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A comparison of hominin teeth from Lincoln Cave, Sterkfontein L/63, and the Dinaledi Chamber, South Africa

Prior to the recovery of *Homo naledi* from the Dinaledi Chamber of the Rising Star Cave system, the Middle Pleistocene fossil record in Africa was particularly sparse. With the large sample size now available from Dinaledi, the opportunity exists to reassess taxonomically ambiguous teeth unearthed at the nearby site of Sterkfontein. Teeth recovered from Lincoln Cave South and area L/63 at Sterkfontein have been considered 'most probably *Homo ergaster*' and 'perhaps Archaic *Homo sapiens*', respectively. Given the similarities shared between Lincoln Cave, area L/63, and the Dinaledi Chamber with regard to climatic/geologic depositional context and age, two teeth from the former sites, StW 592 and StW 585 respectively, were compared with corresponding tooth types of *H. naledi* from the Dinaledi Chamber. The results of our study indicate that the Lincoln Cave and area L/63 teeth are morphologically inconsistent with the variation recognised in the *H. naledi* teeth.

Significance:

- The similar age and climatic/geologic depositional and post-depositional circumstances at Lincoln Cave South, area L/63 at Sterkfontein and the Dinaledi Chamber, Rising Star raise the possibility that these fossils might represent the same species.
- The teeth StW 592 and StW 585 are not consistent with the variation evident in the known *H. naledi* sample.
- The results of the study do not add to the question of the existence of at least two species of the genus *Homo* living in close proximity to each other in South Africa at approximately the same time.

Introduction

Lincoln Cave is located in the Lincoln-Fault Cave system adjacent to the Sterkfontein Cave system.[1] The deposit is divided in two by an old ramp made by limestone miners.[2] One section, dubbed Lincoln Cave North, consists of calcified deposits while Lincoln Cave South is uncalcified. The cave dates to between 252 600±35 600 and 115 300±7700 years ago based on uranium series dating of flowstones.[3] This range of dates has taken on new significance because of the discovery of *Homo naledi* within the nearby Rising Star Cave system, only 2 km from Sterkfontein, dated to between 335 000 and 236 000 years ago.[4,5] If these teeth could be attributed to *H. naledi*, they would show this species in a second cave context.

Excavations at Lincoln Cave began in 1997 and yielded fauna, artefacts and hominin remains.[2] Three hominin teeth have been recovered from Lincoln Cave South: StW 591 is an unerupted permanent left upper first incisor, StW 592 consists of an unerupted left maxillary first molar, and StW 593 is a lower right first incisor.[1] Reynolds et al.[3] suggested that these specimens represent *H. ergaster*. These researchers argued that the fauna and hominin dental material in Lincoln Cave may have resulted in part from the erosion of older Member 5 sediments and redeposition of some of this older fossil material 'into younger infills together with younger artifacts and fauna'[3]. If true, the teeth may be more than 1.5 million years old.

L/63 is an area of the Sterkfontein Cave system that consists of intrusive sediments that separate Member 5 East and West.[2] While Reynolds et al.[3] state that it lacks datable materials, the deposit differs from the surrounding Acheulean breccias and includes fauna suggesting that it includes younger material. That paper noted similarities in stratigraphy, fauna, and artefacts in L/63 and Lincoln Cave South, and proposed that the two deposits 'derived from the same catchment area'[1-3]. StW 585, a right maxillary canine, was recovered from L/63. This tooth is attributed to 'Archaic *Homo sapiens*' based on the short length of the root.[3(p.267)]

The Dinaledi Chamber in the Rising Star Cave system lies approximately 2 km from Sterkfontein and, at 335–236 Ka,[4,5] partially overlaps in time with the Lincoln Cave and L/63 deposits. *Homo naledi* was recovered in uncalcified deposits. The presence of uncalcified deposits in Lincoln Cave South and L/63 may indicate that younger material in these infills may share some aspects of geological history with the Rising Star deposits. Given the possibility that these deposits could potentially be contemporaneous, we carefully assessed whether the dental remains from Lincoln Cave and L/63 represent *H. naledi*. The present research details the similarities and differences between StW 585, StW 592, and specimens attributed to *H. naledi.*

Materials and methods

StW 585 was directly compared with the *H. naledi* maxillary permanent canines from the Dinaledi Chamber at the University of the Witwatersrand. StW 592 was compared with *H. naledi* maxillary first molars based on the description, image and measurements presented in Reynolds et al.[3] StW 591 and StW 593 were not available for study.

Results

StW 585 and the *H. naledi* maxillary permanent canines from the Dinaledi Chamber differ in significant ways. Lingually, StW 585 has a large tuberculum dentale (ASU grade 3) while *H. naledi* does not (Figure 1). The median lingual ridge of StW 585 divides the crown into small mesial and large distal fossae; the pattern is reversed in the *H. naledi* canines. While the distal crest of StW 585 is convex, it is less convex than that of *H. naledi*. StW 585 is

more mesiodistally curved, i.e. the mesial and distal crown edge curve inward toward the midline of the tooth, more than *H. naledi* specimens such as U.W. 101-337 (Figure 2). The crown of StW 585 is short and robust relative to its overall size while *H. naledi* canines appear tall (Figure 2, Figure 3).



Figure 1: Lingual view of StW 585 from L/63 area of Lincoln Cave (centre) and *Homo naledi* maxillary permanent canines from the Dinaledi Chamber. Left to right: U.W. 101-337 RC, U.W. 101-908 RC, StW 585 RC, U.W. 101-501 LC, U.W. 101-412 LC. Arrow shows large tuberculum dentale of StW 585.



Figure 2: Labial view of StW 585 from L/63 area of Lincoln Cave (centre) and *Homo naledi* maxillary permanent canines from the Dinaledi Chamber. Left to right: U.W. 101-337 RC, U.W. 101-908 RC, StW 585 RC, U.W. 101-501 LC, U.W. 101-412 LC.



Figure 3: Mesial view of StW 585 from L/63 area of Lincoln Cave (centre) and *Homo naledi* maxillary permanent canines from the Dinaledi Chamber. Left to right: U.W. 101-337 RC, U.W. 101-908 RC, StW 585 RC, U.W. 101-501 LC, U.W. 101-412 LC.

The StW 585 and *H. naledi* canines do share several traits, including, lingually, a mesial crest that is shorter than the distal crest, and a mesial shoulder that is more apically placed than the distal shoulder (Figure 1). The labial face is minimally curved incisocervically in both StW 585 and *H. naledi* (Figure 3). All have a mesial crest that is more concave than the distal counterpart. Also, the mesial and distal labial grooves are weakly expressed in all canines. A deep groove runs along the mesial length of the root, with a shallow groove along the distal length. StW 585 falls within the absolute size range of variation for *H. naledi* (Table 1). While root length is not a conclusive feature for determining species, StW 585 overlaps in size with the *H. naledi* sample.

Table 1: Measurements (in mm) of maxillary canines used in this study

C^1 Specimens	Mesiodistal	Labiolingual
StW 585	8.5	9.5
U.W. 101-337	7.8	8.3
U.W. 101-347	8.0	9.6
U.W. 101-412	8.7	8.4
U.W. 101-501	7.8	8.4
U.W.101-504B	7.3	
U.W. 101-706	8.5	8.2
U.W. 101-816	8.7	8.0
U.W. 101-908	8.9	8.7
U.W. 101-1277	7.9	8.2
U.W. 101-1548	7.3	
U.W. 101-1566		9.8

Homo naledi maxillary first molars (i.e. U.W. 101-1305 and U.W. 101-1688) were compared with StW 592 from Lincoln Cave South using data from Reynolds et al.[3] StW 592 has a prominent C5, while *H. naledi* maxillary first molars lack a C5 or other accessory cusps (Figure 4). The crista obliqua is continuous between the protocone and metacone in *H. naledi*, unlike StW 592. The StW 592 crown is larger than all *H. naledi* upper first molars (Table 2). Finally, StW 592 exhibits a more 'bulbous' morphology relative to *H. naledi* U.W. 101-1305 or U.W. 101-1688. These differences suggest that StW 592 is not *H. naledi*.

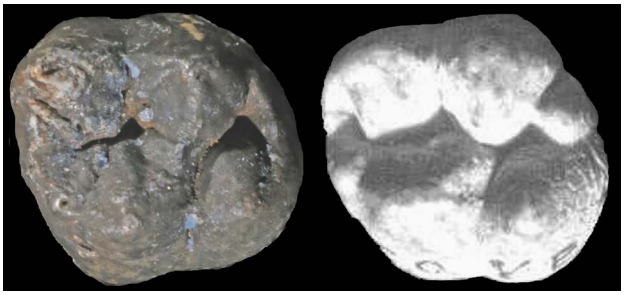


Figure 4: Occlusal view of *Homo naledi* U.W. 101-1305 (left) and StW 592 from Reynolds et al.[3]

Despite these differences, StW 592 and *H. naledi* first molars share a similar size gradient of the principal cusps: protocone > hypocone > metacone = paracone. In addition, occlusal outlines of the StW 592 and *H. naledi* molars are rhomboidal with a distolingual projection of the hypocone.

Table 2: Measurements (in mm) of maxillary first molars used in this study

M^1 Specimens	Mesiodistal	Buccolingual
StW 592	12.3	12.9
U.W. 101-020	11.4	11.6
U.W. 101-445	12.1	11.5
U.W. 101-525	11.5	11.6
U.W. 101-583	11.7	11.8
U.W. 101-708	11.6	11.6
U.W. 101-999	12.1	11.8
U.W. 101-1277	10.5	11.2
U.W. 101-1305	12.3	11.8
U.W. 101-1396		12.4
U.W. 101-1463	11	11.6
U.W. 101-1676	11.7	12.2
U.W. 101-1688	12.4	12

Discussion

Prior to the discovery of *H. naledi*, hominin material from the Middle Pleistocene of southern Africa was universally assumed to represent archaic humans.[6] However, the fragmentary state and poor geological context of the record between 780 Ka and 130 Ka in southern Africa means we must re-evaluate this assumption for all material. In our assessment, the teeth from Lincoln Cave South and L/63 do not fit the morphological pattern of known samples of *H. naledi.* The range of dates from the Dinaledi Chamber, between 335 Ka and 236 Ka, overlaps with the range of dates of flowstone from Lincoln Cave, between roughly 253 Ka and 115 Ka. However, the flowstones may not date the fossil-bearing deposits. We note the conclusion of Reynolds et al.[3] that the Lincoln Cave South and L/63 teeth may have been redeposited from much older Member 5 deposits, which prevents us from concluding that these teeth demonstrate a second, contemporaneous lineage in close proximity to *H. naledi*. With such redeposition and uncertainty of context, it is possible that the teeth do in fact represent a much earlier population of *Homo*. With that said, it is important to keep in mind that this research only examined one tooth from Lincoln Cave and one from area L/63. The recovery and availability of more fossils from Sterkfontein or other sites from this time frame with strong geological context may aid in understanding the normal variation of each tooth type and help resolve the nature of the evolutionary relationship between them and *H. naledi*.

Conclusions

The large sample of *H. naledi* teeth from the Dinaledi Chamber allows us to take a closer look at taxonomically ambiguous fossils from Sterkfontein to determine their similarities or differences. The Lincoln Cave and L/63 teeth, despite some parallels in depositional and post-depositional contexts, are inconsistent with known samples of *H. naledi*. If there is overlap in time, the results would suggest that more than one species of *Homo* was present in the Late Middle Pleistocene of South Africa. If not, the Lincoln Cave and L/63 teeth may represent an earlier species of *Homo*. Unfortunately, given the uncertainty of the dates, at present the Lincoln Cave and L/63 teeth offer little support for either scenario.

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Authors' contributions

J.K.B.: Conceptualisation, methodology, data collection, writing – the initial draft. J.I.: Conceptualisation, methodology, data collection, writing – the initial draft. S.E.C.: Conceptualisation, writing – the initial draft. D.J.d.R.: Methodology, validation, writing – revisions. J.H.: Conceptualisation, validation. L.R.B.: Conceptualisation, validation, project leadership, funding acquisition.

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