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SOCIAL SCIENCES

The taxonomy of *Sahelanthropus tchadensis* from a craniometric perspective

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Abstract: *Sahelanthropus tchadensis* has raised much debate since its initial discovery in Chad in 2001, given its controversial classification as the earliest representative of the hominin lineage. This debate extends beyond the phylogenetic position of the species, and includes several aspects of its habitual behavior, especially in what regards its locomotion. The combination of ancestral and derived traits observed in the fossils associated with the species has been used to defend different hypotheses related to its relationship to hominins. Here, the cranial morphology of *Sahelanthropus tchadensis* was assessed through 16 linear craniometric measurements, and compared to great apes and hominins through Principal Component Analysis based on size and shape and shape information alone. The results show that *S. tchadensis* share stronger morphological affinities with hominins than with apes for both the analysis that include size information and the one that evaluates shape alone. Since TM 266-01-060-1 shows a strong morphological affinity with the remaining hominins represented in the analysis, our results support the initial interpretations that *S. tchadensis* represents an early specimen of our lineage or a stem basal lineage more closely related to hominins than to *Panini*.

Key words: hominin, Homo, paleoanthropology, multivariate analysis.

INTRODUCTION

Sahelanthropus tchadensis represents a controversial species in the discussion about the origins of the hominin lineage (Brunet et al. 2002, Wood & Harrison 2011, Wolpoff et al. 2002), given that its taxonomic position as a basal node in the *hominini* tribe is ambiguous and hard to test. The species is represented by a collection of fossils discovered in Chad and dated to about 7 million years ago (Lebatard et al. 2008). The fossils include a well-preserved (albeit heavily deformed) cranium, mandible fragments, teeth, and fragments of postcrania bones. Since its original publication (Brunet et al. 2002), the phylogenetic relationship of the species with the hominin lineage has been debated and there has been scarcely any aspect of the discovery that has been widely accepted. To start, the old age of the fossils and the fact that they have been discovered in a region far away from fossils representing other hominin species instills already caution about its phylogenetic position (see debate between Brunet et al. 2002 and Wolpoff et al. 2002, as an example). More importantly, the morphological characteristics of the fossils present a combination of primitive and derived traits that make it difficult to position the species within the evolutionary history of hominoids (see discussions in Wood & Harrison 2011 and Lieberman 2022). Much of the initial debate about the taxonomic position of *Sahelanthropus tchadensis* centered around the position of its foramen magnum: in the original publication about the fossil, Brunet et al. (2002)

argued that the morphology and position of the foramen attested to its bipedality. However, inferring posture only based on this trait is not a simple task, especially given that the holotype fossil for *S. tchadensis* (TM 266-01-060-1) was intensely deformed by taphonomic processes, and the interpretation was initially challenged by some authors (Wolpoff et al. 2002, Wood & Harrison 2011).

Zollikofer et al. (2005) reconstructed the skull based on virtual techniques, correcting the deformations present in the original specimen, and their analysis of the position of the foramen magnum suggested an anterior position in the basicranium, reinforcing the idea that *Sahelanthropus* was biped, and hence the earliest hominin ever found. The authors also compared the reconstructed cranial morphology of *S. tchadensis* with those of early hominins and living apes through geometric morphometrics analyses. Their results showed that the cranial morphology of TM 266-01-060-1 presents a strong affinity with other hominins, and not with living apes. Recent studies have further supported that anteriorly located foramen magnum in hominins are discriminatory of bipedality (Neaux et al. 2017, Russo & Kirk 2017), and that *Sahelanthropus* falls within the hominin range (Neaux et al. 2017).

However, while the discussion about locomotion behavior has been initially an important aspect to the identification of *Sahelanthropus* as a hominin, recent studies have challenged whether bipedality is a good indicator of basal hominins. On one hand, bipedality may not have been a unique trait of hominins, as it has been suggested to have evolved in parallel in different lineages of hominoids (Köhler & Moyà-Solà 1997, Böhme et al. 2019), although these conclusions have been contested (Russo & Shapiro 2013, Williams et al. 2020). On the other hand, several studies have shown that the locomotion behavior of early hominin species was significantly different from the locomotion behavior that is observed among *australopithecines* and *Homo* species. For instance, even if habitual bipedality has been supported for early hominin genera, like *Orrorin* and *Ardipithecus* (Richmond & Jungers 2008, White et al. 2009), these species also show adaptations to efficient clambering and climbing.

Within this larger debate, the locomotion habits of *S. tchadensis* have been the focus of several recent studies. Macchiarelli et al. (2020) analyzed the morphology of a partial left femur attributed to another individual of *S. tchadensis*, and concluded that the femur's overall morphology is more similar to that of a chimpanzee than to that of hominins, including modern humans. They also described a great difference between the anteroposterior curvature observed in the new femur from *Sahelanthropus* and the habitual biped *Orrorin tugenensis* (BAR 1002'00). Contrary to Brunet et al. (2002) and Zollikofer et al. (2005), this study contested the idea that *S. tchadensis* was a habitual biped. However, the study was based on a limited number of measurements of the femur and on 2D photographs (Lieberman 2022).

Daver et al. (2022) presented an independent analysis of the same femur, complemented by the analysis of a left and a right ulna attributed to *S. tchadensis*, possibly belonging to the same individual as the skull. Their analyses, based on the cross-sectional geometry, the relative cortical thickness, and the torsion in the femoral shaft, suggest that the morphology of the femur is more congruent with habitual bipedality. The ulnae, on the other hand, show highly curved forearm bones, which is interpreted as evidence of substantial arboreal behavior, and fits the locomotion behavior observed among other early hominins. Meyer et al. (2023) further explored the anatomy of the ulnae of *Sahelanthropus*, proposing that the species shows adaptations consistent with knuckle-walking, and concludes that *S. tchadensis* was not an obligate biped.

Given the conflicting results derived from the analysis of both cranial and postcranial remains, we present in this study new evidence that concur with Brunet et al. (2002), Zollikofer et al. (2005), and Guy et al. (2022) in support of the classification of *S. tchadensis* as more closely related to the hominin lineage than to *Panini*. Our analyses explore the cranial morphological pattern of *S. tchadensis* in relation to the morphological variation seen in other hominin species and apes. As these analyses focus on overall morphology rather than specific synapomorphies, they complement previous studies and contribute to the debate of the phylogenetic position of *Sahelanthropus tchadensis*.

MATERIALS AND METHODS

Cranial morphological affinities of *S. tchadensis* were explored through a Principal Component Analysis (PCA) based on 16 linear craniometric measurements (Table I). The data for TM 266-01-060-1 were extracted from Zollikofer et al. (2005). The cranial morphology of the specimen was compared to those of nine fossil hominin species (represented by 34 specimens), and three living ape species (represented by 156 specimens; Table II). Missing values in the hominin specimens were estimated through linear multiple regressions, following the same method detailed in Hubbe et al. (2011). Centroids for each of the species were calculated as the arithmetic mean of all individuals that belonged to it (Tables III and IV), and the centroids were used as the reference series to compare with TM 266-01-060-1. PCA was conducted on the original data (size and shape) and on data corrected

Table I. **Species and specimens of hominins included in this study.**

Species	N	Specimens	Sources
S. tchadensis †	1	Sa TM 266	Zollikofer et al. (2005)
P. aethiopicus	1	KNM-WT 17000	Kimbel et al. (2004)
P. boisei	4	KNM-ER 406; KNM-ER 407; KNM-ER 732; OH 5.	Wood (1991)
P. robustus	2	SK 48; SK 52.	Wood (1991)
A. afarensis	3	A.L. 333†; A.L 417-1D; 444-2.	Kimbel et al. (2004)
A. africanus	5	MLD 37/38; Sts 5; Sts 52; Sts 71; Stw 13.	Wood (1991)
A. sediba	1	MH1	Berger et al. (2010)
H. erectus	14	D2282; D2700; D3444; D4500; KNM-ER 3733; KNM-ER 3883; KNM-WT 15000; Ng 7; Ng 12; OH 9; Sangiran 4; Sangiran 17; SK 847; Sm 4.	Kaifu et al. (2008) Laird et al. (2017) Wood (1991)
H. habilis	3	KNM-ER 1813; OH 24; Stw 53.	Laird et al. (2017) Wood (1991)
H. rudolfensis	1	KNM-ER 1470.	Wood (1991)

†The data used for this specimen is based on its reconstruction.

for the effect of size (shape alone). Size effect was corrected by dividing each variable by the geometric mean of the species centroid (Darroch & Mosimann 1985). Analyses were done in R (R Core Team 2023), complemented by packages ggplot2 (Wickham 2016) and MASS (Venables & Ripley 2002).

RESULTS

Figure 1 shows the morphospace defined by the first two Principal Components extracted from the original data (size and shape). Together, they explain 78.7% of the original variance. As can be seen, living apes are separated from hominins on the second principal component. TM 266-01-060-1 is clearly positioned in the area occupied by the *Homo* species, differentiating itself from apes and robust australopithecines across PC2. Noteworthy, the *Sahelanthropus* specimen shows stronger morphological affinities with *Homo* species than either Australopithecine and Great Apes, reflecting larger and less prognathic facial morphology. In this analysis, PC1 concentrates size information and has a negative correlation with all measurements (larger skulls have more negative PC1 scores). PC2 is correlated with dimensions of neurocranium and face, being mostly affected by orbital dimensions, superior facial height and skull length (Table

Table II. **Average hominins values for each of the metric variables used in the analyses.**

Variable	*A. afarensis*	*A. africanus*	*A. sediba*	*H. erectus*	*H. habilis*	*H. rudolfensis*	*P. aethiopicus*	*P. boisei*	*P. robustus*	Sa TM 266
Glabella-opisthocranion	**151.87**	137.50	**151.87**	192.03	147	166	**151.87**	167	**151.87**	173
Basion-bregma	**94.12**	96.50	74	108.79	89.50	**94.12**	**94.12**	97.67	**94.12**	86
Basion-nasion	105	99	**103.73**	103.33	77.50	**103.73**	**103.73**	111	**103.73**	105
Biporionic breadth	126	98.50	104	124.26	105.75	127	131	120.83	**119.79**	124
Supramastoid breadth	**122.29**	117	110	141.71	120	**122.29**	**122.29**	130.33	109	128
Superior facial height	100	73.67	68	95.14	68	90	88	100	80	75
Biorbital breadth	88.33	83.60	78	101.18	88.67	101	94	92.67	82	91
Orbital breadth	36.33	26.17	31	35.86	29.75	30.33	36	36.67	33	38
Orbital height	37	30	31	33.94	31	33	37	33.33	30	36
Minimum malar height	**32**	26	**32**	34	25.50	40	**32**	35.33	28.33	26
Maximum nasal width	23.33	22.29	26	33	25	27	26	30.50	24.83	26
Rhinion-nasospinale	30	25.75	22	28.50	27.50	**27.47**	26	35	23.50	32
Foramen magnum length	**30.45**	27.67	**30.45**	36.70	29	**30.45**	**30.45**	28	28	32
Foramen magnum maximum width	**25**	23.67	**25**	29.06	25.50	**25**	**25**	28.67	21	22
Maxillo-alveolar length	66.43	72.50	63	66.14	65	68	78	82	68	76
Maxillo-alveolar breadth	67.50	63.77	63	67.83	70.17	73.33	80	81.67	67.11	60

Numbers in bold are replaced missing values.

V). In the upper part of the morphospace, crania have shorter faces, larger orbits, and longer neurocrania.

Figure 2 shows the morphospace defined by the first two Principal Components (explaining 69.6% of the original variance) extracted from the shape alone data. Similar to the analysis of size and shape, the apes are clearly separated from hominins, in this case occupying the lower-left triangle of the plot. As with the previous analyses, TM 266-01-060-1 is clearly positioned with the hominins, closer to the cluster defined by the genus *Homo*, in stark contrast with the morphology of great apes. In this analysis PC1 is mostly affected by superior facial height and the orbital dimensions (orbital height and breadth), and high values in this PC are associated with smaller facial dimensions. For PC2 the most influential variables are related to the length and breadth of the skull (glabella-opisthocranion, biorbital breadth and maximum nasal width) (Table VI). In the vertical axis of this plot, the lower part is occupied by short and narrow skulls while the upper part is occupied by long and wide skulls. Taken together, these two analyses show a strong morphological affinity of *Sahelanthropus* with hominins.

Table III. **Average great apes values for each of the metric variables used in the analyses.**

Variable	***Pan troglodytes* (Male)**	***Pan troglodytes* (Female)**	***G. gorilla* (Male)**	***G. gorilla* (Female)**	***Pongo pygmaeus* (Male)**	***Pongo pygmaeus* (Female)**
Glabella-opisthocranion	136	131	173	151	130	119
Basion-bregma	90	88	110	97	99	93
Basion-nasion	101	97	136	114	102	94
Biporionic breadth	115	115	144	122	**119.79**	**119.79**
Supramastoid breadth	122.29	122.29	122.29	122.29	122.29	122.29
Superior facial height	90	82	120	98	105	88
Biorbital breadth	90	86	114	96	84	77
Orbital breadth	39	37	49	43	39	36
Orbital height	35	34	42	40	42	39
Minimum malar height	30	26	43	34	38	30
Maximum nasal width	26	24	37	31	26	24
Rhinion-nasospinale	27	25	**27.47**	**27.47**	**27.47**	**27.47**
Foramen magnum length	28	28	33	31	34	30
Foramen magnum maximum width	25	25	25	25	25	25
Maxillo-alveolar length	71	65	**70**	**70**	**70**	**70**
Maxillo-alveolar breadth	60	58	73	65	69	63

Numbers in bold are replaced missing values.

DISCUSSION AND CONCLUSIONS

The cranial morphology of hominins is very derived from the basal bauplan of great apes, especially after the appearance of the genus *Homo*. This derived morphology is associated with the absolute and relative reduction of facial size and projection, reduced dental size, especially of canines, accompanied by an absolute and relative increase in the size of the braincase. Relative to hominins, the evolution of craniofacial shape of great apes has been more constrained (Brunet et al. 2002), which suggests that the last common ancestor between *Hominini* and *Panini* shared higher morphological affinities with the latter. As reviewed by Almécija et al. (2021) this view ignores the fact that Miocene apes have their own adaptations that differentiate them from extant apes, but even when this is considered the overall magnitude of changes in the cranial morphology of hominins is considerably larger than what is observed among apes. In this context, the cranial morphological characteristics of *Sahelanthropus tchadensis* is clearly distinct from the morphological bauplan of great apes, as shown in our analyses, and supports the previous analyzes that group it with hominins (Brunet et al. 2002, Guy et al. 2005, Zollikofer et al. 2005).

However, while the analyses we present confidently reject the hypothesis that *Sahelanthropus tchadensis* shares the same morphological characteristics of great apes, its position as an ancestral species to the hominin lineage is not necessarily supported. As our analyses demonstrate, the TM 266-01-060-1 specimen shows stronger morphological affinities with early *Homo* and late australopithecine species than with the earlier australopithecine species included in our study. A similar result has been observed by Guy et al. (2005). In that sense, if the differentiation between great apes and early Homo can be considered to represent an axis of morphological differentiation towards the derived phenotypic characteristics of later Homo, *Sahelanthropus tchadensis* appears to be very derived towards the bauplan of *Homo*, especially given its early chronology.

Table IV. Correlations between the first two Principal Components and the original variables (size and shape).

Variable	Factor 1	Factor 2
Glabella-opisthocranion	-0.767	0.638
Basion-bregma	-0.731	-0.254
Basion-nasion	-0.799	-0.267
Biporionic breadth	-0.837	-0.278
Supramastoid breadth	-0.560	0.187
Superior facial height	-0.780	-0.590
Biorbital breadth	-0.894	0.030
Orbital breadth	-0.661	-0.517
Orbital height	-0.470	-0.706
Minimum malar height	-0.740	-0.330
Maximum nasal width	-0.879	0.012
Rhinion-nasospinale	-0.454	0.074
Foramen magnum length	-0.598	0.084
Foramen magnum maximum width	-0.371	0.071
Maxillo alveolar length	-0.283	-0.078
Maxillo alveolar breadth	-0.506	0.015

The reconstruction of ancestral morphotypes is challenging (Andrews & Harrison 2005) for several reasons, including the limitations we currently have of testing for the occurrence of homoplasy in the hominin lineage (Wood & Harrison 2011). These challenges ultimately push paleoanthropologists to simplify the evolutionary history of hominins, and in the case of the debate of the phylogenetic relationship of early fossils like *Sahelanthropus*,

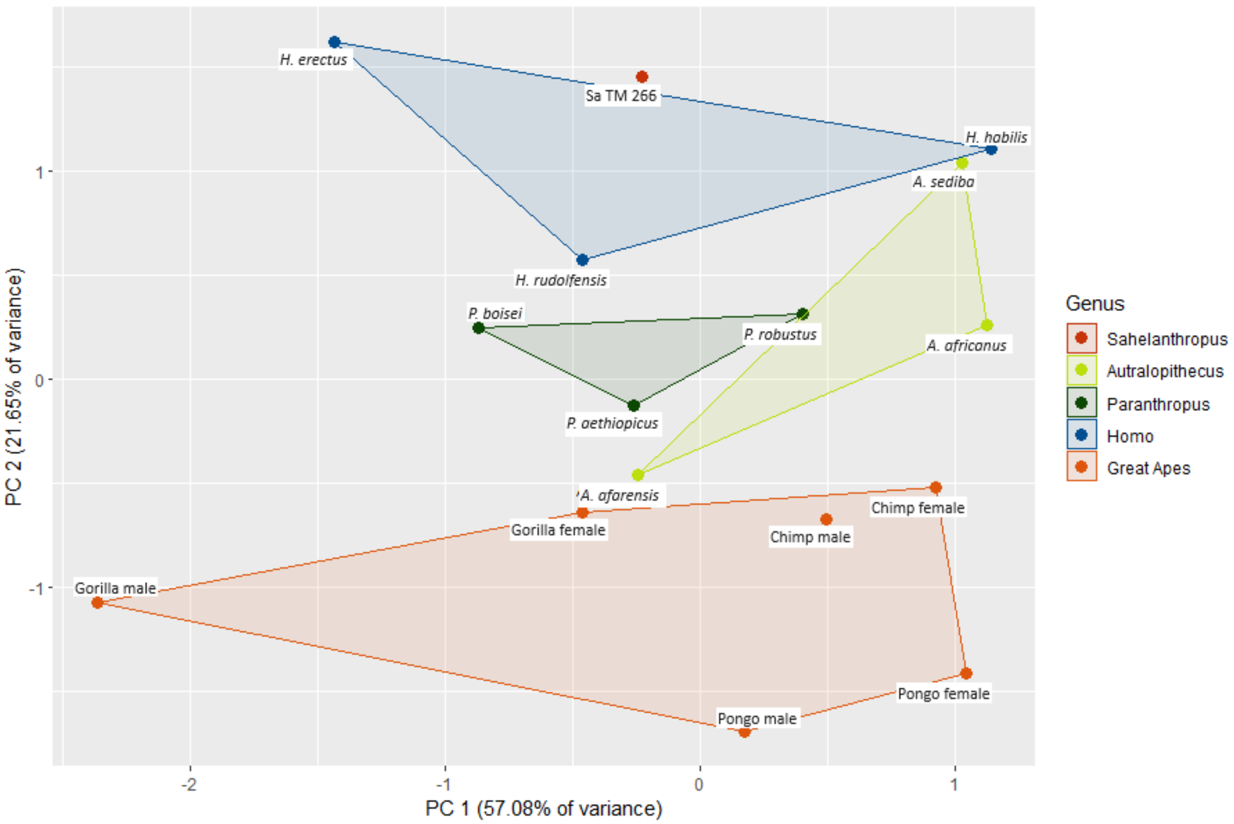

Figure 1. Morphological affinities of *Sahelanthropus tchadensis* (TM 266-01-060-1) in relation to early hominins and great apes according to the first two Principal Components extracted from the original data.

this translates into the idea that there are only two viable evolutionary lineages between 8 and 6 Ma ago: *Hominini* and *Panini*. While this evolutionary scenario can be considered the most parsimonious, it may not be the most likely, especially given that many of the classical synapomorphies for hominins are not exclusive to the tribe (e.g., reduced canines, reduced sexual dimorphism; Wood & Harrison 2011) or can also be explained by changes other than the adoption of bipedality (e.g., anterior position of foramen magnum). This discussion has led Wood & Harrison (2011: 351) to “urge researchers, teachers and students to consider the published phylogenetic interpretations of these taxa as among a number of possible interpretations of the evidence.”

To support this call for considering different phylogenetic scenarios for the beginnings of hominin evolution, the derived cranial morphological characteristics of *Sahelanthropus tchadensis* in our analyses suggest that the classification of the species as a direct ancestor of hominins is not straightforward. If its pattern of morphological affinities represents the axis of differentiation that eventually led to the derived morphology of *Homo*, then we must revisit what are the most parsimonious scenarios for the number of viable evolutionary lineages that were related to or stemming from the *Panini*/*Hominini* clade. The derived position of TM 266-01-060-1 suggests that either they represent an early sister group to Hominin, sharing characteristics with later Homo, or that the Hominin lineage is marked by quick differentiation of craniofacial proportions, followed by a reversion of the morphological bauplan back towards a pattern more similar to the australopithecine’s bauplan.

Table V. **Correlations between the first two Principal Components and the original variables (shape alone).**

Variable	Factor 1	Factor 2
Glabella-opisthocranion	0.623	0.778
Basion-bregma	0.036	-0.211
Basion-nasion	-0.166	0.221
Biporionic breadth	-0.095	-0.010
Supramastoid breadth	0.714	-0.342
Superior facial height	-0.951	0.230
Biorbital breadth	-0.536	0.708
Orbital breadth	-0.806	0.192
Orbital height	-0.847	-0.113
Minimum malar height	-0.744	0.412
Maximum nasal width	-0.560	0.688
Rhinion-nasospinale	-0.262	0.275
Foramen magnum length	-0.313	0.437
Foramen magnum maximum width	-0.264	0.219
Maxillo alveolar length	-0.255	0.107
Maxillo alveolar breadth	-0.358	0.411

The resolution between these models is not possible with the data available, but both scenarios suggest that the discussion about the phylogenetic relationship of *Sahelanthropus tchadensis* must go beyond the question of whether it is or not a hominin. Moreover, the early appearance of a very derived craniofacial bauplan suggests that the morphological differentiation among early Hominins could have appeared fairly quickly, falling in line with the great morphological diversity observed among Miocene apes (Almécija et al. 2021). If this is the case, then our results suggest new possible lines of inquiry towards what were the factors that limited the changes of craniofacial morphology among other pre australopithecine and australopithecine species, as they retained closer morphological affinities to great apes for a long period of time after *Sahelanthropus tchadensis* had already evolved a more derived morphology.

In conclusion, our analyses can safely reject that the craniofacial morphology of *Sahelanthropus tchadensis* is similar to that of great apes, and in that sense they lend support to those studies that place this species within our lineage (Brunet et al. 2002, Guy et al. 2005, Zollikofer et al. 2005). However, from the perspective of overall cranial morphology, *Sahelanthropus* shows a bauplan that is significantly departed from the one observed among apes and early australopithecine, falling closer to the morphospace occupied by early *Homo* species. Despite the fact that morphological traits have shown poor performance in phylogenetic reconstructions of hominids (e.g., Gibbs et al. 2000, Strait & Grine 2004), the analysis of craniofacial morphometric variation has been shown to be effective in reconstruction of hominoid phylogenies (Lockwood et al. 2004, Pugh 2022, Mongle et al. 2023). As such, the derived morphology of *Sahelanthropus* when compared within the framework of great apes and early hominins, supports previous suggestions (e.g., Wood & Harrison 2011) that this species was not a direct ancestor to hominins but represents an early, uniquely derived, side branch in our lineage. This hypothesis, however, cannot be properly tested until other early hominins genera, like *Orrorin* and *Ardipithecus*, can be compared directly with *Sahelanthropus*, as they represent the best reference frame for the morphological diversity of early hominins.

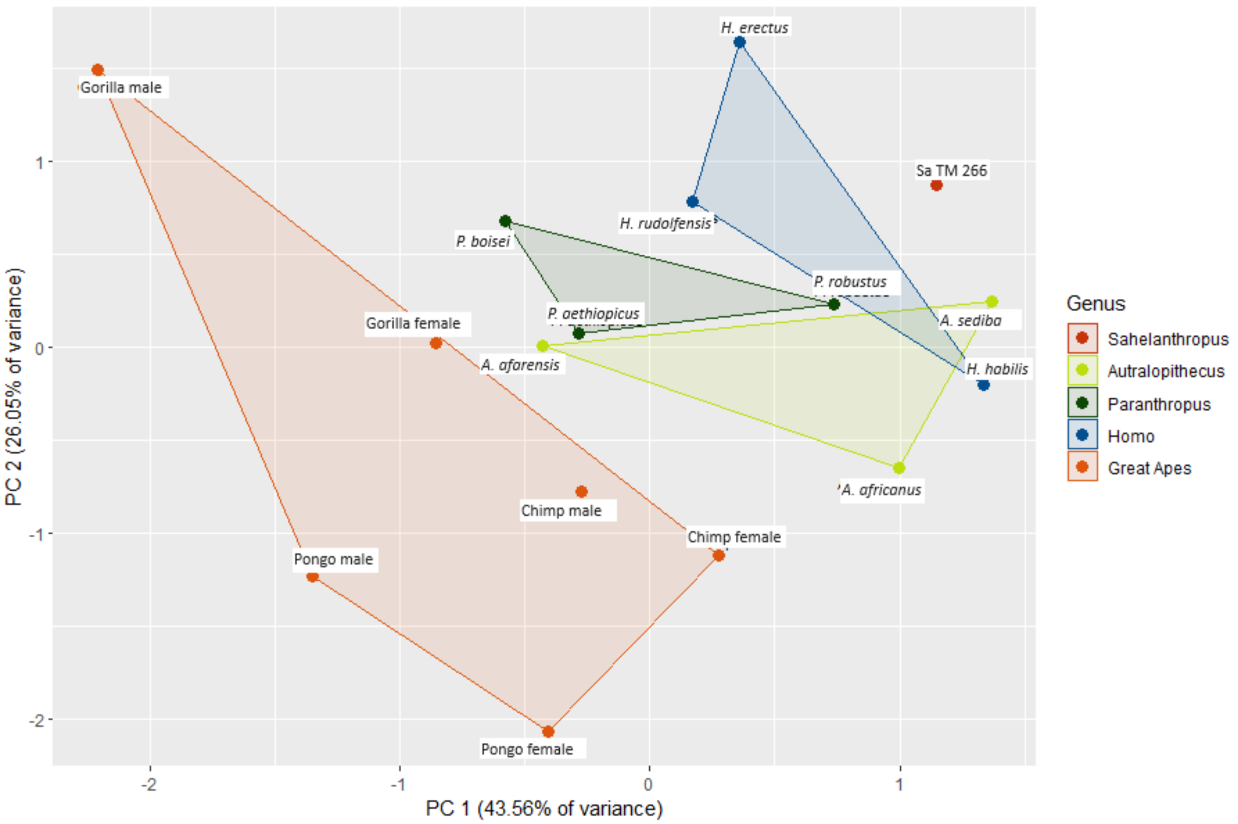

Figure 2. Morphological affinities of *Sahelanthropus tchadensis* (TM 266-01-060-1) in relation to early hominins and great apes according to the first two Principal Components extracted from the size-corrected data.

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REFERENCES

ALMÉCIJA S, HAMMOND AS, THOMPSON NE, PUGH KD, MOYÀ-SOLÀ S & ALBA DM. 2021. Fossil apes and human evolution. Science 372: eabb4363.

ANDREWS P & HARRISON T. 2005. The Last Common Ancestor of Apes and Humans. In: Interpreting the Past, Brill, p. 103-121.

BERGER LR, DE RUITER DJ, CHURCHILL SE, SCHMID P, CARLSON KJ, DIRKS PHGM & KIBII JM. 2010. Australopithecus sediba: a new species of Homo-like australopith from South Africa. Science 328: 195-204.

BÖHME M, SPASSOV N, FUSS J, TRÖSCHER A, DEANE AS, PRIETO J, KIRSCHER U, LECHNER T & BEGUN DR. 2019. A new Miocene ape and locomotion in the ancestor of great apes and humans. Nature 575: 489-493.

BRUNET M ET AL. 2002. A new hominid from the Upper Miocene of Chad, Central Africa. Nature 418: 145-151.

DARROCH JN & MOSIMANN JE. 1985. Canonical and Principal Components of Shape. Biometrika 72: 241-252.

DAVER G, GUY F, MACKAYE HT, LIKIUS A, BOISSERIE J-R, MOUSSA A, PALLAS L, VIGNAUD P & CLARISSE ND. 2022. Postcranial evidence of late Miocene hominin bipedalism in Chad. Nature 609: 94-100.

GIBBS S, COLLARD M & WOOD B. 2000. Soft-tissue characters in higher primate phylogenetics. Proc Natl Acad Sci 97: 11130-11132.

GUY F, LIEBERMAN DE, PILBEAM D, DE LEÓN MP, LIKIUS A, MACKAYE HT, VIGNAUD P, ZOLLIKOFER C & BRUNET M. 2005. Morphological affinities of the Sahelanthropus tchadensis (Late Miocene hominid from Chad) cranium. Proc Natl Acad Sci 102: 18836-18841.

HUBBE M, HARVATI K & NEVES W. 2011. Paleoamerican morphology in the context of European and East Asian late Pleistocene variation: Implications for human dispersion into the new world. Am J Phys Anthropol 144: 442-453.

KAIFU Y, AZIZ F, INDRIATI E, JACOB T, KURNIAWAN I & BABA H. 2008. Cranial morphology of Javanese Homo erectus: new evidence for continuous evolution, specialization, and terminal extinction. J Hum Evol 55: 551-580.

KIMBEL WH, RAK Y & JOHANSON DC. 2004. The Skull of Australopithecus Afarensis, Oxford University Press, 860 p.

KÖHLER M & MOYÀ-SOLÀ S. 1997. Ape-like or hominid-like? The positional behavior of Oreopithecus bambolii reconsidered. Proc Natl Acad Sci 94: 11747-11750.

LAIRD MF ET AL. 2017. The skull of Homo naledi. J Hum Evol 104: 100-123.

LEBATARD AE ET AL. 2008. Cosmogenic nuclide dating of Sahelanthropus tchadensis and Australopithecus bahrelghazali: Mio-Pliocene hominids from Chad. Proc Natl Acad Sci 105: 3226-3231.

LIEBERMAN DE. 2022. Standing up for the earliest bipedal hominins. Nature 609: 33-35.

LOCKWOOD CA, KIMBEL WH & LYNCH JM. 2004. Morphometrics and hominoid phylogeny: Support for a chimpanzee-human clade and differentiation among great ape subspecies. Proc Natl Acad Sci 101: 4356-4360.

MACCHIARELLI R, BERGERET-MEDINA A, MARCHI D & WOOD B. 2020. Nature and relationships of Sahelanthropus tchadensis. J Hum Evol 149: 102898.

MEYER MR, JUNG JP, SPEAR JK, ARAIZA IFX, GALWAY-WITHAM J & WILLIAMS SA. 2023. Knuckle-walking in Sahelanthropus? Locomotor inferences from the ulnae of fossil hominins and other hominoids. J Hum Evol 179: 103355.

MONGLE CS, STRAIT DS & GRINE FE. 2023. An updated analysis of hominin phylogeny with an emphasis on re-evaluating the phylogenetic relationships of Australopithecus sediba. J Hum Evol 175: 103311.

NEAUX D, BIENVENU T, GUY F, DAVER G, SANSALONE G, LEDOGAR JA, RAE TC, WROE S & BRUNET M. 2017. Relationship between foramen magnum position and locomotion in extant and extinct hominoids. J Hum Evol 113: 1-9.

PUGH KD. 2022. Phylogenetic analysis of Middle-Late Miocene apes. J Hum Evol 165: 103140.

R CORE TEAM. 2023. R: A Language and Environment for Statistical Computing, Vienna, Austria: R Foundation for Statistical Computing.

RICHMOND BG & JUNGERS WL. 2008. Orrorin tugenensis Femoral Morphology and the Evolution of Hominin Bipedalism. Science 319: 1662-1665.

RUSSO GA & KIRK EC. 2017. Another look at the foramen magnum in bipedal mammals. J Hum Evol 105: 24-40.

RUSSO GA & SHAPIRO LJ. 2013. Reevaluation of the lumbosacral region of Oreopithecus bambolii. J Hum Evol 65: 253-265.

STRAIT DS & GRINE FE. 2004. Inferring hominoid and early hominid phylogeny using craniodental characters: the role of fossil taxa. J Hum Evol 47: 399-452.

VENABLES WN & RIPLEY BD. 2002. Modern Applied Statistics with S, New York, NY: Springer.

WHITE TD, ASFAW B, BEYENE Y, HAILE-SELASSIE Y, LOVEJOY CO, SUWA G & WOLDEGABRIEL G. 2009. Ardipithecus ramidus and the Paleobiology of Early Hominids. Science 326: 64-86.

WICKHAM H. 2016. ggplot2: Elegant Graphics for Data Analysis, Springer-Verlag New York.

WILLIAMS SA, PRANG TC, MEYER MR, RUSSO GA & SHAPIRO LJ. 2020. Reevaluating bipedalism in Danuvius. Nature 586: E1-E3.

WOLPOFF MH, SENUT B, PICKFORD M & HAWKS J. 2002. Sahelanthropus or "Sahelpithecus"? Nature 419: 581-582.

WOOD B. 1991. Koobi Fora Research Project. Volume 4, Hominid cranial remains, Oxford (England): Clarendon Press, 1 p.

WOOD B & HARRISON T. 2011. The evolutionary context of the first hominins. Nature 470: 347-352.

ZOLLIKOFER CPE, PONCE DE LEÓN MS, LIEBERMAN DE, GUY F, PILBEAM D, LIKIUS A, MACKAYE HT, VIGNAUD P & BRUNET M. 2005. Virtual cranial reconstruction of Sahelanthropus tchadensis. Nature 434: 755-759.

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