|---------------------------------------|-----------|
| Orbital height × width | (36 × 35) |
| Maximum breadth | |
| Bicarotid chord | (45) |
| Bimastoid (at the nuchal crest level) | (108) |
| Biporion | (102) |
| Mastoid mesiodistal length | 54.5 |
| Nuchal plane length (opisthion–inion) | (47) |

Measurements are from TM 266-01-060-1. Parentheses indicate estimated measurements from a preliminary three-dimensional reconstruction.

foramen magnum seems to be longer than wide, and not like the rounded shape typical of *Pan*. As in *A. ramidus*, the basion is intersected by the bicarotid chord; the basion is posterior in large apes and anterior in some of the later hominids. The *Sahelanthropus* basioccipital is correlatively short and shaped like a truncated triangle as in *Ardipithecus*⁶; it is not as triangular as in other early hominids.

Like *Pan*, *Australopithecus*²¹ and *Ardipithecus*⁶, the orientation of the petrous portion of the temporal is approximately 60° relative to the bicarotid chord, instead of 45° as is typical of *Paranthropus* and *Homo*. Unlike *Gorilla*, *Pan* and *Ardipithecus*⁶, the posterior margin of the tympanic tube does not have a crest-like morphology. Compared with known *Ardipithecus* (ARA-VP-1/500)⁶, the glenoid cavity is larger and the postglenoid process mediolaterally wider, so the pronounced squamotympanic fissure is situated more medially to the postglenoid process. The height of the relatively flat temporomandibular joint above the tooth row suggests a high ascending

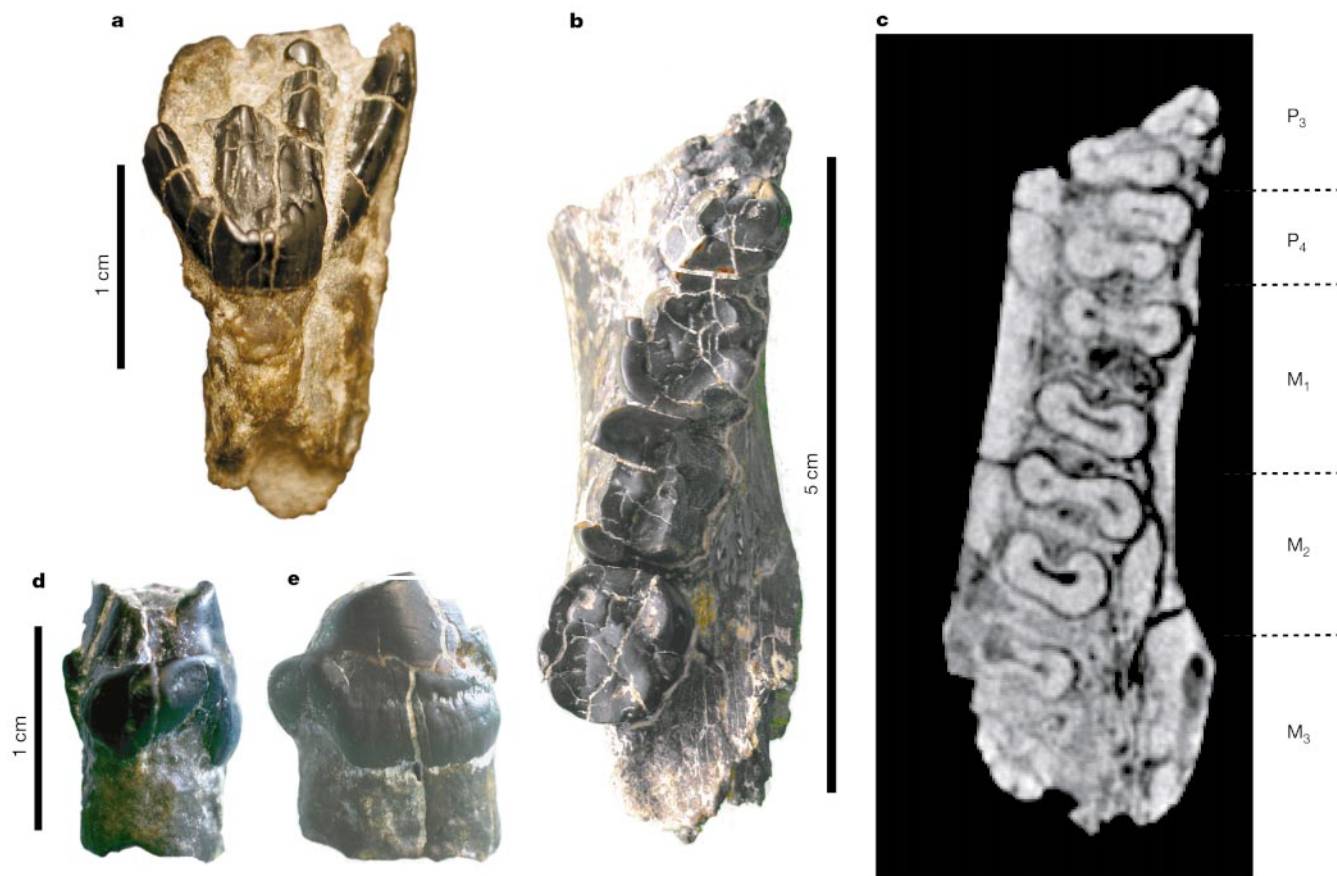


Figure 2 *Sahelanthropus tchadensis* gen. et sp. nov. paratypes. **a**, Right upper I¹, lingual view (TM 266-01-448). **b**, **c**, Right lower jaw (TM 266-02-154-1), occlusal view (**b**) and axial CT scan (**c**). **d**, **e**, Right lower canine (TM 266-02-154-2), distal view (**d**) and buccal view (**e**).

Table 5 Measurements and indices of hominoid frontal bones

| | Post orbital breadth* (a) (mm) | Superior facial breadth† (b) (mm) | Fronto-facial breadth index (a/b × 100) |
|---|--------------------------------|-----------------------------------|---|
| <i>P. troglodytes</i> (10 males) ¹⁹ | 71.0 (62.0–76.5) | 110.1 (99.4–129.0) | 64.4 (58.1–68.5) |
| <i>P. troglodytes</i> (10 females) ¹⁹ | 70.1 (65.0–76.0) | 102.2 (87.3–112.0) | 68.8 (66.6–74.5) |
| <i>G. gorilla</i> (10 males) ¹⁹ | 69.5 (60.5–77.0) | 135.1 (127.7–144.0) | 51.5 (47.4–59.4) |
| <i>G. gorilla</i> (10 females) ¹⁹ | 68.5 (65.5–73.5) | 115.5 (108.0–127.0) | 59.5 (57.0–63.4) |
| <i>P. pygmaeus</i> (5 males) ¹⁹ | 63.8 (59.0–69.5) | 105.7 (88.3–116.2) | 61.2 (51.7–72.5) |
| <i>P. pygmaeus</i> (4 females) ¹⁹ | 64.0 (61.5–65.5) | 90.1 (87.8–94.0) | 71.1 (68.1–74.0) |
| <i>S. tchadensis</i> gen. et sp. nov. (TM 266-01-060-1) | (60) | (102) | (59) |
| <i>A. afarensis</i> (AL 444-2) ²¹ | 77.0 | 118.6 | 64.9 |

Values are mean and range. Values for *S. tchadensis* were estimated from a preliminary three-dimensional reconstruction.

*The least-frontal breadth.

†Left frontomale temporale to right frontomale temporale (outer biorbital breadth).

ramus of the mandible more similar in absolute size to *Gorilla* than to *Pan*. The large pneumatized mastoid process is anteroposteriorly long, more so than in *Ardipithecus*⁶ and *Australopithecus* (AL 444-2, AL 333)^{19,21}. The flat nuchal plane is relatively longer (Fig. 1b, d and Table 4) than in *Pan*, *Gorilla*, AL 444-2 and AL 333, and with crests as marked as those of *Gorilla*, implying the presence of relatively large superficial neck muscles. The horizontally oriented nuchal plane is much flatter than the convex nuchal plane of *Pan*. There is not yet sufficient information to infer reliably whether *Sahelanthropus* was a habitual biped. However, such an inference would not be unreasonable given the skull's other basicranial and facial similarities to later fossil hominids that were clearly bipedal.

Little is preserved of the mandibular corpus in TM-266-02-154-1 or the symphysis in TM-266-01-060-2 to permit much discussion of mandibular anatomy. However, the former, presumably a male, has a thick corpus with a wide extramolar sulcus (Fig. 2a).

In dentition, both lower incisor roots are small. The lingual surface of upper I¹ displays distinct marginal ridges converging basally onto a narrow gingival eminence and with several tubercles extending incisally into the lingual fossa (Fig. 2a). The smaller upper I² alveolus is situated, in frontal view, lateral to the lateral edge of the nasal aperture (Fig. 1a), a probable symplesiomorphy with *Pan*. The upper and lower canines are small (Tables 1, 2). Given the absolutely and relatively massive supraorbital torus of the cranium (Figs 1a and 3), possibly reflecting strong sexual selection, and the thick corpus of the mandible (Fig. 2b, c), which probably indicate male status, we infer that *Sahelanthropus* canines were probably weakly sexually dimorphic. The upper canine (Fig. 1d) has both distal and apical wear facets whereas M³ is unworn. The lower canine (Fig. 2d, e) has a strong distal tubercle that is separated from a distolingual crest by a fovea-like groove; the large apical wear zone at a level above this distal tubercle implies a non-honing C–P₃ complex (the

P₃ is still unknown). The upper canine, judging from the steep, narrow distal wear strip reaching basally, we believe had a somewhat lower distal shoulder than *Ardipithecus*^{6,7}, suggesting an earlier evolutionary stage. Moreover, a small, elliptical contact facet for P₃ on the distobuccal face of the distal tubercle indicates the absence of a lower c–P₃ diastema. *Sahelanthropus* thus probably represents an early stage in the evolution of the non-honing C–P₃ complex characteristic of the later hominids⁷.

The cheek teeth are small (Tables 1, 2), within the size range of *A. ramidus* and the lower end of *A. afarensis*. Lower c and the lower and upper premolars each have three pulp canals and two roots (Fig. 2c). The P₃ has a 2R:MB + D pattern (terminology following ref. 22: R, root; M, mesial; MB, mesiobuccal; D, distal) with a small mesio-buccal root and two partially fused, larger oblique distal roots. The P₄ has two transverse roots (2R:M + D), with the mesial one smaller than the distal; in both premolars the distal root has two pulp canals (Fig. 2c). The P₄ teeth of *Ardipithecus* have more-derived root patterns, with either a Tome's root (*A. r. kadabba*)⁷ or a single root (*A. r. ramidus*)⁶. *S. tchadensis* has a P₄ with a large talonid and well-marked grooves on the buccal face. The molar size gradient is M₂ > M₃ > M₁. The upper molars have three roots, two buccal and one lingual, which is large and mesiodistally elongated. The M³ crowns are triangular whereas the M₃ teeth are rectangular and rounded distally. The lower molar root pattern is 2R:M + D: a mesial root with two pulp canals and a distal root with only one canal (Fig. 2c).

The radial enamel thickness is 1.71 mm at paracone LM³ and 1.79 mm at hypocone LM². The molar enamel is therefore thicker than in *Pan*, possibly thicker than in *Ardipithecus ramidus ramidus*, but thinner than in *Australopithecus*⁶. Given individual and intra-specific variation, further study using high-resolution imaging (CT scanning) is needed for useful comparisons⁷.

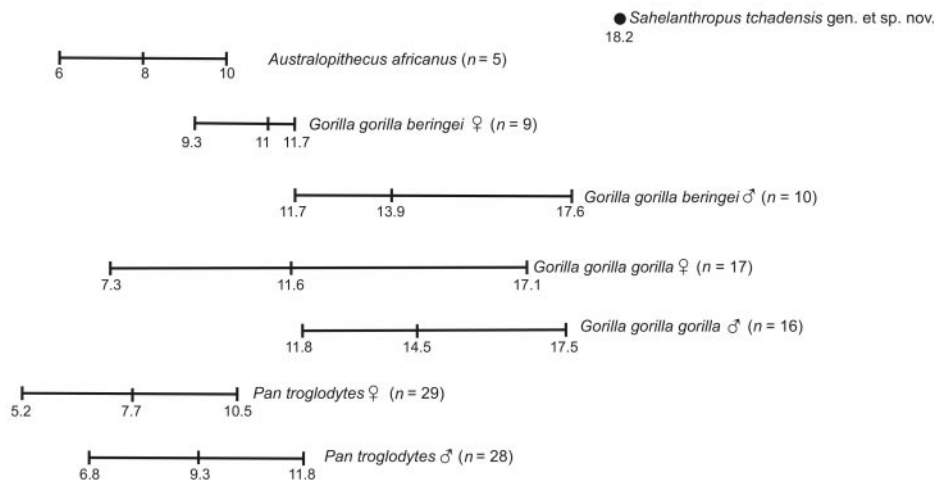


Figure 3 Vertical (superoinferior) thickness of the supraorbital torus in extant hominoids, *A. africanus* and *S. tchadensis* gen. et sp. nov. Measurements are in millimetres at

the highest point of the superior orbital margin. Data for apes and *A. africanus* are from ref. 28.

Discussion

Sahelanthropus has several derived hominid features, including small, apically worn canines—which indicate a probable non-honing C–P₃ complex—and intermediate postcanine enamel thickness. Several aspects of the basicranium (length, horizontal orientation, anterior position of the foramen magnum) and face (markedly reduced subnasal prognathism with no canine diastema, large continuous supraorbital torus) are similar to later hominids including *Kenyanthropus* and *Homo*. All these anatomical features indicate that *Sahelanthropus* belongs to the hominid clade.

In many other respects, however, *Sahelanthropus* exhibits a suite of primitive features including small brain size, a truncated triangular basioccipital bone, and the petrous portion of the temporal bone oriented 60° to the bicarotid chord. The observed mosaic of primitive and derived characters evident in *Sahelanthropus* indicates its phylogenetic position as a hominid close to the last common ancestor of humans and chimpanzees. Given the biochronological age of *Sahelanthropus*, the divergence of the chimpanzee and human lineages must have occurred before 6 Myr, which is earlier than suggested by some authors^{23,24}. It is not yet possible to discern phylogenetic relationships between *Sahelanthropus* and Upper Miocene hominoids outside the hominid clade. *Ouranopithecus*¹⁵ (about 2 Myr older) is substantially larger, with quadrate orbits, a very prognathic and wide lower face, large male canines with a long buccolingual axis, and cheek teeth with very thick enamel. *Samburupithecus*¹⁴ (about 2.5 Myr older) has a low, posteriorly positioned (above M²) zygomatic process of the maxilla, cheek teeth with high cusps (similar to *Gorilla*), lingual cingula, large premolars and a large M³.

Sahelanthropus is the oldest and most primitive known member of the hominid clade, close to the divergence of hominids and chimpanzees. Further analysis will be necessary to make reliable inferences about the phylogenetic position of *Sahelanthropus* relative to known hominids. One possibility is that *Sahelanthropus* is a sister group of more recent hominids, including *Ardipithecus*. For the moment, productive comparisons of *Sahelanthropus* with *Orrorin* are difficult because described craniodental material of the latter is fragmentary and no *Sahelanthropus* postcrania are available. However, we note that in *Orrorin*, the upper canine resembles that of a female chimpanzee. The discoveries of *Sahelanthropus* along with *Ardipithecus*^{6,7} and *Orrorin*⁸ indicate that early hominids in the late Miocene were geographically more widespread than previously thought.

Finally, we note that *S. tchadensis*, the most primitive hominid, is from Chad, 2,500 km west of the East African Rift Valley. This suggests that an exclusively East African origin of the hominid clade is unlikely to be correct (contrary to ref. 8). It will never be possible to know precisely where or when the first hominid species originated, but we do know that hominids had dispersed throughout the Sahel and East Africa¹⁰ by 6 Myr. The recent acquisitions of Late Miocene hominid remains from three localities, as well as functional, phylogenetic and palaeoenvironmental studies now underway, promise to illuminate the earliest chapter in human evolutionary history. *Sahelanthropus* will be central in this endeavour, but more surprises can be expected. □

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Competing interests statement

The authors declare that they have no competing financial interests.

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Competing interests statement

The authors declare that they have no competing financial interests.

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erratum

A new hominid from the Upper Miocene of Chad, Central Africa

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Nature **418**, 145–151 (2002).

Owing to an editorial oversight, the sentence in the second column of page 150 that reads ‘Lower c and the lower and upper premolars each have three pulp canals and two roots’ is in error. Instead, it should read ‘Lower and upper premolars each have three pulp canals and two roots’. □