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# Dental metrics of *Sahelanthropus tchadensis*: A comparative analysis with apes and Plio-Pleistocene hominins

Since discovery and description of the species, *Sahelanthropus tchadensis* has been at the centre of a great discussion around its classification as a hominin – the first of our lineage – or an ape. Many studies have been conducted in order to clarify this question, especially studies based on the morphology of the cranium and the post-cranial remains. In this study, we analysed the posterior dentition of *S. tchadensis* in relation to those of other hominins and chimpanzees, using a multivariate comparative metric analysis. Our results suggest that the posterior dentition of the Chad material lies in the range of well-established early Plio-Pleistocene hominins, supporting its classification as part of the hominin lineage.

**Significance:**

- The subject investigated in this study is important to the understanding of the first steps of human evolution.
- Much has been discussed about this Chadian species. Some believe it is the first hominin, others believe it is an ape.
- This study shows that the posterior dentition of *S. tchadensis* does not preclude it from being a hominin.

## Introduction

Research carried out by the *Mission Paleoanthropologique Franco-Tchadienne* in the Toros Menalla region in Chad, has contributed significantly to the understanding of the evolution of hominins.<sup>1</sup> The main discoveries have occurred in stratigraphic levels dated to the Upper Miocene (7–6 Ma). This chronology was initially based on biostratigraphic correlations with well-dated sites of East Africa<sup>2</sup>, and was recently confirmed using the cosmogenic nuclide method<sup>3</sup> and the authigenic beryllium method<sup>4</sup>.

The most important contribution of Brunet and associates<sup>2</sup> was the finding of hominin fossils ascribed to a new species, *Sahelanthropus tchadensis*, considered by them to be the first representative of our evolutionary lineage. The fossils, including an almost complete cranium (TM 266-01-060), were discovered in 2001 and nicknamed Toumai. A mandible and isolated teeth assigned to the same species were found in the same locality. More recently, Brunet and collaborators<sup>5</sup> described new material found in the same area, which was also ascribed to *S. tchadensis*.

Since the discovery and description of the cranium, its hominin status has been strongly questioned<sup>6</sup>, mainly because the specimen was significantly distorted by taphonomic processes. Among other things, this distortion impeded a clear observation of the position of the foramen magnum, whose anterior orientation is a diagnostic trait for the hominin clade.<sup>7</sup> However, a virtual reconstruction of the cranium<sup>8</sup> confirmed the anterior position of the foramen magnum, and most palaeoanthropologists now accept that *S. tchadensis* was a biped, reinforcing the original suggestion<sup>2</sup>.

Other traits also support the idea that *S. tchadensis* was a hominin, such as a face with an anteroposteriorly short premaxilla, a short basioccipital, a sub-horizontal nuchal plane, a downward lipping of the nuchal crest, a short canine crown, a non-honing C/P<sub>3</sub> complex, and, consequently, an absence of a diastema.<sup>5</sup> However, the derived characters observed in this species are associated with apes, like the size and number of the teeth roots<sup>5</sup>, and a small neurocranium, thus it shows a unique combination of traits.

As to the post-cranial skeleton, little was known until recently. Machiarelli and associates<sup>9</sup> analysed a partial femur (TM 266-01-063), recovered in 2001 at the same location and stratigraphic level as the holotype of *S. tchadensis*, and concluded that it belongs to an individual that was not habitually bipedal, questioning its hominin status. However, Daver and co-authors<sup>10</sup> challenged this interpretation. They analysed the same femur, as well as two ulnae associated with *S. tchadensis*. According to the authors, the morphology of the femur is most parsimonious with habitual bipedality, while the ulnae preserve evidence of arboreal behaviour. Their final conclusion was: “Taken together, these findings suggest that hominins were already bipeds at around 7 Ma.”<sup>10(p.94)</sup> Also, recently, Sevim-Erol et al.<sup>11</sup>, relying on a cladistic analysis of the late Miocene hominids, proposed that *S. tchadensis* is a stem hominid.

As mentioned before, not much has been said about the dentition of *S. tchadensis*, although few complete dental pieces belonging to the species have been found so far. In this study, we undertook a comparative metric analysis of the dentition of the species with those of living apes and Plio-Pleistocene hominins. Our analysis was restricted to the upper posterior dentition because of the limited preservation in the analysed species. Our main goal was to explore the position of *Sahelanthropus*’ dentition in relation to apes and other hominins, considering its metric characteristics under a multivariate perspective. As far as we are aware, this is the first time that this kind of exploratory approach has been carried out toward the discussion on *S. tchadensis*.

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**Table 1:** Species and specimens of hominins included in this study

Species	N	Specimens	References
<i>Pan troglodytes</i> male (M) and female (F)	278	–	12
<i>Sahelanthropus tchadensis</i>	2	TM 266-01-060-1; TM 266-02-154-1	2,5
<i>Orrorin tugenensis</i>	4	BAR 400'01; BAR 380'01'; BAR 210'01; BAR 1900	13
<i>Ardipithecus ramidus</i>	1	ARA-VP- 6/1	14
<i>Australopithecus afarensis</i>	9	A.L. 199-1; A.L. 200-1a; A.L. 333-1; A.L. 333-2; A.L. 417-1d; A.L. 444-2; A.L. 486-1; A.L. 651-1; A.L. 770-1a	15
<i>Australopithecus africanus</i>	13	MLD 6; STS 1; STS 12; STS 17; STS 28; STS 37; STS 52a; STS 53; STS 56; STS 61; STS 8; TM 1511; TM 1512	16
<i>Paranthropus boisei</i>	5	KNM-CH 1; KNM-ER 1804; KNM-WT 17400; OH 30; OH 5	16
<i>Paranthropus robustus</i>	12	DNH 7; SK 13; SK 46; SK 47; SK 48; SK 49; SK 52; SK 65; SK 83; SK 831a; SKX 162; TM 1517	16,17
<i>Homo habilis</i>	7	KNM-ER 1805B; KNM-ER 1813A; OH 13; OH 16; OH 24; OH 39	15
<i>Homo erectus</i>	14	D211; D2600; D2735; KNM-ER 3733; KNM-WT 15000; Sale; Sangiran 15a; Sangiran 17; Sangiran 4; ZHK XIII; ZHLII(XI); ZKD L1-PA98; ZKD L2-PA99; ZKD O1-PA313	16,18

**Table 2:** Average hominin values for each of the dental metrics used in the analyses

Variable	<i>P. troglodytes</i> male	<i>P. troglodytes</i> female	<i>S. tchadensis</i>	<i>O. tugenensis</i>	<i>A. ramidus</i>	<i>A. afarensis</i>	<i>A. africanus</i>	<i>P. boisei</i>	<i>P. robustus</i>	<i>H. habilis</i>	<i>H. erectus</i>
MD P4	7.4	7.2	8	6.8	8.4	8.9	9.7	11.6	10.5	9.1	7.8
BL P4					11.3	12.4	12.9	16.2	15.4	11.7	11.4
MD M1	11	10.7	11.25	11		12	12.6	14.6	13.2	12.4	11.7
BL M1	11.6	11.3	11.9	12.6		13.6	13.4	16	15	13.1	12.6
MD M2	10.4	10.1	12.75	11	11.8	13.2	14.1	15.9	13.8	12.4	12
BL M2	11.8	11.4	12.8	13.2	14.1	14.7	15.6	18.3	15.7	14.2	13.3
MD M3	9.3	9.1	12.05	10.3		13.1	13.7	15.5	14.6	12.1	10.8
BL M3	11	10.7	13.55	12.9		14.7	16	18.4	16.6	14	13.1

MD, mesiodistal length; BL, buccolingual width

Missing values were estimated using multiple linear regressions of the average mean of each variable, following Hubbe et al.<sup>19</sup> The final data matrix was submitted to a principal component analysis (PCA) conducted on the original data (size and shape), performed in R.<sup>20</sup>

## Material and methods

The comparison of *Sahelanthropus*' dentition with those of Pleistocene hominins was carried out based on the mesiodistal and buccolingual diameters of the upper posterior dentition, considering specimens with a minimum of 40% of the variables present. In the case of chimpanzees and *Orrorin tugenensis*, the data used in the analysis are expressed in mean values, as there are just a few dental pieces representing different individuals from the species.

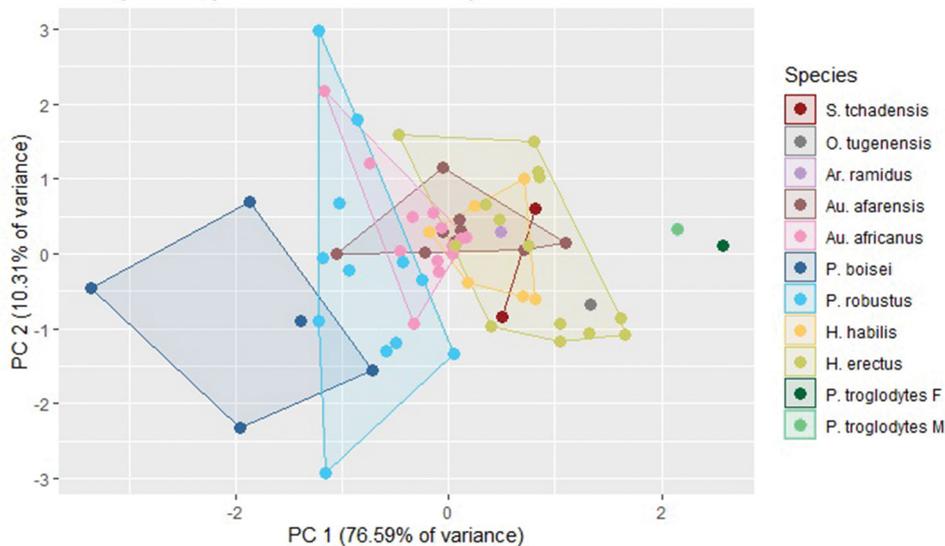
The dental metrics of *Sahelanthropus* were compared to similar measurements of the species shown in Table 1, which also contains the source of the data. Table 2 presents the means of the dental dimensions for each species included in the study. Supplementary table 1 presents the original values for each specimen included in the study.

## Results

Table 3 presents the correlations between the first two principal components (PCs) and the original variables, used to build the plot

**Table 3:** Correlations between the first two principal components and the original variables (size and shape)

Variable	PC 1	PC 2
Mesiodistal length upper P4	-0.869	-0.179
Buccolingual width upper P4	-0.883	-0.381
Mesiodistal length upper M1	-0.790	-0.192
Buccolingual width upper M1	-0.882	-0.393
Mesiodistal length upper M2	-0.870	0.190
Buccolingual width upper M2	-0.911	0.003
Mesiodistal length upper M3	-0.775	0.569
Buccolingual width upper M3	-0.936	0.199



**Figure 1:** Distribution of the species and specimens included in the study along the morphospace defined by PC1xPC2.

in Figure 1. Accordingly, the differentiation between species occurs primarily along the horizontal axis (PC1), which expresses mainly the size of the dentition, and concentrates 76.59% of the original variance. PC2 is residual in nature and does not allow for any interpretation.

The left side of the graph is occupied by hominins with large dentition (*Paranthropus boisei*, *Paranthropus robustus*, and *Australopithecus africanus*). The right side of the morphospace is occupied by *Pan troglodytes*, with small posterior dentition, while the centre of the graph is mainly occupied by hominins with teeth of moderate size (*Homo erectus*, *O. tugenensis*, *Australopithecus afarensis*, *Homo habilis*, and *Ardipithecus ramidus*).

The two specimens of *S. tchadensis* are integrated within the range of hominin variation, with special proximity to *Ar. ramidus*, in the transition between the left and the right clusters, with moderate dental size. In summary, *S. tchadensis* presents a moderate upper posterior dentition, confirming what was inferred originally<sup>2</sup>, based on univariate analysis. There is no remarkable association between *S. tchadensis* and *P. troglodytes*.

## Discussion and final remarks

As we emphasised in the introduction, the taxonomic position of *S. tchadensis* has been discussed since its discovery, and most of these discussions have relied on the cranial characteristics of the holotype.<sup>2,5,6</sup> In terms of dental metrics, not much has been explored thus far.

This study contributes to the understanding of this aspect of the species. For the first time, the morphology of the posterior upper dentition of *S. tchadensis* as a whole was compared using multivariate analysis with an ape and early hominins. Our results indicate that the dentition of the species fits the range of dental variation of our remote ancestors, reinforcing its hominin status.

In general, it can be said that the cheek teeth of *S. tchadensis* are moderate to small, within the range of *Ar. ramidus* and *Au. afarensis*.<sup>2</sup> For the same reason, the size of the dentition of *S. tchadensis* also aligns with those of *H. habilis* and *H. erectus* in the morphospace, species known to display small cheek teeth.

In a nutshell, the moderate to small size of the upper posterior dentition of *S. tchadensis* reinforces its proposed hominin status.<sup>2,5,8,10</sup> Even though the species retain some primitive traits, the derived characteristics described in the cranium and post-cranium, cited in the introduction of this study, corroborate the initial suggestion of *S. tchadensis* as the first representative of our evolutionary lineage.<sup>2</sup>

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## Data availability

All the data supporting the results of this study are included in the article itself.

## Declaration of AI use

No AI was used in this study.

## Authors' contributions

W.N.: Conceptualisation; data analysis; validation; writing – the initial draft; writing – revisions; student supervision; project leadership; project management; funding acquisition. L.V.: Data collection; data analysis; data curation; writing – the initial draft; writing – revisions. C.M.: Data collection; writing – the initial draft. All authors read and approved the final version.

## Competing interests

We have no competing interests to declare.

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