

SITE FORMATION PROCESSES AT RISING
STAR: TAPHONOMY AND 3D SPATIAL
ANALYSES OF THE *HOMO NALEDI*
ASSEMBLAGE

by

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DECLARATION

I declare that this Thesis is my own, unaided work. It is being submitted for the Degree of Doctor of Philosophy at the University of the Witwatersrand, Johannesburg. It has not been submitted before for any degree or examination at any other University.

A handwritten signature in black ink, appearing to be 'Jablon', is written above a horizontal line.

On this 30th day in May 2017 in Johannesburg

ABSTRACT

The recently discovered site of Rising Star in the Cradle of Humankind, Johannesburg, South Africa, has yielded the single largest fossil hominin assemblage on the African continent to have been uncovered to date. Much of the anatomy of the new species, *Homo naledi*, has been described. With a relatively human-like lower limb and strangely primitive-like upper body, *Homo naledi* displays a mosaic of traits in its morphology. A small cranium for a member of the genus *Homo* adds to this unexpected mix of characters. The homogeneity of the collection is notable, particularly with regards to the morphology of the dentition, as almost every aspect of it, including the distinctive form of the lower premolars, the distal accessory cuspule of the mandibular canines, and the expression of nonmetric features that normally vary in human populations, is uniform in every specimen within the Dinaledi assemblage. The assemblage is remarkably homogenous, and almost completely monospecific.

The chamber in which *Homo naledi* was discovered, the Dinaledi Chamber, preserves bone material within clay-rich sediments derived from *in situ* weathering, and exogenous clay and silt, which entered the chamber through fractures that prevented passage of coarser-grained material. This non-brecciated deposit is distinctive from almost all other fossil hominin sites in the Cradle of Humankind. The chamber has always been in the dark zone, and taphonomic analysis of the almost 1550 specimens recovered has shown that the Dinaledi Chamber was not accessible to non-hominins.

In order to further understand the context of the Dinaledi assemblage, and to map and analyse the excavations, a high-resolution three-dimensional (3D) multimodal set of recording strategies was developed and employed for use at the site. Recording of fossils and the excavation process were achieved through the use of white-light photogrammetry, and mapping of the Dinaledi Chamber was

accomplished by means of high-resolution laser scanning, with scans running from the excavation site to both the ground surface and the cave entrance. The integration of conventional surveying techniques as well as photogrammetry with the use of an unmanned aerial vehicle provided further spatial constraints to the landscape above the cave system.

This high-resolution data was then used to provide an accurate 3D spatial reconstruction of two semi-articulated elements recovered from the assemblage, the right Hand 1 (H1) and Foot 1 (F1). The spatial position and displacement of individual bones, and the relative location of both H1 and F1 in the context of the main excavation pit were examined. The spatial disposition of H1 and F1 in relation to surrounding commingled elements creates a testable case study with regards to current models of localised decomposition, disarticulation and dispersal within the Dinaledi Chamber, and does not necessarily imply rapid incorporation into encapsulating sediments, but may instead be a reflection of the natural decomposition of whole body units in a small enclosed space.

High-resolution data of the *in situ* material of the Dinaledi Chamber collected during excavations provided further means for spatial analyses of the commingled assemblage. The analysis of the spatial locations of 792 hominin bone specimens was undertaken. Of these, 283 were recovered from the sediment surface across the chamber floor, while 509 specimens were recovered from within undisturbed floor sediments of the main excavation pit. Three main clusters of surface material were identified which show a concentration of fossils within the central region of the chamber, and a clear dropoff in fossil density in both adjacent passages and up-slope towards the chamber entrance. In the excavated deposits, clusters by body parts were identified which are best attributed to the decomposition and disarticulation of the anatomical regions of multiple individuals in a confined space, with limited winnowing of bones by size or element.

Geological and taphonomic investigations, coupled with the analyses of decomposition and spatial distribution of both surface and subsurface material of the Dinaledi Chamber, precludes site formation attributed to water transport, predator accumulation and mass fatality, and further suggests that post-mortem movement of bones within their encapsulating sediment is the product of downslope movement of floor sediment load within the chamber. The unique challenges presented by the Rising Star cave environment necessitated the design of a novel approach to understanding site formation processes in the Dinaledi Chamber, the results of which can also be applied to new palaeoanthropological cave sites in the Cradle of Humankind as well as other karstic fossil deposits.

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TABLE OF CONTENTS

CHAPTER ONE: INTRODUCTION

Overview of this Thesis.....	1
Background.....	3
Morphology and Dating of <i>Homo naledi</i>	4
Taphonomy of the Dinaledi Assemblage.....	6
Geological Context of Dinaledi Chamber.....	7
Three-Dimensional Data Applied to Palaeontology and Archaeology.....	11
The Role of Spatial Analysis and GIS in Archaeology.....	14
Integration of Geological, Compositional and Spatial Analyses.....	20
Conclusion.....	21

CHAPTER TWO: *HOMO NALEDI*, A NEW SPECIES OF THE GENUS *HOMO* FROM THE DINALEDI CHAMBER, SOUTH AFRICA

Abstract.....	24
Introduction.....	24
Etymology.....	25
Locality.....	25
Horizon and associations.....	25
Holotype, paratypes, and referred materials.....	27
Differential diagnosis.....	29

Cranium, mandible, and dentition (DH1, DH2, DH3, DH4, DH5, U.W. 101-377).....	29
Hand (H1).....	38
Femur (U.W. 101-1391).....	39
Tibia (U.W. 101-484).....	39
Foot (F1).....	39
Description	39
Discussion	45
Materials and methods	47
Comparative hominin specimens examined in this study.....	47
Scanning and virtual reconstruction methods.....	49
Virtual reconstruction of composite crania and estimation of cranial capacity.....	50
Virtual reconstruction of cranial capacity.....	51
Body mass estimation methods.....	52
Stature estimation methods.....	53
Nomenclatural acts.....	54
Acknowledgements	54
Additional information	54
Additional files	55
References	55

CHAPTER THREE: GEOLOGICAL AND TAPHONOMIC CONTEXT FOR THE NEW HOMININ SPECIES *HOMO NALEDI* FROM THE DINALEDI CHAMBER, SOUTH AFRICA

Abstract	59
Introduction	60
The Rising Star cave system.....	62
Results	62
Sedimentology.....	62
Facies 1: horizontally laminated orange-brown mudstone with sandstone lenses.....	64
Facies 2: unconsolidated to consolidated, orange-brown mud clast breccia in a mud matrix.....	65
Flowstones in the Dinaledi Chamber.....	65
Flowstone 1.....	65
Flowstone 2.....	67
Flowstone 3.....	67
Stratigraphic units in the Dinaledi Chamber.....	67
Unit 1.....	67
Unit 2.....	69
Unit 3.....	70
Mineralogy and chemistry.....	71
Taphonomy.....	72
Bone material and its spatial distribution.....	72
Skeletal part representation.....	77

Bone quality and preservation.....	80
Weathering patterns.....	80
Fractures.....	81
Transportation.....	81
Mineral staining.....	81
Surface modifications and vertebrate–bone interactions...	82
Surface modifications and invertebrate–bone interactions.....	82
Discussion.....	83
Sedimentation processes in the Dinaledi Chamber and deposition of <i>H. naledi</i>	83
Environmental constraints in the Dinaledi Chamber based on taphonomy.....	84
Depositional scenarios for the burial of <i>H. naledi</i>	84
Occupation.....	86
Water transport.....	86
Predator accumulation.....	86
Mass fatality or death trap.....	87
Deliberate disposal.....	87
Materials and methods.....	88
Discovery history of the Dinaledi Chamber and mapping of the cave system.....	88
Mineralogical and geochemical analyses of floor sediments.....	89
Excavation approach.....	89

Methodology of taphonomic analyses.....	90
Description of weathering patterns.....	91
Acknowledgements.....	91
Additional information.....	92
Additional files.....	93
References.....	93

CHAPTER FOUR: MULTIMODAL SPATIAL MAPPING AND VISUALISATION OF DINALEDI CHAMBER AND RISING STAR CAVE

Abstract.....	97
Introduction.....	97
Ring Star excavations and <i>Homo naledi</i>	98
Materials and methods.....	99
White-light source photogrammetry.....	100
High-resolution laser scanning.....	100
UAV photogrammetry.....	101
Other scanning techniques.....	101
Workflow for three-dimensional data.....	101
Results.....	102
Discussion.....	105
Strengths and limitations of each scanning method.....	105
Artec Eva white-light scanner.....	105
FARO Focus ^{3D} laser scanner.....	105

Combining different survey and recording modalities: A way forward.....	105
Acknowledgements.....	106
References.....	106

CHAPTER FIVE: POST-MORTEM DISARTICULATION PATTERNS IN *HOMO NALEDI*: TAPHONOMIC SIGNATURES OF DIFFERENTIAL DECOMPOSITION IN THE DINALEDI CHAMBER, RISING STAR CAVE

Abstract.....	110
Introduction.....	111
Physical, Geological, and Sedimentary Context of the Dinaledi Chamber.....	113
Material and Methods.....	115
Results.....	118
Hand 1.....	118
Foot 1.....	119
Discussion.....	121
References.....	128
Figures.....	135
Tables.....	145

CHAPTER SIX: SPATIAL TAPHONOMY OF THE *HOMO NALEDI* ASSEMBLAGE FROM THE DINALEDI CHAMBER, RISING STAR CAVE

Abstract.....	149
Introduction.....	150
Material and Methods.....	151
General aspects of the Dinaledi Chamber.....	151
Data Collection.....	154
Data Plotting.....	154
Cluster Analysis.....	156
RESULTS.....	156
Surface Material.....	156
Excavated Material.....	157
Discussion.....	159
Site Formation Processes.....	159
Future Excavation Strategy.....	163
References.....	164
Figures.....	169
Tables.....	180
 CHAPTER SEVEN: REFERENCES.....	 181
 CHAPTER EIGHT: LETTERS OF SUPPORT.....	 193

Letters of Support for Chapter Two: <i>Homo naledi</i>, a New Species of the Genus <i>Homo</i> from the Dinaledi Chamber, South Africa.....	193
Letters of Support for Chapter Three: Geological and Taphonomic Context for the New Hominin Species <i>Homo naledi</i> from the Dinaledi Chamber, South Africa.....	195
Letters of Support for Chapter Four: Multimodal Spatial Mapping and Visualisation of Dinaledi Chamber and Rising Star Cave.....	197
Letters of Support for Chapter Five: Post-Mortem Disarticulation Patterns in <i>Homo naledi</i>: Taphonomic Signatures of Differential Decomposition in the Dinaledi Chamber, Rising Star Cave.....	200
Letters of Support for Chapter Six: Spatial Taphonomy of the <i>Homo naledi</i> Assemblage from the Dinaledi Chamber, Rising Star Cave.....	205

CHAPTER NINE: SUPPLEMENTAL MATERIALS

Supplemental Material to Chapter Two: <i>Homo naledi</i>, a New Species of the Genus <i>Homo</i> from the Dinaledi Chamber, South Africa.....	210
--	------------

Supplementary file 1. Holotype and paratype specimens and referred materials.

Supplementary file 2. Traits of *H. naledi* and comparative species.

Supplemental Material to Chapter Three: Geological and Taphonomic Context for the New Hominin Species <i>Homo naledi</i> from the Dinaledi Chamber, South Africa.....	211
--	------------

Supplementary file 1. Electron microprobe analyses of spots in fragments of samples UW101-SO-31, UW101-SO-34, UW101-SO-39 and DB-1.

Note that in each of the tables totals below 100% reflect volatile content or porosity of sample, or both.

Supplementary file 2. Summary table listing surface modifications on all morphologically informative specimens. A total of 559 bone and dental specimens were examined for surface modifications.

Supplemental Material to Chapter Six: Spatial Taphonomy of the *Homo naledi* Assemblage from the Dinaledi Chamber, Rising Star Cave.....212

Supplementary file 1. Spatial data coordinates for surface specimens found within the Dinaledi Chamber, by body part.

Supplementary file 2. Spatial data coordinates for subsurface specimens recovered from the main excavation pit of the Dinaledi Chamber.

Supplementary file 3. Spatial data including, vector and vector group data, for subsurface specimens recovered from the main excavation pit of the Dinaledi Chamber.

LIST OF FIGURES

CHAPTER ONE: INTRODUCTION

Figure 1. Map of the Cradle of Humankind, Johannesburg, South Africa, showing known fossil localities.....9

Figure 2. Mapped passageways of the Rising Star Cave system, Cradle of Humankind, Johannesburg, South Africa.....10

CHAPTER TWO: *HOMO NALEDI*, A NEW SPECIES OF THE GENUS *HOMO* FROM THE DINALEDI CHAMBER, SOUTH AFRICA

Figure 1. Dinaledi skeletal specimens. The figure includes approximately all of the material incorporated in this diagnosis, including the holotype specimen, paratypes and referred material. These make up 737 partial or complete anatomical elements, many of which consist of several refitted specimens. Specimens not identified to element, such as non-diagnostic long bone or cranial fragments, and a subset of fragile specimens are not shown here. The ‘skeleton’ layout in the center of the photo is a composite of elements that represent multiple individuals. This view is foreshortened; the table upon which the bones are arranged is 120-cm wide for scale.....26

Figure 2. Holotype specimen of *Homo naledi*, Dinaledi Hominin 1 (DH1). U.W. 101-1473 cranium in (A) posterior and (B) frontal views (frontal view minus the frontal fragment to show calvaria interior). U.W. 101-1277 maxilla in (C) medial, (D) frontal, (E) superior, and (F) occlusal views. (G) U.W. 101-1473 cranium in anatomical alignment with occluded U.W. 101-1277 maxilla and U.W. 101-1261 mandible in left lateral view. U.W. 101-1277 mandible in (H) occlusal, (I) basal, (J) right lateral, and (K) anterior views. Scale bar = 10 cm.....27

- Figure 3.** Cranial paratypes. (A) DH2, right lateral view. (B) DH5, left lateral view. (C) DH4, right lateral view. (D) DH4, posterior view. Scale bar = 10 cm.....28
- Figure 4.** Paratype DH3. (A) Frontal view. (B) Left lateral view, with calvaria in articulation with the mandible (U.W. 101-361). (C) Basal view. Mandible in (D) medial view; (E) occlusal view; (F) basal view. DH3 was a relatively old individual at time of death, with extreme tooth wear. Scale bar = 10 cm.....28
- Figure 5.** U.W. 101-377 mandible. (A) Lateral view; (B) medial view; (C) basal view; (D) occlusal view. (D) The distinctive mandibular premolar morphology with elongated talonids in unworn state. Scale bar = 2 cm.....29
- Figure 6.** Hand 1. Palmar view on left; dorsal view on right. This hand was discovered in articulation and all bones are represented except for the pisiform. The proportions of digits are humanlike and visually apparent, as are the expanded distal apical tufts on all digits, the robust pollical ray, and the unique first metacarpal morphology.....30
- Figure 7.** U.W. 101-1391 paratype femur. (A) Medial view; (B) posterior view; (C) lateral view; (D) anterior view. The femur neck is relatively long and anteroposteriorly compressed. The anteversion of the neck is evident in medial view. Scale bar = 2 cm.....30
- Figure 8.** U.W. 101-484 paratype tibia. (A) Anterior view; (B) medial view; (C) posterior view; (D) lateral view. The tibiae are notably slender for their length. Scale bar = 10 cm.....31
- Figure 9.** Foot 1 in (A) dorsal view; and (B) medial view. (C) Proximal articular surfaces of the metatarsals of Foot 1, shown in articulation to illustrate transverse arch structure. Scale bar = 10 cm.....32
- Figure 10.** Maximum tibia length in *H. naledi* and other hominins. Maximum tibia length for U.W. 101-484, compared to other nearly complete hominin tibia specimens. *Australopithecus afarensis* represented by A.L. 288-1 and KSD-VP-1/1 (Haile-Selassie et al., 2010); *Homo erectus* represented by D3901 from Dmanisi and KNM-WT 15000; *Homo habilis* by OH 35; *Homo floresiensis* by

LB1 and LB8 (Brown et al., 2004; Morwood et al., 2005). Chimpanzee and contemporary European ancestry humans from Cleveland Museum of Natural History (Lee, 2001); Andaman Islanders from Stock (2013). Vertical lines represent sample ranges; bars represent 1 standard deviation.....41

Figure 11. Virtual reconstruction of the endocranium of the larger composite cranium from DH1 and DH2 overlaid with the ectocranial surfaces. (A) Lateral view. (B) Superior view. The resulting estimate of endocranial volume is 560cc. Scale bar = 10 cm.....42

Figure 12. Brain size and tooth size in hominins. The buccolingual breadth of the first maxillary molar is shown here in comparison to endocranial volume for many hominin species. *H. naledi* occupies a position with relatively small molar size (comparable to later *Homo*) and relatively small endocranial volume (comparable to australopiths). The range of variation within the Dinaledi sample is also fairly small, in particular in comparison to the extensive range of variation within the *H. erectus sensu lato*. Vertical lines represent the range of endocranial volume estimates known for each taxon; each vertical line meets the horizontal line representing M1 BL diameter at the mean for each taxon. Ranges are illustrated here instead of data points because the ranges of endocranial volume in several species are established by specimens that do not preserve first maxillary molars.....43

Figure 13. Selected pelvic specimens of *H. naledi*. U.W. 101-1100 ilium in (A) lateral view showing a weak iliac pillar relatively near the anterior edge of the ilium, with no cristal tubercle development; (B) anterior view, angled to demonstrate the degree of flare, which is clear in comparison to the subarcuate surface. U.W. 101-723 immature sacrum in (C) anterior view; and (D) superior view. U.W. 101-1112 ischium in (E) lateral view; and (F) anterior view, demonstrating relatively short tuberacetabular diameter. Scale bar = 2 cm.....44

Figure 14. First metacarpals of *H. naledi*. Seven first metacarpals have been recovered from the Dinaledi Chamber. U.W. 101-1321 is the right first metacarpal of the associated Hand 1 found in articulation. U.W. 101-1282 and U.W. 101-1641 are anatomically similar left and right first metacarpals, which we

hypothesize as antimeres, both were recovered from excavation. U.W. 101-007 was collected from the surface of the chamber, and exhibits the same distinctive morphological characteristics as all the first metacarpals in the assemblage. All of these show a marked robusticity of the distal half of the bone, a very narrow, ‘waisted’ appearance to the proximal shaft and proximal articular surface, prominent crests for attachment of *M. opponens pollicis* and *M. first dorsal interosseous*, and a prominent ridge running down the palmar aspect of the bone. The heads of these metacarpals are dorsopalmarly flat and strongly asymmetric, with an enlarged palmar-radial protuberance. These distinctive features are present among all the first metacarpals in the Dinaledi collection, and are absent from any other hominin sample. Their derived nature is evident in comparison to apes and other early hominins, here illustrated with a chimpanzee first metacarpal and the MH2 first metacarpal of *Australopithecus sediba*.....47

Figure 15. Posterior view of the virtual reconstruction of DH3. The resultant mirror image is displayed in blue. The antimeres were aligned by the frontal crest and sagittal suture using the Manual Registration function in GeoMagic Studio 14.0.....50

Figure 16. Virtual reconstruction of (A) DH2 and (B) occipital portion of DH1. The actual specimen displays its original coloration and the mirror imaged portion is illustrated in blue.....50

Figure 17. Postero-lateral view of the virtual reconstruction of a composite cranium from DH3 and DH4. (A) The surface scan of DH3 was mirror imaged and merged as described in Supplementary Note 8. (B) The scan of DH4 was aligned to the DH3 model. (C) DH4 was then mirror imaged to complete the occipital contour (D).....51

Figure 18. Virtual reconstruction of a composite cranium from DH1 and DH2. The surface model of DH2 (blue), consisting of the original scan merged with the mirror image, was then uploaded and aligned with the mirror imaged DH1 model (pink). Note the similarity in size and shape between DH1 and DH2 observed in the posterior (A) anterior (B) lateral (C) and superior (D) views.....51

Figure 19. Virtual reconstruction of the endocranium of the composite cranium from DH3 and DH4. (A) Lateral view. (B) Superior view. (C) Inferior view. In all views, anterior is to towards the left.....52

Figure 20. Virtual reconstruction of the endocranium of the composite cranium from DH3 and DH4 overlaid with the ectocranial surfaces. (A) Lateral view. (B) Superior view.....52

Figure 21. Virtual reconstruction the DH3/DH4 cranial base using a model of Sts 19. (A) Right lateral view. (B) Left lateral view. (C) Posterior view. (D) Inferior view.....53

Figure 22. Virtual reconstruction the DH3/DH4 endocranial volume using a cranial base model of Sts 19. Right lateral view.....53

CHAPTER THREE: GEOLOGICAL AND TAPHONOMIC CONTEXT FOR THE NEW HOMININ SPECIES *HOMO NALEDI* FROM THE DINALEDI CHAMBER, SOUTH AFRICA

Figure 1. Geological setting of Cradle of Humankind and Rising Star cave system. (A) Geology of Johannesburg Dome and surroundings, showing the Cradle of Humankind world heritage site in bold black outline. (B) surface geology of the immediate surroundings of the Rising Star cave system, showing the fault sets and variable chert content in the dolomite that controlled cave formation. The cave system is confined to a chert-poor stromatolitic dolomite horizon.....61

Figure 2. Geological map and cross-section of the Rising Star cave system. (A) Geological Map showing the distribution of chert-free dolomite and fracture systems controlling the cave. Inset shows the location of the Cradle of Humankind in southern Africa; (B) Northeast-Southwest, schematic cross section through the cave system, relative to several chert marker horizons; (C) Detailed map of the

Dinaledi Chamber showing the orientation of the floor and the position of the excavation and sampling sites.....63

Figure 3. Cartoon illustrating the geological and taphonomic context and distribution of fossils, sediments and flowstones within the Dinaledi Chamber. The distribution of the different geological units and flowstones is shown together with the inferred distribution of fossil material.....64

Figure 4. Stratigraphic units and flowstones observed in the Dinaledi Chamber. (A) Erosional remnant of horizontally laminated Unit 1 strata (Facies 1). (B) Close-up view of Unit 1 (Facies 1a) showing fine laminations and small invertebrate burrows (note fine sand infilling in burrows). (C) Overview photo of the Dinaledi Chamber, directly to the east of the entrance point into the chamber. Photo shows distribution of Flowstones 1–3 and stratigraphic Units 2 and 3. (D) Close-up view of Flowstone 1 encasing sediment of Unit 2. Note that several generations of flowstone (Flowstones 1a–e) are coating Unit 2. The thin, clear lower layer is Flowstone 1a, and the overlying white flowstone is either Flowstone 2 or 3. (E) Close-up view of Unit 2, consisting of generally poorly-cemented Facies 2 sediment. (F) View of the chamber floor near the entry point. On the cave floor, a large erosional remnant of Unit 1 (orange laminated mudstone of Facies 1a), is surrounded by mud-clast breccia of Unit 3 (main hominin bearing unit). Note that Flowstone 2 has been undercut by post-depositional erosion of Unit 3, which, in this location has resulted in a lowering of the floor by as much as 25 cm. (G) Flowstone 2 overlying Unit 3 in one of the chamber’s side passages. In this location Unit 3 has also been partly eroded after depositional from underneath the flowstone drape, leaving a hanging remnant, with some indurated sediment of Unit 3 attached to its base. Note the continued deposition of sediment above Flowstone 2.....66

Figure 5. Data and characteristics of cave floor sediments (Facies 2) from the Dinaledi and Dragon’s Back Chambers. (A) Grain size distribution of sample UW101-SO-39 (Figure 2C). The bulk of the sample material falls within a size fraction corresponding to silt and fine-grained sand. Some coarser mudstone fragments did not disintegrate when immersed in water, likely due to considerable

Mn- and Fe-oxide micro-concretionary development in the orange XRF analyses of bulk samples of three floor sediments from the Dinaledi Chamber (UW101-SO31, -34 and -39) and one from the Dragon's Back chamber (DB-1). The sample from the Dragon's Back Chamber has a radically different composition from those of the Dinaledi Chamber, with the high SiO₂ content reflecting its dominance of quartz. The Dinaledi samples have much higher Al₂O₃ and K₂O contents than DB-1, indicating a higher content of clay minerals and mica, and higher CaO, MgO, MnO, and total Fe oxide contents which reflect alterations and inclusions. The higher P₂O₅ content of the Dinaledi samples is probably located in comminuted bone fragments which are seen macroscopically. The volatiles content (LOI) of the Dinaledi samples is also higher than in DB-1, in accord with a higher total clay mineral and mica content. (C–E) Backscattered electron (BSE) wide-field images of grain mounts from floor sediments. Brighter shades indicate the presence of heavier elements, mainly Mn and Fe in altered grains. (C) DB-1, Dragon's Back Chamber, large fragments are quartz and chert, partly altered. (D) UW101-SO34. (E) UW101-SO39. In these samples the large fragments are almost exclusively clay; note their angular shape which shows these to be locally derived.....68

Figure 6. Views of the Dinaledi Chamber. Clockwise from top left: (A) Photograph taken during initial exploration of the chamber; view to the N. Ellipse 'A' indicates the area where most of the hominid material was excavated. Letter 'B' shows the location of the cranial fragment that was one of the first pieces removed from the chamber. Arrows 'C, D and E' indicate areas of concentrated surface material. Block E is ~ 50 cm across. (B) pre-excavation view of the chamber floor. 'D' and 'E' included hominid teeth, (intrusive) bird bones and several long bone fragments that had been 'arranged' on rocks by an unknown caver prior to discovery by our caving team. Top of the photograph point to the NE. Base of the photograph is 80 cm. (C) view of the primary excavation area prior to excavation looking in a NE direction. The diameter of the ellipse is 1 m for scale (D) the excavation area at the end of the first round of excavations looking in a SSE direction (November 2013). Ellipse A is the same as in previous figures. Arrow B shows the fragment of a long bone that was uncovered after the

cranial fragment had been removed. Arrows C, D and E indicate where surface concentrations had previously been. The diameter of the ellipse is 1 m for scale.....70

Figure 7. Map of the cave chamber showing the distribution of hominin fossils. (A) distribution of concentrations of bone fragments of *H. naledi* along the floor of the Dinaledi Chamber. The positions of maps (B) and (C), (D) are shown relative to survey pegs 1 and 2 respectively. (B) Concentration of long bone fragments encountered next to a rock embedded in Unit 3 sediment. (C) Distribution of fossils in the excavation pit at the start of the excavations in November 2013 (~5 cm below surface). (D) Distribution of fossils in the excavation pit during excavations in March 2014 (~15 cm below surface); the longbone in the central part of the pit is in a near-vertical position and is shown in Figure 9C.....71

Figure 8. Comparison of selected fragments and electron microprobe analytical data of Facies 2 (Unit 3, floor) sediment in the Dinaledi Chamber, and floor sediments in the Dragon's Back Chamber. Analytical spot size is 5 µm diameter, which is generally larger than grain sizes. (A) Chert fragment impregnated with Mn oxi-hydroxide from the Dragon's Back Chamber. (B) Shale fragment from the Dragon's Back Chamber. (C) orange mud clast, typical of Facies 2 sediments from the Dinaledi Chamber, note much finer grain size than seen in (B). (D–G) Plots of K₂O vs Al₂O₃ for mud clast fragments in Facies 2 samples from both chambers show an important difference between them. M, muscovite compositional field. The samples from the Dinaledi Chamber (E–G) yield some data close to the muscovite field, probably indicating sericite grains slightly smaller than the spot size, and all show a trend with K/Al ratios much lower than muscovite, up to a high Al₂O₃ content >30%, which indicates either illite, or mixtures of sericite and kaolinite or other K-free clay minerals. In (E) the analysis of the fragment shown in (C) is indicated. The sample from the Dragon's Back Chamber in (D) shows data in the muscovite field (data point corresponding to [B] is indicated in [D]), but otherwise only low K- and Al-concentrations, which are typical of Mn oxi-hydroxide impregnation (data point corresponding to [a] is

indicated in [D]). No analytical data in d correspond to mudstone fragments such as shown in (C). (H–K), plots of Fe as FeO vs Mn as MnO show similarity between the chambers with respect to Fe-Mn oxi-hydroxide impregnations and alterations within the fragments: in both cases, domains with high Fe rarely coincide with domains high in Mn. (L–O), Plots of F vs Mn as MnO. Some elevated F concentrations at zero Mn values occur, but most data show a correlation for samples from both chambers: elevated Mn content is invariably associated with elevated F, with an atomic ratio $F/Mn \approx 0.14$. No Mn oxi-hydroxide minerals with F have been described, but partial substitution of F^- for OH^- as in apatite might be suspected. The similarity of the F/Mn ratios in Mn oxi-hydroxide impregnated fragments from Facies 2 sediments in both chambers suggests a uniform geochemical environment during the Mn oxi-hydroxide alteration event.....73

Figure 9. Taphonomic spatial patterning within the fossil assemblage exposed in the excavation pit. Taphonomic signatures and spatial orientations suggest that some of the assemblage may be para-authochthonous in nature, rather than primary or in situ. This scenario provides a mechanism for explaining the combination of near- or fully-anatomically articulated skeletal material and elements, which are heavily commingled and in a non-horizontal resting state (from near-vertical to oblique long-axis orientations). (A) Example of an articulated ankle region. (B) Example of an articulated hand. (C) Example of cluster of skeletal elements showing disarticulated elements in a non-horizontal resting state. Note long bone fragment in near-vertical alignment, compared to normal horizontal or near-horizontal alignment of the commingled elements surrounding it. Labels denote specimen numbers.....74

Figure 10. Examples of taphonomic traces recorded on hominin remains. (A) UW101–1288 tibial diaphysis showing evidence of mineral staining adhering to the cortex. The fossil shows evidence of dark zone sub-aerial or sub-surface weathering. Specimen shows a central midline crack with sediment infill, which separates conjoined manganese concretions. (B) UW101–419 (Cranium A [1]) showing iron oxide staining around the external auditory meatus. (C) UW101–312 and 1040 conjoined fragments of a tibial shaft, showing stepped transverse

fracture (post-mortem) of the mid-shaft; note longitudinal crack, and evidence of invertebrate modification. (D) UW101–1288 tibial diaphysis showing a weathering pattern typical of Stage 1 evidenced by fine longitudinal cracks, without concomitant flaking, delamination, or the formation of fibrous texture. (E) UW101–1074 tibial shaft showing manganese mineral concretions overlying yellow staining across the diaphysis. (F) Specimen UW 101–419 Cranium A (1) displaying tide lines of dark brown, reddish brown and yellow staining, which extends across different vault fragment. (G) UW101–498 tibial shaft, showing comminuted post-mortem fracture/crushing preserved by sediment infiltrate. (H) UW101–1070 segment of tibial diaphysis displaying differential mineral staining patterns between conjoined fragments.....75

Figure 11. Taphonomy—surface modifications. (A) Removal of the bone surface with sets of shallow, evenly spaced, multiple parallel striations on fibula (UW101–1037), which run longitudinal with the main axis of the bone and are interpreted as gastropod radula damage. (B) Fibula (UW101–1037) showing removal of the bone surface with sets of shallow, evenly spaced, multiple parallel striations that follow the collagen fibres together with shallow circular pits ranging from 0.1 to 3 mm in diameter, the bases of which may be smooth, cupped, or covered with multiple parallel striations. These features have been attributed to gastropod radula damage. (C) Tibia (UW101–484) showing removal of the bone surface with sets of shallow, striations that show a smooth scalloped edge together with circular pits ranging from 0.1 to 3 mm in diameter interpreted as the result of gnawing by beetle larvae. (D) Tibia (UW101–484) with areas of surface removal that have a straight edge associated with scrape marks interpreted as damage made by a beetle mandible. (E) Fibula (UW101–1037) with sets of shallow, evenly spaced, multiple parallel striations orientated transverse to the long axis of the bone interpreted as gastropod radula damage, resulting in an etched surface appearance that exposes underlying structures. (F) Tibia (UW101–484) showing clusters of large individual striations that are variably arrow-shaped and often overlap, interpreted as damage made by a beetle mandible. Compare with Figure 12 which shows surface modifications made by modern snails and beetles and their larvae. The scale bar in all samples equals 1 mm.....76

Figure 12. Comparative examples of surface modifications on bone made by modern snails and beetles and their larvae after four months in controlled experiments. Gastropods and beetles were found to produce similar modifications to those observed on the Rising Star hominin remains, and remove the surfaces of fresh, dry and fossil bones to an equal degree (see Figure 11). (A) Dry bovid rib showing surface removal associated with evenly spaced, multiple parallel striations made by the radula of an *Achatina* (land snail). (B) Fresh sheep bone that was originally covered with tissue showing how *Helix aspersa* (garden snails) have removed the outer cortical lamellae to produce an etched appearance and create circular shallow pits with smooth and striated bases. (C) Dry bovid rib showing shallow, evenly spaced, multiple parallel striations produced by *Achatina*. (D) Dry bird femur showing large individual striations that are variably arrow-shaped and often overlap, made by *Omorgus squalidus* (hide beetles). (E) A weathered bovid tooth showing surface removal with a scalloped edge produced by *Dermestes maculatus* larvae, and with a straight edge associated with scrape marks. (F) Scrape marks created by a *D. maculatus* adult beetle mandible on a dry medium-sized bovid long bone flake. The scale bar in all samples equals 1 mm.....77

CHAPTER FOUR: MULTIMODAL SPATIAL MAPPING AND VISUALISATION OF DINALEDI CHAMBER AND RISING STAR CAVE

Figure 1. The use of conventional coordinate capture methods during excavations at Malapa Cave, Cradle of Humankind. The excavators are using a Niko NPR-352 total station mounted on a known-position survey point to record the position of fossil material recovered during the excavation process. Site coordinates (x, y and z) are converted to geo-reference coordinates (easting, northing and height above sea level in the WGS 84 map reference system) by the total station.....98

Figure 2. Location of the Rising Star Cave within the Cradle of Humankind, UNESCO World Heritage Site. Other major palaeontological sites are indicated.....	99
Figure 3. Graphic representation of the data collection techniques and specific locations in which they were employed to acquire high-resolution data at the Rising Star Cave.....	100
Figure 4. Photograph of the small confined nature of the ‘Chute’ within the Rising Star Cave.....	101
Figure 5. Workflow of the data collection techniques, data formats and structures employed to acquire high-resolution data at the Rising Star Cave.....	102
Figure 6. (a) Photograph of the adult ‘Hand 1’ of <i>Homo naledi</i> as described by Kivell et al.; (b) adult ‘Hand 1’ of <i>H. naledi in situ</i> , prior to excavation; and (c) in-situ white-light source photogrammetry mesh of the area surrounding adult ‘Hand 1’ of <i>H. naledi</i> accomplished with the Artec Eva after alignment, registration and fusion of four separate scans at an average accuracy of 0.35 mm.....	103
Figure 7. (a) In-situ white-light source photogrammetry mesh of the area surrounding adult ‘Hand 1’ of <i>Homo naledi</i> indicating a reference pin marker (designated with an arrow); and (b) the same mesh converted to the .e57 point cloud data structure, indicating the same pin marker.....	103
Figure 8. Point cloud data generated from scans conducted with the Faro Focus ^{3D} laser scanner indicating the same reference pin marker as shown in Figures 6 and 7 within the excavation area of the Dinaledi Chamber of the Rising Star Cave.....	104
Figure 9. Point cloud data generated from an amalgamation of three-dimensional data collection techniques including unmanned aerial vehicle photogrammetry, high-resolution laser scans and the laser distance meter, showing the accurate position of the Rising Star Cave, including the position of the Dinaledi Chamber, in relation to the above ground level. Scale bar indicates both horizontal and vertical scale.....	104

CHAPTER FIVE: POST-MORTEM DISARTICULATION PATTERNS IN *HOMO NALEDI*: TAPHONOMIC SIGNATURES OF DIFFERENTIAL DECOMPOSITION IN THE DINALEDI CHAMBER, RISING STAR CAVE

Figure 1. Location of the Rising Star Cave within the Cradle of Humankind, UNESCO World Heritage Site. Other major palaeontological sites are indicated.....135

Figure 2. Geological map and cross-section of the Rising Star cave system. (A) Geological Map showing the distribution of chert-free dolomite and fracture systems controlling the cave. Inset shows the location of the Cradle of Humankind in southern Africa; (B) Northeast-Southwest, schematic cross section through the cave system, relative to several chert marker horizons; (C) Detailed map of the Dinaledi Chamber showing the orientation of the floor and the position of the excavation and sampling sites. Reused with permission of Dirks et al., (2015).....136

Figure 3. Consecutive *in situ* white light-source photogrammetry scans of Hand 1 (H1) from the Dinaledi Assemblage. Abbreviations: DP, distal phalanx; IP, intermediate phalanx; MC, metacarpal; PP, proximal phalanx.....137

Figure 4. Consecutive *in situ* white light-source photogrammetry scans of Foot 1 (F1) from the Dinaledi Assemblage. Abbreviations: DP, distal phalanx; MT, metatarsal; PP, proximal phalanx.....138

Figure 5. Three-dimensional recreation of the *in situ* position of the semi-articulated Hand 1 (H1) from the Dinaledi Assemblage. This figure is the combination of three white light-source photogrammetry scans (sediment) and accurately digitally positioned three-dimensional laser surface scans of H1...139

Figure 6. Three-dimensional recreation of the *in situ* position of the semi-articulated Foot 1 (F1) from the Dinaledi Assemblage. This figure is the

combination of three white light-source photogrammetry scans (sediment) and accurately digitally positioned three-dimensional laser surface scans of F1140

Figure 7. A) Digital reconstruction of the *in situ* position of the semi-articulated Hand 1 (H1), and B) Foot 1 (F1), from the Dinaledi Assemblage. Grey indicates carpals, blue - metacarpal rays, and red - phalangeal rays.....141

Figure 8. Displacement of the bones of the semi-articulated Hand 1 (H1) from the Dinaledi Assemblage. Left, normal palmer position of bones, and right, the *in situ* displacement of hand bones prior to excavation.....142

Figure 9. Displacement of the bones of the semi-articulated Foot 1 (F1) from the Dinaledi Assemblage. Left, normal anatomical position of bones, and right, the *in situ* displacement of foot bones prior to excavation.....143

Figure 10. Two-dimensional distribution plot of lower limb (yellow) and upper limb (red) elements within the main excavation pit of the Dinaledi Chamber. The location of Hand 1 (H1) and Foot 1 (F1) is noted. Location of the Pin 2 marker and the borders of the excavation pit are denoted. Axes are in mm.....144

CHAPTER SIX: SPATIAL TAPHONOMY OF THE *HOMO NALEDI* ASSEMBLAGE FROM THE DINALEDI CHAMBER, RISING STAR CAVE

Figure 1: Map of the Dinaledi Chamber, Rising Star cave, depicting the spatial density of surface material found within the chamber.....169

Figure 2: Example of spatial data collection of the Dinaledi assemblage: A) *in situ* three-dimensional white-light source photogrammetry scan of the excavation pit; with B) the corresponding point cloud data structure which spatial coordinates (x, y, and z) were plotted on.....170

Figure 3: A) Expanded surface density map of the Dinaledi Chamber, Rising Star cave, by body part. B) TwoStep Cluster Analysis of the spatial data presented in

A, showing three distinct natural clusters. Location pin markers are denoted in red. Axes are in mm.....171

Figure 4: Plotted two-dimensional distribution map of subsurface material found in the main excavation pit of the Dinaledi Chamber, Rising Star cave, by body parts: A) cranial and dental; B) upper limb; C) lower limb; and D) thorax. Location of the Pin 2 marker and the borders of the excavation pit are denoted. Axes are in mm.....172

Figure 5: Two-dimensional TwoStep Cluster Analysis of subsurface material of the main excavation pit of the Dinaledi Chamber, Rising Star cave, depicting distinct natural clusters by body part: A) all body parts; B) cranial and dental; C) upper limb; and D) lower limb. Spatial data for the thorax do not cluster. Axes are in mm.....173

Figure 6: Three-dimensional TwoStep Cluster Analysis of subsurface material of the main excavation pit of the Dinaledi Chamber, Rising Star cave, depicting distinct natural clusters by body part: A) all body parts; B) cranial and dental; C) upper limb; and D) lower limb. Spatial data for the thorax do not cluster. Axes are in mm.....174

Figure 7: Two-dimensional depth profiles created from alignment spatial data of a number of long bones and other bone material found within the main excavation pit of the Dinaledi Chamber, Rising Star cave. The positions of Hand 1 (H1) and Foot 1 (F1) are noted. Location of the Pin 2 marker and the borders of the excavation pit are denoted. Axes are in mm.....175

Figure 8: Depth profile groups from alignment spatial data of a number of long bones and other bone material found within the main excavation pit of the Dinaledi Chamber, Rising Star cave. The mean, standard deviation and sample number are presented for each depth profile group.....176

Figure 9: Surface material, including modern bird bones and hominin long bone fragments, arranged on rocks within the Dinaledi chamber by an unknown caver, prior to the discovery of this chamber by cavers from the University of the Witwatersrand.....177

Figure 10: Conjoined specimens of *Homo naledi* from the Dinaledi Chamber of the Rising Star Cave. Note the almost 12 m distance between specimen UW-101-020 at Pin 5, and its associated conjoin at Pin 4. Relative height within the chamber is indicated.....178

Figure 11. Surface material found at Pin 1 within the Dinaledi Chamber, Rising Star Cave. A) White light-source photogrammetry scan and B) illustration of a number of elements which have been pushed up to the rock and cave walls within this area, possibly the result of sediment creep and other geological processes which occurred in the chamber.....179

LIST OF TABLES

CHAPTER TWO: *HOMO NALEDI*, A NEW SPECIES OF THE GENUS *HOMO* FROM THE DINALEDI CHAMBER, SOUTH AFRICA

Table 1. Cranial and mandibular measurements for <i>H. naledi</i> , early hominins, and modern humans.....	33
Table 2. Dental measures for <i>H. naledi</i> and comparative hominin species.....	35
Table 3. Dinaledi body mass estimates from femur specimens preserving subtrochanteric diameters.....	40

CHAPTER THREE: GEOLOGICAL AND TAPHONOMIC CONTEXT FOR THE NEW HOMININ SPECIES *HOMO NALEDI* FROM THE DINALEDI CHAMBER, SOUTH AFRICA

Table 1. Element distribution patterns recording the Minimum Number of Individual and Identifiable Elements (MNIE) for skeletal parts of the <i>H. naledi</i> assemblage from the Dinaledi Chamber.....	78
Table 2. Recording activity pathway for Dinaledi Chamber excavations.....	90
Table 3. Taphonomic recording criteria (after Pokines and Symes, 2013).....	91

CHAPTER FOUR: MULTIMODAL SPATIAL MAPPING AND VISUALISATION OF DINALEDI CHAMBER AND RISING STAR CAVE

Table 1. Comparison of three-dimensional data collection methods used at Rising Star Cave and surrounding landscape.....	105
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CHAPTER FIVE: POST-MORTEM DISARTICULATION PATTERNS IN *HOMO NALEDI*: TAPHONOMIC SIGNATURES OF DIFFERENTIAL DECOMPOSITION IN THE DINALEDI CHAMBER, RISING STAR CAVE

Table 1. Recognised articulated anatomical groups recovered from the Dinaledi Chamber to date.....145

Table 2. Recognised decompositional stages of the human body and the physical appearance of remains associated with each stage. Table modified from (Wilson et al., 2007, Bristow et al., 2011).....146

CHAPTER SIX: SPATIAL TAPHONOMY OF THE *HOMO NALEDI* ASSEMBLAGE FROM THE DINALEDI CHAMBER, RISING STAR CAVE

Table 1. Number of surface specimens, by body part, used in the spatial analysis of surface specimens recovered from the Dinaledi Chamber, Rising Star Cave.....180

Table 2. Number of subsurface specimens, by body part, used in the spatial analysis of subsurface specimens recovered from the main excavation pit of Dinaledi Chamber, Rising Star Cave.....180

CHAPTER ONE: INTRODUCTION

Overview of the Thesis

This thesis is the culmination of a series of five papers investigating the morphology and context of the Dinaledi assemblage, and the spatial distribution, spatial taphonomy, and site formation processes at the U.W. 101 site (Dinaledi Chamber) of the Rising Star Cave, Cradle of Humankind, Johannesburg, South Africa. This body of work aimed to understand the site formation processes which took place in the Rising Star Cave and led to the formation of the Dinaledi assemblage. The following hypotheses are put forward, and are tested:

1. The *Homo naledi* assemblage is the result of autochthonous sediment accumulation and the introduction of bone material over a series of time
2. Hominin material from the assemblage was introduced from a single-entry point, at a higher level than the main excavation pit
3. Drainage pits within the Dinaledi Chamber (U.W. 101) assisted the flow and movement of sediment and bone material
4. Sorting of material is due to natural processes occurring within the Dinaledi Chamber such as gravity, sediment creep and movement of the underlying water table
5. The discovery of articulated remains within the assemblage are evidence for the post-mortem deposition of hominin bodies
6. Site formation processes at the U.W. 101 site have resulted in identifiable taphonomic features represented with regularity across the assemblage

Presentation and testing of these hypotheses are done in five separate chapters, entailing 5 papers:

Chapter 2 introduces a new species of hominin: *Homo naledi*. This publication “*Homo naledi*, a New Species of the Genus *Homo* from the Dinaledi Chamber, South Africa” is the morphological description of the species, including the articulated Hand 1 (H1) and Foot 1 (F1), articulated remains which are discussed in later chapters with regards to decomposition

and its implications for understanding site formation processes. This paper also introduces some of the three-dimensional (3D) modelling and data collection techniques used for fossil material from this site. An introduction to the analysis and interpretation of this site at intra-site or excavation level are also provided.

Chapter 3 provides an introduction to the physical and geological context of the Dinaledi Chamber and excavation area in the publication “Geological and Taphonomic Context for the New Hominin Species *Homo naledi* from the Dinaledi Chamber, South Africa”. This includes sedimentology, mineralogy and chemistry, and taphonomy. Chapter 3 outlines the distribution of concentration of fossil material alongside the spatial distribution of some of the material excavated from the main excavation pit. The main approach to excavations at this site are highlighted. The depositional scenarios for the ‘burial’ of *Homo naledi* are introduced in this paper, many of which are tested in later chapters. A number of site formation hypotheses are put forward in this chapter, which are discussed in two subsequent results chapters (Chapter 5 and Chapter 6).

To prevent repetition in this thesis, there is no traditional “materials and methods” section or chapter. This is because Chapter 2 details the material used, and **Chapter 4** features the methods used throughout this study for data collection, specifically 3D data collection. The published article of Chapter 4, “Multimodal Spatial Mapping and Visualisation of Dinaledi Chamber and Rising Star Cave” details the innovative multimodal set of recording and survey methods which were used, developed and employed at the Rising Star Cave, at both site (including excavation) and landscape level. This includes the use of Terrestrial Laser Scanning (TLS), photogrammetry and Unmanned Aerial (UAV) photogrammetry employed for high-resolution data collection, in addition to the workflow used to compile, render and visualise these data. Additional materials or methods used for this study, including statistical and spatial analysis, which are not represented in Chapter 2 or Chapter 4, are detailed in the appropriate chapters, under their own “materials and methods” sections.

Chapter 5 investigates the decomposition patterns of the Dinaledi Chamber. This unpublished manuscript entitled “Post-mortem Disarticulation Patterns in *Homo naledi*:

Taphonomic Signatures of Differential Decomposition in the Dinaledi Chamber, Rising Star Cave” revisits the articulated hand and foot (H1 & F1) of the Dinaledi assemblage and utilises a combination of 3D laser surface scanning of fossil material and 3D photogrammetry of the excavation area, to produce a 3D *in situ* reconstruction of both elements. The analysis presented in this paper aims to explore the decomposition patterns preserved by the semi-articulated hand and foot, their spatial position within the assemblage, and how they aid in understanding site formation processes which occurred within the Dinaledi Chamber.

Lastly, **Chapter 6** is a spatial analysis of the Dinaledi Assemblage presented in the unpublished manuscript “Spatial Taphonomy of the *Homo naledi* Assemblage from the Dinaledi Chamber, Rising Star Cave”. This study details the spatial distribution of fossil material at both surface level within the Dinaledi Chamber, and below the current surface level within the highly fossiliferous excavation pit. Both 2D and 3D GIS plots are used to analyse the spatial distribution of the assemblage including individual elements and associated elements. The relationships between spatial patterning of hominin material from the excavation area are discussed.

Background

Recently, a discovery of an early hominin site was made at Rising Star in the Cradle of Humankind (CoH), situated 2.2 km west of Sterkfontein Cave. This large hominin-specific assemblage is unique, and represents the single largest hominin site on the continent of Africa (Chapter 2: Berger et al., 2015). In addition, only one large mammal taxon is represented by nearly 2,000 well-preserved specimens; a species of hominin named *Homo naledi* (Berger et al., 2015). This body of work aims to understand the processes behind site formation at Rising Star, specifically that of the Dinaledi Chamber and the *Homo naledi* assemblage, whilst also using novel methods and technology to understand the taphonomy and formation of the Dinaledi Chamber. A number of hypotheses were formulated and tested during the course of this work, and these will be discussed independently within each chapter.

In the modern day, the Rising Star Cave system has been utilised by recreational and professional cavers and caving societies for a number of years. However, it was not until

formal investigations by the Evolutionary Studies Institute of the University of the Witwatersrand that excavations in the now-called Dinaledi Chamber commenced. Excavations under the direction of Prof. Lee Berger from the University of the Witwatersrand began in November 2013, when an international team of researchers came together to record the process of retrieving fossil material from the site. Because of the extraordinarily difficult environment of the cave, this chamber lay mostly untouched and unexplored, aiding to the preservation of the scientific wonder of the Dinaledi assemblage. From the moment it was formally discovered, the sheer difficulty in reaching the chamber itself, and therefore the fossil assemblage preserved within it, begged questions about how this site came to be, and what processes occurred in its formation. To understand the species, its context is fundamentally important in answering questions about the environment it may have lived in, and utilised, possibly up to 1 million years ago (Thackeray, 2015, Dembo et al., 2016, Hawks and Berger, 2016).

Morphology and Dating of *Homo naledi*

The Dinaledi assemblage is remarkably homogenous, and almost completely monospecific. Apart from the Sima de los Huesos collection, Atapuerca, Spain (Aguirre and Lumley, 1977, Aguirre 1985, 2001, Arsuaga, 1993) and some later Neanderthal (Stewart, 1977, Trinkaus, 2014) and modern human samples, this new species has the most comprehensive representation of skeletal elements across all life stages, and from multiple individuals, in the hominin fossil record. The morphology of *Homo naledi* places it firmly in the genus *Homo*, rather than in *Australopithecus* or any other early hominin genera (Berger et al., 2015). International teams have described much of the anatomy of *Homo naledi*, including the skull (Laird et al., 2016, Schroeder et al., 2016), upper limb (Feuerriegel et al., 2016), lower limb (Marchi et al., 2016), the vertebrae and ribs (Williams et al., 2017), the hand (Kivell et al., 2015), and the foot (Harcourt-Smith et al., 2015). At the time of submission, a date for the assemblage has not been published (Dirks et al., 2015, Hawks and Berger, 2016), although some efforts have been conducted to produce an estimated age for the assemblage and phylogenetic position of *Homo naledi* (Thackeray, 2015, Dembo et al., 2016, Hawks and Berger, 2016).

With a relatively human-like lower limb and strangely primitive-like upper body, *Homo naledi* displays a mosaic of traits in its morphology. A small cranium for a member of the genus *Homo* adds to this unexpected mix of characters. The homogeneity of the collection is notable, particularly with regards to the morphology of the dentition, as almost every aspect of it, including the distinctive form of the lower premolars, the distal accessory cuspule of the mandibular canines, and the expression of nonmetric features that normally vary in human populations, is uniform in every specimen within the Dinaledi assemblage. The cranial morphology reflects the homogeneity of the assemblage to an even greater degree, as only slight variation is present even for aspects that normally vary among individuals of different body size or between sexes (Berger et al., 2015). This well-preserved assemblage is seemingly the result of a large number of individuals from a single population (Berger et al., 2015). The question remains as to why this population of hominins is found almost 40 m below the present-day surface, within the exceptionally difficult navigational terrain of the Rising Star Cave system.

A number of articulated or semi-articulated remains have been described from the Dinaledi assemblage. The articulated hand and foot (H1 & F1) (Berger et al., 2015, Harcourt-Smith et al., 2015, Kivell et al., 2015) along with an articulated ankle of a juvenile individual suggest that these remains were deposited *in situ* during the accumulation of Unit 3. Chapter 3: Dirks et al. (2015) shows these semi-articulated remains most probably did not weather out from the older Unit 2, as this unit accumulated at the entrance of the Dinaledi Chamber, about 11 m away from the main excavation pit, and about 12 m away from the most concentrated surface material found towards the bottom of the chamber. There is also no evidence of sediments from Unit 2 above or near the main excavation pit and the areas containing the dense surface material. The semi-articulated remains would not have remained semi-articulated if they had indeed weathered out from the Unit 2 sediments (Dirks et al., 2015).

The articulated remains of Hand 1 (H1) and Foot 1 (F1) are important skeletal elements of the assemblage, telling us much about the depositional circumstances taking place in the Dinaledi Chamber. As stated earlier, sedimentology of the Dinaledi Chamber suggests that these remains were deposited *in situ* during the accumulation of Unit 3. The methods outlined in Chapter 4 (Kruger et al., 2016) proved to be a valuable data collection tool as applied to the

context of the Rising Star site and Dinaledi Chamber. These methods, coupled with a three-dimensional *in situ* reconstruction of the hand and foot (H1 & F1) of *Homo naledi*, shed light on the decompositional patterns of the Dinaledi Chamber (Chapter 5). The spatial position and displacement of individual bones, and the relative location of both H1 and F1 in the context of the excavation pit are examined, with implications discussed for the site formation processes which occurred in the Dinaledi Chamber.

Taphonomy of the Dinaledi Assemblage

Analysis of taphonomic processes affecting the formation of the Rising Star hominin fossil assemblage is ongoing. A number of approaches including spatial, geological, sedimentological, contextual and osseous analyses are being used under the guidance of the author in order to understand site formational processes that underpin this unique fossil assemblage (Dirks et al., 2015, Randolph-Quinney 2015a, b). Preliminary analyses have been conducted into the decomposition and subterranean weathering patterns, physical and abiotic traces, and pattern and timing of fractures; surface modifications and invertebrate-bone interactions; spatial context, skeletal distribution patterns and 3D spatial relationships. Such taphonomic analyses are derived from ongoing professional forensic practice in relation to the death process and burial environment; particularly with regard to understanding the consequences of processes of decomposition, bone breakage and spatial distribution within sedimentary units with a degree of resolution usually reserved for medico-legal casework. The co-option of taphonomy into the forensic sphere has been described by Dirkmaat and colleagues as “the most significant development [to] alter the field of forensic anthropology” in the last 20 years (Dirkmaat et al., 2008). Forensic taphonomy is now well situated to provide a scientific and interpretive framework with which to investigate the decompositional and formational histories of extremely ancient deposits by applying analyses of forensically-typical short-duration events into the deep-geological past; such approaches have already been successfully demonstrated elsewhere in the CoH (Randolph-Quinney et al., 2014).

Traditional approaches to taphonomic analyses focus on the application of uniformitarian assumptions in order to understand pattern, process, and mechanism in the past. Such studies were often established to answer or address research problems related to early hominid behaviours, such as the controlled use of fire or hunting versus scavenging ecological niches

(Brain, 1981, 1993). This early work represents a vast corpus of literature relating to aspects of necrology, biostratigraphy, burial, and diagenesis of long-dead organisms (Behrensmeyer 1975, 1985, Lyman 1994, 2010, Behrensmeyer et al., 2000). In contrast, the epistemological and practical basis of forensic taphonomy is unique in that the field marks a shift in the temporal nature of taphonomic studies, away from longitudinal studies of complex time-averaged assemblages, to shorter post-mortem time frames spanning days to years, with the emergence of the individual cadaver as a key unit of analysis (Bristow et al., 2011). In attempting to understand the burial and post-mortem process, taphonomists can be seen to have adopted two complementary lines of approach (Quinney, 2000): (1) neotaphonomy or actualistic taphonomy, which concentrates on the modern environment and applies its results to the past by analogy, and (2) palaeotaphonomy, which examines the context and content of depositional sites in great detail as a means of interpreting formation processes. Forensic taphonomic research or analyses can fall into either category (Bristow et al., 2011); in general, experimental approaches can be considered to be neotaphonomic, while much of the case-based single study reports can be considered as palaeotaphonomic in nature.

Geological Context of Dinaledi Chamber

Representing the remains of an ancient sea, the Malmani Dolomite Subgroup near Johannesburg in South Africa is some 2.5 billion years old (Button, 1973, Eriksson et al., 1976). Forming part of the Transvaal Supergroup, the Malmani Subgroup is divided into five formations: Oaktree, Monte Christo, Lyttelton, Eccles, and Frisco, based on chert content, stromatolite morphology, intercalated shales, and erosion surfaces (Eriksson et al. 1976, 2006). These formations host a number of caves, which developed as cracks and dissolution fissures within the dolomites, due to the action of slightly acidic rainwater percolating through the highly porous and alkaline rock, and the rise and fall in groundwater level (Kullmer, 2007). During the Pliocene-Pleistocene, the caves opened to the surface and admitted sediments containing local fauna and flora in various states of preservation (Kullmer, 2007). Large carnivores and porcupines frequently inhabited the caves and accumulated many of the faunal remains, which in the presence of lime-rich water, underwent diagenesis and fossilised (Dirks and Berger, 2013).

Hominin remains in the CoH, as with all fossils preserved in dolomitic cave systems, are typically encased in breccia, lithified cave sediments which have been folded and broken into angular blocks (Dirks and Berger, 2013), though occasionally these fossils are found in soft sediments after undergoing “de-calcification” (e.g. Lacruz et al., 2002). Hominins found in both situations, and attributed to *Australopithecus africanus*, are known from Sterkfontein (Broom, 1936, Clarke, 1998, Lockwood and Tobias, 2002, Moggi-Cecchi et al., 2006) and Gladysvale (Berger et al., 1993), while those attributed to *Australopithecus robustus* or early *Homo* have been found at Cooper’s Cave (Berger et al. 1995, 2003, Steininger et al., 2008), Drimolen (Keyser, 2000, Keyser et al., 2000), Kromdraai (Broom, 1938, Thackeray et al., 2001), Sterkfontein (Kuman and Clarke, 2000), and Swartkrans (Broom, 1949, Brain, 1981, Grine, 1989, de Ruiter et al., 2006). Other hominid remains have been found at Gondolin (Adams et al., 2007) and the remains of a hominin attributed to *Australopithecus sediba* were discovered at the site of Malapa (Berger, 2010). The most recent discovery of hominin remains are from the Haasgat site (Leece et al., 2016), representing perhaps *Australopithecus* or early *Homo*. Figure 1 is a map of the above-mentioned fossil localities found within the CoH, South Africa.

The Dinaledi Chamber is part of the Rising Star Cave system, a system which spans some 250 m by 150 m of mapped passageways, found within the Bloubank River valley (Figure 2). This system is located within the lower parts of the Monte Christo Formation (Eriksson et al., 2006). The Dinaledi Chamber is approximately 38 m below the ground surface, and bears a significant number of fossilised elements, all of which to date are attributed to the species *Homo naledi* (barring six bird bones of more recent age and some micro-fauna) and are found in soft autochthonous sediments (Dirks et al., 2015). Rising Star differs from all other Pliocene-Pleistocene sites in the region in that the fossils are entombed in a soft mud rather than breccia (Dirks et al., 2015).

The geology of the cave system and chamber are the first clues to deciphering the puzzle that is *Homo naledi*. Investigations of the geology of the system reflect a complex environment, having undergone many cycles which are common to the karstic cave systems of the CoH (Dirks and Berger, 2013). A number of sediment flowstone fill and removal cycles are evident throughout the Rising Star Cave system in the form of erosional remnants,

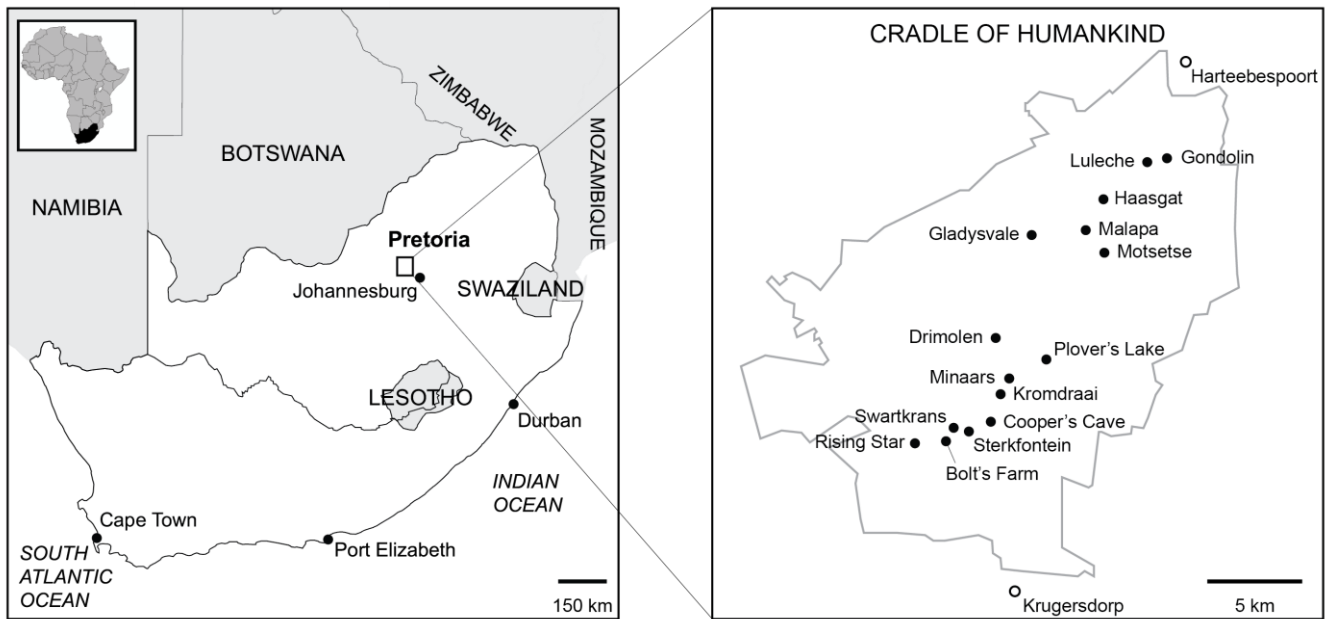


Figure 1. Map of the Cradle of Humankind, Johannesburg, South Africa, showing known fossil localities

RISING STAR SYSTEM

Survey Grade : BCRA 5d

Surveyed By : J Harris N Lindsey
: H Müller C Priddle
: D Rees R van der Hooft

Drawn By : J Harris D Rees
: 1985

© Free Cavers : Rising Star
: Silt
: Bedspring

© CROSA : Empire
: Westminster

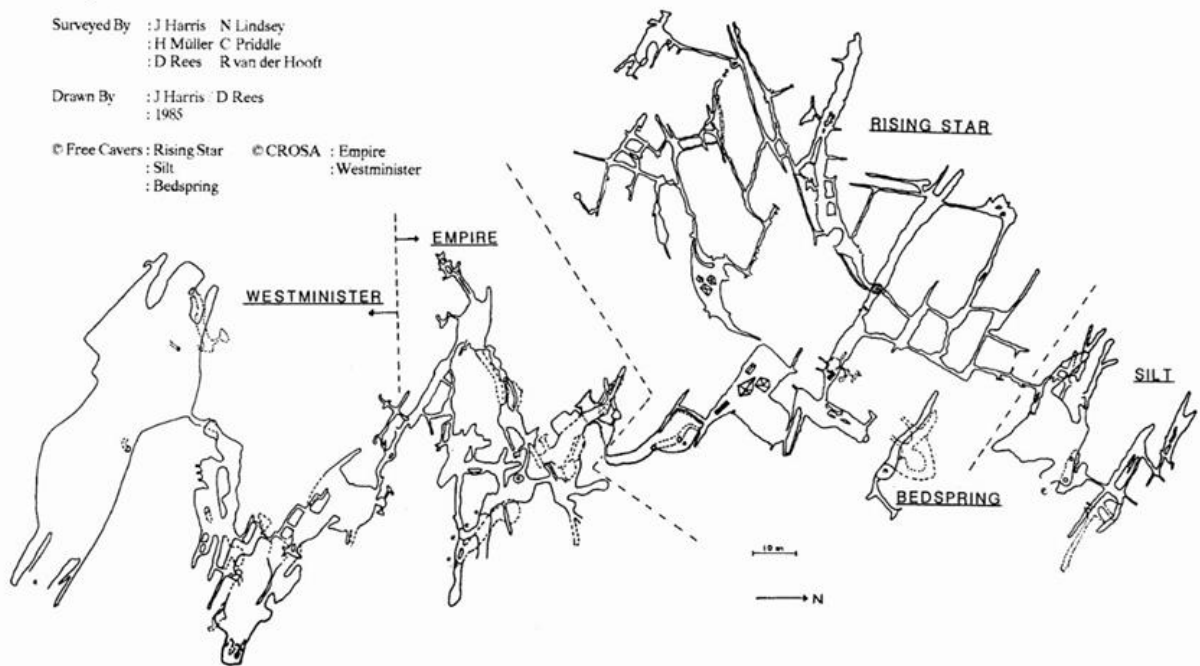


Figure 2. Mapped passageways of the Rising Star Cave system, Cradle of Humankind, Johannesburg, South Africa.

fossiliferous sediment, breccia, and flowstone units (Dirks et al., 2015). From the closet current cave entrance, the sediment deposits become progressively finer-grained towards the Dinaledi Chamber, which itself is filled exclusively by flowstone and fine-grained sediment, the product of two depositional facies (Facies 1 and 2) divided across three stratigraphic Units (1 – 3), which filled the chamber over time (Dirks et al., 2015). The oldest of these Units, Unit 1, is the remnant of laminated mudstones which are preserved as erosional remnants within the Dinaledi Chamber. The composite Unit 2 consists of consolidated sediments containing several hominin bones (including the shafts of a radius and ulna derived from a juvenile hominin). The youngest of the three units, Unit 3, comprises the majority of hominin bone material, and is the main constitute of unconsolidated sediment derived from the weathering and erosion of the two older Units (1 – 2). Unit 3 preserves semi-articulated skeletal material that has not been reworked from older units. The clay-rich sediments making up the units are a combination of *in situ* weathering and exogenous clays and silts, which are the result of filtering through fractures and passages on their way down to the Dinaledi Chamber, effectively screening out larger coarser-grained and clastic materials before reaching the chamber (Dirks et al., 2015, Randolph-Quinney et al., 2016). Geological and taphonomic analyses of the site have precluded the usual site formation processes which occur in the CoH. Taphonomic analyses have shown that the Dinaledi Assemblage is not the product of carnivore accumulations, neither a natural death trap scenario, nor the product of fluvial or gravitational deposits from the surface (Dirks et al. 2015, 2016)

Three-Dimensional Data Applied to Palaeontology and Archaeology

In the Rising Star cave system, squeezes as small as 20 cm occur during the descent from the cave entrance to the Dinaledi Chamber. The chamber itself is reasonably small, and only about 12 m in length. The small confines of this system and chamber therefore required unique recording methodologies and approaches to understanding site formation process. Experienced cavers and excavators able to fit through narrow passageways and shafts were chosen to retrieve surface fossils, and map the cave system and fossil bearing chambers using both terrestrial laser scanning systems (TLS) and a portable high resolution three-dimensional (3D) surface scanner, a system designed and directed by the author. Unable to employ usual mapping techniques because of space limitations, and the knowledge that these methods are time-consuming and prone to error, the author devised a system where a hand-held 3D

scanner was used to capture in time and space the structure and contents of the site, before and after the removal of all fossil remains. Three-dimensional data collection undertaken by an excavator in the cave using the high-resolution scanner were relayed to the surface level in near real time for incorporation in the evolving cave reconstruction using 3D software. This highly technological system was backed up by more conventional systems reliant on photography and measurement.

3D data have transformed the way palaeontologists study extinct organisms and their palaeobiology. The application of 3D data collection such as computed tomography and surface scanning allows for unprecedented insights into fossil remains. Some of these data collection and analysis techniques began in the field of human medicine. For example, in 1895 Wilhelm Conrad Röntgen discovered X-rays at the Institute of Physics of the University of Würzburg. Röntgen found that from a discharge tube and the transport of electricity in gases at high voltages, a penetrating radiation occurred (Haase et al., 1997). In the 1900s this discovery by Röntgen was used extensively for medical purposes. By the 1950s an X-ray image intensifier was created, which allowed the display of the X-rays using a television monitor. The advantage of using this technology for medical application is obvious, and it is clear that it can also benefit fields such as palaeontology, sedimentology, petrology, and soil science.

Computed tomography (CT) was originally applied by Hounsfield (1973) to obtain cross-sectional images of the human head. The application of CT was further applied by Ledley et al. (1974) for the examination of other human body regions. In the same year, the first application of CT to palaeontology was undertaken by Fourie (1974) when he investigated the cranial morphology of *Thrinaxodon liorhinus*. Later, as CT technology and its application become increasingly popular, Conroy and Vannier (1984) examined the hardened matrix infill of four fossil primate skulls. The success of CT data as a means of non-invasive investigation has seen its application to a wide variety of geoscience disciplines, including the non-invasive assessment of *Archaeopteryx* (Haubitz et al., 1988), the examination of fossils and meteorites (Ketcham and Carlson, 2001), non-destructive analysis for geological specimens (Carlson et al., 2003), studies of palaeobotanical remains (DeVore et al., 2006), investigation of arthropod structures (Betz et al., 2007), and the non-invasive exploration of

fossil burrow casts (Fernandez et al., 2013). While CT has proven to be an excellent method for the non-destructive application and analysis of fossilised material, this form of 3D data analysis is only one of many used in this field today.

The use of 3D surface data, which investigates a surface as opposed to the internal morphology or structure of a specimen or site, has been rapidly growing within the fields of palaeontology and archaeology. Its application can be very broad, ranging from the 3D surface reconstruction of therapsid skulls (Kruger et al., 2017), documentation of archaeological finds (McPherron et al., 2009), reconstruction of hominin brain capacity (Berger et al., 2015), body mass estimation of prosauropod dinosaurs (Gunga et al., 2007, Bates et al., 2009), to the analysis of gait in fossilised hominin footprints (Masao et al., 2016). When the interior of a fossil is not required for study, and the external surface features are of most importance, surface scanning techniques are used to collect geometric data from a 3D surface (Cunningham et al., 2014). Surface scanning is especially useful when undertaking studies on fossils which cannot be moved, for example, trace fossils which are *in situ*, or large museum exhibits which are not mobile. The most common of the surface data collection techniques is laser scanning, which uses laser light to produce accurate models of the desired surface. This form of 3D surface modelling is applied later in this study as a means of collection high-resolution 3D data of a palaeoanthropological site (that of the Dinaledi Chamber). Laser scanning of fossil specimens from the *Homo naledi* assemblage was undertaken and included in a spatial analysis.

Photogrammetry, another form of 3D surface data collection, is fast becoming the preferred method in palaeontological studies (Falkingham, 2012). This is largely due to the fact that photogrammetry is easily undertaken, as all that is needed is an appropriate software and a camera, in some cases even a smartphone camera is suitable (Cunningham et al., 2014). Photogrammetry passively reconstructs the geometric properties of the desired fossil or object from a series of photographs. Photogrammetry can also capture colour at the same time, making this form of 3D surface data collection non-invasive and highly informative for research purposes. Photogrammetry has been utilised on a vast array of scientific research, spanning from the taphonomic study of burnt human remains (Pankowská et al., 2016) to the analyses of dinosaur (Remondino et al., 2010), and even hominin footprints (Masao et al.,

2016). This form of 3D surface modelling was applied to collect high-resolution data for the field area surrounding the Rising Star site, and to accurately geo-reference the Rising Star Cave system and Dinaledi Chamber. It was also used with a white-light source photogrammetry scanner, to collect spatial data during excavations at Rising Star, the results of which were spatially analysed.

The very nature of excavation is destructive, at any site, and has thus proved that rigorous recording strategies are imperative to allow for accurate recording during the process. The technologies currently available to the field, which allow for such high-resolution recording, are laser scanning and photogrammetry. The advantages of using these technologies has been discussed above, however, both laser scanning and photogrammetry at archaeological sites provides one other crucial advantage. This is the ability to collect data effectively and efficiently in the field, and processing can be taken at a later stage. This of course reduces the amount of time spent for recording, mapping and taking measurements in the field (Campana, 2014).

The Role of Spatial Analysis and GIS in Archaeology

While archaeologists strive to document excavations and the process of those excavations in great detail, including the spatial arranging of sites and their artefacts, key data can still be lost, ultimately never to be regained again. The complexity of most archaeological excavations demands a rigid form of data collection and analysis. Space and spatial analysis at archaeological sites provides insights into the behaviour, social organization and cognitive structures of past cultures and peoples. Traditionally, spatial analysis in archaeology was undertaken in the quest to explain the correlation between spatial patterning of artefacts and architecture of a particular site or sites. These studies may provide insight into how past societies functioned as systems. Space and spatial analysis became increasingly important, in addressing the relationship between archaeological sites and the natural and ecological landscape surrounding them (Seibert, 2006). This broader sort of investigation is important in deciphering the global context of a site.

The very destructive nature of archaeological excavation can be counteracted to some extent, by incorporation rigorous recording methods and in recent years, a great effort has been seen in the preservation of such data, before, during and after excavations. This is usually accomplished by means of incorporating high-resolution data collection techniques during excavations. High-resolution data collection techniques have been greatly enhanced by the introduction of 3D recording methods. These methods allow for an object, site or even landscape, to be recorded in three dimensions, creating a complex data set that can develop present and future understanding of the entity. In the last decade, the application of such technology to fields such as palaeontology and archaeology have has increased exponentially (Pavlidis et al., 2007). Various modes of 3D modelling have proven to be accurate methods of recording archaeological excavation sites and may include: structure-from-motion based recording (McPherron et al., 2009, Baier and Rando, 2016), satellite and remote sensing (Parcak, 2009, Breeze et al., 2015), surface scanning (Benko et al., 2004, Friess, 2012) and photogrammetry (Drap et al., 2007, Lambers et al., 2007, Guidi et al., 2009, Lerma et al., 2010, Barsanti et al., 2012, Rinaudo et al., 2012, De Reu et al., 2013, 2014). Another key role that 3D modelling can provide is adequate, high resolution mapping. This has been demonstrated by a number of authors, and can be applied to areas that are not specifically archaeological sites, but may prove exceptionally difficult to map due to their circumstances. This is specifically true for caves (Schmid, 2002, Leucci and De Giorgi, 2005, Ma and Zha, 2006, Holenstein et al., 2011, Fabbri et al., 2016).

A large component of archaeological excavation and recording is increasingly relying on Geographic Information Systems (GIS). GIS were first used to understand archaeological excavations in the 1970s, although this was almost exclusively on the analysis of two-dimension (2D) data. With the advances of computer technologies and processing power, coupled with the dramatic reduction of costs for these systems, over the last decade, GIS and 3D data collection, visualisation and analysis has become much more attainable and feasible as applied to archaeology. GIS broadly defined are “a powerful set of tools for collecting, storing, retrieving at will, transforming and displaying spatial data from the real word for a particular set of purposes” (Burroughs, 1986). The application of 3D data and GIS has been limited over the years, as many GIS packages lack a true integration of 3D data (Harris and Lock, 1996).

GIS models can represent spatial data within a set framework. Usually this object-based representation of an item is understood in the guise of an empty box or container, one which holds objects with a set position, described by a set of geometric coordinates (usually in the form of x, y and z). These objects may have a set of properties or characteristics, however with object-based GIS representations, the shape and position of the object is given priority (Merlo, 2016). Field-based representation, on the other hand, is representation of space in a 2D or 3D Cartesian box, and the attribute represented holds more importance than the shape of the entity or object represented (Merlo, 2016). Thus, the type of GIS used to represent and analyse different excavations and spaces must be considered and applied appropriately. GIS analysis is concerned with the investigation and identification of patterns within a spatial data set, and importantly, looking for the possible relationships between these patterns (Merlo, 2016), and then visualising them. These analyses can be statistic or deterministic depending on the variables and types of data and data collection.

In terms of archaeological cave sites, GIS can be an excellent tool for deciphering spatial patterning of artefacts and remains within the system. One such example is that of Moyes (2002) and the investigation of the Actun Tunichil Muknal site, a Mayan ceremonial cave site, situated in the Upper Belize Valley, Belize. At this site, a number of chambers within the cave system were utilised for ritualistic use, and the extent of this utilisation varies from location to location. At this site, the main aim for utilising a GIS was to handle the large quantity of data, that which was in the form of artefacts and human remains. It allowed the data to be manipulated and utilised in a manner that would produce new information, specifically that of spatial analysis. Spatial data collected for the study at the Actun Tunichil Muknal site allowed researchers to test whether artefacts or remains had been placed or assembled in the vicinity of specific morphological features found in the cave (Moyes, 2001). Measuring proximity between artefacts to other artefacts, as well as between spatially created groups and clusters of artefacts or remains, to morphological cave features was key in understanding this site's origins and utilisation. In this example, these data were also able to be tested against and cross-referenced to ethnographical accounts, to either support or dispute them.

GIS has also been utilised in the modelling of magnetic mineralogy, a method with which to test for the event and use of fire in Middle Stone Age (MSA) bearing sea caves in Southern Africa (Herries and Fisher, 2010). At the site of Pinnacle Point 13B, a GIS proved crucial in managing and identifying spatial patterning of burning, a key indicator in the determination of occupation. A combination of data collection for burnt material at this site were recorded in a GIS in order to test spatial models and hypotheses. Testing of spatial clusters and models can also be applied to older sites, such as those found in CoH.

Palaeontological sites in the CoH have used GIS in their own context, to map and analyse fossil deposits. Introduced to manage and analyse a large assemblage of faunal remains, a GIS was relied upon at the Pliocene-Pleistocene site Swartkrans. In order to digitally curate the coordinates of some 400,000 faunal remains, the GIS was not only set up for ongoing excavations at the site, but also to include legacy data, data collected manually and before the application of GIS (Nigro et al., 2003) in the form of field notes and log books. This ‘backwards’ compatibility is most probably one of the most valuable features GIS can provide archaeologists and palaeontologists working in the CoH, as many sites in the area have been excavated over decades. The manipulation of data recorded many years ago, and in many cases without any georeferenced or Cartesian influence, in conjunction with modern day data collection techniques can prove to be exceptionally beneficial. Of course, GIS is not limited to the recording of faunal remains, but can indeed recorded any set of variables desired. This is the case for the Swartkrans GIS, as geological formations, stratigraphy along with stone tools, were also entered and stored for the spatial analyses (Nigro et al., 2003). Similar GIS frameworks have recently been developed and employed at the Sterkfontein Cave sites (Stratford et al., 2016).

Excavations at Sterkfontein rely on legacy data, as excavations have been undertaken at the site since the discovery of the first adult *Australopithecus* specimen in 1936 (Broom, 1936). The integration of both traditional fossil loci and total station generated location data produced a digital, or virtual, grid of the site. This can be done in either 2D or 3D (or both) as new information shares new light on old data. This is becoming common amongst sites in the CoH, as a new way to direct excavation and test spatial hypotheses in order to understand the site formation process that occurred at a particular site.

GIS as applied to the taphonomic aspect of a site is an increasingly utilised form of the systems. While researching burnt burials and the spatial analysis of secondary deposition, studies such as the one conducted by Pankowská et al. (2016) show the reliability of using taphonomy as a set GIS variable. By using photogrammetry as a means of high-resolution 3D data collection, the location of burnt bones *en bloc* was recorded within the context of each urn they were found in. A taphonomic criteria was introduced, and recorded for each bone removed. In this manner, as much spatial data as possible were recorded and then analysed using cluster analyses. In this particular example Pankowská et al. (2016) was able to also produce a spatial distribution based on the weight of anatomical elements, furthering the information that could be extracted from the spatial data.

GIS, whether it be with the integration of 2D, 2.5D or 3D data, is routinely applied successfully to the archaeological and palaeontological context to analyse space and spatial context (Nigro et al., 2003, Channing and Randolph-Quinney, 2006, Isaksen et al., 2007, Simmonds et al., 2008, Egeland et al., 2010, Gallotti et al., 2011, Mainland et al., 2014, McCool, 2014, Birkenfeld et al., 2015, Geiling and Marín-Arroyo, 2015, Pankowská et al., 2016). A GIS is a great tool for inputting a number of different variables, variables which can be specific to a project. The use of 3D GIS allow for more realistic modelling of complex phenomena and environments, exactly what is expected at archaeological sites. 3D GIS can also provide a means for manipulating spatial data, a means for exploring these data further and extracting results otherwise not obtainable through tradition analysis methods.

As outlined by Stratford (2011), methods of excavations at any one site need to be adequate for that site, and these methods may need to change during excavations to accommodate changing circumstances and deposits as they proceed. The main goal is to avoid as much data loss as possible during the excavations. As such, a method and strategy of high-resolution data collection was designed and then applied to the Rising Star site. This was particularly challenging, as the above-mentioned cave environment is extremely difficult and unpredictable in the sense that every chamber is different in some way from the next, and the accessibility of many portions of the pathway towards the Dinaledi Chamber were restrictive to a normal adult's body size. As such, the methods applied by Kruger et al. (2016) form part of an excavation protocol that was appropriate for this particular cave system and fossil site,

and while they may be a suitable data collection methodology to apply to other cave sites and systems, they may not be appropriate to all forms of archaeological or palaeoanthropological sites. However, while the main goals of the data methods outlined by Kruger et al. (2016) were to prevent data loss as best as possible, and another benefit of such high-tech methodology is the inclusion of such data in new data sets and frameworks that may arise in the future. For example, as new questions about the Rising Star Cave and Dinaledi Chamber arise, the data collected by Kruger et al. (2016) can easily be integrated into new Geographic Information Systems (GIS), methodologies, and protocols. Essentially the framework for a site-wide GIS of the Rising Star Cave is already in place, which can be integrated with further geological, sedimentological, archaeological, palaeontological, and spatial investigations that may occur in the future. The methods used, when applied to other sites, can also offer backward compatibility by allowing legacy data to be incorporated into new GIS. This is important for sites that have been excavated for many years prior to the advent of modern technologies, data collection techniques, and GIS. With regards to this study, the methods presented were set up and applied for the high-resolution recording of excavations, mapping of the chamber and parts of the cave system, data collection for the spatial analysis of the semi-articulated remains of the assemblage, and spatial analysis of both the surface and subsurface deposits of the Dinaledi site.

A broader analysis of the assemblage was conducted by way of spatial analysis and is presented in Chapter 6. Spatial data of both surface and subsurface material were collected by means of methods applied in Chapter 4, plotted, and analysed to determine site formation processes in the Dinaledi Chamber. Bone material found on the surface of the Dinaledi Chamber has clearly been moved or transported, as evident from the spatial analyses. The agent of such movement of material is most probably due to sediment creep and slump, processes acting on a number of areas within the chamber. As noted by Dirks et al. (2015) the transportation of skeletal elements into, or within the chamber has been precluded, as no material shows any taphonomic evidence of fluvial modifications such as abrasion patterns caused by the movement of bone in water, smoothing or rounding, the development of polish or frosting, or indications of pitting, denting, and chipping caused by impact. Thus surface material and fragmented remains found in the chamber are products of post-depositional disturbance, a combination of sediment pressure on skeletal elements, human activity, and

geological processes. This is consistent with evidence presented in the spatial analysis of this study (Chapter 6).

Integration of Geological, Decompositional and Spatial Analyses

Each analysis (described in Chapters 3, 5, and 6) contributed unique insights into site formation processes in the Dinaledi Chamber. However, an integration of all three analyses (geological, decompositional and spatial) is most valuable for understanding the Dinaledi assemblage in its present context. Geological and taphonomic analyses conducted as part of this work have asserted that the Dinaledi assemblage is the result of autochthonous sediment accumulation and the introduction of bone material over a series of time, possibly introduced from a single-entry point, at a higher level than the main excavation pit. This in support for both Hypotheses 1 and 2 outlined in the beginning of this chapter. Decompositional analysis of elements from the assemblage suggest that localised decomposition of certain elements took place within the assemblage, lending support to Hypothesis 5. This post-mortem deposition of hominin bodies does not falsify or invalidate the hypothesis of deliberate body disposal set out by Dirks et al. (2015). However, the spatial analysis presented here suggests that at surface and subsurface level, material in the chamber is seemingly commingled as a result of sediment creep and slump (Hypothesis 4). The spatial analysis does not account for the single point of origin of material that has entered the chamber hypothesised by Dirks et al. (2015) (and Hypothesis 2), and suggests further excavation work to be undertaken in specific locations of the chamber in order to address such questions.

Hypothesis 3 presented earlier in this chapter states that drainage pits within the Dinaledi Chamber assisted the flow and movement of sediment and bone material. While the geological analysis (Chapter 3) can to some extent confirm this, it is difficult to draw this conclusion from the spatial analyses (Chapter 6). Taphonomic analyses of the material presented in Chapter 3 supports the hypothesis (Hypothesis 6) that identifiable taphonomic features represent with regularity across this assemblage.

Taken together, analyses show that site formation processes in the Dinaledi Chamber were a series of independent and interdependent processes over time, including the deposition of

autochthonous sediment, with the introduction of multiple periods of post-mortem decomposition of hominin bodies. This supports the hypothesis (Hypothesis 4) that sorting of material is due to natural processes occurring within the Dinaledi Chamber. These processes, coupled with natural processes of sediment creep and slump, and perhaps movement from the underlying water table, have created a commingled assemblage that requires a continuation of the multi-disciplinary investigation applied herein, to fully comprehend natural processes combined with purported hominin interactions leading to the formation of the Dinaledi assemblage, Rising Star Cave, CoH.

Conclusion

This study focuses on three-dimensional data as it can be applied to the palaeontological and archaeological disciplines, and the roles of spatial analysis and GIS in archaeology. It is part of a much larger research project attempting to understand the taphonomic and geological context of the Dinaledi hominin assemblage within the Rising Star Cave system, as well as to describe the morphology of the newly discovered hominin *Homo naledi*. The chapters that follow discuss the morphology and context of the Dinaledi assemblage, and the spatial distribution, spatial taphonomy, and site formation processes at the U.W. 101 site. The unique challenges presented by the Rising Star cave environment necessitated the design of a novel approach to understanding site formation processes in the Dinaledi Chamber, the results of which can also be applied to new palaeoanthropological cave sites in the CoH and elsewhere.

CHAPTER TWO: *HOMO NALEDI*, A NEW SPECIES OF THE GENUS *HOMO* FROM THE DINALEDI CHAMBER, SOUTH AFRICA*

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Homo naledi, a new species of the genus *Homo* from the Dinaledi Chamber, South Africa

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Abstract *Homo naledi* is a previously-unknown species of extinct hominin discovered within the Dinaledi Chamber of the Rising Star cave system, Cradle of Humankind, South Africa. This species is characterized by body mass and stature similar to small-bodied human populations but a small endocranial volume similar to australopiths. Cranial morphology of *H. naledi* is unique, but most similar to early *Homo* species including *Homo erectus*, *Homo habilis* or *Homo rudolfensis*. While primitive, the dentition is generally small and simple in occlusal morphology. *H. naledi* has humanlike manipulatory adaptations of the hand and wrist. It also exhibits a humanlike foot and lower limb. These humanlike aspects are contrasted in the postcrania with a more primitive or australopith-like trunk, shoulder, pelvis and proximal femur. Representing at least 15 individuals with most skeletal elements repeated multiple times, this is the largest assemblage of a single species of hominins yet discovered in Africa.

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Introduction

Fossil hominins were first recognized in the Dinaledi Chamber in the Rising Star cave system in October 2013. During a relatively short excavation, our team recovered an extensive collection of 1550 hominin specimens, representing nearly every element of the skeleton multiple times (**Figure 1**), including many complete elements and morphologically informative fragments, some in articulation, as well as smaller fragments many of which could be refit into more complete elements. The collection is a morphologically homogeneous sample that can be attributed to no previously-known hominin species. Here we describe this new species, *Homo naledi*. We have not defined *H. naledi* narrowly based on a single jaw or skull because the entire body of material has informed our understanding of its biology.

eLife digest Modern humans, or *Homo sapiens*, are now the only living species in their genus. But as recently as 100,000 years ago, there were several other species that belonged to the genus *Homo*. Together with modern humans, these extinct human species, our immediate ancestors and their close relatives, are collectively referred to as 'hominins'.

Now Berger et al. report the recent discovery of an extinct species from the genus *Homo* that was unearthed from deep underground in what has been named the Dinaledi Chamber, in the Rising Star cave system in South Africa. The species was named *Homo naledi*; 'naledi' means 'star' in Sotho (also called Sesotho), which is one of the languages spoken in South Africa.

The unearthed fossils were from at least 15 individuals and include multiple examples of most of the bones in the skeleton. Based on this wide range of specimens from a single site, Berger et al. describe *Homo naledi* as being similar in size and weight to a small modern human, with human-like hands and feet. Furthermore, while the skull had several unique features, it had a small braincase that was most similar in size to other early hominin species that lived between four million and two million years ago. *Homo naledi*'s ribcage, shoulders and pelvis also more closely resembled those of earlier hominin species than those of modern humans.

The *Homo naledi* fossils are the largest collection of a single species of hominin that has been discovered in Africa so far and, in a related study, Dirks et al. describe the setting and context for these fossils. However, since the age of the fossils remains unclear, one of the next challenges will be to date the remains to provide more information about the early evolution of humans and their close relatives.

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Order Primates LINNAEUS 1758
Suborder Anthroidea MIVART 1864
Superfamily Hominoidea GRAY 1825
Family Hominidae GRAY 1825
Tribe Hominini GRAY 1825
Genus *Homo* LINNAEUS 1758
Homo naledi sp. nov. urn:lsid:zoobank.org:pub:00D1E81A-6E08-4A01-BD98-79A2CEAE2411

Etymology

The word *naledi* means 'star' in the Sotho language and refers to the Dinaledi Chamber's location within the Rising Star cave system.

Locality

The Dinaledi chamber is located approximately 30 meters underground, within the Rising Star cave system at about 26°1'13" S; 27°42'43" E. The system lies within the Malmani dolomites, approximately 800 meters southwest of the well-known site of Swartkrans in the Cradle of Humankind World Heritage Site, Gauteng Province, South Africa.

Horizon and associations

The present sample of skeletal material from the Dinaledi Chamber was recovered during two field expeditions, in November 2013 and March 2014.

Six specimens from an ex situ context can be identified as bird bones, and few fragmentary rodent remains have been recovered within the excavation area. Neither of these faunal constituents can presently be associated with the hominin fossil collection (Dirks et al., 2015).

Aside from these limited faunal materials, the Dinaledi collection is entirely composed of hominin skeletal and dental remains. The collection so far comprises 1550 fossil hominin specimens, this number includes 1413 bone specimens and 137 isolated dental specimens; an additional 53 teeth are present in mandibular or maxillary bone specimens. Aside from the fragmentary rodent teeth, all dental crowns (n = 179) are hominin, recovered both from surface collection and excavation. Likewise, aside from the few bird elements, all morphologically informative bone specimens are clearly hominin. In all cases where elements are repeated in the sample, they are morphologically homogeneous, with



Figure 1. Dinaledi skeletal specimens. The figure includes approximately all of the material incorporated in this diagnosis, including the holotype specimen, paratypes and referred material. These make up 737 partial or complete anatomical elements, many of which consist of several refitted specimens. Specimens not identified to element, such as non-diagnostic long bone or cranial fragments, and a subset of fragile specimens are not shown here. The 'skeleton' layout in the center of the photo is a composite of elements that represent multiple individuals. This view is foreshortened; the table upon which the bones are arranged is 120-cm wide for scale.

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variation consistent with body size and sex differences within a single population. These remains represent a minimum of 15 hominin individuals, as indicated by the repetition and presence of deciduous and adult dental elements.

The geological age of the fossils is not yet known. Excavations have thus far recovered hominin material from Unit 2 and Unit 3 in the chamber (Dirks *et al.*, 2015). Surface-collected hominin material from the present top of Unit 3, which includes material derived from both Unit 2 and Unit 3, represents a minority of the assemblage, and is morphologically indistinguishable from material excavated from in situ within Unit 3. In addition to general morphological homogeneity including cranial shape, distinctive morphological configurations of all the recovered first metacarpals, femora, molars, lower premolars and lower canines, are identical in both surface-collected and excavated specimens (see Figure 14 later in the text). These include traits not found in any other hominin species yet described. These considerations strongly indicate that this material represents a single species, and not a commingled assemblage.

Holotype, paratypes, and referred materials

Holotype

Dinaledi Hominin 1 (DH1) comprises the partial calvaria, partial maxilla, and nearly complete mandible of a presumed male individual, based on size and morphology within the sample (Figure 2; Supplementary file 1). The holotype was recovered in situ during excavations within the Dinaledi Chamber in March of 2014, embedded in unconsolidated fine clay matrix (Dirks *et al.*, 2015). The holotype is housed in the Evolutionary Studies Institute at the University of the Witwatersrand, Johannesburg, South Africa.

Paratypes

Dinaledi Hominin 2 (DH2) is a partial calvaria that preserves parts of the frontal, left and right parietals, right temporal, and occipital (Figure 3; Supplementary file 1). Dinaledi Hominin 3 (DH3) is a partial

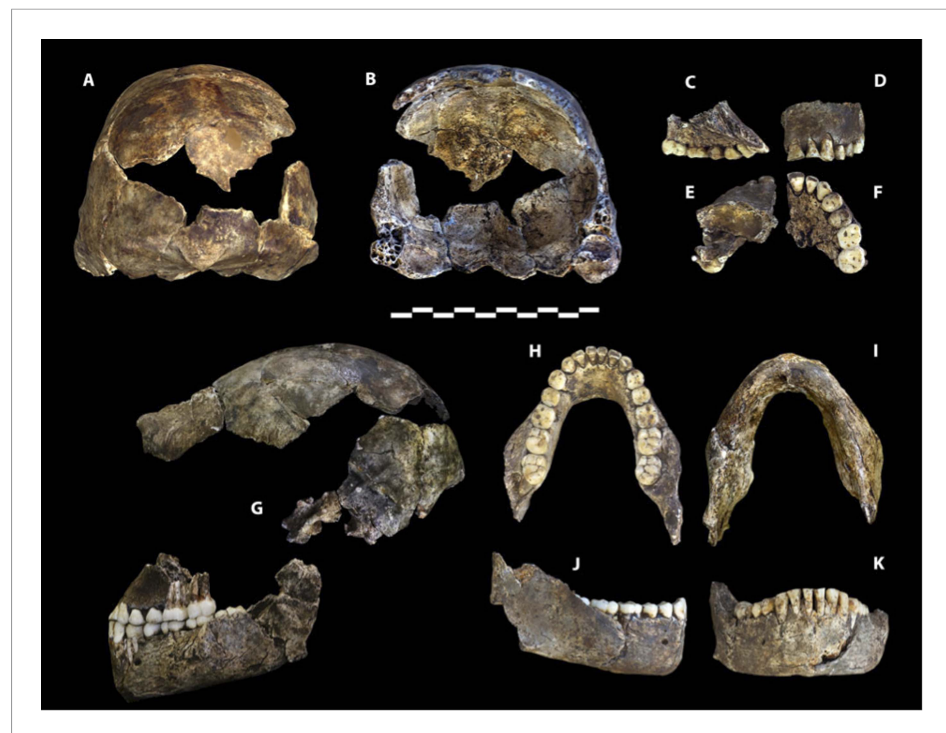


Figure 2. Holotype specimen of *Homo naledi*, Dinaledi Hominin 1 (DH1). U.W. 101-1473 cranium in (A) posterior and (B) frontal views (frontal view minus the frontal fragment to show calvaria interior). U.W. 101-1277 maxilla in (C) medial, (D) frontal, (E) superior, and (F) occlusal views. (G) U.W. 101-1473 cranium in anatomical alignment with occluded U.W. 101-1277 maxilla and U.W. 101-1261 mandible in left lateral view. U.W. 101-1277 mandible in (H) occlusal, (I) basal, (J) right lateral, and (K) anterior views. Scale bar = 10 cm.

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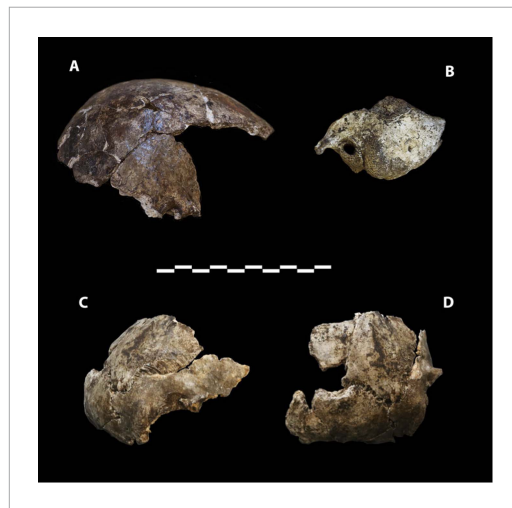


Figure 3. Cranial paratypes. (A) DH2, right lateral view. (B) DH5, left lateral view. (C) DH4, right lateral view. (D) DH4, posterior view. Scale bar = 10 cm.

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calvaria of a presumed female individual that preserves parts of the frontal, left parietal, left temporal, and sphenoid (**Figure 4, Supplementary file 1**). Dinaledi Hominin 4 (DH4) is a partial calvaria that preserves parts of the right temporal, right parietal, and occipital (**Figure 3; Supplementary file 1**). Dinaledi Hominin 5 (DH5) is a partial calvaria that preserves part of the left temporal and occipital (**Figure 3; Supplementary file 1**). U.W. 101-377 is a mandibular fragment that preserves dental anatomy in an unworn state; at present it cannot be definitively associated with any of these Dinaledi Hominin (DH) individuals, and indeed might represent another individual (**Figure 5; Supplementary file 1**). These cranial specimens agree closely in nearly all morphological details where they overlap in areas preserved except those we interpret as related to sex.

Dinaledi hand 1 (H1) is a nearly complete (missing only the pisiform) right hand, found articulated in association, comprising specimens

U.W. 101-1308 to –1311, –1318 to –1321, –1325 to –1329, –1351, –1464, and –1721 to –1732 (**Figure 6; Supplementary file 1**). U.W. 101-1391 is a proximal right femur preserving part of the head, the neck, some of the lesser and greater trochanter, and the proximal shaft (**Figure 7; Supplementary file 1**). U.W. 101-484 is a right tibial diaphysis missing only the proximal end (**Figure 8; Supplementary file 1**). Dinaledi foot 1 (F1) is a partial foot skeleton missing only the medial

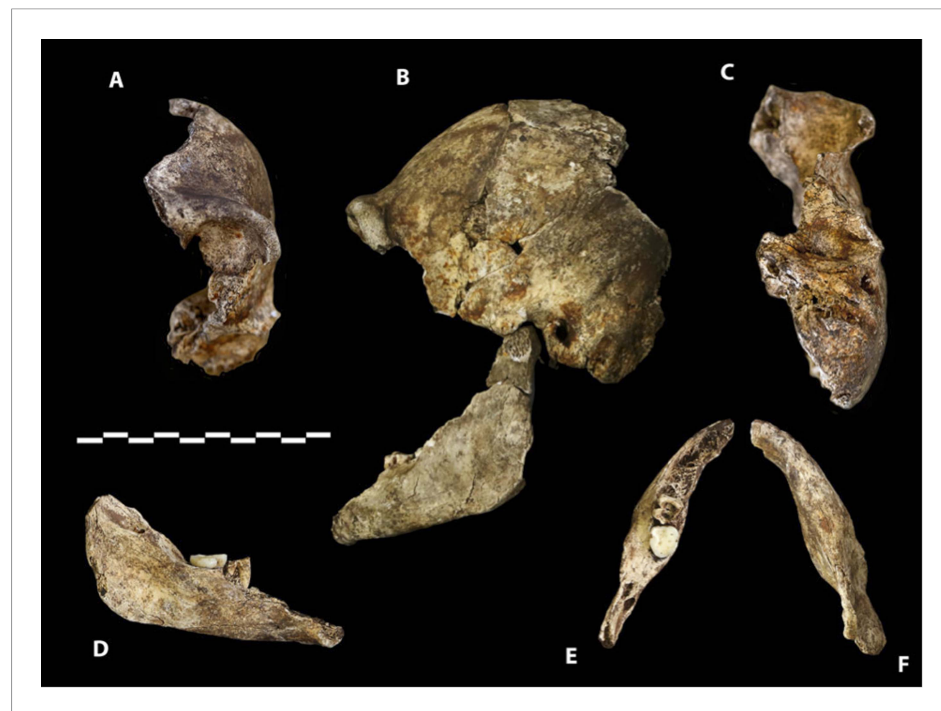


Figure 4. Paratype DH3. (A) Frontal view. (B) Left lateral view, with calvaria in articulation with the mandible (U.W. 101-361). (C) Basal view. Mandible in (D) medial view; (E) occlusal view; (F) basal view. DH3 was a relatively old individual at time of death, with extreme tooth wear. Scale bar = 10 cm.

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Figure 5. U.W. 101-377 mandible. (A) Lateral view; (B) medial view; (C) basal view; (D) occlusal view. (D) The distinctive mandibular premolar morphology with elongated talonids in unworn state. Scale bar = 2 cm. DOI: [10.7554/eLife.09560.007](https://doi.org/10.7554/eLife.09560.007)

cuneiform and the phalanges of rays II–V. Foot 1 is composed of specimens U.W. 101-1322, –1417 to –1419, –1439, –1443, –1456 to –1458, –1551, –1553, –1562, and –1698 (**Figure 9**; **Supplementary file 1**).

Referred material

Referred material is also listed in **Supplementary file 1**. We refer to *H. naledi* all hominin material from the Dinaledi collection that can be identified to element; in total, the holotypes, paratypes and referred material comprise 737 partial or complete anatomical elements.

Specimen numbers in the collection are assigned at the point of excavation. Later laboratory analyses allowed us to refit specimens into more complete elements, which we have used as units of anatomical study. Here we refer to refitted elements by only a single specimen number; either the number of the most constitutive specimen, or the first diagnostic part to be discovered. DH designations are reserved for clearly associated individuals; at this time these are limited to the five partial crania designated

above. Future excavation and analyses will certainly uncover more refits among specimens. As refits are found, all numbers assigned to refitted elements will remain stable, and all numbers in **Supplementary file 1** will be retained.

The collection is morphologically homogeneous in all duplicated elements, except for those anatomical features that normally reflect body size or sex differences in other primate taxa. Therefore, although we refer to the holotype and the paratypes for differential diagnoses; the section describing the overall anatomy encompasses all morphologically informative specimens.

Differential diagnosis

This comprehensive differential diagnosis is based upon cranial, dental and postcranial characters. The hypodigms used for other species are detailed in the 'Materials and methods'. We examined original specimens for most species, except where indicated in the 'Materials and methods'; when we relied on other sources for anatomical observations we indicate this. A summary of traits of *H. naledi* in comparison to other species is presented in **Supplementary file 2**. Comparative cranial and mandibular measures are presented in **Table 1**, and comparative dental measures are provided in **Table 2**.

Cranium, mandible, and dentition (DH1, DH2, DH3, DH4, DH5, U.W. 101-377)

The cranium of *H. naledi* does not have the well-developed crest patterns that characterize *Australopithecus garhi* (Asfaw et al., 1999) and species of the genus *Paranthropus*, nor the derived facial morphology seen in the latter genus. The mandible of *H. naledi* is notably more gracile than those of *Paranthropus*. Although maxillary and mandibular incisors and canines of *H. naledi* overlap in size with those of *Paranthropus*, the post-canine teeth are notably smaller than those of *Paranthropus* and *Au. garhi*, with mandibular molars that are buccolingually narrow.

H. naledi differs from *Australopithecus afarensis* and *Australopithecus africanus* in having a pentagonal-shaped cranial vault in posterior view, sagittal keeling, widely spaced temporal lines, an angular torus, a deep and narrow digastric fossa, an external occipital protuberance, an anteriorly positioned root of the zygomatic process of the maxilla, a broad palate, and a small canine jugum lacking anterior pillars. The anterior and lateral vault of *H. naledi* differs from *Au. afarensis* and *Au. africanus* in exhibiting only slight post-orbital constriction, frontal bossing, a well-developed supraorbital torus with a well-defined supratatorial sulcus, temporal lines that are positioned on the



Figure 6. Hand 1. Palmar view on left; dorsal view on right. This hand was discovered in articulation and all bones are represented except for the pisiform. The proportions of digits are humanlike and visually apparent, as are the expanded distal apical tufts on all digits, the robust pollical ray, and the unique first metacarpal morphology.
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posterior rather than the superior aspect of the supraorbital torus, a root of the zygomatic process of the temporal that is angled downwards approximately 30° relative to the Frankfort Horizontal (FH) and which begins its lateral expansion above the mandibular fossa rather than the EAM, a mandibular



Figure 7. U.W. 101-1391 paratype femur. (A) Medial view; (B) posterior view; (C) lateral view; (D) anterior view. The femur neck is relatively long and anteroposteriorly compressed. The anteversion of the neck is evident in medial view. Scale bar = 2 cm.
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fossa that is positioned medial to the wall of the temporal squame, a small postglenoid process that contacts the tympanic, a coronally oriented petrous, and a small and obliquely oriented EAM. The *H. naledi* mandible exhibits a more gracile symphysis and corpus, a more vertically inclined symphysis, a slight mandibular incurvation delineating a faint mental trigon, and a steeply inclined posterior face of the mandibular symphysis without a post incisive planum. The incisors of *H. naledi* overlap in size with some specimens of *Au. africanus*, though the canines and post-canine dentition are notably smaller, with relatively narrow buccolingual dimensions of the mandibular molars. The maxillary I¹ lacks a median lingual ridge and exhibits a broad and uninflated lingual cervical prominence, the lingual mesial and distal marginal ridges do not merge onto the cervical prominence in the maxillary I², the mandibular canine exhibits only a weak lingual median ridge and a broad and uninflated lingual cervical prominence, and the buccal grooves on the maxillary premolars are only weakly developed. *H. naledi* exhibits a small and isolated Carabelli's feature in the maxillary molars, unlike the more prominent and extensive Carabelli's feature of *Australopithecus*. Moreover, the *H. naledi* mandibular molars possess small, mesiobuccally restricted protostylids that do not intersect the buccal groove, differing from the typically enlarged, centrally positioned protostylids that intersect the buccal groove in *Australopithecus*.

The cranium of *H. naledi* differs from *Australopithecus sediba* (Berger et al., 2010) in exhibiting sagittal keeling, a more pronounced supraorbital torus and supratotal sulcus, a weakly arched supraorbital contour with rounded lateral corners, an angular torus, a well-defined supramastoid crest, a curved superior margin of the temporal squama, a root of the zygomatic process of the temporal that is angled downwards approximately 30° relative to FH, a flattened nasoalveolar clivus, weak canine juga, an anteriorly positioned root of the zygomatic process of the maxilla, and a relatively broad palate that is anteriorly shallow. The *H. naledi* mandible (DH1) has a mental foramen positioned superiorly on the corpus that opens posteriorly, unlike the mid-corpus height, more laterally opening mental foramen of *Au. sediba*. The maxillary and mandibular teeth of *H. naledi* are smaller than those of *Au. sediba*, with mandibular molars that are buccolingually narrow. The lingual mesial and distal marginal ridges do not merge onto the cervical prominence in the maxillary I², the paracone of the

maxillary P³ is equal in size to the protocone, the protoconid and metaconid of the mandibular molars are equally mesially positioned, and the lingual cusps of the molars are positioned at the occlusobuccal margin while the buccal cusps are positioned slightly lingual to the occlusobuccal margin. Also, *Au. sediba* shares with other australopiths a protostylid that is centrally located and which intersects the buccal groove of the lower molars, unlike the small and mesiobuccally restricted protostylid that does not intersect the buccal groove in *H. naledi*.

The cranium of *H. naledi* differs from *Homo habilis* in exhibiting sagittal keeling, a weakly arched supraorbital contour, temporal lines that are positioned on the posterior rather than the superior aspect of the supraorbital torus, an angular torus, an occipital torus, only slight post-orbital constriction, a curved superior margin of the temporal squama, a suprimeatal spine, a weak crista petrosa, a prominent Eustachian process, a small EAM, weak canine juga, and an anteriorly positioned root of the zygomatic process of the maxilla. Mandibles attributed to *H. habilis* show a weakly inclined, shelf-like post incisive planum with a variably developed superior transverse torus, unlike the steeply inclined posterior face of the mandibular symphysis of *H. naledi*, which lacks both a post incisive planum or



Figure 8. U.W. 101-484 paratype tibia. (A) Anterior view; (B) medial view; (C) posterior view; (D) lateral view. The tibiae are notably slender for their length. Scale bar = 10 cm.
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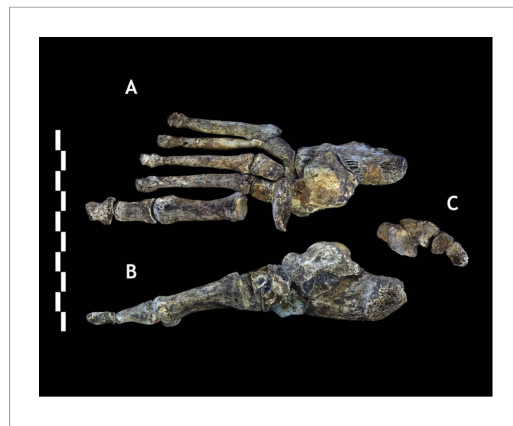


Figure 9. Foot 1 in (A) dorsal view; and (B) medial view. (C) Proximal articular surfaces of the metatarsals of Foot 1, shown in articulation to illustrate transverse arch structure. Scale bar = 10 cm.
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supratoral sulcus, temporal lines that are positioned on the posterior rather than the superior aspect of the supraorbital torus, an occipital torus, an external occipital protuberance, only slight post-orbital constriction, a small postglenoid process, a weak crista petrosa, a laterally inflated mastoid process, a canine fossa, incisors that project anteriorly beyond the bi-canine line, and a shallow anterior palate. As in *H. habilis*, mandibles attributed to *H. rudolfensis* show a weakly inclined, shelf-like post incisive planum with a variably developed superior transverse torus, unlike the steeply inclined posterior face of the mandibular symphysis of DH1, the latter of which lacks either a post incisive planum or superior transverse torus. The mandibular symphysis and corpus of *H. naledi* are more gracile than those attributed to *H. rudolfensis*, and the *H. naledi* mandible (DH1) has a mental foramen positioned superiorly on the corpus that opens posteriorly, unlike the mid-corpus height, more laterally opening mental foramen of *H. rudolfensis*. The maxillary and mandibular dentition of *H. naledi* is smaller than that of most specimens of *H. rudolfensis*, with only KNM-ER 60000 and KNM-ER 62000 appearing similar in size for some teeth (Leakey et al., 2012). The molars of *H. naledi* lack crenulation, secondary fissures, or supernumerary cusps common in *H. rudolfensis*. The buccal grooves of the maxillary premolars are weak in *H. naledi*, and the protoconid and metaconid of the mandibular molars are equally mesially positioned.

H. naledi lacks the typically distinctive long and low cranial vault of *Homo erectus*, as well as the metopic keeling that is typically present in the latter species. *H. naledi* also differs from *H. erectus* in having a distinct external occipital protuberance in addition to the tuberculum lineare, a laterally inflated mastoid process, a flat and squared nasoalveolar clivus, and an anteriorly shallow palate. The parasagittal keeling that is present between bregma and lambda in *H. naledi* (DH1 and DH3) is less marked than often occurs in *H. erectus*, including in small specimens such as KNM-ER 42700 and the Dmanisi cranial sample. Also unlike most specimens of *H. erectus*, *H. naledi* has a small vaginal process, a weak crista petrosa, a marked Eustachian process, and a small EAM. The mandible of *H. erectus* shows a moderately inclined, shelf-like post incisive planum terminating in a variably developed superior transverse torus, differing from the steeply inclined posterior face of the *H. naledi* mandibular symphysis, which lacks both a post incisive planum or a superior transverse torus. The mental foramen is positioned superiorly and opens posteriorly in DH1, unlike the mid-corpus height, more laterally opening mental foramen of *H. erectus*. The maxillary and mandibular incisors and canines of *H. naledi* are smaller than typical of *H. erectus*. The mandibular P₃ of *H. naledi* is more molarized and lacks the occlusal simplification seen in *H. erectus*, they reveal a symmetrical occlusal outline, and multiple roots (2R: MB+D) not typically seen in *H. erectus*. Furthermore, the molars of *H. naledi* lack crenulation, secondary fissures, or supernumerary cusps common in *H. erectus*.

H. naledi lacks the reduced cranial height of *Homo floresiensis*, and displays a marked angular torus and parasagittal keeling between bregma and lambda that is absent in the latter species. *H. naledi*

Table 1. Cranial and mandibular measurements for *H. naledi*, early hominins, and modern humans

Measurement definitions as in Wood (1991)	P. aethiopicus										H. sapiens			
	P.	P.	P.	Au.	Au.	Au.	H. naledi	H. habilis	H. rudolfensis	H. erectus	MP	H.	MP	H.
Cranium														
Cranial capacity	–	410	485	493	457	467	420	513	610	776	865	1266	1266	1330
Porion height	6	72	74	–	86	70	67	81	77	90	94	101	101	112
Posterior cranial length	3	58	47	54	60	44	–	65	60	70	79	99	99	81
Bi-parietal breadth	9	94	98	–	90	99	100	103	107	118	129	142	142	132
Bi-temporal breadth	10	110	109	108	115	104	101	107	112	126	131	146	146	127
Closest approach of temporal lines	–	crest*	crest*	crest*	crest*	21	56	52	35	51	72	101	101	96
Supraorbital height index	–	46	53	50	51	60	56	56	64	59	56	62	62	71
Minimum post-orbital breadth	–	62	66	70	77	67	70	68	75	78	89	96	96	97
Superior facial breadth	49	100	107	109	–	95	86	86	97	113	110	124	124	107
Post-orbital constriction index†	–	62	61	64	–	69	81	79	72	74	81	80	80	91
EAM area (as an ellipse)‡	–	77	80	103	70	96	–	38	76	–	95	85	85	61
Root of zygomatic process origin	–	P4	P4	P3 to M1	P4 to M1	P4 to M1	P4	P3 to P4	P4	P4 to M1	P4 to M1	M1	M1	M1
Petromedian angle	137	50	45	50	31	33	–	55	48	–	52	55	55	46
Maxilloalveolar process														
Maxilloalveolar length	87	94	78	69	67	71	63	57	65	68	66	69	69	55
Maxilloalveolar breadth	88	83	76	69	68	66	63	71	68	72	70	72	72	62
Palate breadth	91	32	40	35	30	36	29	44	38	40	38	56	56	40

Table 1. Continued on next page

Table 1. Continued

Measurement definitions as in Wood (1991)	Measurements											
	P. aethiopicus	P. boisei	P. robustus	Au. afarensis	Au. africanus	Au. sediba	H. naledi	H. habilis	H. rudolfensis	H. erectus	MP Homo	H. sapiens
Palate depth at incisive fossa	3	11	10	10	9	10	5	10	13	11	10	9
Palate depth at M1	7	18	11	11	13	10	10	12	16	15	18	13
Mandible												
Symphysis height	37	49	42	39	37	32	33	31	37	35	34	34
Symphysis width	26	28	25	20	21	18	18	20	24	18	17	14
Symphysis area at M1 (as an ellipse)†	757	1114	835	623	606	452	467	393	723	519	474	365
Corpus height at M1	38	42	36	34	32	30	26	29	36	31	31	28
Corpus breadth at M1	25	29	26	20	21	18	16	20	22	19	19	13
Corpus area at M1 (as an ellipse)‡	742	955	736	540	539	405	326	425	631	458	469	296
Mental foramen height index§	51	50	54	58	53	50	40	46	49	48	48	50

*At least in presumed males.
†Post-orbital breadth/superior facial breadth x 100.
‡Following the formula ($\pi \times (\text{corpus height}/2) \times (\text{corpus breadth}/2)$).
§Height of mental foramen from alveolar border relative to corpus height at the mental foramen.
MP, Middle Pleistocene.
Unless otherwise indicated measurements are defined as in Wood (1991). Chord distances are in mm. Data for *H. naledi* collected from original fossils or laser scans by DJdeR and HMG; comparative data collected by DJdeR on original fossils and casts and supplemented by data from Wood (1991).
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Table 2. Dental measures for *H. naledi* and comparative hominin species

Maxillary

	I ¹			I ²			C			P ³			P ⁴			M ¹			M ²			M ³		
	MD	LL	MD	LL	MD	LL	MD	LL	MD	LL	MD	LL	MD	LL	MD	BL	MD	BL	MD	BL	MD	BL	MD	BL
<i>Au. anamensis</i>	n	3	5	–	–	2	6	7	7	7	6	5	5	3	12	10	10	8	9	8	9	8	9	8
	mean	10.8	8.7	–	–	7.3	11.0	10.6	9.9	9.9	12.6	8.9	8.9	13.6	11.5	12.9	13.0	14.4	12.5	14.2	12.5	14.2	12.5	14.2
	range	9.1–12.4	8.2–9.3	–	–	7.0–7.5	9.9–12.3	9.1–11.8	8.2–11.8	10.1–14.3	7.2–12.1	12.6–14.2	7.8–14.3	9.0–16.7	10.9–16.3	12.9–16.1	11.1–15.7	13.0–15.7	11.1–15.7	13.0–15.7	11.1–15.7	13.0–15.7	11.1–15.7	13.0–15.7
<i>Au. afarensis</i>	n	7	8	9	9	15	15	15	12	10	18	18	18	12	16	13	10	11	11	11	11	11	11	11
	mean	10.7	8.4	7.5	7.2	9.9	10.8	8.8	8.8	12.4	9.1	9.1	9.1	12.4	12.0	13.4	12.9	14.6	12.7	14.5	12.7	14.5	12.7	14.5
	range	9.9–11.8	7.1–9.7	6.6–8.2	6.2–8.1	8.8–11.6	9.3–12.5	7.7–9.7	11.3–13.4	7.6–10.8	11.1–14.5	10.5–13.8	12.0–15.0	12.1–13.6	13.4–15.2	10.9–14.8	13.1–16.3	13.4–15.2	10.9–14.8	13.1–16.3	13.4–15.2	10.9–14.8	13.1–16.3	13.4–15.2
<i>Au. africanus</i>	n	15	15	11	10	16	13	26	26	25	20	21	20	20	21	20	23	24	27	28	27	28	27	28
	mean	10.7	8.3	6.9	6.8	9.9	10.3	9.2	9.2	12.7	9.5	13.4	12.9	13.9	14.1	15.7	14.2	16.0	14.2	16.0	14.2	16.0	14.2	16.0
	range	9.4–12.5	7.4–9.1	5.8–8.0	5.6–7.9	8.8–11.0	8.7–12.0	8.5–10.2	10.7–14.5	7.2–11.0	12.4–15.3	11.7–14.4	12.9–15.3	12.1–16.3	12.8–17.9	11.2–16.9	13.1–18.6	12.8–17.9	11.2–16.9	13.1–18.6	12.8–17.9	11.2–16.9	13.1–18.6	12.8–17.9
<i>Au. sediba</i>	n	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	2	2	1	2	2	2
	mean	10.1	6.9	7.2	6.6	9.0	8.8	9.0	9.0	11.2	9.3	12.1	12.9	12.0	12.9	13.7	13.0	13.7	13.0	13.5	13.7	13.0	13.5	13.7
	range	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	12.6–13.3	12.9–14.1	–	–	–	–
<i>H. naledi</i>	n	–	5	4	8	10	9	10	10	10	7	7	12	13	11	9	7	7	7	7	7	7	7	7
	mean	9.4	6.5	6.6	6.2	8.1	8.6	8.0	8.0	10.5	8.1	11.0	11.6	11.7	12.2	12.8	11.6	12.8	11.6	12.4	12.8	11.6	12.4	12.8
	range	8.8–9.8	6.3–7.0	6.3–7.0	5.8–6.6	7.3–8.9	8.0–9.6	7.7–8.4	9.8–11.0	7.7–8.7	10.5–11.2	10.5–12.4	11.2–12.4	11.0–13.0	11.9–13.6	11.0–12.7	11.4–13.4	11.9–13.6	11.0–12.7	11.4–13.4	11.9–13.6	11.0–12.7	11.4–13.4	11.9–13.6
<i>H. habilis</i>	n	2	2	4	4	2	3	7	7	7	8	8	13	13	7	7	7	7	7	7	7	7	7	7
	mean	10.6	8.0	7.4	6.6	9.0	9.8	9.0	9.0	11.9	9.2	12.1	12.7	13.0	12.7	14.3	12.3	14.3	12.3	14.7	14.3	12.3	14.7	14.3
	range	10.1–11.1	7.3–8.7	6.7–8.1	6.0–7.9	8.5–9.4	8.5–11.6	8.1–9.6	11.0–12.7	8.5–9.9	11.0–13.1	11.6–13.9	12.1–14.1	11.8–13.5	13.5–16.2	11.3–13.9	13.2–16.6	13.5–16.2	11.3–13.9	13.2–16.6	13.5–16.2	11.3–13.9	13.2–16.6	13.5–16.2
<i>H. rudolfensis</i>	n	1	1	–	–	1	1	1	1	1	2	2	2	2	2	2	2	2	1	1	2	1	1	1
	mean	12.3	7.7	–	–	11.5	12.5	10.5	10.5	13.6	10.2	12.5	14.0	14.0	14.3	15.8	13.3	15.8	13.3	13.5	15.8	13.3	13.5	15.8
	range	–	–	–	–	–	–	–	–	–	9.7–10.7	11.1–13.8	13.9–14.2	13.3–14.8	14.1–17.6	14.1–17.6	–	–	–	–	–	–	–	–
<i>H. erectus</i>	n	11	12	6	6	12	12	27	27	27	30	29	34	32	22	22	16	22	16	16	22	16	16	16
	mean	10.3	8.1	7.7	8.0	9.5	10.0	8.5	8.5	11.8	8.1	11.6	12.2	13.2	12.0	13.3	10.5	13.3	10.5	12.8	13.3	10.5	12.8	13.3
	range	8.1–12.6	7.0–11.7	6.0–8.3	6.9–8.5	8.5–11.1	9.0–11.8	7.1–10.1	9.5–13.8	7.0–9.4	9.9–13.4	10.1–14.6	11.0–15.9	10.3–13.6	10.9–15.5	8.7–14.7	10.4–15.8	10.9–15.5	8.7–14.7	10.4–15.8	10.9–15.5	8.7–14.7	10.4–15.8	10.9–15.5
<i>H. neanderthalensis</i>	n	28	37	35	41	28	29	16	16	17	21	19	23	24	27	28	22	28	22	21	28	22	21	21
	mean	9.7	8.5	8.0	8.4	8.8	10.1	8.0	8.0	10.6	7.8	10.6	11.6	12.3	10.9	12.5	9.9	12.5	9.9	12.3	12.5	9.9	12.3	12.5
	range	8.2–11.8	7.3–9.9	5.8–9.3	5.8–9.9	7.2–10.0	7.6–11.4	6.6–9.3	8.4–11.8	5.9–11.5	8.3–11.7	9.5–13.5	11.0–14.2	8.9–15.9	10.8–14.6	8.2–11.4	9.8–14.6	10.8–14.6	8.2–11.4	9.8–14.6	10.8–14.6	8.2–11.4	9.8–14.6	10.8–14.6

Table 2. Continued on next page

Table 2. Continued

Maxillary

	I ¹		I ²		C		P ³		P ⁴		M ¹		M ²		M ³	
	MD	LL	MD	LL	MD	LL	MD	LL	MD	LL	MD	LL	MD	LL	MD	LL
<i>H. heidelbergensis</i>	n 21	23	19	21	27	29	25	25	22	23	25	24	24	23	26	27
	mean 9.6	7.8	7.7	7.8	8.8	9.8	7.9	10.6	7.6	10.3	11.2	11.9	10.2	12.3	8.9	11.6
	range 8.7–10.7	7.1–9.9	7.2–8.4	7.3–8.6	8.1–11.0	8.8–11.8	7.1–9.0	9.2–12.2	7.0–8.8	9.1–11.5	9.9–12.3	10.3–13.2	8.1–12.1	11.1–13.8	7.6–11.0	10.0–13.2
MP/LP African Homo	n 6	6	7	8	4	4	6	6	10	10	14	14	20	20	9	9
	mean 9.0	7.8	7.4	7.2	8.9	9.7	8.4	10.8	8.1	10.8	12.3	13.2	11.0	12.9	9.2	11.7
	range 6.3–10.9	6.6–8.7	6.0–9.3	6.1–8.5	8.2–9.5	8.8–10.0	8.1–8.7	9.9–11.8	7.5–9.3	9.4–12.8	10.4–14.0	12.0–15.0	7.8–13.0	11.0–15.0	7.6–10.2	10.0–13.2

Mandibular

	I ₁		I ₂		C		P ₃		P ₄		M ₁		M ₂		M ₃	
	MD	LL	MD	LL	MD	LL	MD	LL	MD	LL	MD	LL	MD	LL	MD	LL
<i>Au. anamensis</i>	n 2	1	4	3	7	7	8	8	8	8	9	10	7	7	8	8
	mean 6.9	7.4	7.8	8.3	10.0	10.4	12.4	9.2	9.1	11.3	12.9	12.3	14.0	13.4	15.3	13.4
	range 6.8–6.9	–	6.6–8.7	7.9–8.6	6.6–13.9	9.2–11.4	11.3–13.4	8.6–10.0	7.4–9.8	9.6–13.2	11.6–13.8	10.2–14.8	13.0–15.9	12.3–14.9	13.7–17.0	12.1–15.2
<i>Au. afarensis</i>	n 7	8	7	6	13	16	27	26	24	21	32	26	31	27	26	23
	mean 6.7	7.1	6.7	8.0	8.8	10.4	9.6	10.6	9.8	11.0	13.1	12.6	14.3	13.4	15.3	13.5
	range 5.6–7.7	5.6–8.0	6.7–8.8	7.5–11.7	8.0–12.4	7.9–12.6	8.9–13.8	7.7–11.4	9.8–12.8	10.1–14.8	11.0–14.0	12.1–16.5	11.1–15.2	13.4–18.1	11.3–15.3	11.3–15.3
<i>Au. africanus</i>	n 11	12	12	13	23	25	20	21	25	23	29	32	38	38	34	35
	mean 6.2	6.7	7.2	7.9	9.4	10.1	9.7	11.5	10.4	11.6	14.0	13.0	15.7	14.5	16.3	14.6
	range 4.8–6.9	5.7–7.9	5.6–8.1	6.6–9.2	8.5–10.7	8.2–12.1	8.8–11.0	9.9–13.9	8.7–12.3	9.3–13.2	12.4–15.8	11.2–15.1	14.2–17.7	12.8–16.8	13.5–18.5	12.2–16.8
<i>Au. sediba</i>	n –	1	–	1	2	2	1	1	1	1	2	2	2	2	2	2
	mean –	5.9	–	6.6	7.7	8.0	8.1	9.2	8.8	9.7	13.1	11.4	14.5	12.8	14.9	13.2
	range –	–	–	–	7.3–8.0	7.4–8.6	–	–	–	–	13.1–13.1	11.3–11.5	14.4–14.5	12.3–13.2	14.9–14.9	12.5–13.6
<i>H. naledi</i>	n 7	7	5	6	7	7	9	10	6	6	11	11	9	9	6	5
	mean 6.1	5.4	6.9	5.9	7.1	7.1	9.0	8.8	8.7	9.1	12.2	10.7	13.3	11.2	13.4	12.1
	range 5.7–7.0	5.3–5.9	6.6–7.4	5.9–6.0	6.4–7.5	6.9–7.4	8.2–9.4	8.2–9.7	8.3–9.0	8.5–10.2	11.3–12.7	10.3–11.4	12.3–14.0	10.7–12.2	12.9–13.7	11.7–12.8
<i>H. habilis</i>	n 2	2	2	2	3	2	4	4	3	3	5	5	4	4	4	4
	mean 6.4	6.8	7.4	7.6	8.7	9.0	9.6	9.6	9.9	10.5	13.7	11.9	15.0	13.5	15.4	13.3
	range 6.4–6.5	6.7–7.0	7.2–7.7	7.6–7.6	7.6–9.6	7.9–10.0	9.0–10.6	8.6–11.1	9.0–10.5	9.9–11.0	13.0–14.8	10.9–12.8	14.2–15.7	12.0–15.1	14.8–15.9	12.4–14.4

Table 2. Continued on next page

Table 2. Continued
Mandibular

	I ₁		I ₂		C		P ₃		P ₄		M ₁		M ₂		M ₃	
	MD	LL	MD	LL	MD	LL	MD	BL	MD	BL	MD	BL	MD	BL	MD	BL
<i>H. rudolfensis</i>	n	–	1	–	1	–	1	3	6	6	5	5	6	5	3	3
	mean	–	5.4	–	6.7	–	8.3	9.9	10.1	11.4	14.0	12.7	16.0	13.7	16.4	14.1
	range	–	–	–	–	–	–	9.0–10.7	8.8–11.8	9.8–12.2	12.8–15.2	11.4–13.2	14.0–18.3	12.7–14.9	15.6–17.0	13.1–14.6
<i>H. erectus</i>	n	11	12	14	16	14	16	30	25	26	43	43	41	40	26	27
	mean	6.2	6.4	7	7.2	8.7	9	9	10.1	8.7	10.1	12.7	13.3	12.5	12.7	11.7
	range	4.8–7.4	5.8–7.1	5.3–8.1	6.4–8.5	7.0–10.3	8.0–10.4	7.0–12.0	8.2–12.0	7.2–10.3	8.0–12.5	9.9–14.8	10.1–13.3	11.3–15.3	10.8–14.3	10.0–14.2
<i>H. neanderthalensis</i>	n	9	16	23	31	36	41	20	21	23	25	38	26	27	18	20
	mean	5.6	7.2	6.8	7.8	7.8	8.8	7.9	9.1	7.8	9.4	11.8	12.1	11.3	12.0	11.0
	range	4.2–6.4	5.2–8.8	5.9–7.5	6.8–9.0	6.7–8.8	6.8–10.3	6.6–9.1	8.0–10.3	6.5–9.4	8.5–10.5	10.1–13.6	10.2–12.9	9.3–14.0	8.8–12.4	11.2–13.9
<i>H. heidelbergensis</i>	n	21	22	19	20	23	24	22	22	26	29	29	29	29	32	32
	mean	5.6	6.7	6.5	7.3	7.6	8.7	7.9	8.9	7.2	8.7	11.3	11.2	10.5	11.5	10.0
	range	4.8–6.5	6.0–7.5	6.0–7.2	6.6–8.0	6.9–9.0	7.3–10.0	7.2–9.0	7.6–11.6	6.6–8.8	7.2–11.7	10.4–13.8	9.6–13.0	9.7–14.6	8.5–13.9	9.7–13.2
MP/LP African Homo	n	5	5	8	8	8	8	8	8	12	9	16	20	20	13	13
	mean	6.0	6.8	6.8	7.2	8.8	9.6	8.6	9.8	8.6	10.3	13.1	12.5	11.7	12.4	11.5
	range	5.7–6.4	6.1–7.2	5.6–8.3	6.4–8.0	7.8–10.0	8.8–10.3	7.7–9.0	8.6–11.2	6.9–9.6	9.3–11.4	10.7–14.2	10.0–13.0	10.8–15.0	9.2–13.6	10.6–13.5

MP, Middle Pleistocene and LP, Late Pleistocene.
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further has a flat and squared nasoalveolar clivus, unlike the pronounced maxillary canine juga and prominent pillars of *H. floresiensis*. The mandible of *H. floresiensis* shows a posteriorly inclined post incisive planum with superior and inferior transverse tori, differing from the steeply inclined posterior face of the *H. naledi* mandibular symphysis, which lacks both a post incisive planum or a superior transverse torus. Dentally, *H. naledi* is distinguishable from *H. floresiensis* by the mesiodistal elongation and extensive talonid of the mandibular P₄, and the lack of Tomes' root on the mandibular premolars. The molar size gradient of *H. naledi* follows the M1 < M2 < M3 pattern, unlike the M3 < M2 < M1 pattern in *H. floresiensis*, and the mandibular molars are relatively mesiodistally long and buccolingually narrow compared to those of *H. floresiensis*.

H. naledi differs from Middle Pleistocene (MP) and Late Pleistocene (LP) *Homo* (here we include specimens sometimes attributed to the putative Early Pleistocene taxon *Homo antecessor*, and MP *Homo heidelbergensis*, *Homo rhodesiensis*, as well as archaic *Homo sapiens* and Neandertals) in exhibiting a smaller cranial capacity. *H. naledi* has its maximum cranial width in the supramastoid region, rather than in the parietal region. It has a clearly defined canine fossa (similar to *H. antecessor*), a shallow anterior palate, and a flat and a squared nasoalveolar clivus. *H. naledi* lacks the bilaterally arched and vertically thickened supraorbital tori found in MP and LP *Homo*. *H. naledi* also differs in exhibiting a root of the zygomatic process of the temporal that is angled downwards approximately 30° relative to FH, a projecting entoglenoid process, a weak vaginal process, a weak crista petrosa, a prominent Eustachian process, a laterally inflated mastoid process, and a small EAM. The *H. naledi* mandible tends to be more gracile than specimens of MP *Homo*. The mandibular canine retains a distinct accessory distal cuspid not seen in MP and LP *Homo*. Molar cuspal proportions for *H. naledi* do not show the derived reduction of the entoconid and hypoconid that characterizes MP and LP *Homo*. The mandibular M₃ is not reduced in DH1, thus revealing an increasing molar size gradient that contrasts with reduction of the M₃ in MP and LP *Homo*.

H. naledi differs from *H. sapiens* in exhibiting small cranial capacity, a well-defined supraorbital torus and supratoral sulcus, a root of the zygomatic process of the temporal that is angled downwards approximately 30° relative to FH, a large and laterally inflated mastoid with well-developed supramastoid crest, an angular torus, a small vaginal process, a weak crista petrosa, a prominent Eustachian process, a small EAM, a flat and squared nasoalveolar clivus, and a more posteriorly positioned incisive foramen. The *H. naledi* mandible shows a weaker, less well-defined mentum osseum than *H. sapiens*, as well as a slight inferior transverse torus that is absent in humans. The mental foramen is positioned superiorly in *H. naledi*, unlike the mid-corpus height mental foramen of *H. sapiens*. The mandibular canine possesses a distinct accessory distal cuspid not seen in *H. sapiens*. Molar cuspal proportions for *H. naledi* do not show the derived reduction of the entoconid and hypoconid that characterizes *H. sapiens*. The mandibular M₃ is not reduced in *H. naledi*, thus revealing an increasing molar size gradient that contrasts with reduction of the M₃ in *H. sapiens*.

Hand (H1)

H. naledi possesses a combination of primitive and derived features not seen in the hand of any other hominin. H1 is differentiated from the estimated intrinsic hand proportions of *Au. afarensis* in having a relatively long thumb ((Mc1 + PP1)/(Mc3 + PP3 + IP3)) (Rolian and Gordon, 2013; Almécija and Alba, 2014). It is further distinguished from *Au. afarensis*, *Au. africanus*, and *Au. sediba* in having a well-developed crest for both the *opponens pollicis* and first dorsal *interosseous* muscles, a trapezium-scaphoid joint that extends onto the scaphoid tubercle, a relatively large and more palmarly-positioned capitate-trapezoid joint, and/or a saddle-shaped Mc5-hamate joint. *H. naledi* also differs from *Au. sediba* in that it lacks mediolaterally narrow Mc2-5 shafts (Kivell et al., 2011). Manual morphology of *Au. garhi* is currently unknown.

H1 is distinguished from *H. habilis* in having a deep proximal palmar fossa with a well-developed ridge distally for the insertion of the *flexor pollicis longus* muscle on the first distal phalanx, and a more proximodistally oriented trapezium-second metacarpal joint. It also differs from both *H. habilis* and *H. floresiensis* by having a relatively large trapezium-scaphoid joint that extends onto the scaphoid tubercle, and from *H. floresiensis* in having a boot-shaped trapezoid with an expanded palmar surface, and a relatively large and more palmarly-positioned capitate-trapezoid joint (Tocheri et al., 2005, 2007; Orr et al., 2013).

H1 is dissimilar to hand remains attributed to *Paranthropus robustus*/early *Homo* from Swartkrans (Susman, 1988; Susman et al., 2001) in having a relatively small Mc1 base and proximal articular

facet, a saddle-shaped Mc5-hamate joint, and more curved proximal and intermediate phalanges of ray 2–5.

Manual morphology of *H. rudolfensis* is currently unknown, and that of *H. erectus* is largely unknown. Still, H1 differs from a third metacarpal attributed to *H. erectus* s. l., as well as from *Homo neanderthalensis* and *H. sapiens* by lacking a styloid process (Ward et al., 2013).

H1 is further distinguished from *H. neanderthalensis* and *H. sapiens* by its relatively small facets for the Mc1 and scaphoid on the trapezium, its low angle between the Mc2 and Mc3 facets on the capitate, and by its long and curved proximal and intermediate phalanges on rays 2–5.

H1 is differentiated from all known hominins in having a Mc1 that combines a mediolaterally narrow proximal end and articular facet with a mediolaterally wide distal shaft and head, a dorsopalmarly flat and strongly asymmetric (with an enlarged palmar-lateral protuberance) Mc1 head, and the combination of an overall later *Homo*-like carpal morphology combined with proximal and intermediate phalanges that are more curved than most australopiths. H1 also differs from all other known hominins except *H. neanderthalensis* in having non-pollical distal phalanges with mediolaterally broad apical tufts (relative to length).

Femur (U.W. 101-1391)

The femur of *H. naledi* differs from those of all other known hominins in its possession of two well-defined, mediolaterally-running pillars in the femoral neck. The pillars run along the superoanterior and inferoposterior margins of the neck and define a distinct sulcus along its superior aspect.

Tibia (U.W. 101-484)

The tibia of *H. naledi* differs from those of all other known hominins in its possession of a distinct tubercle for the pes anserinus tendon. The tibia differs from other hominins except *H. habilis*, *H. floresiensis*, and (variably) *H. sapiens* in its possession of a rounded anterior border.

Foot (F1)

The foot of *H. naledi* differs from the pedal remains of *Au. afarensis*, *Au. africanus*, and *Au. sediba* in having a calcaneus with a weakly developed peroneal trochlea. F1 also differs from *Au. afarensis* in having a higher orientation of the calcaneal sustentaculum tali. F1 can be further distinguished from pedal remains attributed to *Au. africanus* in having a higher talar head and neck torsion, a narrower Mt1 base, a dorsally expanded Mt1 head, and greater proximolateral to distomedial orientation of the lateral metatarsals. The *H. naledi* foot can be further differentiated from the foot of *Au. sediba* in having a proximodistally flatter talar trochlea, a flat subtalar joint, a diagonally oriented retrotrochlear eminence and a plantar position of the lateral plantar process of the calcaneus, and dorsoplantarly flat articular surface for the cuboid on the Mt4 (Zipfel et al., 2011). Pedal remains of *Au. garhi* are currently unknown, and those of *P. robustus* are too poorly known to allow for comparison.

The *H. naledi* foot can be distinguished from the foot of *H. habilis* by the presence of a flatter, non-sloping trochlea with equally elevated medial and lateral margins, a narrower Mt1 base, greater proximolateral to distomedial orientation of the lateral metatarsals, and a metatarsal robusticity ratio of $1 > 5 > 4 > 3 > 2$. Pedal morphology in *H. rudolfensis* is currently unknown, and that of *H. erectus* is too poorly known to allow for comparison. The *H. naledi* foot can be distinguished from the foot of *H. floresiensis* by a longer hallux and shorter second through fifth metacarpals relative to hindfoot length, and higher torsion of the talar head and neck.

The foot of *H. naledi* can be distinguished from the foot of *H. sapiens* only by its flatter lateral and medial malleolar facets on the talus, its low angle of plantar declination of the talar head, its lower orientation of the calcaneal sustentaculum tali, and its gracile calcaneal tuber.

Description

H. naledi exhibits anatomical features shared with *Australopithecus*, other features shared with *Homo*, with several features not otherwise known in any hominin species. This anatomical mosaic is reflected in different regions of the skeleton. The morphology of the cranium, mandible, and dentition is mostly consistent with the genus *Homo*, but the brain size of *H. naledi* is within the range of *Australopithecus*. The lower limb is largely *Homo*-like, and the foot and ankle are particularly human in their configuration, but the pelvis appears to be flared markedly like that of *Au. afarensis*. The wrists,

fingertips, and proportions of the fingers are shared mainly with *Homo*, but the proximal and intermediate manual phalanges are markedly curved, even to a greater degree than in any *Australopithecus*. The shoulders are configured largely like those of australopiths. The vertebrae are most similar to Pleistocene members of the genus *Homo*, whereas the ribcage is wide distally like *Au. afarensis*.

H. naledi has a range of body mass similar to small-bodied modern human populations, and is similar in estimated stature to both small-bodied humans and the largest known australopiths. We estimated body mass from eight femoral specimens for which subtrochanteric diameters can be measured ('Materials and methods'), with results ranging between 39.7 kg and 55.8 kg (Table 3). No femur specimen is sufficiently complete to measure femur length accurately, but the U.W. 101-484 tibia preserves nearly its complete length, allowing a tibia length estimate of 325 mm (Figure 10). Estimates for the stature of this individual based on African human population samples range between 144.5 and 147.8 mm. Again, this stature estimate is similar to small-bodied modern human populations. It is within the range estimated for Dmanisi postcranial elements (Lordkipanidze et al., 2007), and slightly smaller than estimated for early *Homo* femoral specimens KNM-ER 1472 and KNM-ER 1481. Some large australopiths also had long tibiae and presumably comparably tall statures, as evidenced by the KSD-VP 1/1 skeleton from Woranso-Mille (Haile-Selassie et al., 2010).

The endocranial volume of all *H. naledi* specimens is clearly small compared to most known examples of *Homo*. We combined information from the most complete cranial vault specimens to arrive at an estimate of endocranial volume for both larger (presumably male) and smaller (presumably female) individuals (larger composite depicted in Figure 11). The resulting estimates of approximately 560cc and 465cc, respectively, overlap entirely with the range of endocranial volumes known for australopiths. Within the genus *Homo*, only the smallest specimens of *H. habilis*, one single *H. erectus* specimen, and *H. floresiensis* overlap with these values.

Despite its small vault size, the cranium of *H. naledi* is structurally similar to those of early *Homo*. Frontal bossing is evident, as is a marked degree of parietal bossing. There is no indication of metopic keeling, though there is slight parasagittal keeling between bregma and lambda, and some prelamdboidal flattening. The cranial vault bones are generally thin, becoming somewhat thicker in the occipital region. The supraorbital torus is well developed, though weakly arched, and is bounded posteriorly by a well-developed supratotal sulcus. The lateral corners of the supraorbital torus are rounded and relatively thin. The temporal lines are widely spaced, and there is no indication of a sagittal crest or temporal/nuchal cresting. The temporal crest is positioned on the posterior aspect of the lateral supraorbital torus, rather than on the superior aspect as in australopiths. At the posteroinferior extent of the temporal lines, they curve anteroinferiorly presenting a well-developed angular torus. The crania have a pentagonal outline in posterior view, with the greatest vault breadth located in the supramastoid region. The nuchal region exhibits sexually dimorphic development of nuchal muscle markings and the external occipital protuberance, and there is a clear indication of

Table 3. Dinaledi body mass estimates from femur specimens preserving subtrochanteric diameters

Specimen ID	Side	AP subtrochanteric breadth	ML subtrochanteric breadth	Mass (a)	Mass (b)
U.W. 101-002	R	18.5	23.6	40.0	44.7
U.W. 101-003	R	21.6	31.4	54.5	55.8
U.W. 101-018	R	18.1	23.8	39.7	44.4
U.W. 101-226	L	19.1	24.0	41.3	45.7
U.W. 101-1136	R	16.9	25.5	39.7	44.4
U.W. 101-1391	R	18.8	23.9	40.8	45.3
U.W. 101-1475	L	18.8	29.0	46.5	49.7
U.W. 101-1482	L	20.7	28.9	49.7	52.1

Regression equations described in 'Materials and methods'. Mass (a) based on forensic statures from European individuals. Mass (b) based on multiple population sample. The two estimates diverge somewhat for smaller femora.
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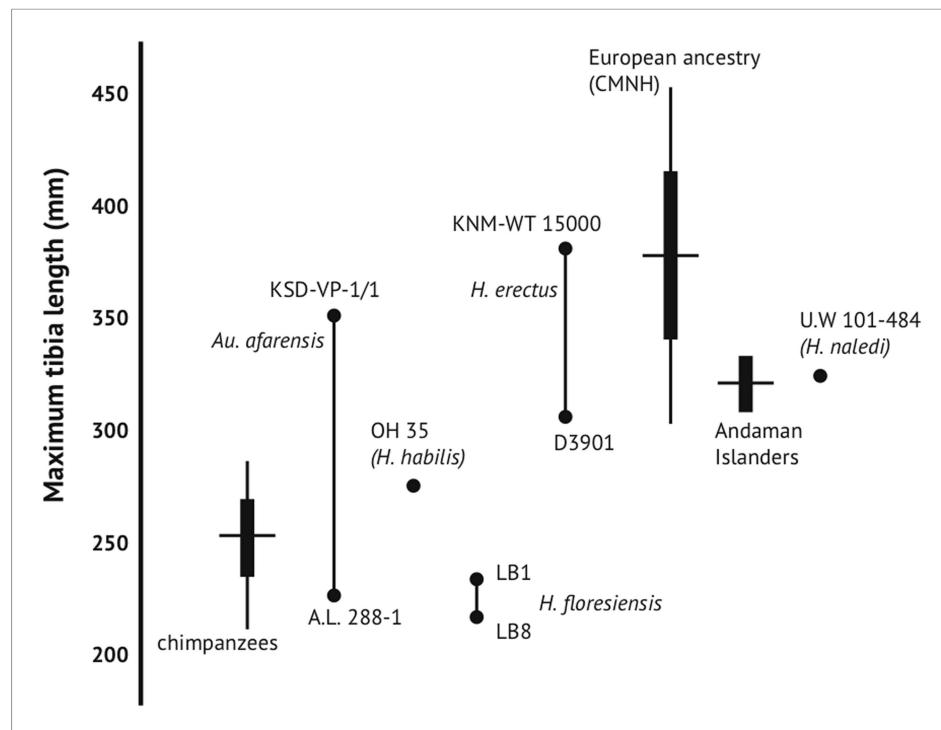


Figure 10. Maximum tibia length in *H. naledi* and other hominins. Maximum tibia length for U.W. 101-484, compared to other nearly complete hominin tibia specimens. *Australopithecus afarensis* represented by A.L. 288-1 and KSD-VP-1/1 (Haile-Selassie et al., 2010); *Homo erectus* represented by D3901 from Dmanisi and KNM-WT 15000; *Homo habilis* by OH 35; *Homo floresiensis* by LB1 and LB8 (Brown et al., 2004; Morwood et al., 2005). Chimpanzee and contemporary European ancestry humans from Cleveland Museum of Natural History (Lee, 2001); Andaman Islanders from Stock (2013). Vertical lines represent sample ranges; bars represent 1 standard deviation. DOI: 10.7554/eLife.09560.015

a tuberculum linearum in addition to the external occipital protuberance. In superior view the vault tapers from posterior to anterior, though post-orbital constriction is slight. The squamosal suture is low and gently curved, and parietal striae are well defined. The lateral margins of the orbits face laterally. A small zygomaticofacial foramen is typically present near the center of the zygomatic bone. The root of the zygomatic process of the maxilla is anteriorly positioned, at the level of the P³ or the P⁴. There is no indication of a zygomatic prominence, and the zygomatic arches do not flare laterally to any extent. The root of the zygomatic process of the temporal is angled downwards approximately 30° relative to FH. The root of the zygomatic process of the temporal begins to laterally expand above the level of the mandibular fossa, rather than above the level of the EAM as in australopithecids. The mandibular fossa is somewhat large, and moderately deep. The articular eminence of the mandibular fossa is saddle-shaped, and oriented posteroinferiorly. Almost the entire mandibular fossa is positioned medial to the temporal squama. The entoglenoid process is elongated and faces primarily laterally. The postglenoid process is small and closely appressed to the tympanic, forming part of the posterior wall of the fossa. The petrotympanic is distinctly coronally oriented. The vaginal process is small but distinct. The crista petrosa is weakly developed and not notably sharpened. There is a strong Eustachian process. The external auditory meatus is small, oval-shaped, and obliquely oriented, and a distinct suprimeatal spine is present. The mastoid region is slightly laterally inflated. The mastoid process is triangular in cross-section, with a rounded apex and a mastoid crest. The digastric groove is deep and narrow, alongside a marked juxtamastoid eminence. The canine jugal are weakly developed and there is no indication that anterior pillars would have been present. A shallow, ill-defined canine fossa is indicated. The nasoalveolar clivus is flat and square-shaped. The parabolic-shaped palate is broad and anteriorly shallow, becoming deeper posteriorly.

The mandibular dentition of *H. naledi* is arranged in a parabolic arch. The alveolar and basal margins of the corpus diverge slightly. A single, posteriorly opening mental foramen is positioned slightly above

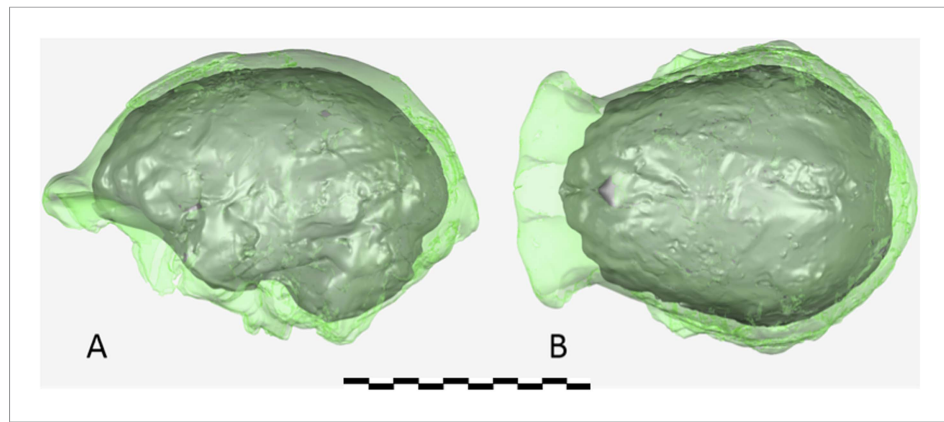


Figure 11. Virtual reconstruction of the endocranium of the larger composite cranium from DH1 and DH2 overlaid with the ectocranial surfaces. **(A)** Lateral view. **(B)** Superior view. The resulting estimate of endocranial volume is 560cc. Scale bar = 10 cm.

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the mid-corpus level, between the position of the P_3 and the P_4 . The mandibular corpus is relatively gracile, with a well-developed lateral prominence whose maximum extent is typically at the M_2 . A slight supreme lateral torus (of Dart) weakly delineates the extramolar sulcus from the lateral corpus. The superior lateral torus is moderately developed, running anteriorly to the mental foramen where it turns up to reach the P_3 jugum. The marginal torus is moderately developed, and defines a moderate intertoral sulcus. The posterior and anterior marginal tubercles are indicated only as slight roughenings of bone. The gracile mandibular symphysis is vertically oriented. A well-developed mental protuberance and weak lateral tubercles are delineated by a slight mandibular incisure, thereby presenting a weak mentum osseum. The post-incisive planum is steeply inclined and not-shelf-like. There is no superior transverse torus, while a weak, basally oriented inferior transverse torus is present. The anterior and posterior subalveolar fossae are continuous and deep, overhung by a well-developed alveolar prominence. The extramolar sulcus is moderately wide. The root of the ramus of the mandible originates high on the corpus at the level of the M_2 . Strong ectoangular tuberosities are indicated. A large mandibular foramen is present, with a diffusely defined mylohyoid groove.

Like the skull, the dentition of *H. naledi* compares most favorably to early *Homo* samples. Yet compared to samples of *H. habilis*, *H. rudolfensis*, and *H. erectus*, the teeth of *H. naledi* are comparatively quite small, similar in dimensions to much later samples of *Homo*. With both small post-canine teeth and a small endocranial volume, *H. naledi* joins *Au. sediba* and *H. floresiensis* in an area distinct from the general hominin relation of smaller post-canine teeth in species with larger brains (**Figure 12**).

In comparison to *H. habilis*, *H. rudolfensis*, and *H. erectus*, the teeth of *H. naledi* are not only small, but also markedly simple in crown morphology. Maxillary and mandibular molars lack extensive crenulation, secondary fissures and supernumerary cusps. The M^1 has an equal-sized metacone and paracone, and has a slight expression of Carabelli's trait represented by a small cusp or shallow pit. I^1 exhibits slight occlusal curvature with trace marginal ridges and variably small *tuberculum dentale*. I^2 exhibits greater occlusal curvature and *tuberculum dentale* expression but neither upper incisor has double shovelling or interruption groove. The mandibular canines of *H. naledi* have a small occlusal area, and have a distal marginal cuspule as a topographically distinct expression of the cingular margin. The P_3 is double-rooted, fully bicuspid with metaconid and protoconid of approximately equal height and occlusal area separated by a distinct longitudinal groove, has a distally extensive talonid, and an occlusal outline approximately symmetrical with respect to the mesiodistal axis. P_4 likewise has a distally extensive talonid and approximately symmetrical occlusal outline (**Figure 5**). M_1 and M_2 lack cusp 6 and cusp 7, except for very slight expression in a small fraction of specimens, and have a very faint subvertical depression rather than a distinct or extensive protostylid. Like australopiths and some early *Homo* specimens, *H. naledi* has an increasing molar size gradient in the mandibular dentition ($M1 < M2 < M3$).

The lower limb of *H. naledi* is defined not only by a unique combination of primitive and derived traits, but also by the presence of unique features in the femur and tibia. Like all other bipedal

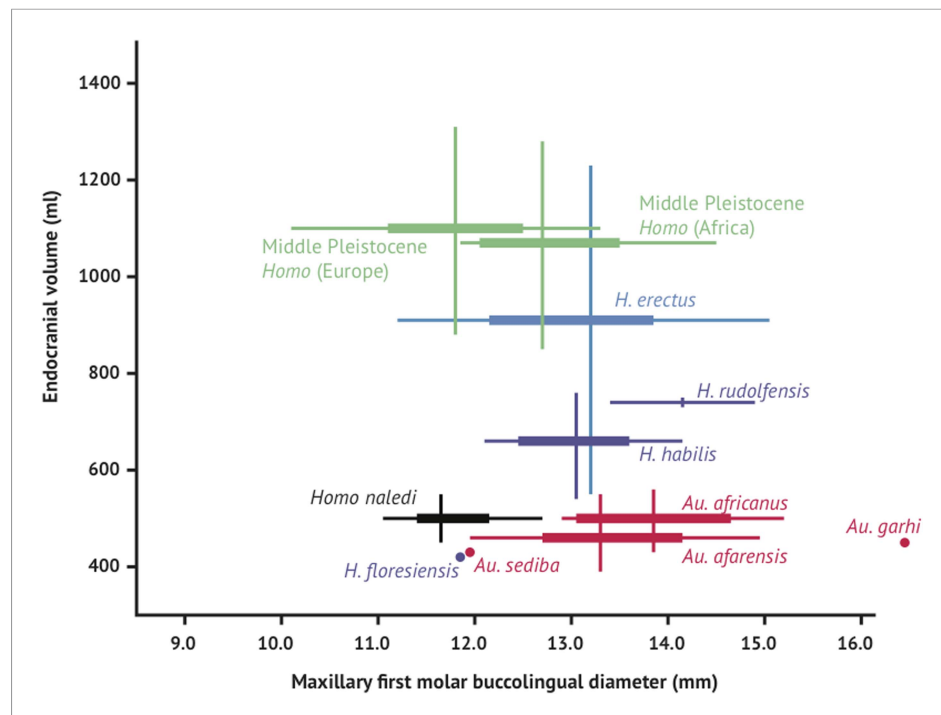


Figure 12. Brain size and tooth size in hominins. The buccolingual breadth of the first maxillary molar is shown here in comparison to endocranial volume for many hominin species. *H. naledi* occupies a position with relatively small molar size (comparable to later *Homo*) and relatively small endocranial volume (comparable to australopithecines). The range of variation within the Dinaledi sample is also fairly small, in particular in comparison to the extensive range of variation within the *H. erectus sensu lato*. Vertical lines represent the range of endocranial volume estimates known for each taxon; each vertical line meets the horizontal line representing M¹ BL diameter at the mean for each taxon. Ranges are illustrated here instead of data points because the ranges of endocranial volume in several species are established by specimens that do not preserve first maxillary molars.

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hominins, *H. naledi* possesses a valgus knee and varus ankle. The femoral neck is long, anteverted, and anteroposteriorly compressed. Muscle insertions for the *M. gluteus maximus* are strong and the femur has a well-marked linea aspera with pilaster variably present. The patella is relatively anteroposteriorly thick. The tibia is mediolaterally compressed with a rounded anterior border, a large proximal attachment for the *M. tibialis posterior*, and a thin medial malleolus. The fibula is gracile with laterally oriented lateral malleolus, a relatively circular neck and a convex surface for the proximal attachment of the *M. peroneus longus*. Unique features in the lower limb of *H. naledi* include a depression in the superior aspect of the femoral neck that results in two mediolaterally oriented pillars inferoposteriorly and superoanteriorly, and a strong distal attachment of the pes anserinus on the tibia.

The foot and ankle of *H. naledi* are largely humanlike (Figure 9). The tibia stands orthogonally upon the talus, which is moderately wedged, with a mediolaterally flat trochlea having medial and lateral margins at even height, a form distinct from the strong keeling seen in OH 8 (*H. habilis*) and several tali from Koobi Fora. The talar head and neck exhibit strong, humanlike torsion; the horizontal angle is higher than in most humans, similar to that found in australopithecines. The calcaneus is only moderately robust, but possesses the plantar declination of the retrotrochlear eminence and plantarly positioned lateral plantar process found in both modern humans and *Au. afarensis*. The peroneal trochlea is small, unlike that found in australopithecines and similar only to that in *H. sapiens* and Neanderthals. The talonavicular, subtalar joints and calcaneocuboid joints are humanlike in possessing minimal ranges of motion and evidence for a locking, rigid midfoot. The intermediate and lateral cuneiforms are proximodistally elongated. The hallux tarsometatarsal joint is flat and proximodistally aligned indicating that *H. naledi* possessed an adducted, non-grasping hallux. The head of the first metatarsal is mediolaterally expanded dorsally, indicative of

a humanlike windlass mechanism. The foot possesses humanlike metatarsal lengths, head proportions, and torsion.

The phalanges are moderately curved, slightly more so than in *H. sapiens*. The only primitive anatomies found in the foot of *H. naledi* are the talar head and neck declination and sustentaculum tali angles, suggestive of a lower arched foot with a more plantarly positioned and horizontally inclined medial column than typically found in modern humans (Harcourt-Smith et al., 2015).

The axial skeleton presents a combination of derived (mainly aspects of the vertebrae) and seemingly primitive (mainly the ribs) traits. The preserved adult T10 and T11 vertebrae are proportioned similarly to Pleistocene *Homo*, with transverse process morphology most similar to Neandertals. The neural canals of these vertebrae are large in comparison to the diminutive overall size of the vertebrae, proportionally recalling Dmanisi *H. erectus*, Neandertals, and modern humans. The 11th rib is straight (uncurved), similar to *Au. afarensis*, and the shape of the upper rib cage appears narrow, as assessed from first and second rib fragments, suggesting that the thorax was pyramidal in shape. The 12th rib presents a robust shaft cross-section most similar to Neandertals. This combination is not found in other hominins and might reflect allometric scaling at a small trunk size.

The Dinaledi iliac blade is flared and shortened anteroposteriorly, resembling *Au. afarensis* or *Au. africanus*. The ischium is short with a narrow tuberoacetabular sulcus, and the ischiopubic and iliopubic rami are thick, resembling *Au. sediba* and *H. erectus*. This combination of iliac and ischiopubic features has not been found in other fossil hominins (Figure 13).

The shoulder of *H. naledi* is configured with the scapula situated high and lateral on the thorax, short clavicles, and little or no torsion of the humerus. The humerus is notably slender for its length, with prominent greater and lesser tubercles bounding a deep bicipital groove, with a small, non-projecting humeral deltoid tuberosity and brachioradialis crest. Distally, the humerus has a wide lateral distodorsal pillar and narrow medial distodorsal pillar, and a medially-displaced olecranon fossa with septal aperture. The Dinaledi radius and ulna diaphyses exhibit little curvature. The radius has a globular radial tuberosity, prominent pronator quadratus crest, and reduced styloid process.

The hand shares many derived features of modern humans and Neandertals in the thumb, wrist, and palm, but has relatively long and markedly curved fingers (Kivell et al., 2015). The thumb is long relative to the length of the other digits, and includes a robust metacarpal with well-developed intrinsic (*M. opponens pollicis* and *M. first dorsal interosseous*) muscle attachments (Figure 6). The pollical distal phalanx is large and robust with a well-developed ridge along the distal border of a deep proximal palmar fossa for the attachment of *flexor pollicis longus* tendon. Ungual spines also project proximopalmarly from a radio-ulnarly expanded apical tuft with a distinct area for the ungual fossa. The wrist includes a boot-shaped trapezoid with an expanded non-articular palmar surface, an enlarged and palmarly-expanded trapezoid-capitate joint, and a trapezium-scaphoid joint that extends further onto the scaphoid tubercle. Overall, carpal shapes and articular configurations are very similar to those of modern humans and Neandertals, and unlike those of great apes and other extinct hominins. However, the *H. naledi* wrist lacks a third metacarpal styloid process, has a more radioulnarly oriented capitate-Mc2 joint, and has a relatively small trapezium-Mc1 joint compared to humans and Neandertals. Moreover, the phalanges are long (relative to the palm) and more curved than most australopiths.



Figure 13. Selected pelvic specimens of *H. naledi*. U.W. 101-1100 ilium in (A) lateral view showing a weak iliac pillar relatively near the anterior edge of the ilium, with no cristal tubercle development; (B) anterior view, angled to demonstrate the degree of flare, which is clear in comparison to the subarcuate surface. U.W. 101-723 immature sacrum in (C) anterior view; and (D) superior view. U.W. 101-1112 ischium in (E) lateral view; and (F) anterior view, demonstrating relatively short tuberoacetabular diameter. Scale bar = 2 cm.

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Discussion

The overall morphology of *H. naledi* places it within the genus *Homo* rather than *Australopithecus* or other early hominin genera. The shared derived features that connect *H. naledi* with other members of *Homo* occupy most regions of the *H. naledi* skeleton and represent distinct functional systems, including locomotion, manipulation, and mastication. Locomotor traits shared with *Homo* include the absolutely long lower limb, with well-marked linea aspera, strong *M. gluteus maximus* insertions, gracile fibula and generally humanlike ankle and foot. These aspects of the lower limb suggest enhanced locomotor performance for a striding gait. The *H. naledi* hand shares aspects of *Homo* morphology in the wrist, thumb and palm, pointing to enhanced object manipulation ability relative to australopiths, including *Au. sediba* (Kivell et al., 2011; Kivell et al., 2015). *H. naledi* lacks the powerful mastication that typifies *Australopithecus* and *Paranthropus*, with generally small teeth across the dentition, gracile mandibular corpus and symphysis, laterally-positioned temporal lines, slight postorbital constriction and non-flaring zygomatic arches. The upper limb, shoulder and ribcage have a more primitive morphological pattern, but do not preclude affiliating *H. naledi* with *Homo*, particularly considering that postcranial remains of *H. habilis* appear to reflect an australopith-like body plan (Johanson et al., 1986). Locomotor, manipulatory, and masticatory systems have both historical and current importance in defining *Homo* (Wood and Collard, 1999; Holliday, 2012; Antón et al., 2014), and *H. naledi* fits within our genus in these respects.

The structural configuration of the *H. naledi* cranium, beyond the functional aspects of mastication, is likewise shared with *Homo*. As in many specimens of *H. erectus* and *H. habilis*, the *H. naledi* vault includes a well-developed and moderately arched supraorbital torus, marked from the frontal squama by a continuous supratatorial sulcus, frontal bossing. Further, as in many *H. erectus* crania, *H. naledi* exhibits a marked angular torus and occipital torus. The *H. naledi* face includes a flat and squared nasoalveolar clivus, comparable to *H. rudolfensis* (Leakey et al., 2012), and weak canine fossae. While its anatomy places it unambiguously within *Homo*, the *H. naledi* cranium and dentition lack many derived features shared by MP and LP *Homo* and *H. sapiens*. The australopith-like features of the postcranium, including the ribcage, shoulder, proximal femur, and relatively long, curved fingers, also depart sharply from the morphology present in MP humans and *H. sapiens*. The similarities of *H. naledi* to earlier members of *Homo*, including *H. habilis*, *H. rudolfensis*, and *H. erectus*, suggest that this species may be rooted within the initial origin and diversification of our genus.

The fossil record of early *Homo* and *Homo*-like australopiths has rapidly increased during the last 15 years, and this accumulating evidence has changed our perspective on the rise of our genus. Many skeletal and behavioral features observed to separate later *Homo* from earlier hominins were formerly argued to have arisen as a single adaptive package, including increased brain size, tool manipulation, increased body size, smaller dentition, and greater commitment to terrestrial long-distance walking or running (Wood and Collard, 1999; Hawks et al., 2000). But we now recognize that such features appeared in different combinations in different fossil samples (Antón et al., 2014). The Dmanisi postcranial sample (Lordkipanidze et al., 2007) and additional cranial remains of *H. erectus* from Dmanisi (Gabunia et al., 2000; Vekua et al., 2002; Lordkipanidze et al., 2013) and East Africa (Spoor et al., 2007; Leakey et al., 2012), demonstrate that larger brain size and body size did not arise synchronously with improved locomotor efficiency and adaptations to long-distance walking or running in *H. erectus* (Holliday, 2012; Antón et al., 2014). Further, the discovery of *Au. sediba* showed that a mosaic of *Homo*-like hand, pelvis and aspects of craniodental morphology can occur within a species with primitive body size, limb proportions, lower limb and foot morphology, thorax shape, vertebral morphology, and brain size (Berger et al., 2010; Carlson et al., 2011; Kivell et al., 2011; Churchill et al., 2013; DeSilva et al., 2013; Schmid et al., 2013). *H. naledi* presents yet a different combination of traits. This species combines a humanlike body size and stature with an australopith-sized brain; features of the shoulder and hand apparently well-suited for climbing with humanlike hand and wrist adaptations for manipulation; australopith-like hip mechanics with humanlike terrestrial adaptations of the foot and lower limb; small dentition with primitive dental proportions. In light of this evidence from complete skeletal samples, we must abandon the expectation that any small fragment of the anatomy can provide singular insight about the evolutionary relationships of fossil hominins.

A recent phylogenetic analysis of fossil hominins based on craniodental morphology placed *Au. sediba* at the base of the genus *Homo* (Dembo et al., 2015), in agreement with earlier analyses of

this species (Berger *et al.*, 2010). The cranial and dental affinities identified between *Au. sediba* and *Homo* include many features shared by *H. naledi*. But *H. naledi* and *Au. sediba* share different postcranial features with other species of *Homo*. Resolving the phylogenetic placement of *H. naledi* will require both postcranial and craniodental evidence to be integrated together. Such integration poses a challenge because of the poor representation of several key species both within and outside of *Homo*, most notably *H. habilis*, for which postcranial evidence is slight, and *H. rudolfensis* for which no associated postcranial remains are known. We propose the testable hypothesis that the common ancestor of *H. naledi*, *H. erectus*, and *H. sapiens* shared humanlike manipulatory capabilities and terrestrial bipedality, with hands and feet like *H. naledi*, an australopith-like pelvis and the *H. erectus*-like aspects of cranial morphology that are found in *H. naledi*. Enlarged brain size was evidently not a necessary prerequisite for the generally human-like aspects of manipulatory, locomotor, and masticatory morphology of *H. naledi*.

Although it contains an unprecedented wealth of anatomical information, the Dinaledi deposit remains undated (Dirks *et al.*, 2015). Considering that *H. naledi* is a morphologically primitive species within our genus, an age may help elucidate the ecological circumstances within which *Homo* arose and diversified. If the fossils prove to be substantially older than 2 million years, *H. naledi* would be the earliest example of our genus that is more than a single isolated fragment. The sample would illustrate a model for the relation of adaptive features of the cranium, dentition and postcranium during a critical time interval that is underrepresented by fossil evidence of comparable completeness. A date younger than 1 million years ago would demonstrate the coexistence of multiple *Homo* morphs in Africa, including this small-brained form, into the later periods of human evolution. The persistence of such a species with clear adaptations for manipulation and grip, alongside MP humans or perhaps even alongside modern humans, would challenge many assumptions about the development of the archaeological record in Africa.

The depth of evidence of *H. naledi* may provide a perspective on the variation to be expected within fossil hominin taxa (Lordkipanidze *et al.*, 2013; Bermúdez de Castro *et al.*, 2014). The entire Dinaledi collection is remarkably homogeneous. There is very little size variation among adult elements within the collection. Eight body mass estimates from the femur (Table 2) have a standard deviation of only 4.3 kilograms, for a body mass coefficient of variation (CV) of only 9%. The CV of body mass within most human populations is substantially higher than this, with an average near 15% (McKellar and Hendry, 2009). Likewise, the size variation of cranial and dental elements is minimal. With 11 mandibular first molars, the CV of buccolingual breadth is only 3.2% and for 13 maxillary first molars the CV of buccolingual breadth is only 2.0% (buccolingual breadth is used because it is not subject to variance from interproximal wear). Not only size, but also anatomical shape and form are homogeneous within the sample. Almost every aspect of the morphology of the dentition, including the distinctive form of the lower premolars, the distal accessory cuspule of the mandibular canines, and the expression of nonmetric features that normally vary in human populations, is uniform in every specimen from the collection. The distinctive aspects of cranial morphology are repeated in every specimen, and even the aspects that normally vary among individuals of different body size or between sexes exhibit only slight variation among the Dinaledi remains. One of the most unique aspects of *H. naledi* is the morphology of the first metacarpal; the derived aspects of this anatomy are present in every one of seven first metacarpal specimens in the collection (Figure 14). Unlike any other fossil hominin site in Africa, the Dinaledi Chamber seems to preserve a large number of individuals from a single population, one with variation equal to or less than that found within local populations of modern humans.

The Dinaledi collection is the richest assemblage of associated fossil hominins ever discovered in Africa, and aside from the Sima de los Huesos collection and later Neanderthal and modern human samples, it has the most comprehensive representation of skeletal elements across the lifespan, and from multiple individuals, in the hominin fossil record. The abundance of evidence from this assemblage supports our emerging understanding that the genus *Homo* encompassed a variety of evolutionary experiments (Antón *et al.*, 2014), with diversity now evident for fossil *Homo* in each of the few intensively explored parts of Africa (Leakey *et al.*, 2012). But as much as it advances our knowledge, *H. naledi* also highlights our ignorance about ancient *Homo* across the vast geographic span of the African continent. The tree of *Homo*-like hominins is far from complete: we have missed key transitional forms and lineages that persisted for hundreds of thousands of years. With an increasing pace of discovery from the field and the laboratory, more light will be thrown on the origin of humans.



Figure 14. First metacarpals of *H. naledi*. Seven first metacarpals have been recovered from the Dinaledi Chamber. U.W. 101-1321 is the right first metacarpal of the associated Hand 1 found in articulation. U.W. 101-1282 and U.W. 101-1641 are anatomically similar left and right first metacarpals, which we hypothesize as antimeres, both were recovered from excavation. U.W. 101-007 was collected from the surface of the chamber, and exhibits the same distinctive morphological characteristics as all the first metacarpals in the assemblage. All of these show a marked robusticity of the distal half of the bone, a very narrow, ‘waisted’ appearance to the proximal shaft and proximal articular surface, prominent crests for attachment of *M. opponens pollicis* and *M. first dorsal interosseous*, and a prominent ridge running down the palmar aspect of the bone. The heads of these metacarpals are dorsopalmarly flat and strongly asymmetric, with an enlarged palmar-radial protuberance. These distinctive features are present among all the first metacarpals in the Dinaledi collection, and are absent from any other hominin sample. Their derived nature is evident in comparison to apes and other early hominins, here illustrated with a chimpanzee first metacarpal and the MH2 first metacarpal of *Australopithecus sediba*.

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Materials and methods

Comparative hominin specimens examined in this study

In the differential diagnosis of *H. naledi*, we have compared the holotype DH1, paratypes, and other referred material to fossil evidence from previously-identified hominin taxa. Our goal is to provide a diagnosis for *H. naledi* that is clear in reference to widely recognized hominin hypodigms. Different specialists continue to disagree about the composition and anatomical breadth represented by these hominin taxa and attribution of particular specimens to them (see e.g., [Wood and Collard, 1999](#); [Lordkipanidze et al., 2013](#); [Antón et al., 2014](#) on early *Homo* taxa). We do not intend to take any position on such disagreements by our selection of comparative samples for *H. naledi*.

We have been cautious in our attribution of postcranial specimens to hominin taxa, particularly in the African Plio-Pleistocene, where it has been demonstrated multiple hominin taxa coexisted in time, if not in geographical space. Because the purpose of this study is differential diagnosis in reference to known taxa, unattributed specimens are not germane, although in certain cases there are well-accepted attributions to genus for specimens (e.g., *Homo* sp. or *Australopithecus* sp.) as cited below. We have included some specimens in comparisons because they are relatively complete, even if they cannot be attributed to a species, because few hominin taxa are represented by evidence across the entire skeleton. For some anatomical characters, parts are preserved only for MP or later hominin samples, so we have included such comparisons to make clear how *H. naledi* compares in these elements to the (few) known fossil examples.

This study relies upon observations and measurements taken from original fossils by the authors, observations taken from casts, and observations taken from the literature. These observations are in large part standard anatomical practice; where features are specially described in previous studies we have referenced those here. For this study, a cast collection was assembled including the Phillip V. Tobias research collection at the University of the Witwatersrand and loans of cast materials from the University of Wisconsin–Madison, University of Michigan, American Museum of Natural History, New York University, University of Colorado–Denver, University of Delaware, Texas A&M University, and the personal collections of Peter Schmid, Milford Wolpoff and Rob Blumenschine. We extend our gratitude to the curators of fossil

collections and the generosity of these institutions in facilitating this research, both in South Africa and throughout the world.

This list of skeletal materials extends the list of craniodental comparative material used in diagnosing *Au. sediba*, with many of the hypodigms identical to that study (Berger et al., 2010). Where we have had first-hand access to original specimens, we rely upon our own observations; we therefore do not refer readers to other sources for these data.

Australopithecus afarensis

The samples attributed to *Au. afarensis* from Hadar, Laetoli, the Middle Awash, Woranso-Mille and Dikika were utilized. For this taxon we relied upon published reports (Johanson et al., 1982; Kimbel et al., 2004; Drapeau et al., 2005; Alemseged et al., 2006; Haile-Selassie et al., 2010; Ward et al., 2012), in addition to our own observations on original fossils and casts.

Australopithecus africanus

The samples attributed to *Au. africanus* from Taung, Sterkfontein and Makapansgat were employed. Original specimens were examined first-hand by the authors.

Australopithecus garhi

The cranium BOU-VP-12/130 from Bouri was included, with data taken from a published report (Asfaw et al., 1999).

Australopithecus sediba

The partial skeletons MH1 and MH2 from Malapa, South Africa were included in this study, based on examination of the original specimens by the authors.

Paranthropus aethiopicus

The cranium KNM-WT 17000 was examined first-hand for this study.

Paranthropus boisei

Samples from the Omo Shungura sequence, East Lake Turkana, Olduvai Gorge and Konso were included in this study. Original specimens from Olduvai Gorge and East Lake Turkana were examined first-hand, while casts and published reports (Tobias, 1967; Suwa et al., 1996, 1997; Domínguez-Rodrigo et al., 2013) were used to study the Omo and Konso materials. Our postcranial considerations of *P. boisei* are very limited and we did not rely upon the association of KNM-ER 1500 (Grausz et al., 1988) to derive information about the postcranial skeleton of *P. boisei*.

Paranthropus robustus

The samples from Kromdraai, Swartkrans, Sterkfontein, Drimolen, Gondolin, and Coopers were included in this study. First-hand observations of original specimens from all localities were used with the exception of Drimolen fossils, which were compared using published reports (Keyser, 2000; Keyser et al., 2000).

Homo habilis

Samples from Olduvai Gorge, East Lake Turkana, the Omo Shungura sequence, Hadar, and Sterkfontein were included in this study. Original Olduvai Gorge and East Lake Turkana fossils were examined first-hand, while for the Omo and Hadar materials we relied on our original observations on casts and originals and published reports (Boaz and Howell, 1977; Tobias, 1991; Kimbel et al., 1997). We include the following fossils in the hypodigm of *H. habilis*: A.L. 666-1, KNM-ER 1478, KNM-ER 1501, KNM-ER 1502, KNM-ER 1805, KNM-ER 1813, KNM-ER 3735, OH 4, OH 6, OH 7, OH 8, OH 13, OH 15, OH 16, OH 21, OH 24, OH 27, OH 31, OH 35, OH 37, OH 39, OH 42, OH 44, OH 45, OH 62, OMO-L894-1, and Stw 53. We recognize that some authors (including some of the authors of this paper) prefer to classify OH 62, Stw 53 and A.L. 666-1 outside of *H. habilis*, (e.g., as *Homo gautengensis* which we do not recognize as valid), or even outside the genus *Homo*; these specimens expand the morphological and temporal variability encompassed within *H. habilis*.

Homo rudolfensis

Samples from Olduvai Gorge, East Lake Turkana, and Lake Malawi were included in this study. The East Lake Turkana fossils available prior to 2010 were examined first-hand, while for the Olduvai and Lake Malawi fossils and KNM-ER 60000, 62000, and 62003 we relied on original observations on fossils and casts as well as published reports (Schrenk et al., 1993; Blumenschine et al., 2003; Leakey et al., 2012). We include the following fossils in the hypodigm of *H. rudolfensis*: KNM-ER 819,

KNM-ER 1470, KNM-ER 1482, KNM-ER 1483, KNM-ER 1590, KNM-ER 1801, KNM-ER 1802, KNM-ER 3732, KNM-ER 3891, KNM-ER 60000, KNM-ER 62000, KNM-ER 62003, OH 65, and UR 501. We do recognize that KNM-ER 60000 and KNM-ER 1802 present some conflicting anatomy that some authors have argued precludes them as conspecific specimens (Leakey et al., 2012); by considering both, we aim to be conservative as they encompass more variation within *H. rudolfensis*.

Homo erectus

Samples from Buia, Chemeron, Daka, Dmanisi, East and West Lake Turkana, Gona, Hexian, Konso, Mojokerto, Olduvai Gorge, Sangiran, Swartkrans, Trinil, and Zhoukoudian were included in this study. South African material is of special interest in this comparison because of the geographic proximity, and because of the difficulty of clearly identifying *Homo* specimens within the large fossil sample from Swartkrans. In particular, the following specimens from Swartkrans are considered to represent *H. erectus*: SK 15, SK 18a, SK 27, SK 43, SK 45, SK 68, SK 847, SK 878, SK 2635, SKW 3114, SKX 257/258, SKX 267/2671, SKX 268, SKX 269, SKX 334, SKX 339, SKX 610, SKX 1756, SKX 2354, SKX 2355, SKX 2356, and SKX 21204. It has been suggested (Grine et al., 1993, 1996) that SK 847 and Stw 53 might represent the same taxon, and that this taxon is a currently undiagnosed species of *Homo* in South Africa. However, we agree with Clarke (1977; 2008) that SK 847 can be attributed to *H. erectus*, and that Stw 53 cannot. Because there is no clear indication that more than one species of *Homo* is represented in the Swartkrans sample, we consider all this material to belong to *H. erectus*. We considered '*Homo ergaster*' (and also '*Homo aff. erectus*' from Wood, 1991) to be synonyms of *H. erectus* for this study; Turkana Basin specimens that are attributed to *H. erectus* thus include KNM-ER 730, KNM-ER 820, KNM-ER 992, KNM-ER 1808, KNM-ER 3733, KNM-ER 3883, KNM-ER 42700, KNM-WT 15000. Olduvai specimens include OH 9, OH 12 and OH 28. Original fossil materials from Chemeron, Lake Turkana, Swartkrans, Trinil, and Dmanisi were examined first-hand by the authors, while the remainder were based on casts and published reports (Weidenreich, 1943; Wood, 1991; Antón, 2003; Rightmire et al., 2006; Suwa et al., 2007).

A large number of postcranial specimens have been collected from the Turkana Basin and appear consistent with the anatomical range otherwise found in *Homo*, and inconsistent with known samples of *Australopithecus* and *Paranthropus* from elsewhere. These include KNM-ER 1472, KNM-ER 1481, KNM-ER 3228, KNM-ER 737, and others. We may add other fossils from other sites lacking association with craniodental material, such as the partial BOU-VP 12/1 skeleton and even the Gona pelvis. These specimens attributable to *Homo* but not necessarily to a particular species did inform our understanding of variability within the genus, but for the most part these specimens do not inform our differential diagnosis of *H. naledi* relative to particular species. For example, the key element of femoral morphology of *H. naledi* in contrast to other species is the presence of two well-defined mediolaterally running pillars in the femoral neck; the isolated specimens of early *Homo* do not contradict this apparent autapomorphy. Likewise, no isolated specimens inform us about the humanlike aspects of foot morphology in *H. naledi*. In these cases, the lack of associations for this evidence actually is less important than the lack of specimens that replicate the distinctive features of the *H. naledi* morphology.

Middle Pleistocene *Homo*

Specimens from the latest Lower Pleistocene and MP of Europe and Africa that cannot be attributed to *H. erectus* were included in our comparisons. These include fossils that have been attributed to *H. heidelbergensis*, *H. rhodesiensis*, 'archaic *H. sapiens*', or 'evolved *H. erectus*' by a variety of other authors. Specimens attributed to MP *Homo* include materials from Eliye Springs, Arago, Atapuerca Sima de los Huesos, Bodo, Broken Hill, Cave of Hearths, Ceprano, Dali, Elandsfontein, Jinniushan, Kapthurin, Mauer, Narmada, Ndutu, Petralona, Reilingen-Schwetzingen, Solo, Steinheim, Swanscombe. This grouping includes the following specimens: KNM-ES 11693, Arago 2, Arago 13, Arago 21, Atapuerca 1, Atapuerca 2, Atapuerca 4, Atapuerca 5, Atapuerca 6, Cave of Hearths, SAM-PQ-EH1, Kabwe, Mauer, Ndutu, Salé, Petralona, Reilingen-Schwetzingen, Steinheim.

Homo floresiensis

Specimens from Liang Bua, Flores as described by Brown et al., 2004; Morwood et al., 2005, Jungers et al., 2009a, Jungers et al., 2009b, and Falk et al., 2005 were included in this study.

Scanning and virtual reconstruction methods

The calvariae (DH1-4) were scanned using a NextEngine laser surface scanner (NextEngine, Malibu, CA) at the following settings: Macro, 12 divisions with auto-rotation, HD 17k ppi. Depending on the

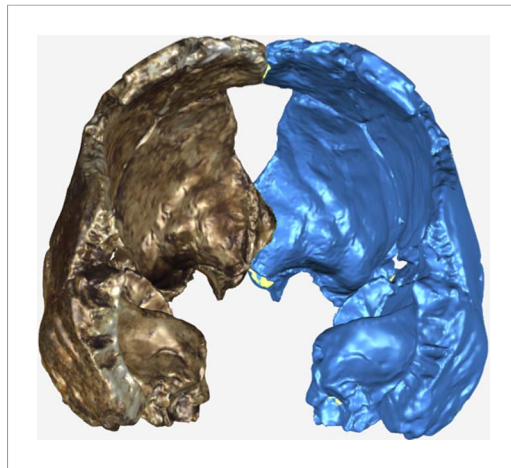


Figure 15. Posterior view of the virtual reconstruction of DH3. The resultant mirror image is displayed in blue. The antimeres were aligned by the frontal crest and sagittal suture using the Manual Registration function in GeoMagic Studio 14.0.

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complexity of the surface relief, either two or three complete scanning cycles were completed per specimen, resulting in multiple 360° scans. Each individual scan was trimmed, aligned, and fused (volume merged) in the accompanying ScanStudio HD Pro software. For each specimen, the individual 360° scans were then aligned and merged in GeoMagic Studio 14.0 (Raindrop Geomagic, Research Triangle Park, NC), creating a final three-dimensional model of the specimen. Given the fragmented nature of the calvariae specimens, both the ectocranial and endocranial surfaces were captured in the scans.

DH3 consisted primarily of portions of the right calvaria. However, a small section of the frontal and the parietal crossed the mid-sagittal plane. For this reason, it was possible to mirror image the surface scan to approximate the left calvaria and obtain a more complete visualization of the complete calvaria (**Figure 15**). The virtual specimen of DH3 was mirrored in GeoMagic Studio, and manually registered (aligned) using common points along the frontal crest and sagittal suture. The registration procedure in GeoMagic Studio is an iterative process that refines the alignment of specimens to minimize spatial differences between corresponding surfaces. In this manner, the program is able to match the position overlapping surfaces, in addition to their angulation and curvature.

The same procedures were used to mirror image and create a virtual reconstruction of DH2 and the occipital portion of DH1 (**Figure 16**). The occipital and vault portions of DH1 were reconstructed based on the anatomical alignment of the sagittal suture, sagittal sulcus, parietal striae, and the continuation of the temporal lines across both the specimens.

Virtual reconstruction of composite crania and estimation of cranial capacity

In order to virtually estimate the cranial capacity, composite crania were constructed from the surface scans and mirror imaged scans of the calvariae. Two separate composite crania were created; the relatively smaller-sized calvariae (DH3 and DH4) were combined into one composite, and the larger-sized calvariae (DH1 and DH2) composed the larger composite cranium.

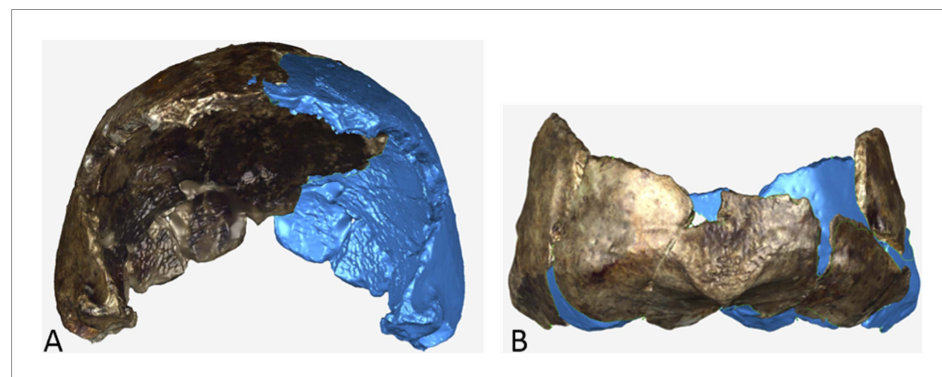


Figure 16. Virtual reconstruction of (A) DH2 and (B) occipital portion of DH1. The actual specimen displays its original coloration and the mirror imaged portion is illustrated in blue.

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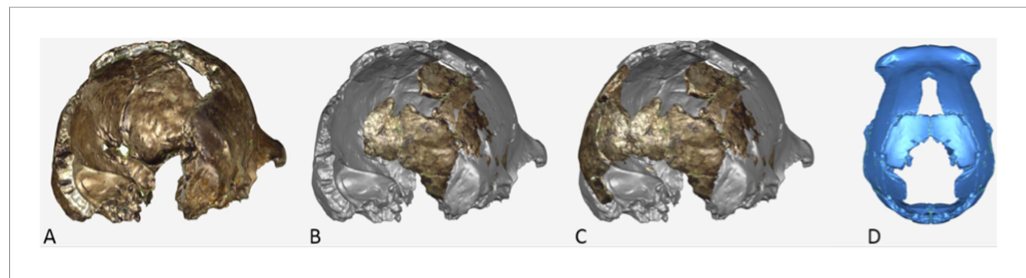


Figure 17. Postero-lateral view of the virtual reconstruction of a composite cranium from DH3 and DH4. (A) The surface scan of DH3 was mirror imaged and merged as described in Supplementary Note 8. (B) The scan of DH4 was aligned to the DH3 model. (C) DH4 was then mirror imaged to complete the occipital contour (D).

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The smaller composite cranium, DH3 was mirrored in GeoMagic Studio 14.0, and merged with the original scan as outlined above. The surface scan of DH4 was uploaded and registered (aligned) to the DH3 model using overlapping temporal features (e.g., the external auditory meatus). No scaling was performed. DH4 was then mirror imaged to complete the occipital contour. The resultant model suggests a general concordance between the specimens in both size and shape with a close alignment of vault surfaces and anatomical features between specimens (Figure 17).

For the larger composite cranium, the surface model of DH2 and its mirror image was then uploaded, registered (aligned), and merged with the mirror-imaged model of DH1. No scaling was performed. The congruency between the specimens in the resultant model suggests that DH1 and DH2 are similar in both size and vault shape (Figure 18).

Virtual reconstruction of cranial capacity

The composite model of DH3 and DH4 was used to estimate the cranial capacity for the smaller morphotype. In GeoMagic Studio 14.0, the endocranial surface of the composite was carefully selected from the ectocranial surface and copied as a new object. In order to obtain a volume calculation the model has to be a closed surface, meaning that all of the holes in the surface model had to be filled. Small holes in the model were filled using the 'Fill by Curvature' function. Larger holes were filled in by sections. For example, the cranial base was filled in using a number of transverse sections, so that in the absence of the cranial base the contour of the various cranial fossae and the petrous portions of the temporal could be preserved as best as possible. When appropriate (e.g., around angular portions of the petrous bone), small sections were filled using a flat hole filling function. The new surfaces created by the hole-filling mechanism were carefully monitored and repeated until an acceptable model that appeared to best approximate the missing portions was obtained. The result is a closed model approximation of the endocranium, of which a volume can be

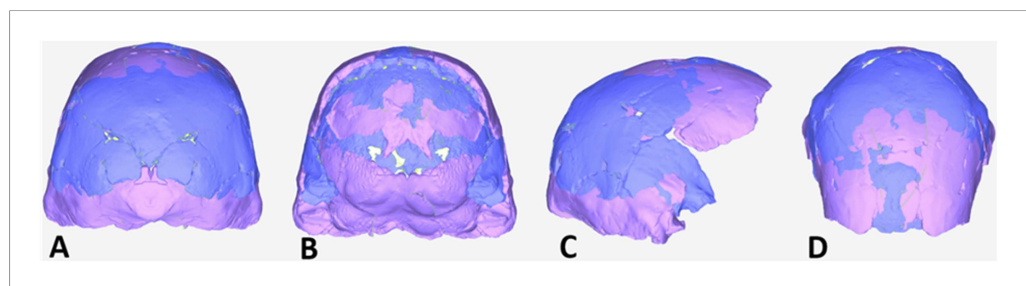


Figure 18. Virtual reconstruction of a composite cranium from DH1 and DH2. The surface model of DH2 (blue), consisting of the original scan merged with the mirror image, was then uploaded and aligned with the mirror-imaged DH1 model (pink). Note the similarity in size and shape between DH1 and DH2 observed in the posterior (A) anterior (B) lateral (C) and superior (D) views.

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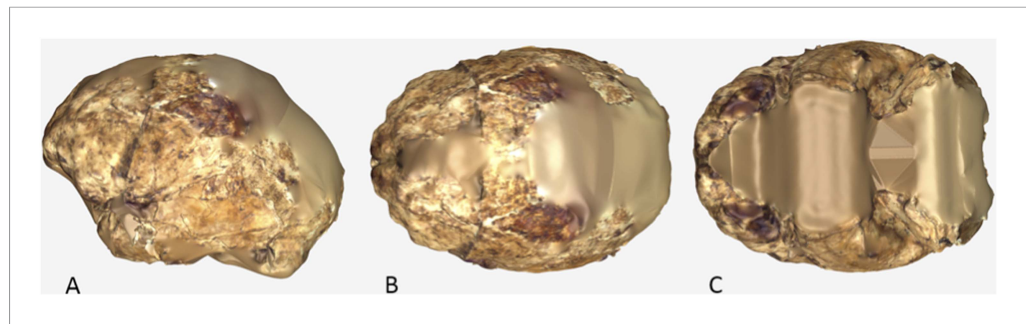


Figure 19. Virtual reconstruction of the endocranium of the composite cranium from DH3 and DH4. (A) Lateral view. (B) Superior view. (C) Inferior view. In all views, anterior is to the left.

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calculated by GeoMagic Studio (**Figure 19, Figure 20**). The volume of the smaller composite cranium (DH3 and DH4) indicates a cranial capacity of approximately 465 cm³.

In order to determine whether significant errors were being introduced in the manner that the cranial base was filled in the above procedures, the endocranial volume of DH3/DH4 was also virtually calculated using the cranial base of Sts 19 as a model. A 3D model of Sts 19 was mirrored and aligned to the DH3/DH4 model using the external auditory meatus and common points on the internal surface of the petrous portion as a guide (**Figure 21**). The Sts 19 model was then scaled by 0.97 to obtain an optimal fit between the two models.

After the Sts 19 model was merged with the DH3/DH4 model, the endocranial surface was extracted and reconstructed as described above (**Figure 22**). The resultant endocranial volume using the Sts 19 cranial base was 465.9 cm³. This value is in agreement with the first estimate and suggests that using a model cranial base did not significantly alter the results.

The larger composite cranium, consisting of DH1 and DH2, lacks most of the frontal region. In order to create a closed endocranial surface for a volume estimate, the frontal region from the smaller composite cranium was scaled by 5%, and then registered (aligned) and merged to the model of the larger composite cranium. As with the smaller composite cranium, the endocranial surface was then selected and converted to a new object, and the remaining holes filled based on the curvature of the surface. The volume of the closed endocranial model was calculated using GeoMagic Studio. The cranial capacity (endocranial volume) of the larger composite model is approximately 560cc.

Body mass estimation methods

Eight femoral fragments from the Dinaledi collection allow a direct measurement of the subtrochanteric anteroposterior and mediolateral diameters (**Table 3**). We developed two regression

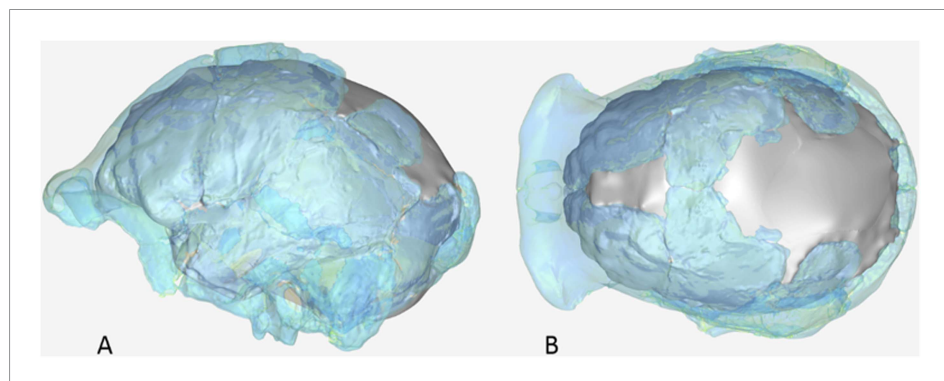


Figure 20. Virtual reconstruction of the endocranium of the composite cranium from DH3 and DH4 overlaid with the ectocranial surfaces. (A) Lateral view. (B) Superior view.

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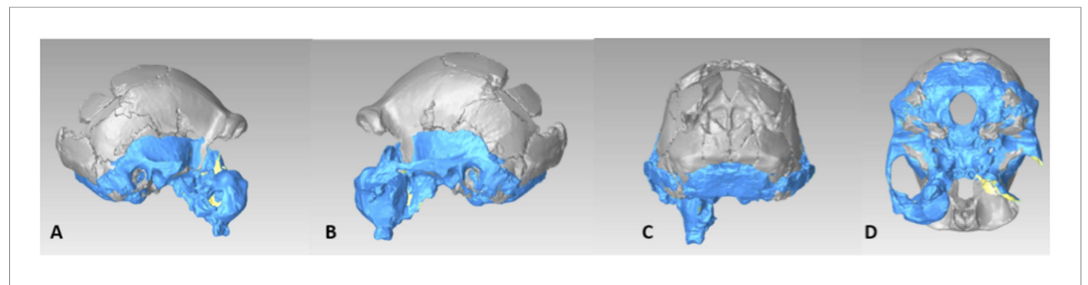


Figure 21. Virtual reconstruction the DH3/DH4 cranial base using a model of Sts 19. (A) Right lateral view. (B) Left lateral view. (C) Posterior view. (D) Inferior view.

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equations to estimate body mass from these diameters based on the masses of modern human samples. MCE measured body masses of a sample of 253 modern European individuals, 128 males and 125 females, collected from the Institute for Forensic Medicine in Zurich, Switzerland. Body masses were taken at time of forensic evaluation. This sample yields the following regression equation relating body mass to subtrochanteric diameter, where FSTpr refers to the product of the femoral subtrochanteric mediolateral and anteroposterior breadths:

$$\text{Body Mass} = 0.060 \times \text{FSTpr} + 13.856, \text{SEE} = 6.78, r = 0.50, p = <0.001.$$

We further examined a broader sample of 276 modern humans taken from a number of populations around the world, with data measured by TWH. The body masses of individuals were estimated from femur head diameter, using the average of results obtained from *Grine et al. (1995)* and *Ruff et al. (1997)*. The sample includes 115 females, 155 males, and 6 individuals of indeterminate sex.

$$\text{Body Mass} = 0.046 \times \text{FSTpr} + 24.614, \text{SEE} = 5.82, r = 0.82, p < 0.001.$$

Stature estimation methods

We collected data from skeletal material representing two African population samples. We use only African populations in this comparison because the ratio of tibia length to femur length, and thereby the proportion of stature constituted by tibia length, varies between human populations both today and prehistorically. Although we do not know this proportion for *H. naledi*, we adopt the null hypothesis that they likely had tibia/femur proportions similar to other African population samples.

95 male and female Kulubnarti individuals from medieval Nubia are curated at the University of Colorado, Boulder. Data were collected by HMG, including estimates of living stature based on the Fully method (*Fully, 1956; Raxter et al., 2006*), and these were used to develop a regression equation relating tibia length to stature. The resulting equation is:

$$\text{Stature} = 0.295 \times \text{TML} + 48.589, \\ \text{SEE} = 3.13, r = 0.90, p < 0.001.$$

We (HMG and TWH) collected measurements from 38 African males and 38 females curated within the Dart Collection of the University of the Witwatersrand. Specimens were randomly chosen with no preference for specific African ethnic groups. Cadaveric statures are documented for this collection, the regression equation relating tibia length to stature in this sample is:

$$\text{Stature} = 0.223 \times \text{TML} + 75.350, \\ \text{SEE} = 6.50, r = 0.63, p < 0.001.$$

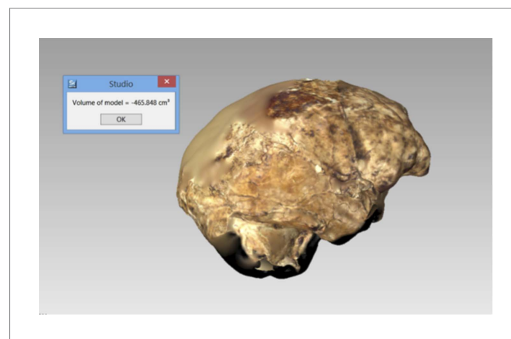


Figure 22. Virtual reconstruction the DH3/DH4 endocranial volume using a cranial base model of Sts 19. Right lateral view.

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Nomenclatural acts

The electronic edition of this article conforms to the requirements of the amended International Code of Zoological Nomenclature, and hence, the new name contained herein is available under that Code from the electronic edition of this article. This published work and the nomenclatural acts it contains have been registered in ZooBank, the online registration system for the ICZN. The ZooBank LSIDs (Life Science Identifiers) can be resolved and the associated information viewed through any standard web browser by appending the LSID to the prefix 'http://zoobank.org/'. The LSID for this publication is: urn:lsid:zoobank.org:pub:00D1E81A-6E08-4A01-BD98-79A2CEAE2411. The electronic edition of this work was published in a journal with an ISSN (2050-084X) and has been archived and is available from the following digital repositories: PubMed Central and LOCKSS.

Access to material

All Dinaledi fossil material is available for study by researchers upon application to the Evolutionary Studies Institute at the University of the Witwatersrand where the material is curated (contact Bernhard Zipfel [Bernhard.Zipfel@wits.ac.za]). Three-dimensional surface renderings and other digital data are available from the MorphoSource digital repository (<http://morphosource.org>).

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Additional files

Supplementary files

- Supplementary file 1. Holotype and paratype specimens and referred materials.
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- Supplementary file 2. Traits of *H. naledi* and comparative species.
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CHAPTER THREE: GEOLOGICAL AND TAPHONOMIC CONTEXT FOR THE NEW HOMININ SPECIES *HOMO NALEDI* FROM THE DINALEDI CHAMBER, SOUTH AFRICA*

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Geological and taphonomic context for the new hominin species *Homo naledi* from the Dinaledi Chamber, South Africa

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Abstract We describe the physical context of the Dinaledi Chamber within the Rising Star cave, South Africa, which contains the fossils of *Homo naledi*. Approximately 1550 specimens of hominin remains have been recovered from at least 15 individuals, representing a small portion of the total fossil content. Macro-vertebrate fossils are exclusively *H. naledi*, and occur within clay-rich sediments derived from in situ weathering, and exogenous clay and silt, which entered the chamber through fractures that prevented passage of coarser-grained material. The chamber was always in the dark zone, and not accessible to non-hominins. Bone taphonomy indicates that hominin individuals reached the chamber complete, with disarticulation occurring during/after deposition. Hominins accumulated over time as older laminated mudstone units and sediment along the cave floor were eroded. Preliminary evidence is consistent with deliberate body disposal in a single location, by a hominin species other than *Homo sapiens*, at an as-yet unknown date.

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eLife digest Modern humans, or *Homo sapiens*, are now the only living species in their genus. But as recently as 20,000 years ago there were other species that belonged to the genus *Homo*. Together with modern humans, these extinct human species, our immediate ancestors and their close relatives are collectively referred to as 'hominins'.

Now, Dirks et al. describe an unusual collection of hominin fossils that were found within the Dinaledi Chamber in the Rising Star cave system in South Africa. The fossils all belong to a newly discovered hominin species called *Homo naledi*, which is described in a related study by Berger et al. The unearthed fossils are the largest collection of hominin fossils from a single species ever to be discovered in Africa, and include the remains of at least 15 individuals and multiple examples of most of the bones in the skeleton.

Dirks et al. explain that the assemblage from the Dinaledi Chamber is unusual because of the large number of fossils discovered so close together in a single chamber deep within the cave system. It is also unusual that no other large animal remains were found in the chamber, and that the bodies had not been damaged by scavengers or predators. The fossils were excavated from soft clay-rich sediments that had accumulated in the chamber over time; it also appears that the bodies were intact when they arrived in the chamber, and then started to decompose.

Dirks et al. discuss a number of explanations as to how the remains came to rest in the Dinaledi Chamber, which range from whether *Homo naledi* lived in the caves to whether they were brought in by predators. Most of the evidence obtained so far is largely consistent with these bodies being deliberately disposed of in this single location by the same extinct hominin species. However, a number of other explanations cannot be completely ruled out and further investigation is now needed to uncover the series of events that resulted in this unique collection of hominin fossils.

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Introduction

The Pliocene-Pleistocene cave deposits in the Cradle of Humankind World Heritage Site (South Africa) preserve a diversity of hominin fossils in a varied set of contexts (Hughes and Tobias, 1977; Clarke, 1998; Partridge et al., 2003; Berger et al., 2010; Bruxelles et al., 2014; Berger et al., 2015). Hominin remains in the area are generally encased in lithified clastic deposits in caves that are situated in stromatolite-rich dolomite of the Malmani Subgroup (Eriksson et al., 2006) (Figure 1). Sedimentological and taphonomic descriptions of notable fossil sites (Brain, 1981; de Ruiter et al., 2009; Dirks et al., 2010; Pickering and Kramers, 2010; Pickering et al., 2011a, 2011b) indicate that fossils were trapped and preserved in caves as a result of a range of processes including death traps, scavenging, mud flows and predation. Distribution patterns of fossiliferous caves in the area suggest that fossil deposition occurred in caves that are close to critical resources such as water (Reynolds et al., 2011; Dirks and Berger, 2013).

The cave deposits represent sediment traps that have collected fossils for at least 3 Ma, and possibly longer, thus, providing a unique window into Pliocene-Pleistocene ecosystems, and how they evolved over time as the climate and the landscape changed (Hopley et al., 2007; Pickering et al., 2007, 2011a; Pickering and Kramers, 2010; Bailey et al., 2011; Reynolds et al., 2011; Dirks and Berger, 2013; Bruxelles et al., 2014; Granger et al., 2015). For the past 3 Ma, hominin-bearing deposits in caves formed in broadly similar settings involving debris cone accumulations near cave openings (Partridge and Watt, 1991; Brain, 1993; Pickering et al., 2007; Dirks et al., 2010; Bruxelles et al., 2014). Deposition of these debris cones resulted from granule- to boulder-sized breakdown of ceilings and walls mixed with allochthonous and autochthonous, sand- to clay-sized sediment, as well as peloids and other biogenic debris, by rock falls, debris flow and sheet wash. The clastic sediments vary in texture and composition depending on their position on or near the talus cone, and have been cemented by carbonate-rich waters dripping from cave ceilings.

The sedimentary deposits in the Rising Star cave system that host the remains of the new hominin species of *Homo naledi* (Berger et al., 2015) are anomalous when compared to all other deposits of hominin remains in the Cradle of Humankind in a number of significant ways. Not only are the remains extremely numerous and concentrated, but they also occur in largely unconsolidated mud-rich sediments deep inside the cave away from any obvious cave opening, which suggests that a special

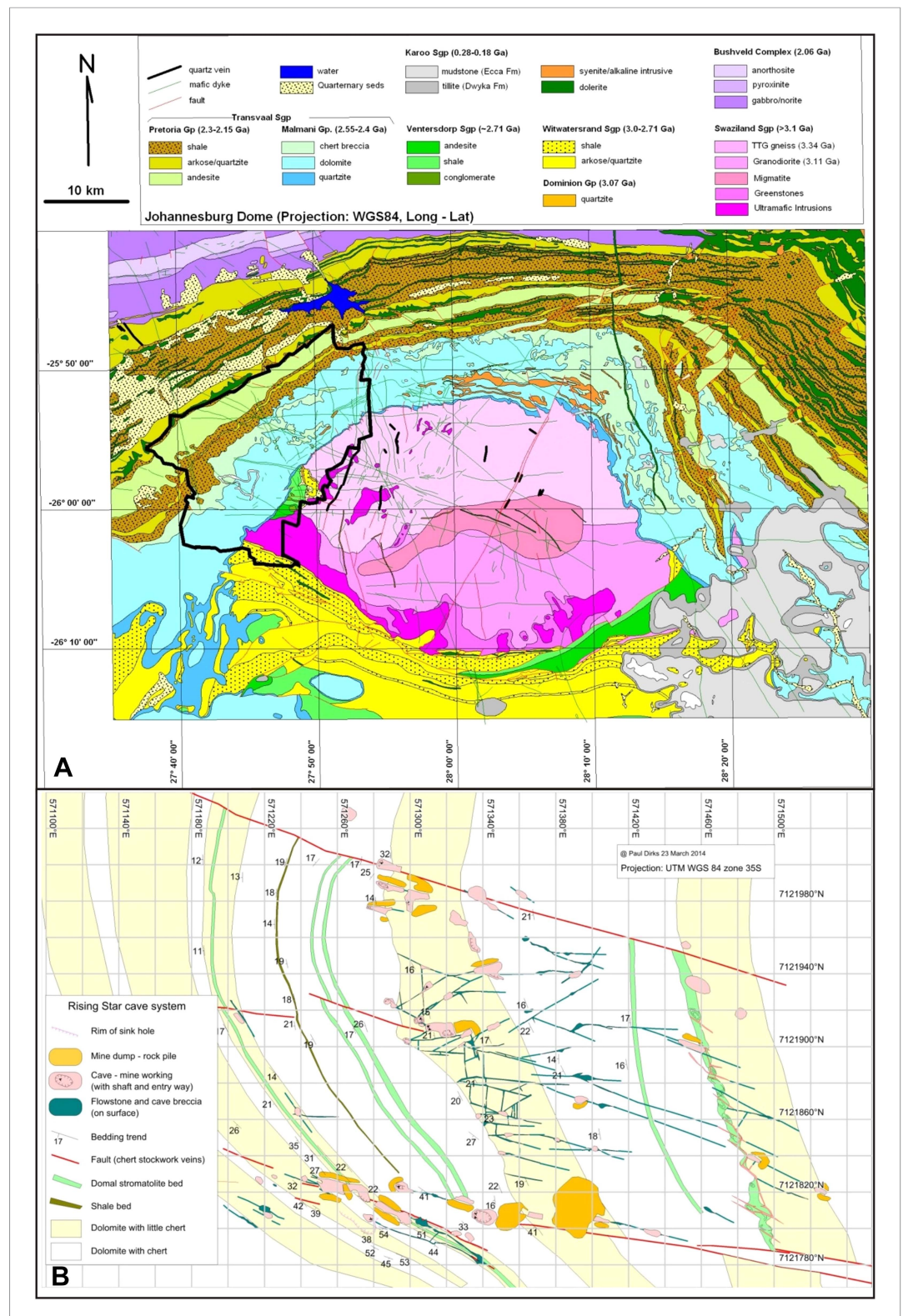


Figure 1. Geological setting of Cradle of Humankind and Rising Star cave system. **(A)** Geology of Johannesburg Dome and surroundings, showing the Cradle of Humankind world heritage site in bold black outline. **(B)** surface geology of the immediate surroundings of the Rising Star cave system, showing the fault sets and variable chert content in the dolomite that controlled cave formation. The cave system is confined to a chert-poor stromatolitic dolomite horizon.

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confluence of circumstances contributed to their accumulation. This paper provides the geological and taphonomic context to the unusual fossil assemblage of *H. naledi* in the Rising Star cave system, and provides possible scenarios to explain their deposition.

The Rising Star cave system

The Rising Star cave system lies in the Bloubaank River valley, 2.2 km west of Sterkfontein cave. It comprises an area of 250 × 150 m of mapped passageways situated in the core of a gently west dipping (17°) open fold, and is stratigraphically bound to a 15–20 m thick, stromatolitic dolomite horizon in the lower parts of the Monte Christo Formation (Eriksson *et al.*, 2006; Figures 1B and 2A). This dolomite horizon is largely chert-free, but contains five thin (<10 cm) chert marker horizons that have been used to evaluate the relative position of chambers within the system (Figure 2B). The upper contact is marked by a 1–1.3 m-thick, capping chert unit that forms the roof of several large cave chambers. Surface mapping indicates that cave openings and flowstone-filled fractures do not penetrate this capping chert unit, except where a dextral fault truncates the stratigraphy to the south of the system (Figure 2). The network of cavities is developed along west-northwest, north and northwest trending fractures and joints.

The fossil-bearing chamber, named the Dinaledi Chamber ('Chamber of Stars' in the Sotho language; Figure 2A), is ~30 m below surface and ~80 m, in a straight line, away from the present, nearest entrance to the cave (Figure 2B). It is situated in the central part of the system and was found during speleological surveys (see methodology section). The only identified access point into the Dinaledi Chamber involves an exposed, ~15 m climb from the bottom of a large ante-chamber (the Dragon's Back Chamber), up the side of a sharp-edged dolomite block that has dislodged from the roof (the Dragon's Back; Figure 2B). From the top of the Dragon's Back, the Dinaledi Chamber is accessed via a narrow, northeast-oriented vertical fissure, and involves a ~12 m vertical climb down, with squeezes as tight as ~20 cm, to reach the floor (Figure 2B,C). The main passage forming the Dinaledi Chamber is ~25–50 cm wide at its narrowest and ~10 m long, and expands in width near the intersections with cross-cutting passages (Figure 2C). The roof of both the Dinaledi and Dragon's Back chambers is formed by the capping chert (Figure 2B). The Dragon's Back Chamber can currently be accessed in two ways, both involving steep climbs along narrow fractures and tight passages (Figure 2A): route 1, along an east-northeast trending passage that follows a fracture for a horizontal distance of ~50 m past a narrow access point called the 'postbox'; and route 2, along a more complicated set of broadly east-trending passages, via a network of southeast, east and north trending fractures for ~120 m, and past a narrow access point called 'superman crawl'. Route 1 is the most direct and contains abundant sediment accumulations once the deeper part of the cave is accessed (i.e., ~20 m into the cave); route 2 has a gentler gradient, but is longer and involves a descent along narrow fissures largely devoid of sediment accumulations. An exhaustive search by a professional caving team and researchers has failed to find any other plausible access points into the Dinaledi Chamber, and there is no evidence to suggest that an older, now sealed, entrance to the chamber ever existed. Furthermore, detailed surface mapping of the landscape overlying the Rising Star cave system (Figure 2A) illustrates that no large flowstone-filled fractures occur in the region above the Dinaledi Chamber.

The skeletal material recovered from the Rising Star cave was collected during two field expeditions in November 2013 and March 2014, and includes 1550 identifiable fossil hominin specimens as well as six bird and several rodent specimens. Of the 1550 hominin specimens, ~300 numbered bone fragments were collected from the surface of the Dinaledi Chamber, and ~1250 numbered fossil specimens were recovered from a small excavation pit in that chamber.

Results

Sedimentology

Throughout the Rising Star cave system erosional remnants of fossiliferous sediment, breccia, and flowstone units provide evidence for several cycles of sediment-flowstone fill and removal/dissolution as the level of the water table in the cave changed repeatedly. On approaching the Dinaledi Chamber from the closest current cave entrance, sediment deposits in the cave become progressively finer-grained. The coarse-grained clastic deposits encountered furthest into the cave are in the Dragon's Back Chamber, and include channelized sandstone and quartz/chert pebble conglomerate units that terminate against the Dragon's Back. The fill generally dips gently west (<5°) in the down slope

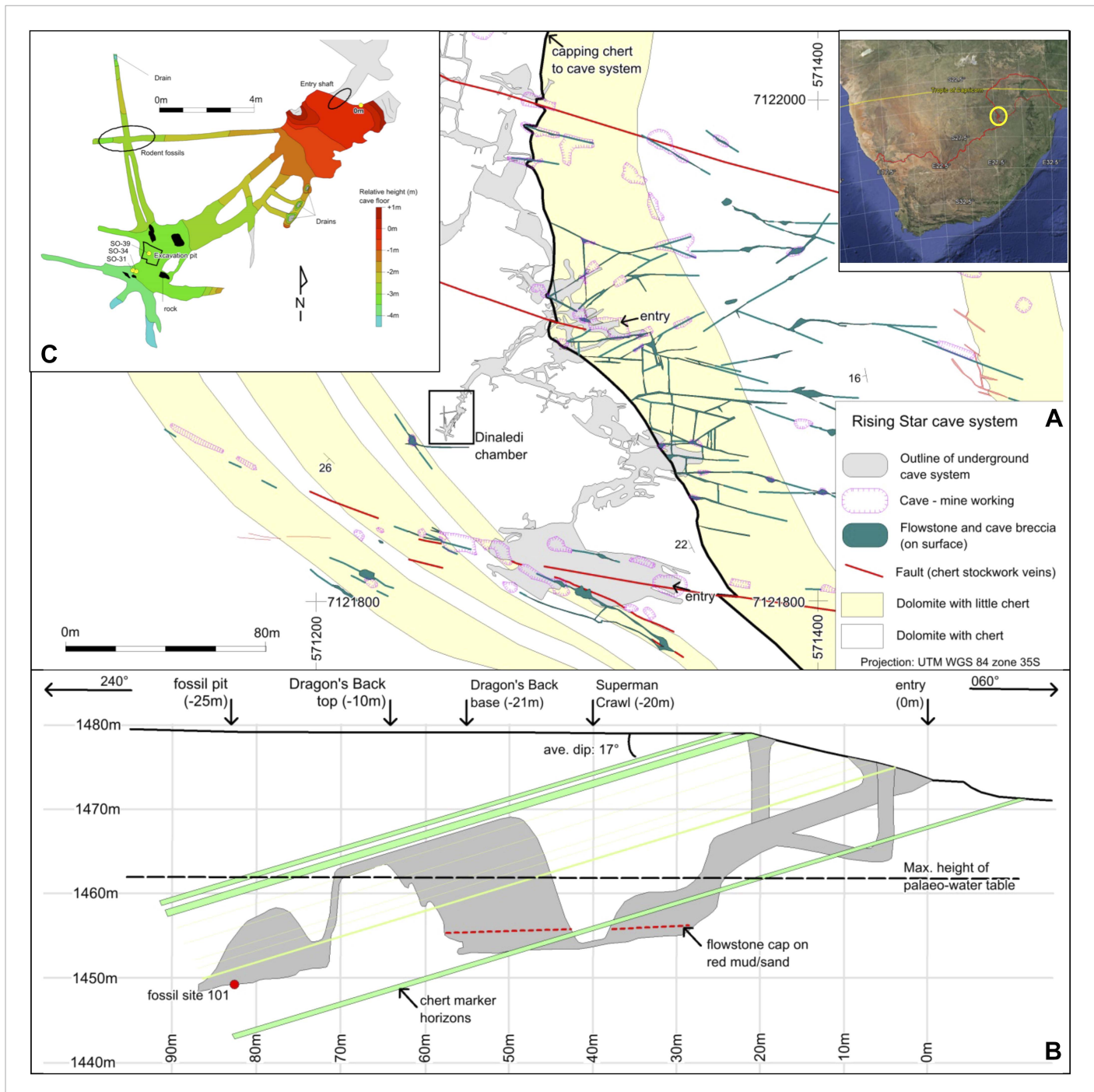


Figure 2. Geological map and cross-section of the Rising Star cave system. **(A)** Geological Map showing the distribution of chert-free dolomite and fracture systems controlling the cave. Inset shows the location of the Cradle of Humankind in southern Africa; **(B)** Northeast-Southwest, schematic cross section through the cave system, relative to several chert marker horizons; **(C)** Detailed map of the Dinaledi Chamber showing the orientation of the floor and the position of the excavation and sampling sites.

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direction of the passages, and becomes near horizontal in the Dragon's Back and Dinaledi chambers. These chambers contain no evidence of sediment input from proximal sources that would indicate a nearby vertical shaft connecting these chambers to surface (Pickering et al., 2007). Mapping reveals no large cave openings on surface above these chambers, although narrow, flowstone-filled fractures

occur (**Figure 2A**) that may have allowed passage of water and some fine-grained sediment into caverns below.

The Dinaledi Chamber is exclusively filled by flowstone and fine-grained sediment involving two depositional facies distributed across three stratigraphic units that filled the chamber over time. Stratigraphic units are separated by erosional unconformities, or laterally continuous flowstone intercalations. Erosion remnants of the units occur in a variety of stratigraphic positions, and there is extensive evidence of reworking with older units being re-deposited into younger units. Each of the facies and units, and each of the flowstone phases that are interlayered with the various units, are described below (**Figures 3, 4**).

Facies 1: horizontally laminated orange-brown mudstone with sandstone lenses

Facies 1 has been sub-divided into two sub-facies. Facies 1a consists of unlithified, horizontally laminated, orange mud, with very low sand content (**Figure 4A,B**). The composition is dominated by fine sericite clay with subordinate amounts of silt-sized chert and dolomite grains (**Figure 5**). Facies 1a is generally unconsolidated, but contains secondary Mn- and Fe- oxide phases that locally form weakly cemented concretions. Facies 1a has a patchy distribution, occurring both in undisturbed, isolated areas as accumulations atop blocks and in fissures (e.g., **Figure 4A**), and more commonly as erosional remnants of formerly more extensive deposits that filled the Dinaledi Chamber and side passages. Outcrops of Facies 1a (e.g., near the entry point at the top of the chamber, **Figure 4F**) show evidence of in situ auto-brecciation of orange mudstone around exposed margins, due to desiccation, and/or formation of Fe-Mn concretions.

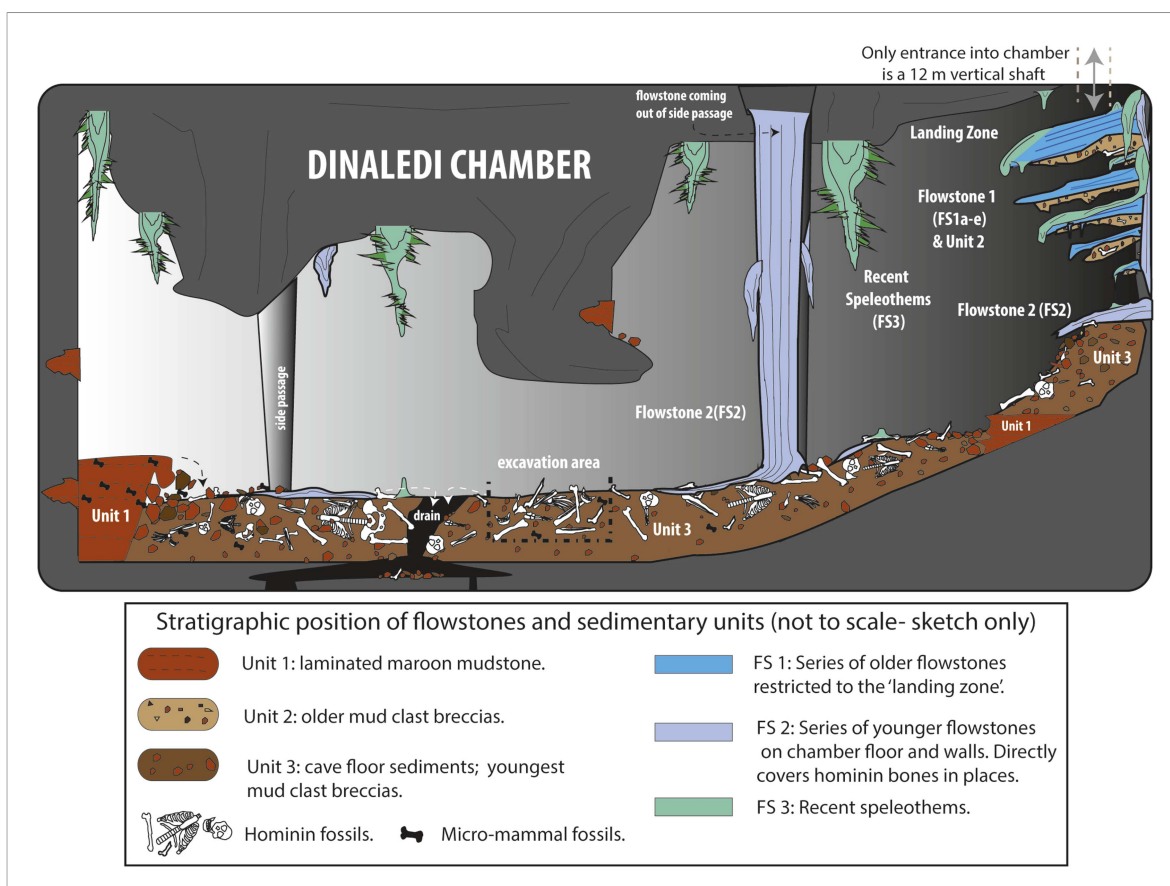


Figure 3. Cartoon illustrating the geological and taphonomic context and distribution of fossils, sediments and flowstones within the Dinaledi Chamber. The distribution of the different geological units and flowstones is shown together with the inferred distribution of fossil material.

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Facies 1b consists of orange-brown mudstone interlaminated with thin lenses of silt to fine- to medium-grained sand with angular to sub-rounded grains of chert and quartz, and abundant micromammal fossils. The sandstone/siltstone layers are a few mm thick, and in some places display small-scale current ripple laminations. Facies 1b is restricted to isolated erosion remnants in the floor and to crevices in the dolostone above the floor (**Figure 3**). An extensive search for hominin and other macro-vertebrate bones in Facies 1a and 1b was conducted within the Dinaledi Chamber, but none were found.

The horizontally laminated deposits of Facies 1a have been interpreted as autochthonous suspension deposits associated with a low energy environment as water laden with mud gradually filtered into the cave chamber. Deposits of Facies 1a have also accumulated on ledges in isolated fissures where mud filtered through narrow cracks.

Deposits of Facies 1b are interpreted to represent a higher energy environment involving pulses of para-autochthonous and/or allochthonous sediment deposited in the cave by minor sheet flow, which alternated with periods of quiescence during which Facies 1a muds were deposited. The source of micromammal fossils and sand in Facies 1b has not been determined with any certainty, but considering that Facies 1b deposits occur in isolated locations within the chamber, we assume that the sand and fossils may have entered from narrow passageways that drain higher up into the chamber.

Facies 2: unconsolidated to consolidated, orange-brown mud clast breccia in a mud matrix

Facies 2 consists of massive, that is, non-layered, mud clast breccia surrounded by a matrix of brown mud with localised patches of sparry carbonate cement. Clasts in Facies 2 are predominantly composed of laminated, orange-brown mud fragments (Facies 1a), which are weakly consolidated, angular to sub-angular in shape, and variable in size, but typically <3 cm in diameter (**Figure 4D,E**). Facies 2 locally contains pebble to cobble-sized, angular clasts of dolomite and chert, derived from the surrounding cave walls. No reworked flowstone clasts have been observed in Facies 2 deposits. Sediments of Facies 2 may be clast-supported (e.g., near the landing zone) or matrix supported (e.g., in parts of the cave floor), and the size and angularity of mud clasts varies, as does the degree of matrix and cementation. Macro-vertebrate bones, including all the remains of *H. naledi*, are found within stratigraphic units composed of Facies 2.

Facies 2 deposits are interpreted as accumulations of largely autochthonous debris derived from within the cave chamber through weathering (auto-brecciation) and erosion of Facies 1 deposits, or through reworking of older deposits of Facies 2. The typically angular nature of the soft mud clasts in Facies 2 indicates minimal transport and low-energy processes in the cave chamber. The few fragments of dolomite and chert were sourced from within the chamber, dropped from the cave roofs and walls. Deposits of Facies 2 accumulated in the area beneath the fissure that forms the entry point into the Dinaledi Chamber, to form a debris cone that sloped into the chamber. This debris cone largely developed in the absence of either sustained flowing or standing water to explain its topography and the preservation of angular mud fragments.

Flowstones in the Dinaledi Chamber

A number of different flowstone formations can be identified in the Dinaledi Chamber. These formed at separate times, and help demarcate stratigraphic units. Each type of flowstone is described below starting with the oldest.

Flowstone 1

The oldest flowstones in the cave are a group of five, spatially associated flowstone drapes (Flowstones 1a–e) that appear to be genetically related, and remain as hanging erosion remnants with rounded shapes, near the entrance into the chamber (**Figure 4C**). Remains of Flowstone 1 are preserved to the east of the entry point into the Dinaledi Chamber, where a large, south dipping, dripstone apron (Flowstone 1a) and four partly dissolved, closely spaced flowstone sheets 30–100 cm beneath it (i.e., Flowstones 1b–e) build out from the back of the entry point. All remnants of Flowstone 1 dip ~20–30° south towards the bottom of the cave chamber. Flowstone 1a, which is the topmost and thickest (<15 cm) of the early flowstone units covers a 10–15 cm thick remnant of well-indurated Facies 2 sediment assigned to Unit 2 (see below; **Figure 4D**). Flowstones 1b–e cover poorly consolidated remnants of Unit 2 sediment that are partly covered themselves by deposits of younger flowstone

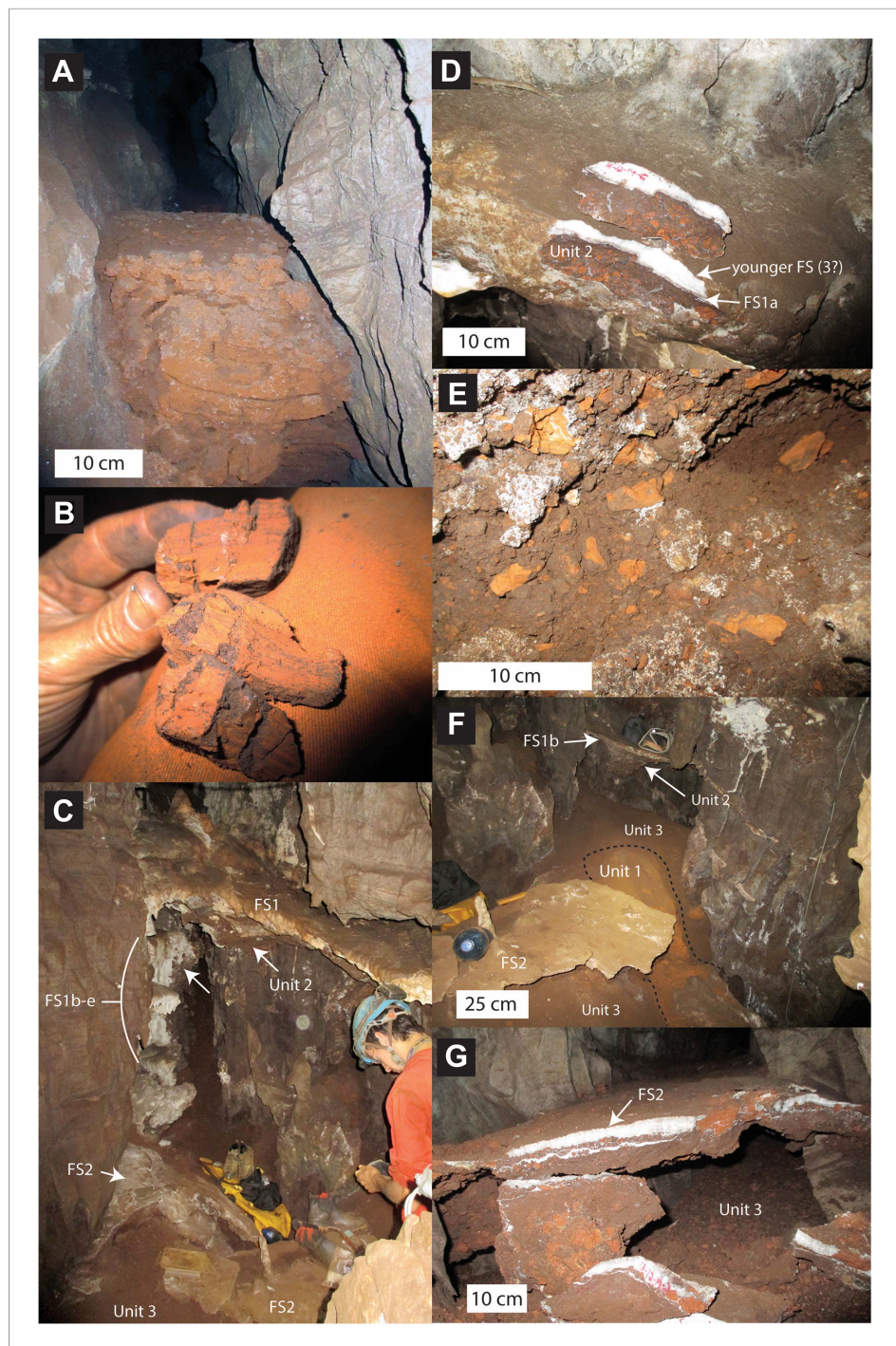


Figure 4. Stratigraphic units and flowstones observed in the Dinaledi Chamber. (A) Erosional remnant of horizontally laminated Unit 1 strata (Facies 1). (B) Close-up view of Unit 1 (Facies 1a) showing fine laminations and small invertebrate burrows (note fine sand infilling in burrows). (C) Overview photo of the Dinaledi Chamber, directly to the east of the entrance point into the chamber. Photo shows distribution of Flowstones 1–3 and stratigraphic Units 2 and 3. (D) Close-up view of Flowstone 1 encasing sediment of Unit 2. Note that several generations of flowstone (Flowstones 1a–e) are coating Unit 2. The thin, clear lower layer is Flowstone 1a, and the overlying white flowstone is either Flowstone 2 or 3. (E) Close-up view of Unit 2, consisting of generally poorly-cemented Facies 2 sediment. (F) View of the chamber floor near the entry point. On the cave floor, a large erosional remnant of Unit 1 (orange laminated mudstone of Facies 1a), is surrounded by mud-clast breccia of Unit 3 (main hominin bearing unit). Note that Flowstone 2 has been undercut by post-depositional erosion of Unit 3, which, in this location has resulted in a lowering of the floor by as much as 25 cm. (G) Flowstone 2 overlying Unit 3 in one of the chamber's side passages. *Figure 4. continued on next page*

Figure 4. Continued

In this location Unit 3 has also been partly eroded after depositional from underneath the flowstone drape, leaving a hanging remnant, with some indurated sediment of Unit 3 attached to its base. Note the continued deposition of sediment above Flowstone 2.

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(i.e., Flowstones 2 or 3). In fresh breaks, Flowstone 1a shows a basal 3–8 mm thick layer of laminated, crystalline calcite, which is covered by an outer layer of mostly white, coarse-crystalline calcite, which varies significantly in thickness and in places forms a fringe of small stalactites along the outer lip of Flowstone 1a (**Figure 4D**). This outer layer likely represents a younger generation of flowstone (Flowstone 3?) that covered Flowstone 1a.

Flowstone 2

Flowstone 2 represents the most significant phase of flowstone development in the Dinaledi Chamber, and forms cascades emanating from fractures in cave walls and the cave roof throughout the chamber. Deposits of Flowstone 2 partly cover remains of Flowstone 1a–e, and portions of the floor of the cave. This can be observed near the landing zone, but is particularly prominent in the bottom of the chamber. In most side passages, where the dolomite walls narrow to thin fractures, large cascades of Flowstone 2, flow down the cave walls and spread out across the cave floor forming thin flowstone drapes on top of poorly consolidated sediment of Facies 2 containing hominin fossils (Unit 3; **Figure 4F,G**). Locally (e.g., in a side passage on the northwest side of the Dinaledi Chamber) floor drapes of Flowstone 2 cover erosional remnants of Facies 1a (Unit 1). In various places in the chamber, significant undercutting of these floor drapes has occurred due to more recent erosion of the cave floor, creating hanging sheets of Flowstone 2 (**Figure 4F,G**). In fresh breaks, Flowstone 2 varies from white, coarse-crystalline calcite to grey and brown laminated calcite contaminated with mud. Some of the floor drapes have a sugary texture due to post-depositional recrystallisation. In places, Flowstone 2 has been covered by thin deposits of Flowstone 3.

Flowstone 3

Deposits of Flowstone 3 are currently active flowstone formations in the Dinaledi Chamber, and are primarily restricted to the chamber ceiling in the area around the entrance, where they form delicate needle- and rod-like forms that include well-formed crystals of aragonite. Near the chamber entrance, minor dripstone is also forming on the walls and on top of Flowstone 1 and 2. Lower in the chamber, there are small dripstone accumulations (stalagmites), which have resulted in localised patches of Flowstone 3 on the chamber floor and covering Flowstone 2.

Stratigraphic units in the Dinaledi Chamber

Using the distribution of flowstones, sedimentary facies (e.g., the presence of Facies 1 mud clasts inside Facies 2), and erosional contacts, a basic stratigraphy of three separate units has been established in the Dinaledi Chamber. This stratigraphic interpretation is preliminary and based solely on geological reasoning (i.e., stratigraphic superposition of individual units, textural variations in Facies 2 sediment and the presence or absence of dissolution features), because of an absence of reliable age data. It is important to note that the facies described above are not synonymous with stratigraphic ordering although in general Facies 1 sediments appear to be older than Facies 2 sediments. Variations in texture, composition and degree of lithification of Facies 2 sediments, as well as direct contact relationships, make it possible to define different stratigraphic units composed of Facies 2. Because we do not yet have a clear understanding of the age relationships, nature of disconformable surfaces or the extent of reworking between the units, we refrain from defining these as discrete allostratigraphic units and instead prefer the use of lithostratigraphic units. The three lithostratigraphic units and their distribution in the Dinaledi Chamber are described below.

Unit 1

The oldest stratigraphic unit preserved in the Dinaledi Chamber, Unit 1, is represented by outcrops of laminated orange mudstone of Facies 1a, which are preserved as isolated erosion remnants in several places in the Dinaledi Chamber (**Figure 4A,F**). The first significant remnant of Unit 1 is located on the

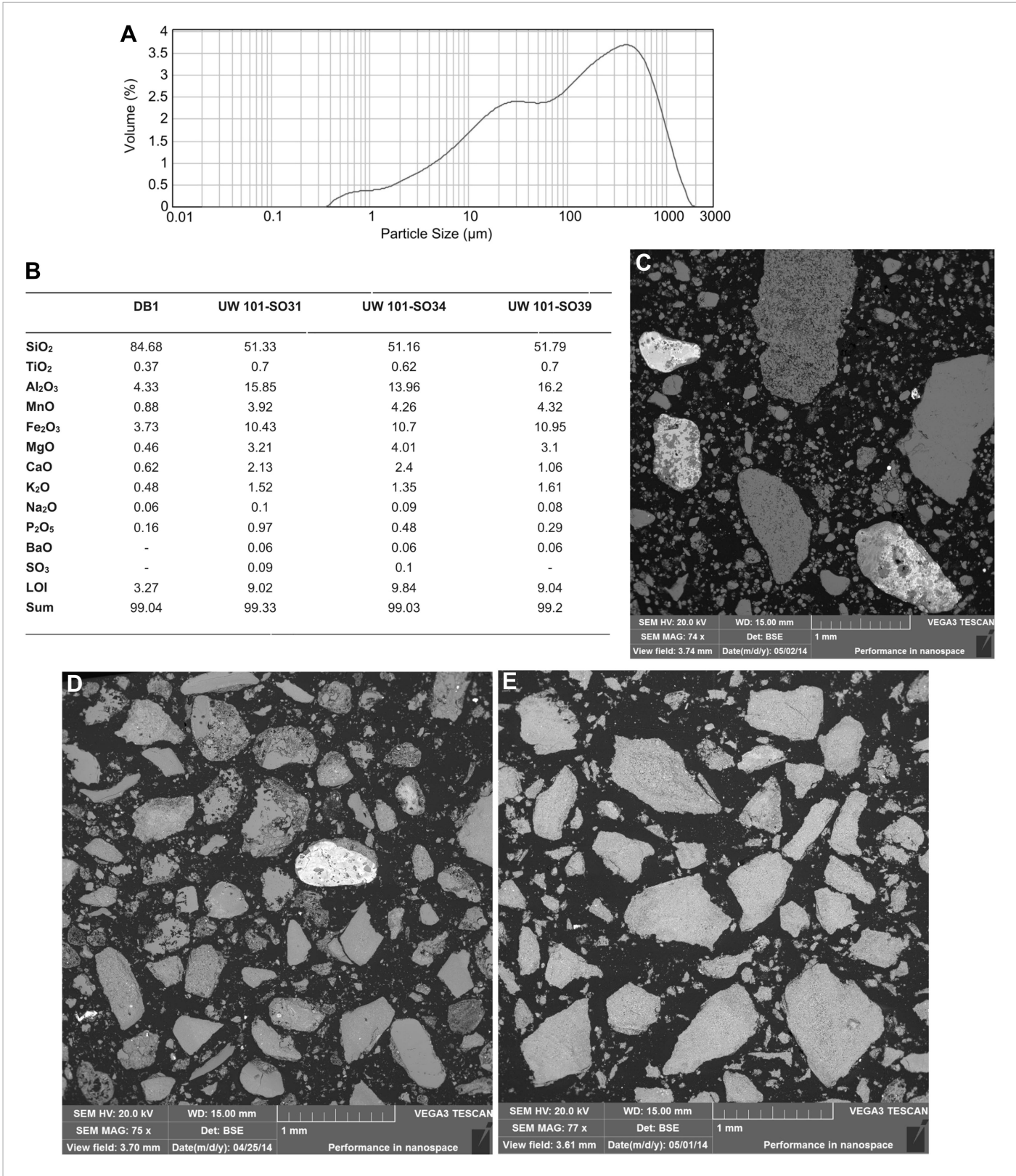


Figure 5. Data and characteristics of cave floor sediments (Facies 2) from the Dinaledi and Dragon’s Back Chambers. **(A)** Grain size distribution of sample UW101-SO-39 (**Figure 2C**). The bulk of the sample material falls within a size fraction corresponding to silt and fine-grained sand. Some coarser mudstone fragments did not disintegrate when immersed in water, likely due to considerable Mn- and Fe-oxide micro-concretionary development in the orange **Figure 5. continued on next page**

Figure 5. Continued

mudstone. Because some mudstone fragments are well lithified the particle size distribution is skewed towards the coarser grain-size values. **(B)** Results of XRF analyses of bulk samples of three floor sediments from the Dinaledi Chamber (UW101-SO31, -34 and -39) and one from the Dragon's Back chamber (DB-1). The sample from the Dragon's Back Chamber has a radically different composition from those of the Dinaledi Chamber, with the high SiO₂ content reflecting its dominance of quartz. The Dinaledi samples have much higher Al₂O₃ and K₂O contents than DB-1, indicating a higher content of clay minerals and mica, and higher CaO, MgO, MnO, and total Fe oxide contents which reflect alterations and inclusions. The higher P₂O₅ content of the Dinaledi samples is probably located in comminuted bone fragments which are seen macroscopically. The volatiles content (LOI) of the Dinaledi samples is also higher than in DB-1, in accord with a higher total clay mineral and mica content. **(C–E)** Backscattered electron (BSE) wide-field images of grain mounts from floor sediments. Brighter shades indicate the presence of heavier elements, mainly Mn and Fe in altered grains. **(C)** DB-1, Dragon's Back Chamber, large fragments are quartz and chert, partly altered. **(D)** UW101-SO34. **(E)** UW101-SO39. In these samples the large fragments are almost exclusively clay; note their angular shape which shows these to be locally derived.

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floor of the cave chamber, to the east of the entry point below outcrops of younger units composed of Facies 2, and remnants of Flowstones 1–3. This exposure of Unit 1 is largely buried by younger sediment belonging to Unit 3 (**Figure 4F**).

A second large outcrop of Unit 1 occurs in a northwest-trending side passage of the Dinaledi Chamber, where it forms a ~4 m long portion of cave floor composed of finely laminated orange mud. At some point in time, deposits of Unit 1 would have filled much of the Dinaledi Chamber, and erosion products (i.e., mud clasts) from this unit are the source for much of the mud clast breccia (i.e., deposits of Facies 2; **Figure 4E**) observed in the cave chamber.

The isolated outcrop of micromammal-bearing, orange mudstone-sandstone (Facies 1b) in one of the side passages may represent a further outcrop of Unit 1, in which case it provides evidence for lateral facies variations in Unit 1. Alternatively the outcrop of Facies 1b represents local reworking of Unit 1, and hence a younger stratigraphic unit. Because of this uncertainty, we presently do not include Facies 1b within Unit 1.

Small pockets of Facies 1a sediment (a few tens of cm long and wide by up to 10 cm thick) are preserved in crevices and as hanging remnants, high-up in the Dinaledi Chamber, up to 4 m above the chamber floor. These outcrops may represent isolated erosion remnants of Unit 1, but in the absence of direct stratigraphic relationships we cannot be sure. Alternatively, Facies 1a has a long depositional history, and these isolated outcrops represent in situ accumulations of 'wad' formed as a result of weathering of the dolomite wall rock (**Martini et al., 2003**).

Unit 2

The next stratigraphic unit, Unit 2, is the oldest unit composed of Facies 2 sediment, and is restricted to small outcrops below the entrance shaft into the Dinaledi Chamber. Unit 2 is a composite unit that consists of variably consolidated, clast-supported Facies 2 sediment, dominated by reworked mud clasts derived from Unit 1, mixed with rare chert and dolomite fragments (**Figure 4D**). The mud clasts in this unit are composed of a combination of fresh (orange), angular clasts, and more oxidized (brown), sub-angular to sub-rounded clasts (**Figure 4E**), set in an oxidized, brown muddy matrix with some silt- to sand-sized particles, and locally cemented by sparry carbonate.

Outcrops of Unit 2 are preserved as erosional remnants of limited size that are attached below the hanging aprons of Flowstones 1a–e. The topmost outcrop of Unit 2 occurs below Flowstone 1a, and consists of a 10–15 cm thick erosion remnant of consolidated mud clast breccia (**Figure 4D**). The outer surface of this outcrop has a smooth appearance as a result of dissolution after deposition and lithification. In contrast, erosion remnants of Unit 2 that are preserved underneath aprons of Flowstones 1b–e (**Figure 4C**), are mostly unconsolidated and have a rubbly appearance.

Like the overlying flowstone sheets, outcrops of Unit 2 dip southwest at ~20–30° into the Dinaledi Chamber (**Figure 4C**), which indicates that Unit 2 accumulated on a debris cone or rubble deposit that sloped into the chamber and developed below the entry shaft. Sediments that accumulated on this debris cone gradually slumped into the Dinaledi Chamber at a time that flowstone was forming, resulting in the progressive formation of Flowstones 1a–e. This process of progressive erosion is described in more detail in the discussion section.

Outcrops of Unit 2 contain several, in situ macro-fossil bones that can be identified as hominin, but are otherwise undiagnostic. This includes the shafts of a juvenile hominin ulna and radius contained in

a collapsed portion of unconsolidated Unit 2 sediment derived from below Flowstone 1b, which are consistent with the remains of *H. naledi*.

Unit 3

Unit 3 is the youngest stratigraphic unit in the Dinaledi Chamber, and is represented by sediment that accumulated along the floor of the chamber and along the bottom of many, but not all of the side passages (**Figure 4G**). Unit 3 is composed of largely unconsolidated sediment of Facies 2 dominated by reworked orange mud clasts embedded in a brown muddy matrix. This unit is massive and displays no evidence of layering or grading, and is commonly matrix supported (as opposed to the mostly clast-supported Unit 2). It has been derived from weathering and erosion of Units 1 and 2. Unit 3 partly covers exposures of Unit 1 in several side passages and near the entry point into the cave.

Upon initial discovery of the Dinaledi Chamber, Unit 3 contained dozens of hominin bones exposed along its surface and partially buried within it, in most portions of the chamber where Unit 3 has formed (**Figure 6**). A series of minor test pits (a few cm deep) were dug into Unit 3 at various areas of the cave floor, which revealed that abundant additional hominin bones are buried at shallow depths within Unit 3 throughout much of the chamber. The abundance and density of *H. naledi* bones in the chamber is demonstrated in the single excavation, where most (1250 out of 1550 elements) of the fossil material documented from the Dinaledi Chamber was collected (**Figure 7**). Unit 3 also contains rare disarticulated rodent remains that are undiagnostic of age, and that are possibly derived as an erosional product from Unit 1 (Facies 1b) or that were deposited directly into Unit 3 as it accumulated.

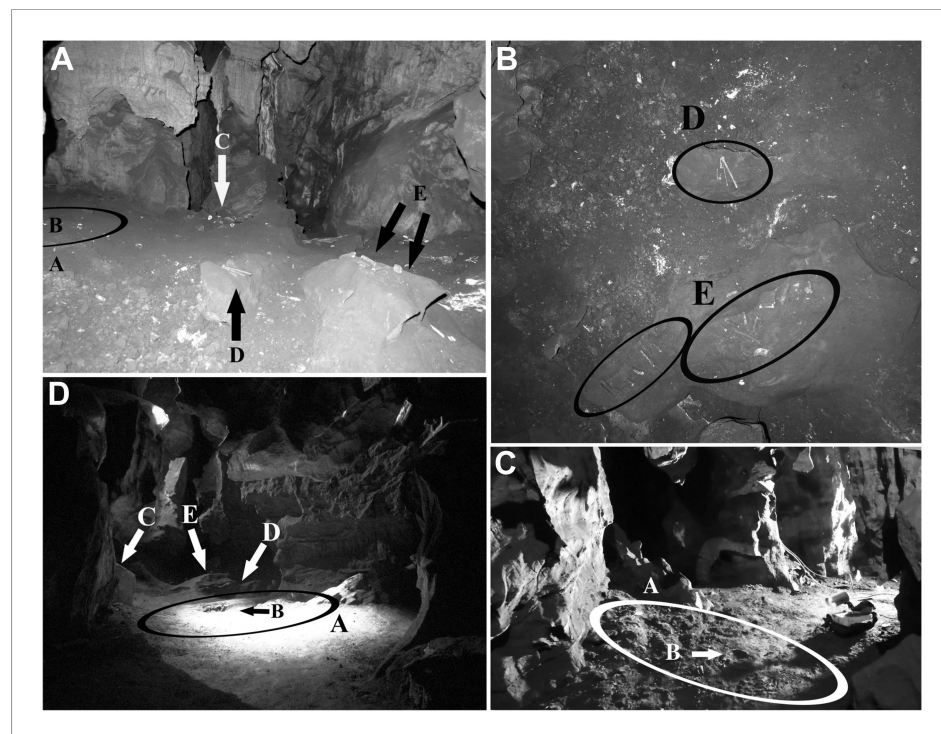


Figure 6. Views of the Dinaledi Chamber. Clockwise from top left: **(A)** Photograph taken during initial exploration of the chamber; view to the N. Ellipse 'A' indicates the area where most of the hominid material was excavated. Letter 'B' shows the location of the cranial fragment that was one of the first pieces removed from the chamber. Arrows 'C', 'D' and 'E' indicate areas of concentrated surface material. Block E is ~ 50 cm across. **(B)** pre-excitation view of the chamber floor. 'D' and 'E' included hominid teeth, (intrusive) bird bones and several long bone fragments that had been 'arranged' on rocks by an unknown caver prior to discovery by our caving team. Top of the photograph point to the NE. Base of the photograph is 80 cm. **(C)** view of the primary excavation area prior to excavation looking in a NE direction. The diameter of the ellipse is 1 m for scale **(D)** the excavation area at the end of the first round of excavations looking in a SSE direction (November 2013). Ellipse A is the same as in previous figures. Arrow B shows the fragment of a long bone that was uncovered after the cranial fragment had been removed. Arrows C, D and E indicate where surface concentrations had previously been. The diameter of the ellipse is 1 m for scale.

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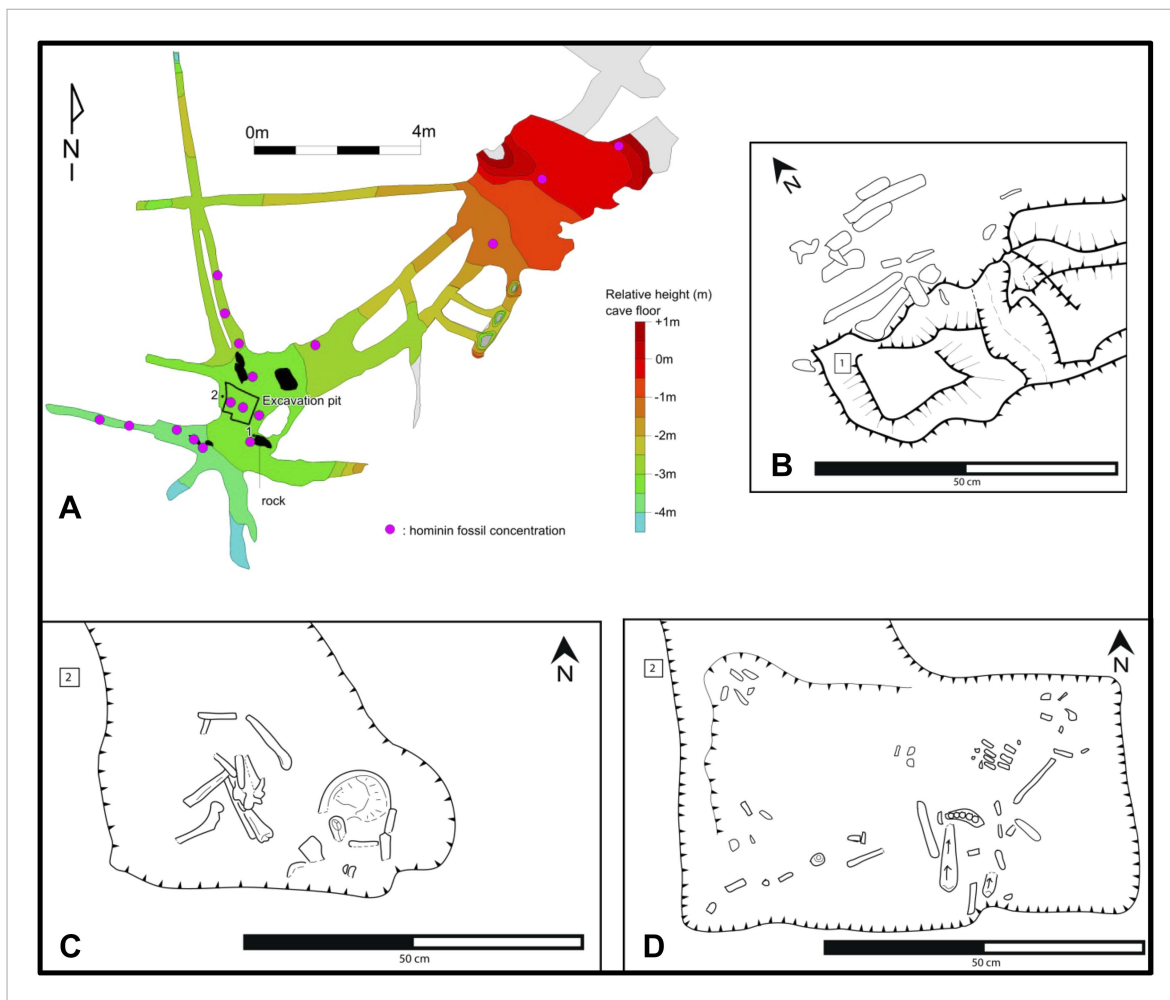


Figure 7. Map of the cave chamber showing the distribution of hominin fossils. (A) distribution of concentrations of bone fragments of *H. naledi* along the floor of the Dinaledi Chamber. The positions of maps (B) and (C), (D) are shown relative to survey pegs 1 and 2 respectively. (B) Concentration of long bone fragments encountered next to a rock embedded in Unit 3 sediment. (C) Distribution of fossils in the excavation pit at the start of the excavations in November 2013 (~5 cm below surface). (D) Distribution of fossils in the excavation pit during excavations in March 2014 (~15 cm below surface); the long-bone in the central part of the pit is in a near-vertical position and is shown in **Figure 9C**.

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In many parts of the chamber, Unit 3 is covered by a thin sheet of Flowstone 2, which spread across the top of Unit 3 from a number of separate drip points. When dated, these cover sheets of Flowstone 2 will constrain the youngest possible age for the *H. Naledi* fossil assemblage. The formation of drapes of Flowstone 2 atop Unit 3 was followed by localized, post-depositional erosion of the cave floor, a process that continues today, as sediment is periodically washed down floor drains in the chamber. As a result, hanging erosion remnants of Flowstone 2 are preserved in several places along the walls of the cave chamber (e.g., directly north of the excavation pit), where they remain up to 20 cm above the present cave floor (**Figure 4F,G**).

Mineralogy and chemistry

Mineralogical and chemical studies were carried out on sediment samples from the floors of the Dinaledi and Dragon's Back chambers (Facies 2; Unit 3) to assess the nature of the sediment encasing the Dinaledi fossils and to determine whether these chambers were connected at the time of deposition of Units 2 and 3 (see **Supplementary file 1** for analytical results).

Four samples of cave sediment were studied using different techniques to obtain data on their size fraction, mineralogy and geochemical characteristics. Samples UW101-SO-31, UW101-SO-34 and

UW101-SO-39 were collected near the excavation pit in the Dinaledi Chamber, from brown matrix-supported mud clast breccia of Unit 3 (**Figures 2C and 7**). UW101-SO-31 is light-brown in colour, and contains sand grains and has bone fragments. UW101-SO-34 consists of dark-brown mud and is not gritty to feel. UW101-SO-39 is a medium- to dark-brown mud that is slightly gritty to feel. One additional sample, DB-1, was collected for analysis from unconsolidated floor sediment in the Dragon's Back chamber (**Figure 2B**). This is a brown silty mud with a fine-gritty feel, containing sub-mm sized bone fragments.

The three samples of Unit 3 from the Dinaledi Chamber (SO31, 34, 39; **Figures 2C and 5D,E, 8**) are dominated by reworked, angular mud clasts in a clay matrix, with some chert fragments, but with little externally derived detrital quartz. The sample from the Dragon's Back Chamber is dominated by detrital quartz, with some detrital muscovite, as well as shale and chert fragments, of which some are altered and impregnated and/or coated with Mn- and Fe-oxides. Mudstone fragments are rare in DB-1 (**Figures 5C and 8**). Elevated MnO (3.9–4.2%) and Fe₂O₃ (10.3–11%) levels in the floor sediments of both chambers are associated with alteration of chert or mudstone prior to their comminution, with Mn- and Fe oxides/hydroxides occurring as replacement and micro-vein infilling. XRD diffractograms identified both quartz and muscovite in all samples with high scores compared to other minerals. Hematite was identified with high scores in all the Dinaledi samples. Goethite (FeO(OH)) and birnessite ((Na,Ca,K)(Mn⁴⁺,Mn³⁺)₂O₄·1.5H₂O) were only identified in UW101-SO-31, with low scores, but high certainty. Other minerals identified with low scores and high certainties are dolomite ((CaMg)(CO₃)₂) in UW101-SO-34 and kaolinite (Al₂Si₂O₅(OH)₄) in UW101-SO-39. Using XRD, only quartz and muscovite were identified in DB-1. Acid tests showed all samples to be free of calcite or aragonite. All analysed Mn oxi-hydroxides in both chambers contain fluorine, with similar (atomic) F/Mn ratios of ≈ 0.14, indicating a similar chemical environment during their formation. Different patterns in K₂O vs Al₂O₃ plots reflect a dominance of mudstone fragments consisting mainly of clay minerals, in the Dinaledi Chamber, and the presence of muscovite in the Dragon's Back Chamber (**Figure 8**). The contrasting composition in particulate matter of floor sediments in the two chambers, suggests that the Dinaledi Chamber was an isolated sedimentary environment at the time of deposition of Unit 3, with no or very limited transfer of sediment between the two chambers.

Flowstone samples from the Dinaledi Chamber were analysed for uranium to assess the possibility of U-Pb dating. Although analysed samples mostly contain sufficient U for this (0.3–0.7 ppm), a fine dusting of a detrital component derived from associated muds is present in all tested pilot samples. This has confounded preliminary attempts at U-Pb dating, because of the high, and isotopically variable, background of common Pb it carries.

Taphonomy

A detailed taphonomic study of the hominin remains is ongoing, and initial results have been provided in this study to illustrate the broader context of the fossil assemblage. Analyses of taphonomic processes affecting the Dinaledi hominin fossil assemblage have been conducted to describe decomposition, weathering and fracture patterns, surface modifications as a result of invertebrate–bone interactions (as well as the lack of vertebrate–bone interactions), and spatial context including skeletal distribution patterns (**Behrensmeyer et al., 1986; Galloway, 1999; Straus and Porada, 2003; Loe, 2009; Symes et al., 2013; Figures 7, 9–12**). Summary tables of results are presented in **Table 1** and **Supplementary file 2**.

Bone material and its spatial distribution

Figure 7 shows the general distribution of fossil material within the Dinaledi Chamber, together with more detailed maps of fossil distributions in the excavation pit and nearby surficial areas. When the Dinaledi Chamber was first entered, the sediments along the cave floor (i.e., Unit 3) consisted largely of loosely packed, semi-moist, clay-rich clumps of varying sizes in which bone material was distributed. Where people had moved through the chamber, the sediment along the floor had been compacted down to a flat, semi-hard surface. The hominin bone material was distributed in Unit 3, across the surface in almost every area of the chamber, including narrow side passages and offshoots, with the highest concentration of bone material encountered near the southwest end of the chamber, about 10–12 m downslope from the entry point, where the floor levels out.

Hominin bones were found at the surface of, and within Unit 3, distributed across the floor of most of the Dinaledi Chamber, and short distances down many side passages (**Figures 6, 7**). In parts of the

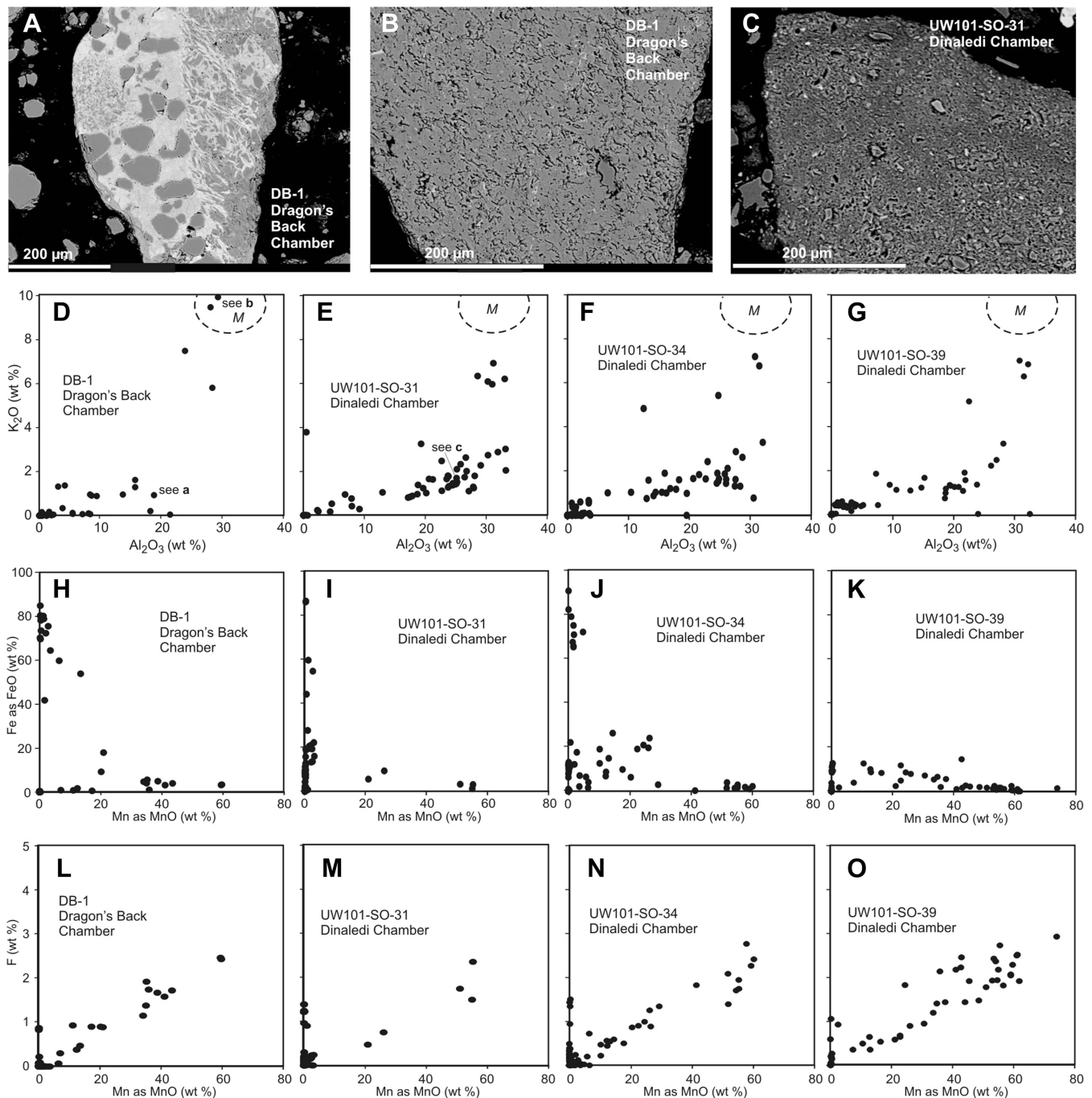


Figure 8. Comparison of selected fragments and electron microprobe analytical data of Facies 2 (Unit 3, floor) sediment in the Dinaledi Chamber, and floor sediments in the Dragon's Back Chamber. Analytical spot size is 5 μm diameter, which is generally larger than grain sizes. (A) Chert fragment impregnated with Mn oxi-hydroxide from the Dragon's Back Chamber. (B) Shale fragment from the Dragon's Back Chamber. (C) orange mud clast, typical of Facies 2 sediments from the Dinaledi Chamber, note much finer grain size than seen in (B). (D–G) Plots of K_2O vs Al_2O_3 for mud clast fragments in Facies 2 samples from both chambers show an important difference between them. M, muscovite compositional field. The samples from the Dinaledi Chamber (E–G) yield some data close to the muscovite field, probably indicating sericite grains slightly smaller than the spot size, and all show a trend with K/Al ratios much lower than muscovite, up to a high Al_2O_3 content >30%, which indicates either illite, or mixtures of sericite and kaolinite or other K-free clay minerals. In (E) the analysis of the fragment shown in (C) is indicated. The sample from the Dragon's Back Chamber in (D) shows data in the muscovite field (data point corresponding to [B] is indicated in [D]), but otherwise only low K- and Al-concentrations, which are typical of Mn oxi-hydroxide impregnation (data point corresponding to [a] is indicated in [D]). No analytical data in d correspond to mudstone fragments such as shown in (C). (H–K), plots of Fe as

Figure 8. continued on next page

Figure 8. Continued

FeO vs Mn as MnO show similarity between the chambers with respect to Fe-Mn oxi-hydroxide impregnations and alterations within the fragments: in both cases, domains with high Fe rarely coincide with domains high in Mn. (L–O), Plots of F vs Mn as MnO. Some elevated F concentrations at zero Mn values occur, but most data show a correlation for samples from both chambers: elevated Mn content is invariably associated with elevated F, with an atomic ratio $F/Mn \approx 0.14$. No Mn oxi-hydroxide minerals with F have been described, but partial substitution of F^- for OH^- as in apatite might be suspected. The similarity of the F/Mn ratios in Mn oxi-hydroxide impregnated fragments from Facies 2 sediments in both chambers suggests a uniform geochemical environment during the Mn oxi-hydroxide alteration event.

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chamber, Flowstone 2 covers Unit 3 along the surface of the cave floor, encasing some hominin bones. A few hominin bones were also collected from loose sediment accumulated on top of Flowstone 2, and represent re-deposited material derived from recently eroded and transported deposits of Unit 3. In situ bone fragments exist in Unit 2, which are hominin and contributed to the assemblage found in Unit 3.

To date, most hominin bones have been collected from Unit 3. A single excavation of Unit 3 was conducted in a 0.8×0.8 m pit, ~20–25 cm deep (with a 50 cm deep central sondage; **Figure 2C**), near

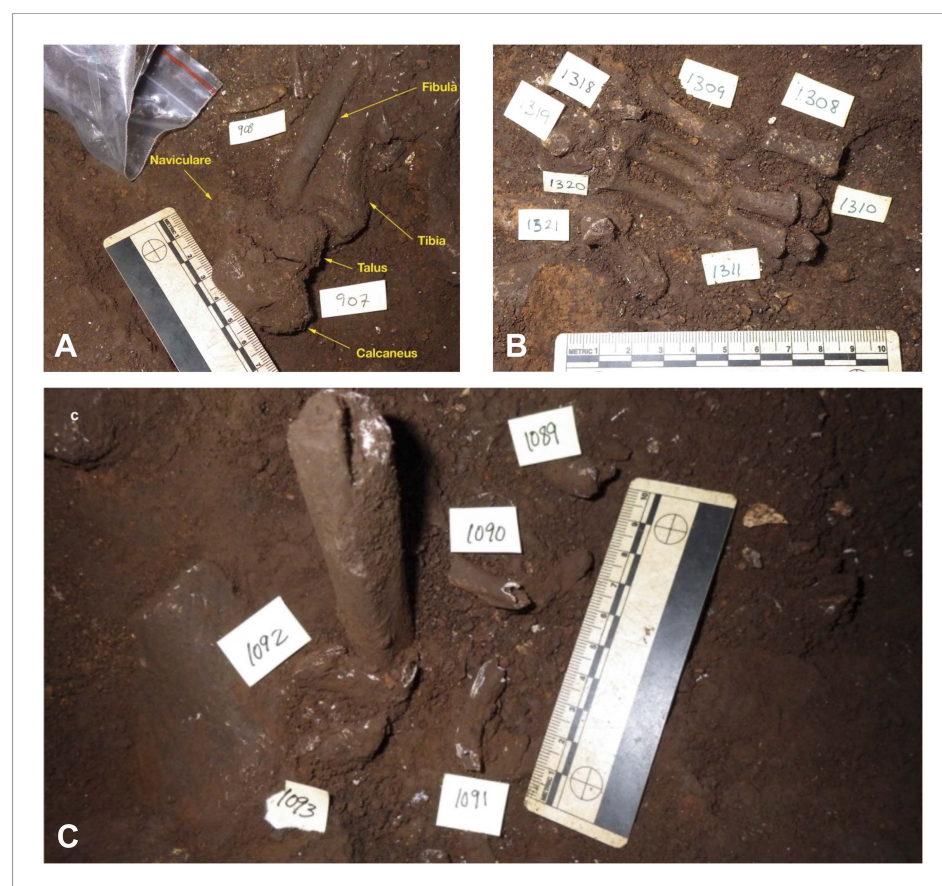


Figure 9. Taphonomic spatial patterning within the fossil assemblage exposed in the excavation pit. Taphonomic signatures and spatial orientations suggest that some of the assemblage may be para-authochthonous in nature, rather than primary or in situ. This scenario provides a mechanism for explaining the combination of near- or fully-anatomically articulated skeletal material and elements, which are heavily commingled and in a non-horizontal resting state (from near-vertical to oblique long-axis orientations). (A) Example of an articulated ankle region. (B) Example of an articulated hand. (C) Example of cluster of skeletal elements showing disarticulated elements in a non-horizontal resting state. Note long bone fragment in near-vertical alignment, compared to normal horizontal or near-horizontal alignment of the commingled elements surrounding it. Labels denote specimen numbers.

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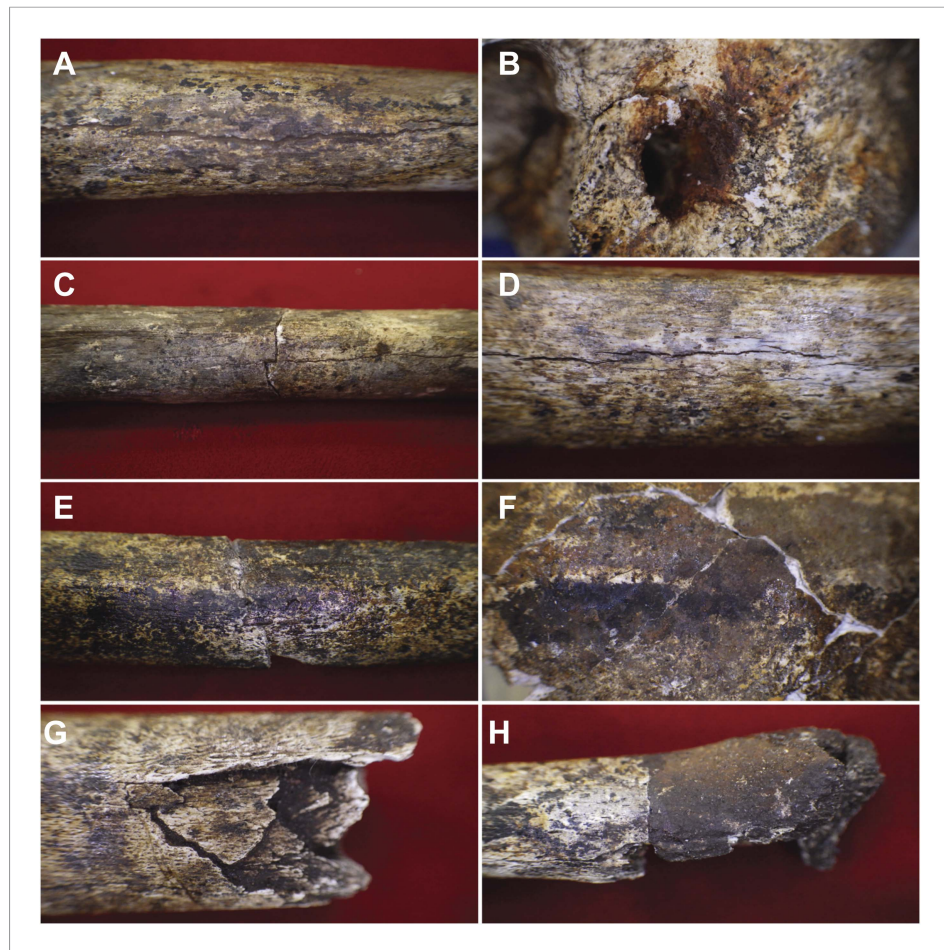


Figure 10. Examples of taphonomic traces recorded on hominin remains. (A) UW101–1288 tibial diaphysis showing evidence of mineral staining adhering to the cortex. The fossil shows evidence of dark zone sub-aerial or sub-surface weathering. Specimen shows a central midline crack with sediment infill, which separates conjoined manganese concretions. (B) UW101–419 (Cranium A[1]) showing iron oxide staining around the external auditory meatus. (C) UW101–312 and 1040 conjoined fragments of a tibial shaft, showing stepped transverse fracture (post-mortem) of the mid-shaft; note longitudinal crack, and evidence of invertebrate modification. (D) UW101–1288 tibial diaphysis showing a weathering pattern typical of Stage 1 evidenced by fine longitudinal cracks, without concomitant flaking, delamination, or the formation of fibrous texture. (E) UW101–1074 tibial shaft showing manganese mineral concretions overlying yellow staining across the diaphysis. (F) Specimen UW 101–419 Cranium A(1) displaying tide lines of dark brown, reddish brown and yellow staining, which extends across different vault fragment. (G) UW101–498 tibial shaft, showing comminuted post-mortem fracture/crushing preserved by sediment infiltrate. (H) UW101–1070 segment of tibial diaphysis displaying differential mineral staining patterns between conjoined fragments.

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a dense surface accumulation of bone where the floor levels out and the chamber widens (**Figure 6C,D, 7**). The approximately 1250 specimens recovered from this excavation consist of a variety of articulated, disarticulated and commingled cranial and postcranial material (**Figure 7**). Articulated elements appear more common in the lower 10 cm of the excavation and include critical elements such as a hand, ankle and foot (**Berger et al., 2015; Figure 9**). At ~15 cm depth, skeletal material was found less frequently, and after reaching a depth of 20 cm, no further fossil remains were recovered. It is not presently known whether fossil concentrations and depths are consistent through the remainder of the chamber.

Within the excavation pit the recovered elements present a mixture of skeletal material in near-primary (autochthonous) and secondary (re-deposited) context (**Figure 9**). The excavation revealed

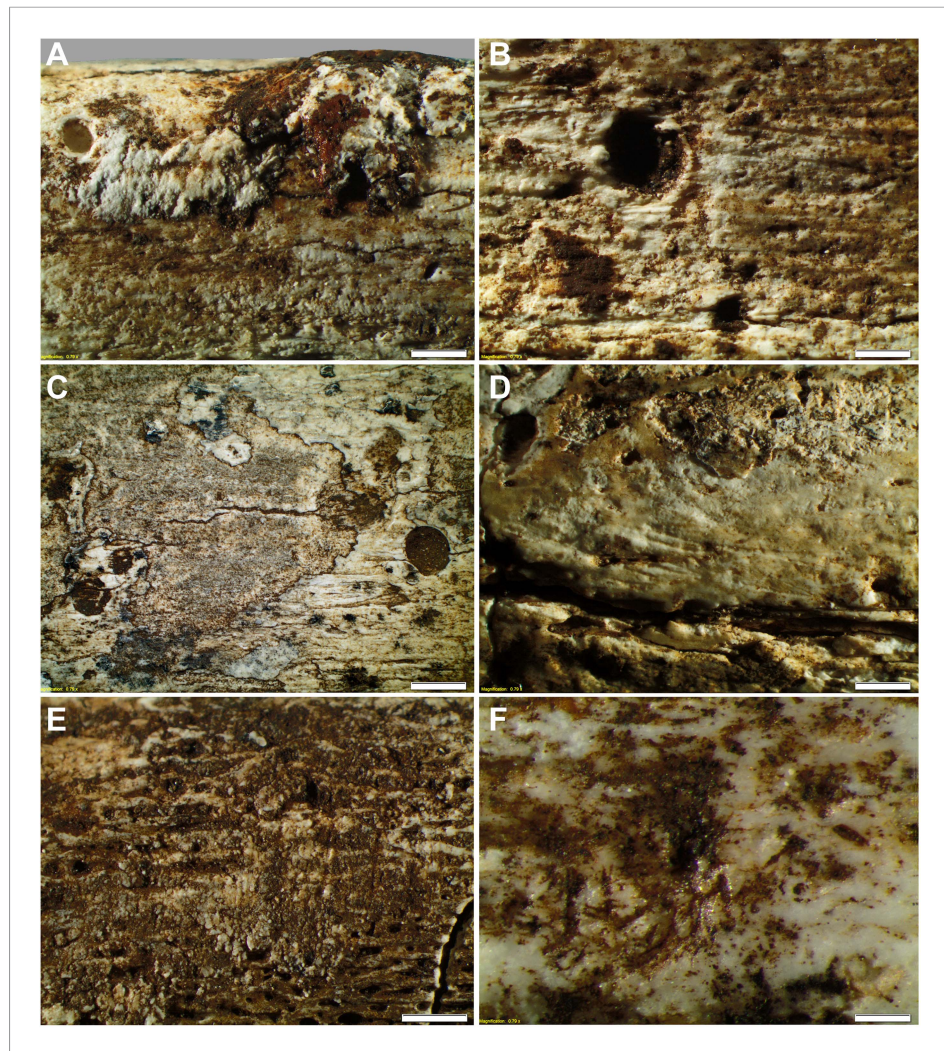


Figure 11. Taphonomy—surface modifications. (A) Removal of the bone surface with sets of shallow, evenly spaced, multiple parallel striations on fibula (UW101–1037), which run longitudinal with the main axis of the bone and are interpreted as gastropod radula damage. (B) Fibula (UW101–1037) showing removal of the bone surface with sets of shallow, evenly spaced, multiple parallel striations that follow the collagen fibres together with shallow circular pits ranging from 0.1 to 3 mm in diameter, the bases of which may be smooth, cupped, or covered with multiple parallel striations. These features have been attributed to gastropod radula damage. (C) Tibia (UW101–484) showing removal of the bone surface with sets of shallow, striations that show a smooth scalloped edge together with circular pits ranging from 0.1 to 3 mm in diameter interpreted as the result of gnawing by beetle larvae. (D) Tibia (UW101–484) with areas of surface removal that have a straight edge associated with scrape marks interpreted as damage made by a beetle mandible. (E) Fibula (UW101–1037) with sets of shallow, evenly spaced, multiple parallel striations orientated transverse to the long axis of the bone interpreted as gastropod radula damage, resulting in an etched surface appearance that exposes underlying structures. (F) Tibia (UW101–484) showing clusters of large individual striations that are variably arrow-shaped and often overlap, interpreted as damage made by a beetle mandible. Compare with **Figure 12** which shows surface modifications made by modern snails and beetles and their larvae. The scale bar in all samples equals 1 mm.

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a range of long bones, teeth and various other skeletal fragments as well as a nearly complete, but highly fragmented cranium at the upper levels of the deposit, immediately underlain by a nearly complete and articulated lower limb of a child (including articulated tibia, fibula and talus), in turn underlain by a fully articulated hand of an adult. Within the pit the vast majority of long bones were found in horizontal to near-horizontal positions, with limited orientational alignment. The horizontal bones were found interspersed with a small number of long bones positioned in a non-horizontal

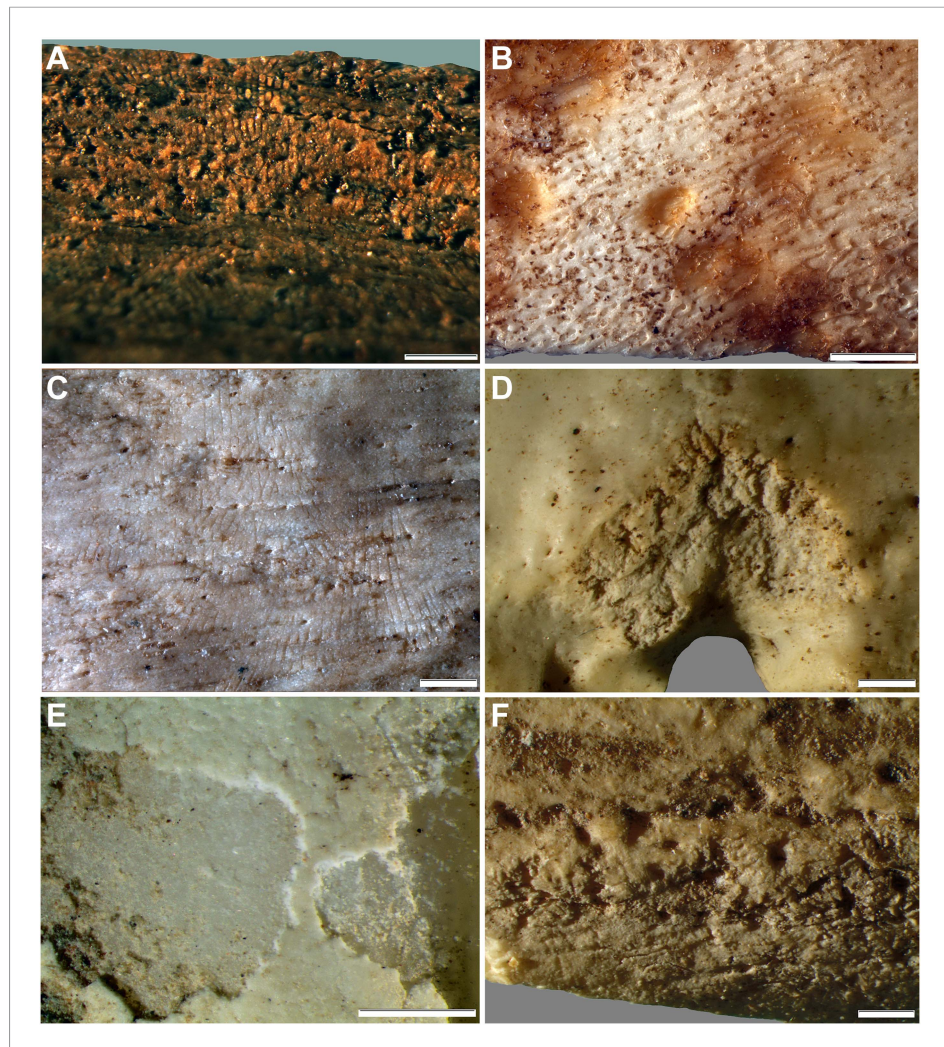


Figure 12. Comparative examples of surface modifications on bone made by modern snails and beetles and their larvae after four months in controlled experiments. Gastropods and beetles were found to produce similar modifications to those observed on the Rising Star hominin remains, and remove the surfaces of fresh, dry and fossil bones to an equal degree (see **Figure 11**). **(A)** Dry bovid rib showing surface removal associated with evenly spaced, multiple parallel striations made by the radula of an *Achatina* (land snail). **(B)** Fresh sheep bone that was originally covered with tissue showing how *Helix aspersa* (garden snails) have removed the outer cortical lamellae to produce an etched appearance and create circular shallow pits with smooth and striated bases. **(C)** Dry bovid rib showing shallow, evenly spaced, multiple parallel striations produced by *Achatina*. **(D)** Dry bird femur showing large individual striations that are variably arrow-shaped and often overlap, made by *Omorgus squalidus* (hide beetles). **(E)** A weathered bovid tooth showing surface removal with a scalloped edge produced by *Dermestes maculatus* larvae, and with a straight edge associated with scrape marks. **(F)** Scrape marks created by a *D. maculatus* adult beetle mandible on a dry medium-sized bovid long bone flake. The scale bar in all samples equals 1 mm.

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resting state (from near-vertical to oblique long-axis orientations (**Figure 9C**), suggesting a burial history involving multiple depositional events (**Manhein et al., 2006**).

Skeletal part representation

With the exception of six avian bones and isolated non-diagnostic rodent elements, all identifiable, macro-skeletal specimens recovered to date from the Dinaledi Chamber are clearly hominin, and all the distinctive morphological aspects of *H. naledi* are near identical in excavated and surface-collected specimens and are considered part of the hypodigm of *H. naledi*. The collection of 1550 catalogued hominin specimens (**Berger et al., 2015**) includes ~1413 hominin fossil bone specimens,

Table 1. Element distribution patterns recording the Minimum Number of Individual and Indentifiable Elements (MNIE) for skeletal parts of the *H. naledi* assemblage from the Dinaledi Chamber

Element	MNIE left	–	MNIE right
Mandible		7	
Calvaria		6	
C1		2	
C2		2	
Other cervical		3	
Thoracic		13	
Lumbar		3	
First rib	2		
Second rib	1		1
Sternum		1	
Clavicle	3		2
Scapula	2		3
Humerus	3		5
Radius	2		4
Ulna	2		3
Scaphoid	1		3
Lunate	1		2
Capitate	1		2
Trapezoid	1		2
Trapezium	1		2
Triquetral			1
MC1	4		3
MC2	3		4
MC3	3		3
MC4			1
MC5	1		1
Proximal manual phalanges		35	
Intermediate manual phalanges		27	
Distal manual phalanges		14	
Ilium	4		5
Ischium	4		5
Pubis	3		2
Sacrum		1	
Coccyx		1	
Femur	5		9
Patella			4
Tibia	4		5
Fibula	4		4
Talus	6		2
Calcaneus	2		2
Navicular	3		3
Medial cuneiform	3		0
Intermediate cuneiform	3		4

Table 1. Continued on next page

Table 1. Continued

Element	MNIE left	–	MNIE right
Lateral cuneiform	2		1
Cuboid	1		2
MT1	3		3
MT2	1		3
MT3	2		2
MT4	1		3
MT5			3
Proximal pedal phalanges		12	
Intermediate pedal phalanges		14	
Distal pedal phalanges		6	

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including mandibles and maxillae bearing 53 teeth, and 137 isolated dental specimens. All dental crowns ($n = 179$), both from surface collection and in situ excavation, are hominin, and all are morphologically consistent with each other. Likewise, all morphologically informative bone specimens are clearly hominin. In all cases where multiple examples are present, they exhibit little variability, consistent with a single population sample. In general, the *H. naledi* assemblage contains many articulated elements, including articulated epiphyses of juvenile limb elements, and it contains a high number of infant and juvenile dental and postcranial remains (Berger et al., 2015). The remains represent a minimum of 15 hominin individuals, as indicated by the repetition and presence of deciduous and adult dental elements (Berger et al., 2015).

The avian bones (UW 101-40 a–f; Aves gen. et sp. indet.) represent lower limb elements (including femur, tibiotarsus and tarsometatarsus) consistent with coming from a single individual. The avian specimens were part of a group of bones that had been ‘arranged’ on rocks by an unknown caver prior to discovery by our caving team (Figure 6B), and are taphonomically distinct from the hominin assemblage. They lack surface modification and stain patterns, and are characterised by the adhesion of a thin film of calcite crystals over much of the surface of the bone, suggesting they were deposited more recently. A small number of isolated and non-diagnostic rodent incisors occur together with the hominin remains.

Using the bone elements recovered to date, we have analysed the composition of the *H. naledi* assemblage, based on the observed frequency of various elements as a function of the expected sequence of disarticulation of various skeletal regions, as well as intrinsic survival characteristics of elements (Lyman, 1994; Pokines and Symes, 2013). Table 1 presents the Minimum Number of Individual and Identifiable Elements (MNIE) for the hominin skeletal material from the Dinaledi Chamber. This table is conservative and only lists elements that are clearly duplicated. Dental remains have not been included.

For long bone fragments, the MNIE is generally based on the repetition of the proximal shaft morphology (e.g., sub-trochanteric femur morphology), but, in some cases (e.g., the humerus) the MNIE is based on the distal articular morphology. In the current collection, this procedure underestimates the number of elements represented: for example, the total length of identifiable fibula shaft fragments is substantially greater than expected for the four left and four right fibulae that are duplicated in the assemblage based on proximal shaft morphology. Also, bone fragments, such as partial metacarpals, that are identifiable at regional scale, but that cannot be exactly identified at the scale of the element, have not been included in Table 1.

Whereas many long-bones are fragmentary, many of the hand, wrist, foot and ankle elements in the collection are complete, or nearly so. In several instances it is possible to identify immature and adult remains as representing duplicate elements even if they do not preserve the same anatomical area. We did not attempt an MNIE count with rib fragments beyond the first and second ribs; as such, there are 48 total rib fragments or refitted partial ribs aside from the two examples of first and second ribs.

What is most obvious from the general assemblage quantification is that all regions of the skeleton are represented within the cave assemblage, in spite of potential preservation and/or recovery bias. More importantly, in some of the material we observed, regions that conventionally disassociate both early and late in the decomposition process are represented as anatomically aligned and articulated groups, suggesting limited post-mortem spatial alteration and disaggregation within the chamber in both the proximate putrefactive (early) and distal decompositional (late) periods. Although much of the fossil material is disarticulated, the deposit contains articulated or near-articulated examples such as the maxilla and mandible of single individuals and the bones of the hands and feet, which normally disarticulate very early in the decomposition sequence (**Figure 9**). These elements are found in anatomical position and in spatial articulation with elements (e.g., vertebral components) that normally disarticulate later.

The observed patterns indicate a formational process that did not involve a high degree of winnowing. The sedimentary system in which the fossils were deposited was closed, or nearly closed, and skeletal disarticulation and movement of elements was largely restricted to the Dinaledi Chamber only (although some bone fragments may have washed down floor drains).

Bone quality and preservation

The hominin assemblage is homogeneous in terms of surface preservation and condition (**Figures 10 and 11**), suggesting that the remains share a similar depositional history (i.e., the disarticulated vs articulated material does not vary significantly in terms of surface preservation). The structural state of the material is classified as good, and surface morphology is retained for many of the specimens (i.e., no plastic deformation has been observed), even though they were water logged and friable at recovery. The bones are generally, partially mineralised; there is no evidence of calcite crystal formation in or on bones, but some bones and teeth are dotted with black iron-manganese oxi-hydroxide deposits and coatings (e.g., **Figure 10**), and an orange-colour residue of iron oxide (e.g., **Figure 10B**). Colouration of the bone underlying surficial mineral deposits ranges from light grey to red-brown. The internal structure of bones is bright white in colour.

Whilst the overall structural integrity of the bone is good, few specimens preserve a pristine surface morphology. The overall surface quality of bone material corresponds to McKinley's Grades 3 and 4 (**McKinley, 2004**). As such, the majority of external surfaces of the cranial elements and long bones preserve the morphology of the bone, but display evidence of varying degrees of bone surface (cortical) removal (**Figure 11**; **Supplementary file 2**), striated patterns and pitting (**Figure 11**), and post-mortem fracturing resulting in multiple conjoins (**Figure 10**; **McKinley, 2004**)—expressions of these traits are discussed below.

Weathering patterns

The skeletal assemblage of *H. naledi* displays little variation in surface structure and condition, indicating that the hominin material has been exposed to a limited range of environmental fluctuation during its depositional history. Analysis of the weathering patterns of the Dinaledi assemblage indicates that most of the bones show weathering stages 1 or 2 (after **Behrensmeyer, 1978**); while 18% have an etched appearance and 11% exhibit dissolution (**Supplementary file 2**). No element exceeds weathering stage 3 with the majority of elements displaying stage 1 weathering patterns. Most elements show no signs of cracking or flaking, although some deeper cracks may be present due to post-depositional effects. Stage 1 weathering is evidenced in most specimens of long bones, rib fragments, and mandibular fragments as fine longitudinal cracks (**Figure 10D**), without concomitant flaking and the formation of a fibrous texture.

None of the bone fragments studied preserve evidence of bleaching, cortical exfoliation, delamination or deep patination, indicating that the bones were not affected by solar radiation (**Lyman and Fox, 1989, 1997**); that is, no bone fragment was exposed to weathering on surface outside the cave, which is consistent with sedimentation patterns observed in the chamber. We interpret the observed weathering patterns to result from fluctuations in moisture content in the Dinaledi Chamber, causing swelling and shrinkage of the osseous material, with larger longitudinal cracking being caused by sediment loading. As bone is repeatedly exposed to wet and dry conditions in seasonally/periodically wet environments, crack formation may be enhanced by the shrinking and swelling of the material (**Junod and Pokines, 2013**; **Pokines and Symes, 2013**). Overall, weathering patterns of the bone surfaces are consistent with the effects of sub-aerial and sub-surface processes in a periodically wet or water-saturated, dark depositional environment that experienced stable temperatures.

Fractures

The *H. naledi* assemblage recovered from the Dinaledi Chamber is characterised by a high-degree of bone breakage and fragmentation (e.g., **Figure 10G**). Examination of the entire fossil assemblage for fracture patterns indicates that all of the fractures in the *H. naledi* assemblage resulted from dry bone (or mechanically incompetent) breakage, with many bones displaying recent or weathering related (19%) breakage patterns (**Villa and Mahieu, 1991; Symes et al., 2013**). Significantly, no examples of spiral (green) fractures have been documented (**Supplementary file 2**), which indicates that post-depositional processes are the primary agents of skeletal damage. Fracturing has led to disassociation and spatial dispersal of many of the skeletal elements (**Figures 6,7**). Refitting fragments of bone indicates that breakage occurred at different times in the depositional history of the assemblage. For some elements, neighbouring bone fragments display unique patterns of weathering and surface modification (e.g., **Figure 10H**); that is, breakage occurred relatively early in the depositional history and preceded periods of surface exposure. In other instances separate fragments that can be refitted to display matching staining patterns (e.g., **Figure 10F**) indicating that breakage occurred relatively late in the weathering history; that is, after the element had been lying on surface long enough for mineral stains to be deposited. These patterns are consistent with the geological observation that sediment in Units 2 and 3 with fossil remains were affected by reworking, with some bone material being re-deposited several times. We, therefore, interpret the observed dry-bone fracture patterns to be due to post-depositional sediment movement within the chamber as Units 2 and 3 are reworked, as well as unintentional damage by cavers or others entering the chamber; and we find no evidence for green fractures associated with trauma in the *H. naledi* fossil assemblage.

Transportation

The matrix sediments surrounding the fossils do not present evidence for sedimentation processes that involved significant water action able to transport coarse-grained material including bone fragments. Likewise, the assemblage presents no evidence of fluvial modifications such as abrasion patterns caused by the movement of bone in water. No element shows evidence of physical smoothing or rounding, the development of polish or frosting, or indications of pitting, denting, and chipping caused by impact (**Supplementary file 2; Pokines and Symes, 2013**). Grooves, scratches, and gouges are common, but are the result of invertebrate action (see below; **Figure 11**), and the distribution of these defects across the bone surface is random. We therefore preclude transportation by water as a major taphonomic factor associated with the delivery of skeletal elements into, or within the cave system.

Mineral staining

Staining and mineral deposition is common on most elements that preserve an external surface (**Supplementary file 2**). In the main, staining consists of irregular low-profile clusters or concretions of dark brown to black mineral deposit (a combination of manganese and iron oxy-hydroxides). This can occur as a surface deposit overlying the cortex directly (e.g., **Figure 10A**) and is seen as a surface sheen or cortical infiltrate, though more commonly it occurs as a deposit overlying existing areas of staining (yellow to ochre in colour (e.g., **Figure 10E**). This indicates a multi-staged history of mineralisation and chemical exchange between bone and the environment (**Pokines and Symes, 2013**), consistent with the episodic reworking of the bones.

A number of specimens preserve linear, and in some cases, parallel mineral precipitate stains or 'tide marks' that attest to the dynamic burial history of the fossils. These stains are visible as single or multiple linear deposits of manganese and iron oxy-hydroxide phases (**Figure 10F**), and are artefacts of the burial environment of osseous remains. They mark a contact boundary between the bone surface and surrounding sediment, and indicate the resting orientation of the bone during precipitation of the stains. They demonstrate that portions of individual bones were sub-aerially exposed for long periods of time during formation and erosion of Unit 3 (**Junod and Pokines, 2013; Pokines and Symes, 2013**). The outer and inner surface of the A1 cranium (UW 101–419) show at least two phases of cross-cutting mineral deposits, that formed when the cranium was complete (i.e., skeletonized and un-fragmented) and lying on its left side in contact with surrounding sediment that eroded and shifted over time. This clearly illustrates that at least part of the fossil assemblage in Unit 3 was reworked and redistributed as a result of erosion and re-deposition.

Surface modifications and vertebrate–bone interactions

No evidence is noted of vertebrate modifications such as those caused by carnivores, rodents or other hominins. The specimens were assessed for evidence of edge polish from repeated gnawing, tooth pits or punctures perpendicular to the surface of the bone, tooth scores, striations and/or furrows (V or U-shaped in cross section), and traces of gastric corrosion (Haynes, 1983; de Ruiter and Berger, 2000; Pickering et al., 2004; Pokines and Symes, 2013; [Supplementary file 2](#)). There is no evidence of stone tool inflicted cuts, scrapes, impact or chop marks (White, 2014). Tooth scores and pits, crenulated edges and splintered shafts associated with carnivore damage (Kuhn, 2011) are absent. None of the specimens are burnt (Stiner et al., 1995) or shows signs of trampling other than limited incidental recent breakage by cavers that is readily evident (Behrensmeyer et al., 1986).

Surface modifications and invertebrate–bone interactions

The collection bears clear traces of invertebrate activity, with most of the bones ($n = 553$) exhibiting microscopic removal of the bone surface, and evenly spaced, multiple parallel striations (35%) associated with smooth-based pits (34%), a pattern consistent with damage made to bone by modern gastropods. Sixty-two specimens (10%) record large individual, variably arrow-shaped and randomly oriented striations, consistent with those made by modern beetles ([Supplementary file 2; Figures 11,12](#)).

Many specimens in the assemblage show that the bone surface has been removed over a relatively large area, in various stages of elimination; from the outer lamellae to underlying cortical bone. Removal of the bone surface exposes underlying structures, enlarging features such as Haversian canals, and creating an etched appearance (e.g., [Figure 11B,E](#)). Fossil specimens retaining outer cortical lamellae show that a scraping mechanism was applied to the bone surface. This is indicated by the association of post-fossilisation incision marks with areas of bone surface removal ([Figure 11A](#)), and a bone fraction adhering to the fossil surface, its shape and distribution reflecting a scraping action.

Sets of shallow, evenly spaced, multiple parallel striations of equal width and length are a common feature on the fossils. When oriented parallel to the long axis of the bone, individual striations appear as relatively broad, variably arrow or lens-shaped. They follow the collagen fibres, creating an etched surface appearance. When oriented at an angle to the main axis of the bone, the morphology and arrangement of the parallel striations are more clearly visible, revealing multiple evenly spaced linear incisions, in places overlapping, and extending over a large area of the bone surface ([Figure 11B,E](#)). The multiple parallel striations locally manifest as short evenly spaced incision marks.

Shallow circular pits, ranging from about 0.1 to 3 mm in diameter are common. They are associated with bone surface removal ([Figure 11B,C](#)) and multiple parallel striations, in places in the base of pits. The margins of pits are generally smooth and rounded, and commonly scalloped, in a similar manner to the edge pattern observed on some outer cortical lamellae ([Figure 11C](#)). Some pits are fresh, exposed by recent removal of the sedimentary coating and fossilised bone surface. Straight edged scrape marks ([Figure 11D](#)) and clusters of large v-shave, overlapping striations ([Figure 11F](#)) are locally involved with bone surface removal.

The features observed on the Dinaledi collection were compared to surface modifications produced by 16 invertebrate taxa on bones in controlled experiments. Fresh, dry and fossil bones were placed with each type of invertebrate in separate tanks, and data on the resulting modifications recorded after four months. Our experiments show that land snails (*Achatina* sp.), garden snails (*Helix aspersa*), hide beetles (*Omorgus squalidus* and *Dermestes maculatus*) and their larvae produce a similar set of modifications to those observed on the Rising Star material, characterised by evenly spaced multiple parallel striations ([Figure 12A–C](#)), circular shallow pits with scalloped edges and smooth, cupped or striated bases ([Figure 12B,E](#)), scraping of the bone ([Figure 12D,F](#)), and an etched surface appearance ([Figure 12A,B](#)). This suggests that the observed surface modifications are most likely the result of gastropod and beetle damage.

At least two modification events have been observed on some of the fossils. Recent surface removal is evident on top of manganese and sedimentary fossil coatings, creating a white patina on bone ([Figure 11A](#)). Circular shallow pits and grooves, associated with multiple parallel striations and surface removal, are commonly in-filled with consolidated sediment ([Figure 11B,C](#)), indicating that the pits were created prior to the formation of the sedimentary coatings.

Discussion

Sedimentation processes in the Dinaledi Chamber and deposition of *H. naledi*

Whereas Unit 1, is a distinct older stratigraphic unit, Units 2 and 3 appear to have formed in a continual manner involving the interaction of three separate sedimentary processes: (a) sediment accumulation below access points into the cave chamber (i.e., near the current vertical entrance shaft); (b) erosion of the accumulating sedimentary pile, as sediment slumped down-slope, into the chamber towards floor drains; and (c) stabilisation by flowstone formation.

The accumulation of poorly consolidated Facies 2 sediment in Units 2 and 3, alternated with periods of flowstone deposition. Each of the Flowstones 1a-e interpreted to have formed as crust on top of a debris pile of Facies 2 sediment, starting with the formation of Flowstone 1a on top of a debris cone forming Unit 2. Formation of Flowstone 1a was followed by a period of erosion during which the poorly consolidated sediment pile, slumped inwards into the cave, probably as a result of the removal of sediment through floor drains deeper down in the cave chamber. This erosional process would have undercut the sediment pile of Unit 2, leaving behind partly indurated erosional remnants of Unit 2 covered by remnants of Flowstone 1a. As the sedimentary pile below this erosion remnant stabilized and flowstone formation continued, a new crust formed on top of the pile of Facies 2 sediment, to once more, weakly indurate the top-layer. This was followed by the next phase of erosion, slumping and undercutting of the sediment pile, leaving behind erosional remnants of Flowstone 1b again covering the remains of partly indurated Facies 2 mudstone breccia assigned to Unit 2. This progressive erosional process repeated itself at least three more times to form Flowstones 1c-e, as sediment of Unit 2 was gradually reworked and spread out across the floor of the Dinaledi Chamber, where it accumulated as Unit 3 (**Figure 4**). This process was concomitant with continued weathering, auto-brecciation and erosion of remnants of Unit 1, which also contributed to formation of Unit 3.

Deposition of Unit 3 was followed by a major phase of flowstone formation that formed cascades, curtains and flowstone crusts atop Unit 3 across the entire chamber (Flowstone 2). In the lower parts of the chamber and in many of the lower side passages, large areas of the cave floor (i.e., Unit 3) are still covered by Flowstone 2 (and to a lesser extent, more recent patches of Flowstone 3), including areas where the flowstone directly covers *H. naledi* bones. However, in the upper and central parts of the main chamber, Unit 3 has been locally eroded, undercutting and partly removing the cover of Flowstone 2; for example, near the fossil excavation pit, erosion remnants of Flowstone 2 along the chamber wall are positioned several cm's above the present chamber floor surface, indicating erosion of the uppermost part of Unit 3 since deposition of Flowstone 2 (**Figure 4F,G**). In addition, collapsed sediment containing hominin bones derived from hanging remnants of Unit 3 have locally washed down to be re-deposited atop Flowstone 2 lower down in the chamber, where the floor is level and no erosion has occurred. Thus, the erosional and re-depositional processes that led to the formation of Units 2 and 3, is on-going today, and the distribution of fossils on the cave floor is, in part at least, the result of erosional winnowing.

The remains of *H. naledi* are concentrated in Unit 3, but remains also occur in Unit 2. Four hominin bone fragments were observed in situ within Unit 2, and the shafts of a radius and ulna derived from a juvenile hominin were found in loose material slumped from hanging remnants of Unit 2. The large number of hominin bones collected from around the weathered base of Unit 2 also suggests that this unit contained a significant number of the fossils that contributed to the *H. naledi* assemblage.

However, many of the remains of *H. naledi* were probably not eroded out of Unit 2 to be re-deposited in Unit 3. Unlike Unit 2, which is limited to small erosion remnants near the cave entrance, Unit 3 is distributed across the Dinaledi Chamber and preserves well-articulated skeletal elements that have not been reworked from older units. This is illustrated by the presence of an articulated ankle, foot and hand in the excavation pit in Unit 3 (**Berger et al., 2015**this volume; **Figure 9**), which suggests that these remains were deposited in situ during the accumulation of Unit 3. It is highly unlikely that these remains weathered out from older sediments of Unit 2, because Unit 2 accumulated near the entrance to the chamber, that is, ~11 m away from the pit (**Figure 2C**), and there are no accumulations of Unit 2 above or near the excavation pit. In addition, if a hand or foot would have weathered out of the unconsolidated sediment of Unit 2, they would not have remained perfectly

articulated as the sediment slumped downslope into the chamber, past floor drains. Also, there have not been any flowstone fragments found within Unit 3 that would suggest that reworked skeletal material from unit 2 may have been transported *en bloc* deep into the chamber from the entrance area. Furthermore, the orientation of the chamber passages and presence of drain systems likely precludes such a possibility.

Thus, the fossils of *H. naledi* were probably deposited over an extended period of time during deposition and reworking of Units 2 and 3, and before deposition of Flowstone 2. Continual reworking of these units and the fossils they contain is consistent with taphonomic evidence (element distribution; breakage patterns, mineral staining). The distribution of Unit 2 below the current entry shaft into the Dinaledi Chamber, and the orientation of Flowstones 1a–e that cover Unit 2 and slope into the chamber, together strongly suggest that the current entry shaft has always been the main entry point for sediment into the chamber. This also indicates that the fossils of *H. naledi* entered via this route.

Environmental constraints in the Dinaledi Chamber based on taphonomy

The Dinaledi collection displays taphonomic characteristics indicative of a depositional history that involved several stages of burial with surface modifications and breakage patterns consistent with repeated reworking of at least part of the assemblage within the confines of the Dinaledi Chamber, involving both biotic and abiotic agents (**Supplementary file 2**). The distribution of bone material and skeletal part representation indicative of limited winnowing (**Table 1**) indicate that the fossils of *H. naledi* must have found their way into the chamber via a difficult route that precluded any other large vertebrates from finding a way in. The distribution of the fossils within reworked material derived from Unit 2, as well-articulated remains in Unit 3 suggests that *H. naledi* fossils entered the chamber over an extended period of time; that is, not all remains were deposited at once. The presence of articulated, functional anatomical units that conventionally disassociate early in the decompositional sequence (**Figure 9B**) also suggests that bodies were fresh or in the early stages of decomposition when they entered the chamber and were encapsulated in the matrix (**Haglund, 1993; Lyman, 1994**). The lack of green fractures on any of the elements in the assemblage suggests that the bodies did not enter the chamber due to catastrophic accident such as falling into the chamber or due to flooding, or suffered trauma in any other way shortly before or after death.

Limited weathering (physical and chemical) indicative of sub-aerial, sub-surface processes in a periodically wet or water-saturated, dark environment (**Figure 10**) indicate that the bones were never exposed to the earth's surface and elements (the sun and rain) outside the cave (**Lyman and Fox, 1989; Backwell et al., 2012; Junod and Pokines, 2013**). The preservation of primary and secondary context patterns of skeletal elements, the fragmented nature of many fossil bones, overprinting tide marks of minerals stains on skull fragments (**Figure 10F**), invertebrate damage on bones by gastropods and beetles (**Figure 11**), and bone breakage patterns indicative of post-mortem (dry bone) or mechanically incompetent fractures (**Lyman and Fox, 1989**) probably due to re-working of some of the fossil-bearing sediments (**Figure 10**) all indicate that the fossils experienced significant periods of exposure and reworking after deposition (**Lyman, 1994; Manhein et al., 2006**). This multi-staged internment history is best understood in terms of the continual reworking of Units 2 and 3 due to the gradual erosion of the cave floor as it slumps toward floor drains in the chamber (the geological process explained above).

The collection is also notable for the absence of large vertebrate remains, and the taphonomic processes that are not evidenced through surface and structural modifications and skeletal part representation most importantly there is no evidence for carnivore or rodent modification; no evidence of cut marks or burns and no (geological or taphonomic) traces of fluvial transportation or long-distance movement or traces of green bone fractures (**Haglund, 1992; Lyman, 1994; Fernández-Jalvo and Andrews, 2003; Pickering et al., 2011a**).

Depositional scenarios for the burial of *H. naledi*

Considering the geological and taphonomic context described above, the Dinaledi hominin site represents a depositional scenario that deviates from all other hominin localities in the region (**Brain, 1981; Partridge et al., 2003; Dirks et al., 2010; Pickering and Kramers, 2010; Pickering et al., 2011a**) in two important ways. First, the Dinaledi Chamber appears to have never had unimpeded

access, with fossil material deposited in muddy sediment in a geologically and geochemically isolated environment, and second the large vertebrate assemblage is comprised solely of hominin material (Berger *et al.*, 2015). Each of these points will be discussed in more detail below.

Unlike other southern African cave sites where hidden shafts and sinkholes acted as death-traps to numerous species (Brain, 1981; Partridge *et al.*, 2003; Dirks *et al.*, 2010; Pickering and Kramers, 2010; Pickering *et al.*, 2011a), there is no indication of a direct vertical passageway to surface into the Dinaledi Chamber. The chert layer forming the roof of the chamber is unbroken and coarse-grained clastic deposits transported by water action are absent, as are externally derived sediments. Instead, the Dinaledi Chamber represents an isolated sedimentary environment with fossils preserved in fine-grained, semi-consolidated mudstone breccia that is texturally and chemically distinct from fill in the upper chambers of the cave and that appears to have largely accumulated below the current entry shaft into the chamber.

Flowstone formation continues today (Flowstone 3), changing the morphology of cave passages. This makes it possible that a more direct access-way or easier passage may have existed when hominins entered. A different entrance into the chamber may also explain the presence of rodent bone concentrations in Facies 1b. However, sedimentation patterns indicate that the accumulation of Unit 2 with fossils occurred below the current entry point into the chamber, and alternate routes did not involve vertical access shafts that connected directly to surface in either the Dinaledi Chamber or nearby Dragon's Back Chamber. The lack of other contemporaneous fauna in the assemblage, and complete lack of surface modifications by vertebrates (carnivores, scavengers or rodents) further suggests that the Dinaledi Chamber remained undisturbed by other animals, which could not reach the chamber. Taken together, this means *H. naledi* would have had to traverse difficult terrain to reach the Dinaledi Chamber, with the chamber and the proximal entrance to the chamber positioned in the dark zone.

Mono-specific assemblages have been described from Tertiary and Mesozoic vertebrate fossil sites (Kidwell *et al.*, 1986; Rogers, 1990; Behrensmeyer, 1991), linked to catastrophic events (Turnbull and Martill, 1988). Among deposits of non *H. sapiens* hominins, where evidence of catastrophic events is lacking, mono-specific assemblages have been associated typically with deliberate cultural deposition or burial (Arsuaga *et al.*, 1997; Carbonell and Mosquera, 2006; Gaudzinski, 2006). Every previously known case of cultural deposition has been attributed to species of the genus *Homo* with cranial capacities near the modern human range. Unlike the Dinaledi assemblage, each of these hominin associated occurrences also contains at least some medium- to large-sized, non-hominin fauna (Arsuaga *et al.*, 1997; Carbonell and Mosquera, 2006; Gaudzinski, 2006; Behrensmeyer, 2008).

There are a number of sites in Europe that represent accumulations of hominin fossils in caves that can be compared with the Dinaledi assemblage. The fossil hominins from Sima de los Huesos, Atapuerca, Spain, are presently believed to have accumulated within a single event (Aranburu *et al.*, 2015). The assemblage also includes carnivore remains, including the remains of (an extensive number of) cave bears and smaller carnivores. The Sima de los Huesos bone assemblage is highly fractured, with most fractures consistent with post-depositional breakage, but a small portion (~4%) consistent with peri-mortem breakage that might be explained as a result of fall-down a 13 m shaft into the cave (Sala *et al.*, 2015a). Alternatively, there is some evidence that peri-mortem trauma may have resulted from lethal interpersonal violence (Sala *et al.*, 2015b). Both hominin and carnivore bones in the Sima de los Huesos bear carnivore tooth marks at low frequency (less than 4%), which has been interpreted as the sporadic action of carnivores trapped after falling into the chamber (Sala *et al.*, 2014). Cut marks have not been reported on the hominin remains (Andrews and Jalvo, 1997).

Another example is presented by Level TD6-2 of Gran Dolina, Spain, which represents an accumulation of hominin and faunal bones in a ~30 cm thick layer across an excavated extent of 7 m². The remains of at least six hominin individuals are present in this assemblage, with cut marks and evidence of intentional de-fleshing similar to associated fauna, as well as tooth marks from carnivores (Saladié *et al.*, 2014). The accumulation of hominin bone is interpreted as the result of cannibalism, with later carnivore scavenging at a smaller scale. A similar instance of cannibalism appears to be evidenced at El Sidron, Spain. Here, an almost exclusively hominin assemblage comprises a minimum of 13 individuals bearing cut marks, percussion pitting, and conchoidal scars typical of intentional processing of carcasses (Rosas *et al.*, 2012).

The Krapina rock shelter in Croatia represents the earliest-excavated large hominin sample. Here remains of a minimum of 23 individual Hominins were recovered with extensive associated fauna from several stratigraphic layers, with most hominin material coming from a single layer, the 'Homo Zonus'. Breakage patterns of the Krapina hominin assemblage are mostly consistent with post-depositional fracturing, including excavation damage and prehistoric fracturing due to sedimentary loading (Russell, 1987a). Many of the hominin bones bear cut marks, which have been variably interpreted as evidence of cannibalism or mortuary practices (Russell, 1987b; Villa, 1992).

Pliocene and Early Pleistocene occurrences of single-species hominin bone deposits in Africa thus far contrast with these European cave sites. The AL 333 assemblage from Hadar, Ethiopia includes the fragmentary remains of some 17 hominin individuals and fauna, which appear to have been redeposited within a shallow streambed after possibly having been subject to predation (Behrensmeyer, 2008). Malapa, in the Cradle of Humankind, South Africa has been interpreted as a 'death trap', with several partial hominin skeletons and associated fauna (Dirks et al., 2010). The Malapa hominin and faunal assemblages lack evidence of carnivore activity, and include a disproportionate fraction of climbing species, suggesting that access to the cave was formerly limited and possibly hazardous for ungulates (Val et al., 2015), but a broad array of faunal species have been recovered from the site.

The Dinaledi assemblage shows no evidence of accumulation by either cannibalism or carnivore activity (Supplementary file 2), making it different from El Sidron, the Aurora Stratum of Gran Dolina, AL 333, and Krapina. The Dinaledi situation shows similarities with the Sima de los Huesos assemblage in several respects. However, the Dinaledi hominins recovered to date are entirely free of cut marks, tooth marks, or peri-mortem fractures while each of these is present at low frequencies in the Sima de los Huesos sample.

Few previously recognised scenarios operating in South African caves could have produced the selectivity for hominin remains as observed in the Dinaledi Chamber (Brain, 1981; de Ruiter and Berger, 2000; Dirks et al., 2010); a depositional situation common in no species other than modern humans. Below we will briefly discuss five alternative hypotheses for the accumulation of the hominin material in the Dinaledi Chamber, presented in order of what we consider to be reverse likelihood.

Occupation

There are no signals of occupation debris or evidence of occupation within the Dinaledi Chamber, or anywhere else in the Rising Star cave. Based on our current assessment, occupation would have required accessing the chamber in the dark through an entrance similar to the current one, through an area inaccessible to other medium- to large-sized mammals. Thus, if hominins were traveling to the chamber, it is assumed that they would almost certainly have required artificial light. Given the physical challenges associated with access into the chamber and the lack of evidence for longer-term use, we consider occupation an unlikely explanation for the presence of the hominin remains.

Water transport

Sedimentological evidence excludes the transport of coarse-grained material into the chamber by water action. The cave has been inundated in the past by rising water tables, but there is no evidence within the Dinaledi Chamber of depositional processes that involved high-energy transport mechanisms capable of transporting the large hominin bones, let alone do so in a uniquely selective manner. The high abundance and diversity of predominantly non-hominin fossil remains preserved throughout the adjacent Dragon's Back Chamber not only refute sediment transport by water flow between the two chambers, but also indicates that a considerable barrier between the two chambers was in place at time of deposition of *H. naledi*, and indeed throughout the history of the Dinaledi Chamber. The Dinaledi Chamber has been a closed depositional system for a long time, and did not allow the sudden ingress of water and sediment; only fine-grained muddy sediment accumulated, which accessed the chamber through narrow cracks that filtered out coarser material. Thus, the accumulation of the hominin remains in the chamber does not fit the pattern of a flood or fluvial event (Behrensmeyer, 2008; Dirks et al., 2010).

Predator accumulation

In this hypothesis a carnivore either killed or scavenged the hominins, and brought them into the Dinaledi Chamber. In doing so, the predator would need to overcome the challenges of navigating the dark zone of the cave described earlier, in order to access a remote chamber, all while

transporting a large hominin carcass. Despite abundant fossil material available for taphonomic study, we have, thus far, found no trace of carnivore damage on the Dinaledi remains. Nor have we found any trace of carnivore remains or the remains of other likely prey animals. Thus, the predator would have had to select a single prey species—*H. naledi*—carrying into the chamber all age and size categories (Berger et al., 2015) without leaving a trace of its own presence. We consider this very unlikely.

Mass fatality or death trap

As with other mono-specific assemblages in the fossil record (Kidwell et al., 1986; Rogers, 1990; Behrensmeyer, 1991, 2008) the remains of *H. naledi* could have accumulated as a result of a catastrophic event during which a large group of animals was trapped in the cave. This could have happened either during a single event when a large number of hominin individuals were in the chamber, or in a death trap scenario over a period of time as individuals repeatedly entered the Dinaledi Chamber and died. Either scenario would have to explain why the animals chose to penetrate this deep into the cave, into the dark zone, moving away from all entrance points into the cave system. The sedimentological evidence presented suggests that accumulation of the fossils occurred over a period of time during deposition and reworking of Units 2, and 3, which refutes a single event hypothesis. Apart from this, and noting that the assemblage recovered to date represents only a small part of the total fossil content in the chamber, the sheer number of remains encountered in the Dinaledi Chamber, is hard to explain as the result of a single calamity. The individual entry hypothesis would require individuals or small groups to enter repeatedly and succumb to some form of, as yet unidentified, mortality event. The demographics of the assemblage—which includes individuals of practically every developmental age, from neonate to senile, is inconclusive in terms of providing definitive evidence towards either attritional or catastrophic mass fatality events.

The individuals represented within the Dinaledi chamber died at a range of ages from infant to old adult. The distribution of age-at-death within a sample of remains may potentially test hypotheses about the causes of mortality. For example, attritional mortality tends to over-represent old adults and very young children in comparison to their proportions within a living population, while the age-at-death distribution resulting from a catastrophic event tends to be representative of the age structure in a living population with more young adults and older juveniles than the attritional profile. The mortality profiles of the Sima de los Huesos and Krapina hominin samples have been argued as consistent with a catastrophic profile using statistical tests (Bocquet-Appel and Arsuaga, 1999). Most of the information to distinguish catastrophic from attritional age profiles in an age-at-death distribution is contained in the proportion of older juveniles and sub-adults. In both the Krapina and Sima de los Huesos assemblages, sample sizes are small and near the numerical limit to test statistically. In the Dinaledi assemblage, we presently can assess the age class (and, therefore, the approximate age-at-death distribution) for only 13 individuals, with 3 infants, 3 young juveniles, 1 old juvenile, 1 sub-adult, 4 young adults and 1 old adult (two additional individuals are represented by isolated teeth that cannot be attributed to an age class) (Berger et al., 2015). We found no significant result when comparing the currently available distribution to either catastrophic or attritional mortality profiles, and therefore a mass death scenario involving some sort of calamity or death trap cannot be completely excluded to explain the Dinaledi assemblage. The large number of immature individuals (8 out of 13) does allow us to reject hypotheses that would strongly over-represent adults, such as repeated cave exploration by socially isolated adult males. Further work in this regard will be required.

Deliberate disposal

In the deliberate body disposal hypothesis, bodies of the individuals found in the cave would either have been carried into, or dropped through an entrance similar to, if not the same as, the one presently used to enter the Dinaledi Chamber. If individuals were dropped either whole or in part into the present entrance chute to the chamber, then physical entry would not be required. None of the bone elements studied shows evidence of green fracture (Supplementary file 2), indicating lack of trauma. Therefore, if bodies were dropped down the entrance, it is unlikely that they would have fallen rapidly, or landed with any force; perhaps because the entry is too irregular and narrow to allow a body to freefall and gain speed, or perhaps because a pile of soft muddy sediment had accumulated below the entry way, breaking the momentum of any falling object. Note that accessing the entry point to the chamber to drop bodies down the chute would have still entailed a complex climb in the

dark zone. In this scenario, the distribution of skeletal material, as well as the evidence for partial articulation, could be explained by the slow slumping of fleshed or semi-fleshed remains, downslope into the chamber. Alternatively, the hominins could have entered the chamber directly, carrying the bodies or dying there, which would explain, not only the absence of green fractures, but the presence of delicate, articulated remains in the excavation pit, deep in the chamber, well away from the entrance point, on the other side of floor drains.

Considering the geological and taphonomic context of the Dinaledi Chamber, the occupation, predator accumulation and water transport hypotheses cannot adequately explain the fossil assemblage. Both the mass mortality or death trap scenario (although possibly not involving a single event) and deliberate disposal hypothesis are considered plausible interpretations and require additional investigation. Based on current evidence, our preferred explanation for the accumulation of *H. naledi* fossils in the Dinaledi Chamber is deliberate body disposal, in which bodies of the individuals found in the cave would either have entered the chamber, or were dropped through an entrance similar to, if not the same as, the one presently used to enter the Dinaledi Chamber. Reconstructions of the cave environment indicate that reaching even the entrance of the Dinaledi Chamber would always have been difficult, particularly in the absence of artificial light.

Our interpretation of events raises questions about the meaning of deliberate and repeated body disposal to this ancient group of individuals. Recent evidence has extended the record of complex behaviour from archaic and modern humans (Haglund, 1993; Arsuaga et al., 1997; Carbonell and Mosquera, 2006) to earlier hominins (McBrearty and Brooks, 2000; Douka and Spinapolice, 2012; Joordens et al., 2015). Deliberate disposal of bodies in the Dinaledi Chamber implies that morphologically primitive hominins like *H. naledi* may have had their own distinctive patterns of behavioral complexity, even though the reason why *H. naledi* may have ventured deep into the cave system remains unresolved.

This leaves the important question of how old the *H. naledi* remains are. At this point we do not want to speculate on the age of the deposit considering the reworked nature of the sediments resulting in mixed stratigraphic signatures that impede faunal dating of the fossil rodent remains, and the limited amount of clean flowstone suitable for U-Pb dating (Pickering et al., 2011a, 2011b). Further method development is underway to circumvent this problem.

Materials and methods

Discovery history of the Dinaledi Chamber and mapping of the cave system

The original mapping of the Rising Star cave system was conducted by a group of cavers from the Free cavers and CROSA caving societies in Johannesburg, who produced a base map that was used by our caving team when exploring the cave system. This map did not show the location of the Dinaledi Chamber.

The Dinaledi Chamber was discovered as a result of detailed speleological surveys of a series of chambers known to contain macro-fossils including the Dragon's Back Chamber. Once discovered, the Dinaledi Chamber and access routes into the chamber were mapped in more detail using traditional mapping techniques involving tape-measures, compass-clinometers, and laser-inclinometers. Prior to our work there is no evidence that excavations for fossils were ever undertaken in the Rising Star cave.

When the Dinaledi Chamber was first entered, it was clear that cavers had been in the chamber before, because they had re-arranged some of the bones (Figure 6B), and had left behind several survey pegs. It is unknown to what degree earlier caving expeditions may have disturbed the original context of the fossils, or damaged some of the bone material, by walking over them, although it was noted that upon first entry much of the rubbly floor of the Dinaledi Chamber had remained undisturbed (i.e., not walked on before). None of the earlier expeditions into the Dinaledi Chamber have left a record of the chamber itself on any survey maps, or have mentioned the fossils in the chamber. Further investigation has established only one confirmed entry into the chamber in the early 1990s (responsible for leaving the survey pegs). Given the complex nature of the entryway, it is unlikely that many, if any, expeditions would have entered the Dinaledi Chamber before or after that one confirmed entry. Since the discovery of the fossils, the entrances into the Dragon's Back Chamber have been locked off, and entry by recreational cavers is no longer physically possible.

Mineralogical and geochemical analyses of floor sediments

Analytical work was carried out at the SPECTRUM central analytical facility of the University of Johannesburg. Grain-size analysis and petrography, were carried out at James Cook University. Bulk chemical analyses of 4 samples were carried out by X-ray fluorescence (XRF) using a Philips PANalytical MagiX Pro instrument and standard borate fusion (**Figure 5B**). The bulk mineralogical composition of four samples was determined by X-ray diffraction (XRD) using a Philips PANalytical X'Pert instrument. The High Score Plus software was used to refine the XRD diffractograms to identify the various mineral phases within the sediment samples.

The cave sediment samples were mounted in 30 mm epoxy blocks and polished for textural analysis using scanning electron microscopy (SEM; **Figures 5, 8**) and electron microprobe analysis. SEM studies were carried out using a Tescan Vega3 scanning electron microscope equipped with an Oxford Instruments X-max 50 mm² EDS detector. Quantitative spot chemical analyses were carried out using a CAMECA SX100 electron microprobe with 4 wavelength dispersive spectrometers and an EDS detector. The instrument was operated at 15 kV with a 5 µm beam width. As many phases within the fragments constituting the samples are not resolvable even at the µm scale, most of the analytical results represent mixtures, and information on their constituent minerals can be obtained from element correlations. The data are given in **Supplementary file 1**. Relevant two-element plots are shown in **Figure 8**. For the quartz-dominated sample DB-1 from the Dragon's Back Chamber, the non-quartz components were investigated.

Excavation approach

Following discovery of the fossil deposits, permission for excavation and recovery of fossils was issued by the South African Heritage Resource Agency, Department of Arts and Culture (PermitID: 952). Excavations are coordinated through the Evolutionary Studies Institute and the National Centre for Excellence in PalaeoSciences, at the University of the Witwatersrand, where all specimens are curated and stored in the fossil vault, and can be studied and accessed by researchers.

Due to the difficult operating conditions, and limited physical access to the excavation chamber by the field crew, a unique system of recording and recovery was developed to assist excavation in the Dinaledi Chamber. The excavation and recording strategy focused on maximizing the retrieval of stratigraphic and spatial information during the recovery process by the excavators, and at the same time allowing reflexive supervision from senior investigators in a physically remote location. The technical strategy included the use of high-resolution 3D non-contact scanning, live digital video streaming of the excavation process to an above-ground supervisory team, as well as more conventional archaeological recording methods to facilitate post-excavation analysis.

Although the recovery process utilised conventional archaeological methodologies, an explicitly forensic archaeological approach (**Hunter and Cox, 2005**) was applied to the resolution of the Dinaledi Chamber. We adopted a multidisciplinary framework, bringing a wide range of expertise in buried environments, to ensure that the most complete range of evidence was collected. The excavation strategy proceeded on a single-context recording and recovery basis (**MOLAS, 1994**). The limits of the excavation were defined within the site, and sketch plans produced where appropriate. Excavation was undertaken with non-metallic tools in order to limit the possibility of recovery damage to highly fragile and friable skeletal material, and the exposure and recovery of any sediment surface was limited to the production of one or two hand-brush trays of spoil only. All excavated matrix sediment was double-bagged and recovered for analysis. In situ metric measurements were taken where specimens were highly fragmented or fragile. Taphonomic traces were noted where seen. All bone fragments were lifted from the surrounding sediment, double bagged, wrapped in bubble plastic, taped securely, boxed and lifted to the surface for cleaning, photographic recording, and consolidation or preservation of the remains where necessary. Recording pathways adopted are presented in **Table 2**.

A photographic record of the excavation was taken, augmented with high-resolution, 3D surface scanning to document the location, orientation (axial and surface) of every bone. We used an Artec Eva (<http://www.artec3d.com/hardware/artec-eva/>), 3D white light scanner with the capacity to capture surface colour and texture (surface resolution: 0.5 mm; 3D point accuracy: 0.1 mm) in order to record and analyze the spatial position and orientation of bones within Unit 3 matrix material. The post-scan process was managed in Artec Studio 9. Each scan sweep comprised a number of separate

Table 2. Recording activity pathway for Dinaledi Chamber excavations

Material or action	Assign and record	Forms
In cave: excavator and recorder		
Sediment context	Context number and attributes	Context form
	Photography	Photo register
	Sketch plan and/or section	Section log
	Scan	Scan register
	Sample	Sample register
Bone	Element number	Skeletal form
	Spatial properties	Area sketch
	Physical properties	Taphonomy
		Peri-M trauma
		Post-M trauma
		Metric form
	Recovery	Recovery log
Excavation scan	Record all observed contexts and elements	Scan form
Above ground: recorder		
Context or element	Record of assigned number	Context log
Excavation scan	Record all observed contexts and elements	Scan log
Bone element	Preliminary ID, spatial attributes and location	Element log
Recovered material	What is lifted and boxed	Recovery log

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images compiled into a single layer. Each scan was then registered to acquire 3D triangulated points. Once registration was complete, the separate layers were manually aligned, by using a minimum of three reference points. The reference points are fixed survey markers within the Dinaledi Chamber, which were captured in each scan to provide optimal registration. Once alignment was complete, a global registration process allowed for the scan data to be merged accurately. This produced a 3D mesh representation of the scanned area. The 3D scan was then overlain with a photographic texture map, which was captured by the Artec Eva at the time of scanning.

Methodology of taphonomic analyses

The entire *H. naledi* assemblage has been analysed at macroscopic scale, and a reduced sample of specimens from 11 individuals has been studied by microscope. Specimens were viewed at magnifications between 7 and 50 times using an Olympus SZX16 Zoom Stereo Microscope fitted with a DFC420 digital camera and equipped with Stream software. Modifications observed on the Rising Star material were compared with those recorded on bones in a reference collection held at the University of the Witwatersrand, which comprises bones and teeth modified by 58 known agents, including humans and a wide range of other vertebrates; 17 invertebrate taxa; and geological processes, including different forms of sedimentary abrasion, from trampling by large animals to the overall rounding and polishing caused by moving water. Characteristics and traces evaluated in the taphonomic analysis are listed in **Table 3** (after **Pokines and Symes, 2013**).

In undertaking the analyses we have adopted a taphonomic approach derived from forensic practice in relation to the death process and burial environment with a degree of resolution usually reserved for medico-legal casework. The co-option of forensic taphonomy into palaeo-taphonomy provides a framework with which to investigate the decompositional and formational histories of ancient deposits by applying analyses of short-period events into the geological past (**Symes et al., 2013**).

Table 3. Taphonomic recording criteria (after *Pokines and Symes, 2013*)

Signature	Characters or taphonomic traces for recording
Preservational	General state of remains (excellent, good, fair, or poor)
	Cortical erosion/exposure of cancellous bone
	Cortical exfoliation (bone loss in thin, spalling layers)
	Postmortem breakage
	Perimortem breakage/fragmentation or trauma
	Rounding (erosion/tumbling in an abrasive environment)
	Decalcified
	Postmortem cracking of desiccated tooth enamel
	Incidental surface striations/scratches
Soil surface exposure	Surface cracking/longitudinal splitting from drying of waterlogged bone
	Weathering (bleaching and cracking; sensu Behrensmeyer)
Mineral deposition	Copper (green), iron (red), calcium (white), manganese (black), or other mineral oxide staining
	Vivianite formation
	Concretion
	Water staining (presence of a water line from mineral deposits, colour differential line)
Mechanical	Excavation damage
	Micro-abrasion
Soil/burial substrate	General soil staining
	Warping/flattening of elements (especially the cranial vault)
	Crushing/compaction from overburden
	Adhering/infiltrating sediments
Faunal	Adhering fauna
	Carnivore puncture and gnawing
	Gastric corrosion, winnowing, or windowing of bone
	Rodent gnawing
	Invertebrate surface modification and damage

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Description of weathering patterns

The remains of *H. naledi* were analysed following the six stage classification system of *Behrensmeyer (1978)* based on faunal remains that weathered on the landscape in Kenya. Although this classification system has been developed for surface deposits, and is therefore less suitable for South African cave deposits, we have chosen to apply this recording system, because it allows us to address issues of possible bone transport into the Dinaledi Chamber from surface. *Behrensmeyer (1978)* described six weathering stages (Stages 0–5) based on the progressive pattern of linear cracking and flaking of the cortical surface, followed by formation of a rough fibrous texture, and eventual collapse of bone integrity and structure (i.e., greasy bone with tissue is designated as Stage 0, and splintered fragile bone falling apart in situ is designated as Stage 5). The progressive weathering stages are broadly indicative of the period of surface exposure in sub-aerial conditions, with bone exposed to the elements, including sunlight.

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Author contributions

PHGMD, Responsible for geological mapping, wrote the original draft of the manuscript, and coordinated all subsequent edits, and assisted with overall interpretations; LRB, Conceived the overall project, assisted with taphonomic interpretations and wrote interpretive parts of the manuscript; EMR, Mapped the geology and lay-out of the Dinaledi Chamber, provided sedimentological input and assisted with the interpretations and geological writing; JDK, Provided the geochemical and sedimentological input and assisted with the interpretations; JH, Analysed the spatial context and skeletal distribution patterns of elements; Provided input on interpretations of behavior and taphonomy; Helped draft sections of the discussion; PSR-Q, Contributed to the excavation and body recovery protocols and drafted the taphonomic sections; Conducted analyses of weathering, skeletal damage patterns and other taphonomic processes in deposition and formation of the assemblage; ME, Conducted the excavations and fossil recovery, supervised by JH and LRBe; Assisted with detailed sampling and cave mapping; CMM, Conducted analyses of weathering, skeletal damage patterns and other taphonomic processes in deposition and formation of the assemblage; SEC, DJR, PS, Assisted with the interpretations related to behavior; LRB, Provided input on surface modification and with JGH conducted experiments on invertebrate–bone interactions; Conducted analyses of weathering, skeletal damage patterns and other taphonomic processes in deposition and formation of the assemblage; GAB, Provided the geochemical and sedimentological input and assisted with the interpretations; PB, Helped map the cave system; KLH, Conducted the excavations and fossil recovery supervised by JH and LRBe, Acquisition of data; EMF, AG, HM, BP, Conducted the excavations and fossil recovery supervised by JH and LRBe; JGH, Conducted experiments on invertebrate–bone interactions; RH, ST, RH and ST were the cavers who discovered the fossils, and together with PB mapped the cave system; AK, Helped with the analyses of the spatial context and skeletal distribution patterns; TVM, Collected geochemistry data on sediments

Additional files

Supplementary files

- Supplementary file 1. Electron microprobe analyses of spots in fragments of samples UW101-SO-31, UW101-SO-34, UW101-SO-39 and DB-1. Note that in each of the tables totals below 100% reflect volatile content or porosity of sample, or both.

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- Supplementary file 2. Summary table listing surface modifications on all morphologically informative specimens. A total of 559 bone and dental specimens were examined for surface modifications. This sample includes all of the larger specimens and most of the complete elements in the collection, from both surface and excavation contexts. At low magnification (7×) most of the bones show weathering stage 1 or 2 (Behrensmeyer, 1978), while 18% have an etched appearance and 11% exhibit dissolution. No bone in this sample has edges consistent with a spiral (fresh) fracture. Instead, they show weathered (19%) or recent breakage patterns (Villa and Mahieu, 1991). None of the specimens are burnt (Stiner et al., 1995) or shows signs of trampling (Behrensmeyer et al., 1986). There is no evidence of stone tool inflicted cut, scrape, impact or chop marks (White, 2014). Tooth scores and pits, crenulated edges and splintered shafts associated with carnivore damage (Kuhn, 2011) are absent. The collection bears clear traces of invertebrate activity, with most of the bones (n = 553) exhibiting microscopic removal of the bone surface, and evenly spaced, multiple parallel striations (35%) associated with smooth-based pits (34%), a pattern consistent with damage made to bone by modern gastropods (Figure 12). Sixty-two specimens (10%) record large individual, variably arrow-shaped and randomly oriented striations, consistent with those made by modern beetles (Figure 12).

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CHAPTER FOUR: MULTIMODAL SPATIAL MAPPING AND VISUALISATION OF DINALEDI CHAMBER AND RISING STAR CAVE*

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Multimodal spatial mapping and visualisation of Dinaledi Chamber and Rising Star Cave

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The Dinaledi Chamber of the Rising Star Cave has yielded 1550 identifiable fossil elements – representing the largest single collection of fossil hominin material found on the African continent to date. The fossil chamber in which *Homo naledi* was found was accessible only through a near-vertical chute that presented immense practical and methodological limitations on the excavation and recording methods that could be used within the Cave. In response to practical challenges, a multimodal set of recording and survey methods was thus developed and employed: (1) recording of fossils and the excavation process was achieved through the use of white-light photogrammetry and laser scanning; (2) mapping of the Dinaledi Chamber was accomplished by means of high-resolution laser scanning, with scans running from the excavation site to the ground surface and the cave entrance; (3) at ground surface, the integration of conventional surveying techniques as well as photogrammetry with the use of an unmanned aerial vehicle was applied. Point cloud data were used to provide a centralised and common data structure for conversion and to corroborate the influx of different data collection methods and input formats. Data collected with these methods were applied to the excavations, mapping and surveying of the Dinaledi Chamber and the Rising Star Cave. This multimodal approach provides a comprehensive spatial framework from individual bones to landscape level.

Introduction

The field recovery of hominin fossils and other skeletal remains is a process which owes much of its practical and epistemological background to prehistoric archaeology and archaeological field techniques. As such, searching for, recovering and collecting evidence from a sub-surface or surface scatter of bones are disruptive processes that occur during field investigation. Field archaeology is, by its very nature, a destructive process¹ – once a fossil (or stone tool) has been removed, it can never be put back in its original place, and the link to its context of deposition is broken. As a result, the goal of spatial field recording is to ensure that all items and samples taken from a site can be sourced to their particular context and modelled in three dimensions. Adequate survey and mapping techniques allow investigators to maintain a record of where every item of evidence was found within a defined area, allowing the investigator to recreate the order of events that took place from when the deposit was first exposed, to final recovery. The recording process of any site usually follows the traditional archaeological field recording and requires at least two fixed reference points from which the fieldworker can extrapolate the position of any bone or sample within a deposit, using basic spatial geometry. In many respects the practical fundamentals of field recording of bones, artefacts, dating and sediment samples, is a largely unchanged component of archaeological field skills, and can use items as simple as tape measures, plumb-bobs, and pencil and drafting film, up to the level of electronic distance measuring devices, the Global Positioning System (GPS), photogrammetry and non-contact surface laser scanning.¹ Regardless of the level of technology utilised, it is critical that any recording system allows the archaeologist or palaeoanthropologist to accurately record, plot and model the contexts and contents of a site as precisely as possible in three dimensions. Whether the expected outcome is hand-drawn maps and plans, or three-dimensional computerised models of a site, the fundamental principles are the same.

Historically, work conducted in the Cradle of Humankind with three-dimensional recording methods aimed for visualisation of geological structures, taphonomic associations, and linkages between in-situ and ex-situ fossils. With respect to early hominin sites, mapping the cave systems with reference to the excavation process is essential to understanding the development and movement of sediments and geological units, and has been advanced by several researchers in Africa and Europe.²⁻²⁰ Because of the brecciated nature of the primary fossil deposits of the Cradle of Humankind (Taung, Gladysvale, Sterkfontein, Kromdraai, Swartkrans, Makapansgat and Malapa), conventional archaeological recovery techniques using traditional methods of recording and planning of discrete contexts (production of single-context plans, overlays and sections, e.g. those used by fieldworkers in the UK) have been difficult to apply in South Africa. Many historical excavations, such as the central component of Sterkfontein^{21,22} or Cave of Hearths (Makapansgat)^{23,24}, have traditionally used an above-site fixed-grid system from which metal poles or markers are suspended, allowing for an approximation of spatial location to the level of the nearest cubic yard or cubic metre, or using offsets from the grid to determine x-y-z location within a square or cubic unit with greater precision. With the advent of laser-rangefinder technology later South African excavators have often sought to record the general position of fossils and fossil blocks within the cave by means of broader coordinate systems, using instruments such as electronic distance measuring devices, laser theodolite or total stations (although the adoption of this technology has been relatively late in South African palaeoanthropology as a result of the prohibitive cost of purchasing such equipment).

Three-dimensional digitisation of caves has been undertaken by many researchers since the late 1990s, and has often been used in conjunction with other archaeological and palaeontological data collection methods. Some of the earliest uses of three-dimensional recording within the Cradle of Humankind were undertaken by Quinney and Calabrese in mapping the 'Little Foot' StW 573 skeleton at Sterkfontein in 1998²⁵, using a Leica total station in conjunction with PenMap surveying software. This undertaking allowed for the precise three-dimensional collection of coordinate data (x, y and z axes) and the reconstruction of contour maps of the exposed geological units within which the skeleton was entombed. Other work (1997 to 2001) by Quinney, Sinclair and colleagues at sites within the Makapansgat Valley

(including the Limeworks australopithecine site and the Cave of Hearths) used the same Leica/PenMap system to assist in the construction of archaeological site plans within individual excavation units, and to combine these with landscape-level surveys of river terraces, sinkholes and fossil-bearing caves, in order to build up broadscale spatial data of the landscape and karstic features.^{26,27} In combination with aerial survey data from microlight aircraft, photogrammetry and Geographical Positioning System (GPS) data, the spatial data was integrated into a geographical information system (GIS) model of landscape archaeology in IDRISI.²⁷

Later work in 2002 by Lacruz and colleagues²⁸ at the site of Gladysvale provided a three-dimensional surface (mesh) visualisation of the cave system extrapolated from total station coordinate data, and, more importantly, situated the cave system in direct spatial reference to the current landscape surface. This was followed by Nigro and colleagues¹³, who developed an integrated GIS framework in order to map and analyse the fossil deposits at Swartkrans.

Methods of spatial coordinate capture and three-dimensional visualisation of hominin-bearing deposits are now routinely applied at palaeo-anthropological fieldschools such as those undertaken at Drimolen and Sterkfontein. All excavations at the site of Malapa (including work on ex-situ dump deposits) have utilised three-dimensional recording from total station equipment (Figure 1). Recent research excavations by Stratford at the site of Sterkfontein have focused on the use of three-dimensional coordinate systems for the mapping of geological units, artefactual and fossil deposits, integrated into a GIS framework.²⁹ This work has resulted in significant methodological advances compared to earlier approaches and has led to practical frameworks comparable to those applied at European cave excavations.³⁰ Most recently, Subsol and colleagues³¹ applied surface laser scanning to capture the in-situ three-dimensional morphology of the StW 573 skeleton. This work included a test of different laser scanners in order to judge the efficacy and efficiency of different technical set-ups, with resulting recommendations for best practice in such environments.

Such work within the Cradle of Humankind has been mirrored elsewhere in South Africa and beyond, with laser scanning in particular being used in an

increasing capacity to record fragile cultural heritage, or to facilitate public understanding of the past through three-dimensional reconstruction. Within cave environments, laser scanning (combined with GIS data) has been applied to spatial reconstructions and mapping, often in conjunction with conventional spatial survey.^{2-20,29-32}

Three-dimensional data can also be used in the reconstruction of previously worked sites which were excavated before technology such as terrestrial laser scanning existed. In one such case study, Puchol and colleagues⁵ virtually recreated an archaeological excavation site using three-dimensional laser scan data and integrating the data with previously recorded archaeological data, to analyse the spatial context from over 60 years earlier. This amalgamation of 'old' and 'new' data allowed the researchers to extract entire data sets which might not have even been considered in the past. This increases the need for accurate three-dimensional recording of sites, as the better the quality and resolution of recorded data, the easier it will be to relate to new and developing methods of data capture in the future.

Rising Star excavations and Homo naledi

The Rising Star Cave system is located in the Cradle of Humankind World Heritage Site, some 50 km outside of Johannesburg, South Africa (Figure 2). Whilst amateur cavers had been periodically visiting the Cave for a number of years, an incursion by a caving team from the Evolutionary Studies Institute in September 2013 was the first to formally investigate the system for the fossil remains of early hominins. Excavations in November 2013 and March 2014 yielded 1550 identifiable fossil elements representing a minimum of 15 individuals; 300 bone specimens were collected from the surface of the Dinaledi Chamber and 1250 fossil specimens were recovered from a small excavation pit in the chamber floor. This assemblage is the largest single collection of fossil hominin material found on the African continent to date, and has been assigned to the *de novo* hominin taxon, *Homo naledi*. The taxonomy of this new species is detailed by Berger and colleagues³³, with the geological and taphonomic context by Dirks and colleagues³⁴. The latter includes a detailed description of the recovery and recording methods applied to the excavation, with aspects detailed in additional commentaries on inferred mortuary behaviours by Randolph-Quinney^{35,36}.



Figure 1: The use of conventional coordinate capture methods during excavations at Malapa Cave, Cradle of Humankind. The excavators are using a Nikon NPR-352 total station mounted on a known-position survey point to record the position of fossil material recovered during the excavation process. Site coordinates (x , y and z) are converted to geo-reference coordinates (easting, northing and height above sea level in the WGS 84 map reference system) by the total station.

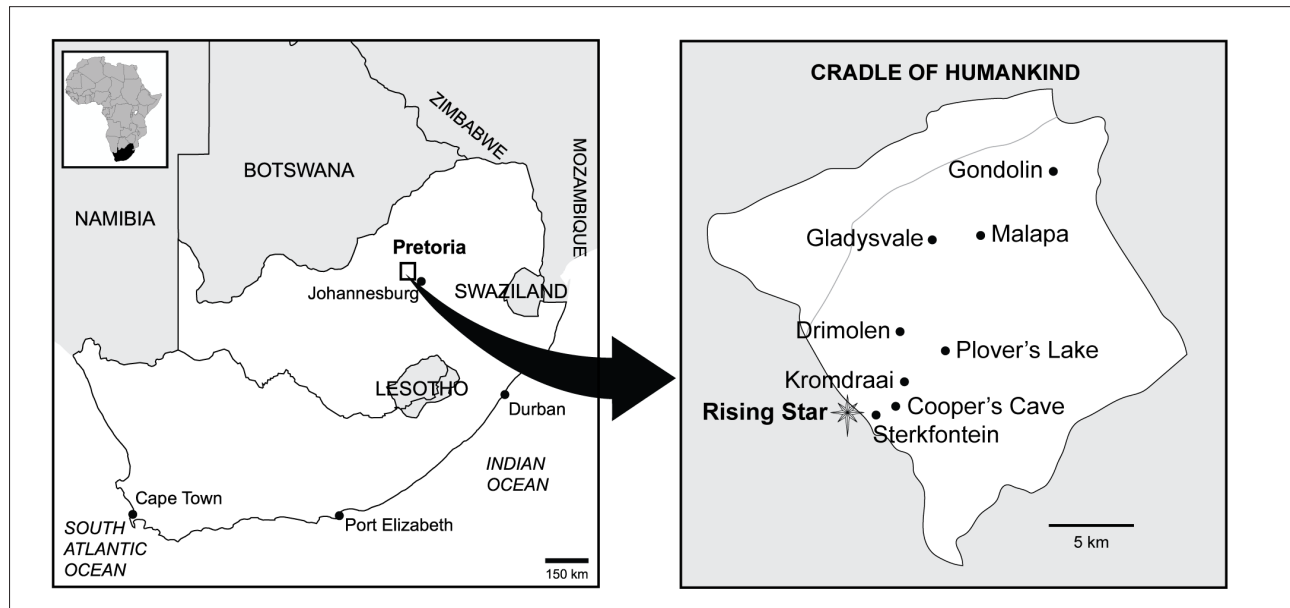


Figure 2: Location of the Rising Star Cave within the Cradle of Humankind, UNESCO World Heritage Site. Other major palaeontological sites are indicated.

Taphonomically, the assemblage presents a unique situation compared to other South African early hominin-bearing karstic cave sites for three reasons: (1) the hominin remains are numerous and concentrated in a very small area; (2) with the exception of a small number of recent intrusive rodent and bird bones, only hominin bones are found within the Chamber; and (3) the assemblage is unique by what it lacks – there is no evidence of carnivore modifications, sub-aerial exposure or weathering, peri-mortem breakage or trauma, cut marks, or fluvial transport, and no evidence of burning or charring of remains.

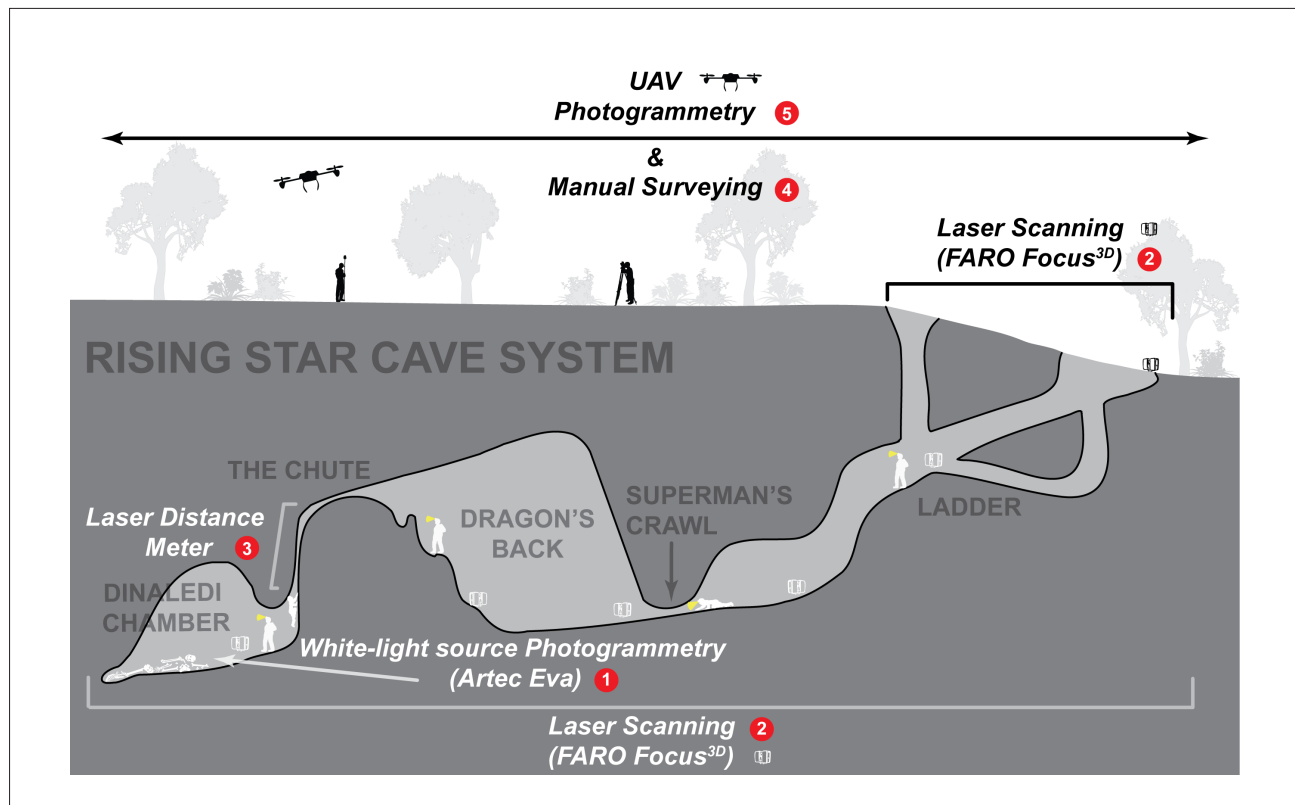
Furthermore, the Dinaledi Chamber presents an anomalous depositional environment in comparison to the primary historical hominin sites of the Cradle of Humankind in Gauteng – Sterkfontein, Kromdraai and Swartkrans.^{34,37} The latter sites are noted for fossil remains contained in lithified breccia or found in decalcified sedimentary units derived ultimately from clastic breccias. The Dinaledi Chamber is unique in that the fossils were recovered from unconsolidated sediments, and appear never to have been lithified during their depositional history. The basic stratigraphic development of the cave infill is divided into two facies (Facies 1 and 2, with 1 being the oldest) subdivided into three stratigraphic units (1–3, from old to young). Unit 1 comprises reworked laminated mudstones preserved as erosion remnants within the Chamber. Unit 2 is a composite unit that consists of remnant outcrops of variably consolidated sediments containing hominin bones. Unit 3 is the youngest stratigraphic unit, composed of largely unconsolidated sediment derived from weathering and erosion of Units 1 and 2. The majority of the hominin bones was derived from Unit 3. The clay-rich sediments making up the units were derived from in-situ weathering, and from exogenous clays and silts, which entered the Chamber through fractures that prevented passage of coarser-grained materials. Thus, the infill of the Dinaledi Chamber is largely endogenous, fine grained and unconsolidated in nature.³⁴ Because of the sedimentary environment, recovery of fossils could proceed relatively rapidly using methods more akin to bioarchaeology, rather than the traditional palaeontology of the Cradle in which fossils are extracted from calcified breccia blocks. Unfortunately, the size of the Chamber and the difficulty of the access route precluded the use of conventional surveying equipment such as total stations and necessitated a trade-off in conventional excavation recording strategies. This situation presented immense practical and methodological limitations on the excavation and recording methods

that could be used within the cave, where conventional methods of high-resolution spatial data retrieval proved impossible.

Materials and methods

As historical work at sites such as Gladysvale, Makapansgat and Sterkfontein has demonstrated, three-dimensional coordinate data are seen as essential in placing fossil remains in context. At Rising Star, this contextualisation includes collecting three-dimensional data, visualising and understanding the location of fossil material in relation to (1) other material in the Dinaledi Chamber, (2) other chambers within the Rising Star Cave system and (3) the position of the Chamber relative to the landscape surface and surrounding structural geology. Collection of such data demanded high-resolution acquisition, and necessitated the use of equipment of considerable monetary value. Data collection techniques used at the Rising Star Cave ranged from landscape level, down to scanning in-situ fossils (Figure 3). A centralised data structure, in the form of point cloud data, was fundamental to integrating these different formats and data types, many of which have not been integrated in this way at any palaeontological site before.

In response to the practical challenges noted above, a multimodal set of recording and survey methods was developed and employed for use at Rising Star: (1) recording of spatial distribution of the fossils (spatial taphonomy) and the excavation process was achieved through the use of white-light photogrammetry and laser scanning; (2) mapping of the Dinaledi Chamber in landscape context, with scans running from the excavation site to the ground surface and the cave entrance, was accomplished by means of high-resolution laser scanning; (3) at surface level, the integration of conventional surveying techniques as well as photogrammetry with the use of an unmanned aerial vehicle (UAV) was applied. Point cloud data were used to provide a centralised and common data format for conversion and to corroborate the influx of different data collection methods and input formats. Data collected with these methods pushed the boundaries of both technology and image reconstruction as applied to the excavations, mapping and surveying of the Dinaledi Chamber and the Rising Star Cave. This multimodal approach represents the first time that such a seamlessly integrated three-dimensional survey has been applied to a South African hominin site, and provides a comprehensive spatial framework from individual bones within the excavation context, up to the landscape level.



UAV, unmanned aerial vehicle

Figure 3: Graphic representation of the data collection techniques and specific locations in which they were employed to acquire high-resolution data at the Rising Star Cave.

White-light source photogrammetry

The constraints of the Rising Star Cave and Dinaledi Chamber affected both excavators and equipment and demanded an innovative approach to collecting high-resolution spatial data. These data are important for documenting spatial orientation, but can also be used for mapping and surveying. During excavations in November 2013 and March 2014, a handheld Artec Eva (Luxembourg City, Luxembourg; <http://www.artecthree-dimensional.com/hardware/artec-eva/>) white-light source photogrammetry device was employed for this purpose. 'Painting' or 'sweeping' the desired area with the Artec Eva produces a real-time visualisation of the scan area on an accompanying laptop computer. The Eva has its own white-light source, which is activated in a series of strobe-like flashes during data capturing. Documenting the excavations within the Dinaledi Chamber with the Eva served two purposes. Firstly, spatial data on the location and orientation (axial and surface) of every bone were collected, with a surface resolution of approximately 0.5 mm and a three-dimensional point accuracy of approximately 0.1 mm. Secondly, the data recorded during this process were transported to the surface after every scan, allowing the scientists above ground to provide guidance and direction to the excavators concerning excavations and recovery.

Fossil material from Unit 3 of the Dinaledi Chamber³¹ was scanned at approximately 50-mm intervals, or before and after large amounts of material were removed from the sediments. This meant that the excavation recordings were limited to a maximum interval of 50 mm or less. To date, the main excavation area has been excavated to an average depth of 100 mm, and is represented by 151 Artec scans. Fossil material from other parts of the Dinaledi Chamber (i.e. not from the main excavation area, and found mostly at surface level) was also scanned before and after recovery using the same equipment and method.

The post-scan process was managed in Artec Studio 9 (and more recently Artec Studio 10 Professional). Each scan 'sweep' comprised a number of separate images compiled into a single layer. Each scan was

then registered to acquire three-dimensional triangulated points. Once registration was complete, the separate layers were manually aligned, using a minimum of three reference points. These reference points were a combination of fixed survey markers within the Dinaledi Chamber, and physical features of the excavation area, which were captured in each scan to provide optimal registration. Once alignment was complete, a global registration process allowed for the scan data to be merged accurately. This produced a three-dimensional mesh representation of the scanned area. The three-dimensional mesh was then overlain with a photographic texture map, captured by the Artec Eva concurrently at the time of scanning. The final product resembles a realistic, photo-like, overlay of the three-dimensional scan. After compiling each three-dimensional scan, the surface scan was exported as a PLY (polygon file format, also known as the Stanford triangle format), which was then stitched together to create a composite surface scan from multiple scans. This composition allowed for the excavation areas and Chamber to be visualised in a three-dimensional environment, through time. Each individual three-dimensional scan, once registered, aligned and fused, was then converted to the E57 file format³⁸ for three-dimensional imaging data exchange for effortless visualisation and coordinate system manipulation in Autodesk Recap.

High-resolution laser scanning

Data capture of large areas proved to be cumbersome with the Eva as even small areas (e.g. <1 m²) of the cave walls or floor, could produce gigabytes of scan data, and in turn many hours of data rendering, fusion and meshing. As a result, a FARO Focus^{3D} X330 laser scanner (Lake Mary, FL, USA; <http://www.faro.com/products/three-dimensional-surveying/laser-scanner-faro-focus-three-dimensional/>) was used to scan the Dinaledi Chamber, as well as the route between the Chamber and the entrance of the Rising Star Cave system. The Focus^{3D} scanner is physically larger than the Eva and is capable of scanning areas or objects from 0.6 m to a maximum of 330 m. This range was advantageous as large portions of the Rising Star Cave could be scanned relatively quickly.

With a distance accuracy of about 2 mm, the Focus^{3D} scanner was able to produce ultra-high resolution, accurate scans of the cave.

To allow the best possible registration and geo-referencing while scanning in the Rising Star Cave, each scan with the Focus^{3D} scanner was undertaken with the use of 145-mm diameter spheres. These spheres have a magnetic base that attaches to a steel bracket and allows for secure placement. As the cave surfaces are extremely rough and inconsistent, the team modified a number of JOBY GorillaPods (Petaluma, CA, USA; <http://joby.com/gorillapod>) for positioning the spheres throughout the cave. In this manner, it was possible to attach the spheres securely and safely to various formations and features in the cave. The spheres were placed strategically throughout the cave to complete the scanning as efficiently and accurately as possible, with a minimum of 3 and a maximum of 10 spheres present in each scan.

The Dinaledi Chamber was scanned in its entirety with six scans, each of which took 10–12 min to complete at a resolution of 3.086 mm per 10 m scanned. At this resolution, a point cloud of 173 million points per scan was achieved. A set of 37 scans was completed on a slightly lower resolution of 6.136 mm per 10 m scanned, producing a point cloud of 43 million points per scan. A total of 43 scans was completed, to capture the entire path from the entrance of the Rising Star Cave system to, and including, the Dinaledi Chamber, with the exception of the very confined 'Chute' area (discussed later). Each scan totalled approximately 300 MB and all 43 were combined to create an ultra-accurate point cloud, map and digitisation of the Rising Star Cave. Scans were processed with FARO's SCENE software and were then exported to the Pointools POD file format (.pod) with a compression accuracy of 1 mm. The .pod files were visualised and given a coordinate system with the utilisation of Autodesk Recap.

UAV photogrammetry

A UAV was used to capture data of the land surface above the Rising Star Cave system. The UAV used was the Aerialtronics ATX8 (Den Haag, the Netherlands) with a full-frame Nikon D610 digital single-lens reflex (DSLR) camera attached. A total of 1031 time-lapse images were taken over three flights, at a height of 103 m. Each flight lasted approximately 8 min. Calibration and corroboration of the data were accomplished using four ground control points, as well as a Nikon GP-1A GPS unit. The program Agisoft Photoscan was used to generate the three-dimensional spatial data, which were then exported as .tif and .txt data formats. The data were imported to Autodesk Recap (.rcp) and assigned a coordinate system, which was then overlaid on the Eva and FARO scanner data. In this way, it was possible to accurately locate the Dinaledi Chamber in relation to the ground above it.

Other scanning techniques

The 'Chute' is an extremely difficult and confined 12-m fissure leading down into the Dinaledi Chamber (Figure 4). Despite several attempts, the nature of this passageway proved to be too difficult to scan using either the Artec Eva or FARO Focus^{3D} scanners. Consequently, in order to link the three-dimensional spatial data of the two systems, the Chute was manually mapped and measured using a Leica DISTO S910 laser distance meter. Points were measured at intervals between the top and bottom of the Chute, in the form of x, y and z coordinates at a resolution of approximately 1 mm. Known points collected with the Focus^{3D} were shot in with the S910 and used to align the Dinaledi Chamber scan data with the rest of the laser scan data acquired from the top of the Chute all the way back to the entrance of the Cave.

Manual surveying of the ground above the cave system was also conducted, using traditional surveying techniques. Data acquired in this way were compiled in Autodesk AutoCad (.dwg file format) and once again overlaid on the data collected with the white-light source photogrammetry, high-resolution laser scanning and UAV

photogrammetry. Above ground, two fixed beacons were erected, and assigned UTM coordinates.



Figure 4: Photograph of the small confined nature of the 'Chute' within the Rising Star Cave.

Workflow for three-dimensional data

An integral part of combining the many different formats and scan data presented in this paper was ensuring a centralised and common data structure for conversion. In this case, point cloud data served as an amenable arrangement for data processing, as sets of local, global or arbitrary coordinates could be used to tie data sets together. In addition, a number of different data formats such as .txt, .xyz, .e57, .pod or .rcp can be configured as point cloud data.

A workflow was introduced to handle all the data collected from the excavations and surveys of the Dinaledi Chamber and Rising Star Cave (Figure 5). As noted previously, scan data using the Artec Eva white-light source photogrammetry were processed and rendered in Artec studio. Once the final scan of each layer of excavations was completed and ready for export, a positioning tool was used to set the horizontal plane of the surface. These data were exported to the .e57 file format and imported into Autodesk Recap as a Recap project (.rcp). Now comprising point cloud data, these data were then given arbitrary, local position coordinates. Coordinates were all set to millimeters and the origin of the coordinates was set to a feature in the cave. This process allowed the excavation area, as well as features and fossil material in the Dinaledi Chamber, to be located and expressed as points, each one with an x, y and z coordinate. By simply selecting a point in Recap, the x, y and z coordinate for a specific point is shown, and the data recorded for spatial data analyses.

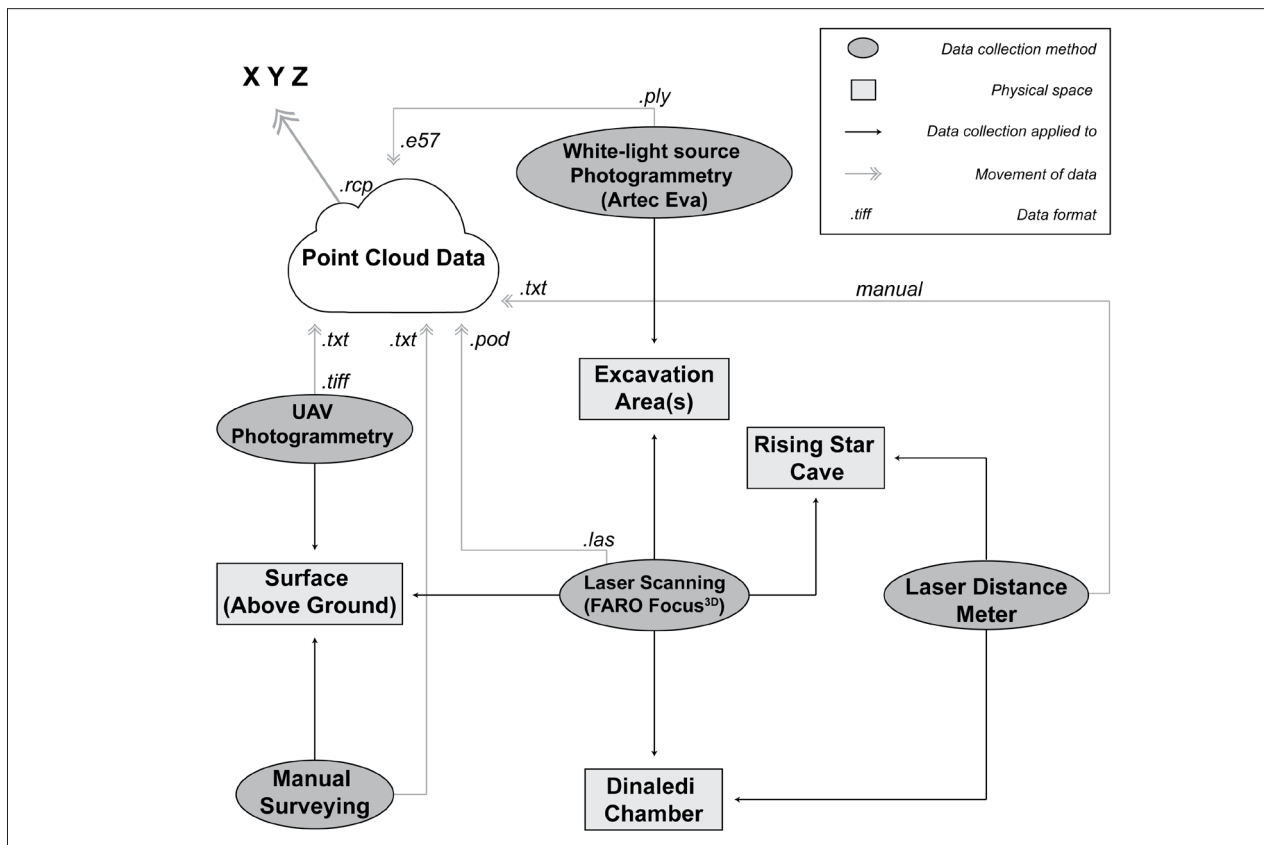


Figure 5: Workflow of the data collection techniques, data formats and structures employed to acquire high-resolution data at the Rising Star Cave.

Data collected with the FARO high-resolution laser scanner were exported as .pod and also imported to Recap as a .rcp project. These data were then linked to the Eva white-light source photogrammetry data by updating a point in the point cloud data, and setting it to the same coordinate as it appeared in the photogrammetry data. In this way, a point in the white-light scans would have the same coordinate x, y and z position as the same point in the laser scans. As data from the excavation area are limited to that region, and are constantly changing as excavations proceed, the linking of this data with the rest of the Dinaledi Chamber and the laser scan data, was essential for alignment and fitting of the coordinates to the larger coordinate system of the Cave's point cloud. Thus, if a point in the white-light source photogrammetry data was 'missing' (for example, a fixed marker was not scanned in a particular scan) it still had a coordinate value in the form of x, y and z.

This procedure allowed fossil material to be assigned an x, y and z value in the form of points. Each in-situ fossil was given a number of coordinates for different spatial attributes, such as proximal, distal or centre of a bone, before excavation. The layered point clouds produced from the white-light and laser scanners were then used to record the fossils' positional attributes in three dimensions while they were still in place.

Laser scan data collected inside the Rising Star Cave system were linked to the ground surface by scanning fixed markers at the entrance to the cave. These reference markers served two purposes. Firstly, they allowed the data collected above ground, by means of manual surveying and UAV photogrammetry, to be synced with data below ground for accurate location of underground features on the surface. Secondly, the reference markers provided a set coordinate system to allow new sections of the cave to be scanned and linked to the existing cave scans, thus expanding the three-dimensional knowledge of the system.

As with the other methods, the UAV photogrammetry data were converted to point cloud data and imported to Recap. Visualisation of these data is more simplified compared to the others as most of it is represented by x and z coordinates only. By locating the fixed markers at the entrance of the

cave, the UAV photogrammetry point cloud data could be assigned the same coordinate system as the other systems, and the coordination of data by the various methods presented in this paper could be achieved. As the UAV captures global coordinates for its data (in the same way as GPS and ground control points are assigned GPS coordinates), it was possible to assign global (GPS) coordinates to the point cloud data, essentially assigning GPS coordinates for fossil material in the Dinaledi Chamber. However, assigning such GPS coordinates to the fossil material offered little benefit above that of assigning arbitrary points and this method was not applied. The GPS coordinate data were, however, instrumental in coordinating the manual surface surveys, in accurately locating the underground chambers, and in visualising underground features in relation to the ground surface. This visualisation is important as the positions of chambers relative to the surface, as well as their relationship to geological features above ground, may bear on how material was deposited or accumulated in the system.

Results

Ongoing analyses are underway to fully describe the context of each fossil element recovered from the excavations in the Dinaledi Chamber. An example of the results obtained by means of the scanning techniques presented here can be seen in Figure 6. Figure 6a is a photograph of the adult 'Hand 1' of *H. naledi*, as described by Kivell and colleagues³⁹. Beside it is the hand in situ prior to excavation (Figure 6b). Figure 6c shows the in-situ white-light source photogrammetry mesh accomplished with the Eva after alignment, registration and fusion from four separate scans at an average accuracy of 0.35 mm. The location of the articulated hand is clearly visible, and its spatial context, in relation to the broader excavation area, is captured. Accurate measurements are obtainable through the Artec Studio software, including the distance (in any direction) between specimens within the excavation chamber. Figure 7a shows the broader context of 'Hand 1' in relation to the excavation area and a fixed registration marker ('Pin 2') within the Chamber.



Figure 6: (a) Photograph of the adult 'Hand 1' of *Homo naledi* as described by Kivell et al.³⁹; (b) adult 'Hand 1' of *H. naledi* in situ, prior to excavation; and (c) in-situ white-light source photogrammetry mesh of the area surrounding adult 'Hand 1' of *H. naledi* accomplished with the Artec Eva after alignment, registration and fusion of four separate scans at an average accuracy of 0.35 mm.

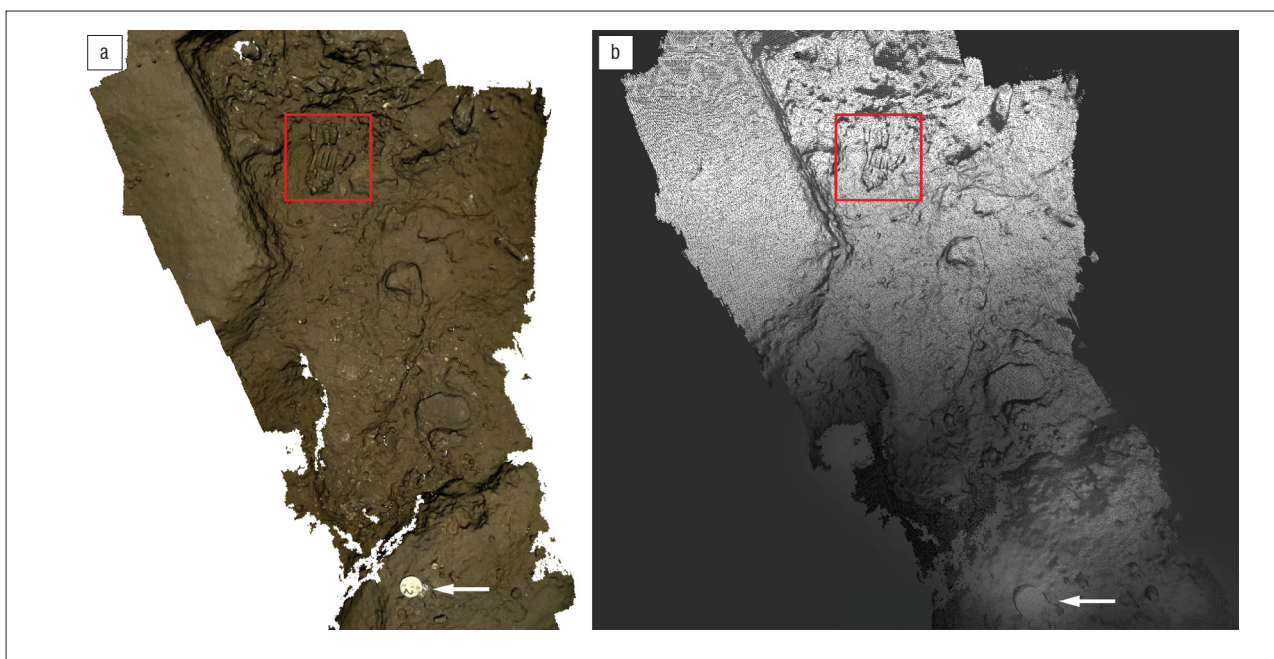


Figure 7: (a) In-situ white-light source photogrammetry mesh of the area surrounding adult 'Hand 1' of *Homo naledi* indicating a reference pin marker (designated with an arrow); and (b) the same mesh converted to the .e57 point cloud data structure, indicating the same pin marker.

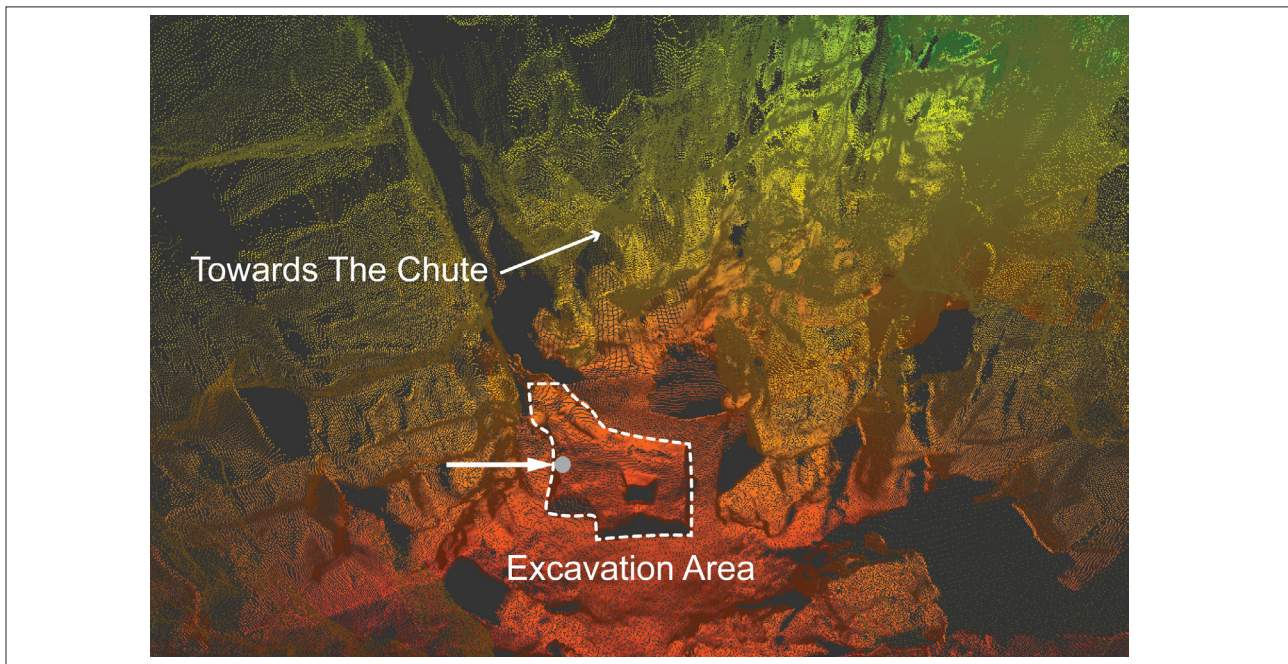


Figure 8: Point cloud data generated from scans conducted with the Faro Focus^{3D} laser scanner indicating the same reference pin marker as shown in Figures 6 and 7 within the excavation area of the Dinaledi Chamber of the Rising Star Cave.

Figure 8 displays one of six point cloud areas generated from the high-resolution laser scanning within the Dinaledi Chamber. As it shows, each point in this cloud has a coordinate, and the location of 'Pin 2' is indicated as in Figure 7. Multiple shared points in each of the different scanning methods allowed for scans and coordinates to be tied together. If a fixed marker within the cave was not represented in an Artec scan, its coordinates were still available in the Focus^{3D} scans. For example, the marker assigned as 'Pin 1' is not present in Figures 6 and 7, which only covers the 'Pin 2' area. However, through the multi-method registration

process, fossil material found in scans relating to 'Pin 1' can still be measured and placed in context to fossil material found in scans relating to 'Pin 2'.

Figure 9 shows the accurate placement of the Dinaledi Chamber in relation to the ground surface in high resolution. This image combined data from the Focus^{3D} scans and the point cloud data generated by the UAV photogrammetry and illustrates how the Dinaledi Chamber, and the fossil material recovered from it, relates to the rest of the Rising Star Cave system and the ground above.

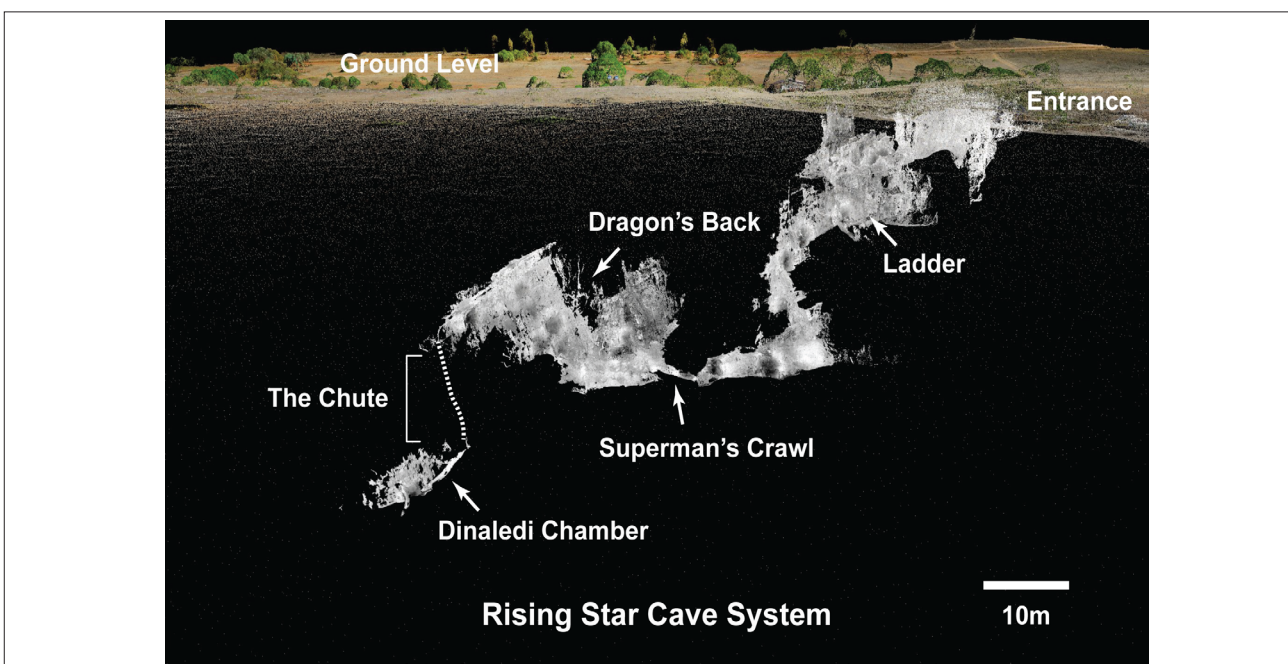


Figure 9: Point cloud data generated from an amalgamation of three-dimensional data collection techniques including unmanned aerial vehicle photogrammetry, high-resolution laser scans and the laser distance meter, showing the accurate position of the Rising Star Cave, including the position of the Dinaledi Chamber, in relation to the above ground level. Scale bar indicates both horizontal and vertical scale.

Discussion

The multimodal approach to the acquisition of three-dimensional data as applied to palaeontology will, we hope, become commonplace, as advancements in technology continue to unfold. As methods for collaborating these data also advance, it would be fortuitous to incorporate these methods into new and existing fieldwork at fossil and archaeological sites. As three-dimensional modelling processes improve, post-processing of extremely large data sets will become much more efficient and less time consuming. At this stage, the requirements for three-dimensional data processing are extremely expensive – in terms of monetary output and processing power and time – and are thus not always attainable. As the advancement of three-dimensional scanners continues, the cost will undoubtedly become more affordable and such equipment will earn its place in archaeological and palaeontological tool kits.

Strengths and limitations of each scanning method

Table 1 highlights the relative format and precision (static accuracy) of each method utilised in the three-dimensional data collection at Rising Star. However, in practice, it was found that each recovery method had a series of inherent strengths and weaknesses in in-field recovery, post-hoc processing, or subsequent data analysis and presentation. The strengths and limitations of the Artec Eva and the FARO Focus^{3D} systems are discussed below.

Artec Eva white-light scanner

Although the small, handheld Artec Eva is a more than adequate scanning device for medium-sized objects (e.g. a human skull), the work resolution and static accuracy is inadequate for rendering smaller objects. For example, isolated human teeth and small fossil fragments were exceptionally hard to visualise in the post-processing stage as they simply did not stand out against the sedimentary ‘background’. In addition, the Eva is challenged when presented with right angles, such as the edges of the excavation pit. This inadequacy led to missing data in these areas. The accompanying laptop computer was both a hindrance and an aid during excavations at Rising Star. Because the laptop required an active power source, the Eva unit was unable to operate independently. In addition, the power cabling had to be run into the excavation chamber from the surface because a generator could not be brought into the cave. However, the live display of the scanning area that the laptop provided, allowed the person scanning to make sure the areas or objects scanned were captured correctly. The minimum working distance for the Eva (approximately 400 mm) meant that extremely tight spaces, such as that of the Chute, could not be scanned with this method. The Eva is relatively expensive and perhaps not financially viable for all researchers; however, it is a useful and powerful scanner ideal for creating three-dimensional models of large surfaces as well as smaller objects, not only in the field but also in the laboratory. Rendering larger models takes considerable time, much of which is determined by the computer and graphical processing power at hand.

FARO Focus^{3D} laser scanner

The FARO Focus^{3D} has its own power source, and a replaceable battery pack should extra power be needed. Independent power made for easier scanning in the cave and Dinaledi Chamber, as no cords or cabling were required and the power pack provided power for a substantial period of time. In addition, all data were recorded onto a secure digital (SD) memory card, further reducing its bulk. The Focus^{3D}, however, relies on the use of multiple spheres for registration in the post-processing stage. These spheres are relatively expensive and fragile, which is not ideal in a cave environment. In addition, the requirement for multiple spheres to be visualised in more than one scan presented significant challenges for placement within the tight confines of the cave. The Focus^{3D} is larger than the Eva and requires a tripod and platform in order to conduct its scans. However, its size did not hinder its transportation through the cave, and the tripod–platform assembly was detachable. The need for a line-of-sight connection between the spheres meant that the Focus^{3D} was still incapable of scanning the Chute and x, y and z data for this section of the cave had to be captured with the DISTO S910. This meant that high-resolution data were acquired for the entire path to the Dinaledi Chamber, with the exception of the Chute. The Focus^{3D} is exceptionally expensive, and is usually rented out for a prescribed number of days. Rendering the resulting point cloud from scans is remarkably quick.

Combining different survey and recording modalities: A way forward

The large amounts of data collected with the methods presented in this paper, will serve to answer a number of key questions around the formation of the site (UW-101) at Rising Star and the deposition of the material found within the Dinaledi Chamber. Laser scanning has been used successfully in many archaeological sites for GIS^{12,13} and heritage preservation^{5,9,10,17}. Work conducted at Wonderwerk Cave in the Northern Cape Province of South Africa by Rüther and colleagues¹⁷ shows the extent to which laser scan data can be useful. The main aims of this project were to collect data for the ‘African Cultural Heritage and Landscape Database’ – a database of information for heritage preservation. Non-contact laser and photogrammetric recovery methods served as an ideal form of data collection as the process is exceptionally rapid, and the data set compiled from it can be used for a variety of other uses, including scientific ones. The data from this project were found to be useful for three-dimensional grid plotting, three-dimensional mapping and the reconstructions of lithic, faunal, botanical and geological associations.¹⁷ As with the work carried out at Rising Star, and the Dinaledi Chamber, the data collected with laser scanning have allowed the creation of a three-dimensional map of the cave system and three-dimensional grid plotting (should it be necessary) and will be used in the mapping of natural and geological features occurring in the Rising Star Cave and their association to features above ground. Accurate placement of the cave system in relation to the ground above it will allow for other technologies to be used on the surface, including ground penetrating radar and geological magnetism studies. We will report on these developments in due course.

Table 1: Comparison of three-dimensional data collection methods used at Rising Star Cave and surrounding landscape

Data collection method	Scanner/ equipment	Applicable area	Data format output (post-processing)	Data format input (point cloud data)	Software for processing	Static accuracy
Laser distance meter	Leica DISTO S910	Chute		x,y,z / .txt		1 mm
White-light source photogrammetry	Artec Eva	Dinaledi Chamber	.ply	.e57	Artec Studio 9 / Artec Studio 10 Professional	0.1–0.5 mm
Laser scanning	Faro Focus ^{3D} X330	Rising Star Cave; Dinaledi Chamber; above ground	.las	.pod	Faro SCENE	~2 mm
Unmanned aerial vehicle photogrammetry	Aerialtrionics ATX8 / Nikon D610	Above ground	.tiff	.txt	Agrisoft	N/A

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Authors' contributions

A.K. conducted the research and wrote the original draft of the manuscript. PR-Q. supervised and developed the original recovery protocols. M.E. supervised the infield recovery of three-dimensional data. All authors contributed equally to manuscript rewrites and editing.

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**CHAPTER FIVE: POST-MORTEM DISARTICULATION PATTERNS IN
HOMO NALEDI: TAPHONOMIC SIGNATURES OF DIFFERENTIAL
DECOMPOSITION IN THE DINALEDI CHAMBER, RISING STAR
CAVE***

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Post-mortem disarticulation patterns in *Homo naledi*: taphonomic signatures of differential decomposition in the Dinaledi Chamber, Rising Star Cave

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ABSTRACT

The Rising Star cave system lies in the Bloubaank River valley, just 2.2 km west of Sterkfontein. Here, within the Dinaledi Chamber, the single largest collection of fossil hominin material on the African continent has been uncovered. The fossil assemblage, almost exclusively comprises material of the newly described hominin *Homo naledi*, preserves a minimal amount of articulated remains. Of these, Dinaledi Hand 1 (H1) is a nearly complete (missing only the pisiform) right hand, found semi-articulated in close spatial association, and Foot 1 (F1) is a semi-articulated adult right foot. The preservation of the articulated or semi-articulated remains of the manual and pedal skeleton of *Homo naledi* is important, both in terms of the rarity of these anatomical units in the fossil record, but also as to what critical information these associations yield with regards embedded taphonomic information and site formation processes of the Dinaledi assemblage.

This paper reports an innovative approach to understanding skeletal articulation and spatial arrangement of fossils from the chamber. *In situ* scanning of the fossil deposit was accomplished with white-light photogrammetry, integrated into a multi-modal, multi-source capture of spatial data. Laser surface scanning of individual bones of H1 and F1 after recovery, allowed for the three-dimensional digital placement of these bones back into spatial position, by combining individual laser scanned bones with the white-light source photogrammetry scans of the excavation area. Effectively this high-resolution method allows for the digital recreation of the excavation space and placement of digital surface models back into the original resting position of actual fossil material, prior to excavations. The spatial position and displacement of individual bones, and the relative location, of both H1 and F1 in the context of the excavation pit is examined. The spatial disposition of H1 and F1 in relation to surrounding commingled elements creates a testable case study with regards to current models of localised decomposition, disarticulation and dispersal within the Dinaledi chamber and does not necessarily imply rapid incorporated into encapsulating

sediments, but may instead be a reflection of the natural decomposition of whole body units in a small enclosing space. Thus, patterns of differential decomposition expressed within the Dinaledi Chamber assemblage do not falsify or invalidate the hypothesis of deliberate body disposal (Dirks et al., 2015) by *Homo naledi*.

INTRODUCTION

Excavations within the Dinaledi Chamber of Rising Star Cave have produced more than 1550 identifiable fossil elements attributed to the extinct hominin taxon *Homo naledi* (Berger et al., 2015). The fossil assemblage comprises 300 numbered bone specimens collected from the surface of the Dinaledi Chamber and roughly 1250 numbered fossil specimens recovered from a small excavation pit in the chamber. This discovery is the largest single fossil hominin assemblage found on the African continent to date (Dirks et al., 2015, Randolph-Quinney, 2015b), with the remains of a minimum number of 15 individuals present, representing all age groups from juveniles to old adults (Berger et al., 2015).

Geologically, the Dinaledi Chamber presents an anomalous depositional environment in comparison to the ‘classic’ sites of the Cradle of Humankind (CoH) in Gauteng Province, South Africa. Sites such as Sterkfontein, Kromdraai, Swartkrans and Malapa are noted for yielding fossil remains contained in lithified breccias, or found in decalcified sedimentary units derived ultimately from clastic breccia (Partridge, 1978, Brain, 1993a, Berger et al., 1994, Clarke, 1994, Kuman et al., 1997, de Ruiter, 2003). In the majority of CoH fossil-bearing caves, skeletal material has been brought into the system through a variety of agents, before it is ultimately lithified. Such agents can be biotic or abiotic, and include processes such as the effects of gravity (such as a fatal fall into a natural death trap, or downslope movement on talus slopes), vertebrate accumulation (predation or scavenging by carnivores, or accumulation by rodents), mass movement of sediments, fluvial transportation, or a combination of such processes. These

processes generally produce taphonomic markers within a fossil assemblage, the role in site formation of which, can be inferred from factors such as body-part representation, bone breakage patterns, or traces of surface modification (Lyman, 1994, Lyman and Fox, 1997, Lyman, 2010, Bristow et al., 2011, Pokines, 2013, Pokines and Baker, 2013).

In the case of the Dinaledi Chamber assemblage, these signatures are distinctly different when compared to other South African early hominin-bearing karstic cave sites for a number of reasons: **(1)** hominin remains are numerous and concentrated in space; **(2)** the assemblage is mono-specific in nature, with the exception of a small number of recent intrusive animal bones; and **(3)** the assemblage presents no evidence of peri-mortem breakage or trauma, carnivore modifications, cut marks, sub-aerial weathering, water or fluvial transportation, and no evidence of burning. Based on taphonomic, sedimentological, and geological constraints, Dirks et al. (2015) interpret that the assemblage was not carried in by carnivores, water or mudflow, was not exposed on the surface before being brought into the cave, and shows no evidence of having fallen into a death trap. Whilst Dirks and colleagues do not reject mass mortality or death trap scenarios as possible explanations, based on currently available evidence they consider deliberate body disposal by conspecifics over an extended timescale to be the most plausible formational process operating on the assemblage (Dirks et al., 2015, Dirks et al., 2016), a ritualised behavioural mortuary process which can perhaps be best classed as funerary caching (Randolph-Quinney, 2015a) *sensu* Pettitt (2011).

In only a limited number of cases have articulated hominin skeletons been recovered from CoH karstic systems, and these have varied in terms of overall completeness, and the degree of specific regional anatomical articulation that the skeletons present. The degree and pattern of anatomical articulation (and its obverse, disarticulation) provides significant information as to the processes of site and assemblage formation, preservation, and peri- and post-mortem processes

affecting fossil assemblages. Somewhat complete, semi-articulated skeletons have been recovered from the sites of Sterkfontein (StW 573 (Clarke, 1998) and StW 431 (Toussaint et al., 2003)) and Malapa (MH1 and MH2 (Berger, 2010, Dirks et al., 2010), and each instance provides some degree of taphonomic information with regards to the biotic or abiotic agents responsible for the ingress of the individuals into their respective cave systems (Brain, 1985, Clarke, 1994, Pickering, 1999, Pickering et al., 2004, L'Abbé et al., 2015, Val et al., 2015). In the case of the Dinaledi Chamber, the presence of anatomically associated or articulated skeletal elements provides significant information as to the process of ingress into the cave, as well as the post-mortem depositional physical processes affecting the assemblage as a whole.

This paper focusses on a detailed spatial analysis of two sets of articulated remains recovered from excavations of *in situ* deposits, and discusses how the process of differential decomposition may account for the spatial patterning and survivability of skeletal material within the Dinaledi Chamber.

Physical, Geological, and Sedimentary Context of the Dinaledi Chamber

The Rising Star cave system lies in the Bloubank River valley (Figure 1), some 2.2 km west of Sterkfontein cave, and comprises an area covering some 37,500 m² of explored passageways. The morphology of the cave system is detailed in Dirks et al. (2015). The hominin-bearing Dinaledi Chamber is located some 38 metres below the current ground surface, and some 80 metres from the nearest extant entrance to the cave. The Dragon's Back Chamber is considered the deepest part of the cave in which sediment from the surface can accumulate by gravitational means through the flow of water. The route from the Dragon's Back Chamber into the Dinaledi Chamber is blocked by a dolomite wall that must be climbed before tapoint, and involves a 15 metre climb from the bottom of the Dragon's Back Chamber, followed by a 12-metre vertical drop (the Chute) in order to reach the floor of the fossil chamber. The main passage forming the Dinaledi Chamber is 10

metres in length (Figure 2), being some 25–50 cm wide at its narrowest, and which expands in width near the intersections with crosscutting passages.

The Dinaledi Chamber is unique in the CoH in that the fossils were recovered from soft unconsolidated sediments within the karstic system, and appear never to have been breccified during their depositional history. The sedimentological makeup and stratigraphy of the chamber is reported by Dirks et al. (2015). The chamber infill comprises two Facies (1 and 2, with 1 being the oldest) subdivided into three stratigraphic Units (1-3, from old to young). Unit 1 comprises laminated mudstones preserved as erosion remnants along the walls of the chamber. Unit 2 is a composite unit that consists of remnant outcrops of variably consolidated sediments which contains several hominin bones. Unit 3 is youngest unit, and is from where the bulk of the hominin bones were recovered; it is composed of largely unconsolidated sediment derived from weathering and erosion of Units 1 and 2.

The walled-off configuration between Dragon's Back and Dinaledi chambers ensures that direct flow of sediments and sediment-laden water from the Dragon's Back Chamber into the Dinaledi Chamber is not physically possible, and the mineralogy and texture of the sediments in the Dinaledi Chamber have been shown to be distinct from the infill of the Dragon's Back Chamber.

Sedimentological analyses have demonstrated that the clay-rich sediments making up the Units were derived from *in situ* weathering, and from exogenous clays and silts, which entered the chamber through fractures that prevented passage of coarser-grained materials; thus the infill of the Dinaledi Chamber is the end product of a series of filters or traps, which winnowed out all large grained sediments or clastic material, en route to final deposition within the chamber. This winnowing process did not include the hominin fossil material, which must therefore have been transported into the chamber by a mechanism other than sedimentary accumulation processes.

The Dinaledi Chamber is unique in that only hominins are represented, and the skeletons show no evidence of transportation into the cave by gravity, other vertebrates or flowing water, and which thus represents a depositional scenario that deviates from all other hominin localities in the region (Brain, 1993b, Watson, 1993, Pickering et al., 2004). Under the body disposal (funerary caching) scenario, the bodies of the individuals found in the cave would either been carried into the chamber, or were dropped through an entrance similar to, if not the same as, the one presently used to enter the Dinaledi Chamber.

MATERIAL AND METHODS

As noted in the introduction, the degree and pattern of anatomical articulation or disarticulation, can provide significant information as to processes of site and assemblage formation. The initial descriptive papers of *Homo naledi* and its depositional context (Berger et al., 2015, Dirks et al., 2015) detailed the presence of four groups of anatomical associations within the chamber sediments. Subsequent commentaries (Dirks et al., 2016) or regional analyses (Harcourt-Smith et al., 2015, Kivell et al., 2015), have gone on to identify three additional partial foot associations and two partial hand associations (Table 1). The articulated manual and pedal remains suggests that at least some of the fossil material in Unit 3 was not significantly reworked after deposition, and a spatial analysis of these associations forms the basis of this paper.

To this end, a unique set of methodologies were employed for high-resolution spatial recording, in order to document excavations and provide a link for the material recovered to its context of deposition. It is imperative to collect such high-resolution data at large assemblages such as that at Rising Star, in order to provide contextualisation within deposits, and to assist in preservation by archive following archaeological recovery. Anatomical positions of skeletal material, once

recorded and analysed, also provide much needed information on the context and micro-stratigraphy of the site, and site formation processes, as well as enabling future excavations to be built on an objective spatial framework. This allows, with the aid of three-dimensional data recovery, the relationships within a particular site or assemblage to be analysed in developmental perspective, and to be viewed holistically. Much like forensic investigations, the events leading up to the formation of a particular site can then possibly be recreated and reconstructed with the aid of this technology and visualised as an aid to site interpretation; the use of such recording and visualisation techniques has become more important in palaeoanthropology and palaeontology, and the reader is directed to Cunningham et al. (2014) for a comprehensive review of 3D data use in such contexts.

In situ scanning of the fossil deposits in the Dinaledi Chamber was accomplished primarily with white-light photogrammetry, integrated into a multi-modal, multi-source capture of spatial data to assist in both spatial recording (preservation by archive) as well as visualisation as an aid to stratigraphical and taphonomic analyses. The technical methods behind the multimodal high-resolution data collection techniques employed at Rising Star can be found in Kruger et al. (2016). These scanning methodologies were applied to record the absolute and relative positions of fossils within the sedimentary profile of the chamber.

Dinaledi Hand 1 (H1) is a nearly complete (missing only the pisiform) right hand, found semi-articulated in close spatial association (specimens comprise U.W. 101-1308 to -1311, -1318 to -1321, -1325 to -1329, -1351, -1464, and -1721 to -1732) (Berger et al., 2015, Kivell et al., 2015). H1 was found at c.130 mm below the surface of the main excavation pit, with the palmar surface facing upwards (Figure 3).

Dinaledi Foot 1 (F1) is a semi-articulated adult right foot. F1 is represented by a calcaneus (U.W. 101-1322); talus (-1418); cuboid (-1418); proximal hallucial

phalanx (-1419); 5th metatarsal (-1439); 1st metatarsal (-1443); 4th metatarsal (-1456); 3rd metatarsal (-1457); 2nd metatarsal (-1458); Distal hallucial phalanx (-1551); flexor hallucis brevis (FHB) sesamoid (-1553); navicular (-1562) and lateral cuneiform (-1698). The fossil was found at an excavation depth of 160 mm, in a somewhat more disarticulated state than H1 (Figure 4).

Scanning of the fossils within their soil matrix was enacted with a handheld Artec Eva 3D surface scanner. A series of separate *in situ* white light source photogrammetric scans were taken of H1 and F1 prior to excavation, and then at different stages during the excavation process as sediment was removed, prior to recovery of the fossils. Following excavation, lifting, cleaning and conservation, each bone was surface scanned using the NextEngine 3D Laser Scanner in axial and transverse major axes using the macro focus function, with 14 incremental divisions. This captured high-definition surfaces and texture at 40k ppi. Using the accompanying ScanStudio HD Pro software, each individual scan was trimmed of unwanted data and aligned to its corresponding scan to create a 360-degree model. The aligned models were volume merged (fused) and exported as Polygon File Format (ply - also known as the Stanford Triangle Format). Ply files were imported into Artec Studio 10 Professional for translation and global alignment.

The excavation (*in situ*) scans were subsequently registered, aligned and volume merged with Artec Studio 10 Professional, before being exported as .ply format files. Once exported, these scans were then re-imported into Artec Studio 10 Professional along with the 3D models of each individual hand and foot bone as noted above. Translation and rotation of each 3D model of the individual hand bones was guided and aligned by surface models of the excavation. By layering each white-light source photogrammetry scan of the *in situ* hand and foot, a virtual three-dimensional representation of the excavation area surrounding H1 and F1 was produced, representing a cube of sediment within which the precise anatomical resting and relative position of each bone element can be seen (Figs. 5 and 6). Rotation, translation and alignment of individual hand bones could thus be

accomplished over multiple depths within the virtual excavation area. This produced an accurate 3D reconstruction of the placement of H1 and F1 as they lay *in situ*, by virtually placing the bones of H1 and F1 back into the underground excavation pit. This allows for a precise and accurate visualisation of the relative position of each elemental part, which imparts significant spatial information which can assist in taphonomic analyses and interpretation.

The encapsulating sediment was then extracted from the scan volume, leaving the precise spatial arrangement of each element as they would have been in the ground, prior to excavation and recovery. This ‘reverse engineering’ of the fossil deposits allows for the investigation of spatial taphonomic patterns within the surviving assemblage, as well as clear visualisation of small-scale anatomical articulations and disjunctions between bones.

RESULTS

The extracted H1 and F1 spatial volumes demonstrate the resting (post-mortem) position of each anatomical group within their supporting Unit 3 matrix (Figs. 7A and 7B).

Hand 1

As noted above, Dinaledi Hand 1 (H1) is a nearly complete right hand, found at a depth of 130mm below the cave floor surface, with the palmar surface facing upwards. Figure 5 demonstrates the relative anatomical position of each element (excluding the missing pisiform) preserved prior to recovery, with Figure 7A the arrangement of elements with sedimentary matrix digitally removed.

Structurally the hand can be broken down into three anatomical zones – carpals, metacarpal rays, and phalangeal rays. The first of these comprises the surviving scaphoid, lunate, triquetral, trapezium, trapezoid, capitate and hamate bones. All of these elements are in near anatomical position, with clear articulation between the majority of joint facets, with only marginal displacement and slight lateral rotation of the trapezoid and trapezium out of normal anatomical alignment. A narrow gap has opened up post-mortem between the four distal carpals (hamate, capitate, trapezoid and trapezium) and the proximal articular facets of the metacarpal array. The metacarpals (MC2 to MC5) are in close to normal anatomical position, with only MC1 having moved both further laterally and distally from the rest of the hand, with concomitant slight ventral rotation (Figure 8).

With regards to the phalangeal array. The proximal phalanges (PP) of rays 1 to 4 have retained close anatomical articulation in their recovery position, with either direct articulation with their corresponding metacarpal distal head, or near articulation. The intermediate and distal phalanges are out of strict anatomical articulation, attest to the position of flexure, with a closed, or semi-closed hand at time of skeletisation. These elements were located above the level of PP 1–4, with their proximal ends displaced slightly to the palmer side. The distal phalanges (DP) exhibit more post-mortem movement, as only DP2 resembles the closed hand scenario. DP3 was found displaced with the proximal portion being found below PP3 in the sediment, and the distal end of DP2 pointing down within the excavation area. IP4 has been somewhat displaced from PP3, having being found slightly laterally from the rest of H1. The pollical bones of H1 suggests that the thumb was not flexed during skeletisation, and was open as the hand rested. PP, IP and DP5, as well as DP4 were all found lower within the excavation area, and not articulated with the rest of H1.

Foot 1

Dinaledi Foot 1 (F1) is a semi-articulated adult right foot, reconstructed by Harcourt-Smith et al. (2015) as the calcaneus, talus, cuboid, navicular, intermediate and lateral cuneiform, all five metatarsals, the proximal hallucial phalanx, the distal hallucial phalanx, and a sesamoid (likely to be associated with flexor hallucis brevis). The fossil was found in a somewhat more disarticulated state than the H1 fossil hand, with much of the pedal unit found within a relatively small area, but with differing degrees of displacement. Only the talus, cuboid, metatarsals and hallucial phalanges were found in association with the remaining pedal elements (calcaneus, navicular, cuneiforms and sesamoid) recovered from elsewhere in the excavation pit, and subsequently introduced into the reconstruction by Harcourt-Smith and colleagues. The preserved spatial arrangement of semi-articulated elements in the ground can be seen as following a general anatomical alignment (Figure 6) with displacement and rotation of individual elements apparent.

Figure 7B demonstrates the broad structural arrangement of the three pedal anatomical zones – tarsals, metatarsals, and phalanges – reflecting the hindfoot, midfoot and forefoot respectively. In general, the foot was found in an inverted position (i.e. resting upon the dorsum) with anatomical disassociation having taken place within the broad pedal structure. The associated hindfoot is present as the only the talus and cuboid. These elements are displaced from normal anatomical position, with the talus laterally rotated and inverted from normal position; it was recovered resting on the trochlear surface, with the distal hallucial phalanx in close association (Figure 7B). The cuboid was found close to the head of the talus, and was also inverted compared to normal anatomical position. The metatarsals (MT1 to MT5) are in close to normal anatomical position, with slight medial displacement of MT1. In keeping with the hindfoot, the metatarsals were all found with the dorsal surface downwards. With regards to the phalangeal array. Only the phalanges of rays 1 were recovered, and these were somewhat displaced regarding the hallux. The overall configuration of the foot suggests that it came to rest post-mortem on the dorsal surface, with subsequent disassociation of individual elements (Figure 9).

DISCUSSION

The preservation of the articulated or semi-articulated remains of the manual and pedal skeleton of *Homo naledi* is important, both in terms of the rarity of these anatomical units in the fossil record, but also as to what critical information these associations yield with regards embedded taphonomic information. Critically, there are only a few relatively complete or complete hominin hands in the South African fossil record available to us. These comprise the left hand of *Australopithecus prometheus* (Clarke, 2013) StW 573 from the Silberberg Grotto of Sterkfontein Caves, the right hand of *Australopithecus sediba* MH2 (Churchill et al., 2013) from Malapa, and the complete right hand (barring only the pisiform) of *Homo naledi* (Kivell et al., 2015) as discussed here. Complete or partial feet are equally scarce, and largely confined to specimens recovered from Sterkfontein and Malapa (Clarke, 1998, Berger et al., 2010). Perhaps, and more importantly, the preservation of these complex anatomical regions provides significant information with regards to the numerous post-mortem processes acting on cadaveric remains deposited in the Dinaledi Chamber.

Historically, disarticulation is characterised as one of the four primary categories of taphonomic concern (the other being dispersal, fossilisation and mechanical modification (Lyman, 1994)). These categories are understood from the starting point of a complete unmodified skeleton, on which subsequent taphonomic processes operate. Disarticulation refers to the anatomical disassociation of skeletal elements from each other, and is often seen as the first step in the loss of anatomical integrity of a body or skeleton. The process of disarticulation specifically relates to the destruction, decomposition, or removal of (primarily) soft tissues which hold bony elements or joint surfaces of a skeleton together. Depending on the organism under consideration and anatomical region, these soft tissues may comprise tendons, ligaments, muscles or skin, or components of joint

capsules such as synovial membrane; the breakdown of these anatomical components allows individual bones, or complete elements and limbs, to disarticulate from the body. Because soft tissue anatomy varies from joint to joint, the process of disarticulation is highly complex. Subsequent dispersal is the increase or the decrease of the distance between bones. Dispersal of skeletal elements may precede, be simultaneous with, or subsequent to disarticulation (Lyman, 1994); models of dispersal have been constructed for fluvial transport, carnivore transport, raptor transport, human transport and natural abiotic processes (Coard and Dennell, 1995, Mondini, 1995, Nawrocki et al., 1997, Bassett and Manhein, 2002, Marean and Cleghorn, 2003, Cleghorn and Marean, 2004, Faith et al., 2009, Pante and Blumenschine, 2009).

The extent of preservation of articulated elements – the degree of articulation as opposed to disarticulation – is directly influenced by the decomposition process that a cadaver or carcass undergoes, and this in turn is influenced by a host of covarying abiotic and biotic processes which either retard or accelerate the pattern, mode and tempo of decomposition. Decomposition can be described as the process by which the body breaks down and decays, finally resulting in skeletonisation. It is a continuous process that is often difficult to divide into discrete defining categories, though an adequate understanding of the processes that influence decomposition and the stages through which a body passes as it decomposes can be used to estimate time since death (PMI or post-mortem interval). Decompositional changes to a body that occur immediately after death are often much more rapid than those occurring later in the process. Furthermore, decomposition can be retarded by several processes, including physical and chemical barriers and climatic factors. The factors that affect the rate at which post-mortem changes occur were suggested by Prieto et al. (2004) as falling into two groups: those dependent on the cadaver (intrinsic factors), or extrinsic factors such as temperature, humidity, insect activity, and scavenging – it is the interplay between these factors which influences the pattern and rate of decay and skeletonisation (Bristow et al., 2011).

In the early post-mortem period, enzymatic digestion (autolysis) is the primary driving factor (Table 2). This initiates widespread cell degradation via anaerobic microorganisms such as bacteria, fungi, and protozoa (Vass, 2001, Vass et al., 2002, Vass, 2010) within the gastrointestinal tract and the respiratory system (Carter et al., 2007, Carter et al., 2008, Carter et al., 2010), leading to saturation of body tissues (haemolysis) (Fielder and Graw, 2003) with decomposition products. These products result in colour changes seen on the dermis with concomitant bloating of the body, signalling the onset of the putrefactive stage of decomposition (Bristow et al., 2011). A continued internal build-up of decomposition gases eventually leads a build-up of internal pressure, leading to purging through body orifices, such as the mouth, nose, and anus, and possible tissue rupturing (Carter et al., 2007). The active decay process is most often associated with a decrease in body mass (Adlam and Simmons, 2007).

Putrefaction processes function under anaerobic conditions (Adlam and Simmons, 2007, Cross and Simmons, 2010, Simmons et al., 2010a, Simmons et al., 2010b). Further decay by bacteria and fungi is purely anaerobic and it is this which leads to full skeletonization of the cadaver (Fielder and Graw, 2003). The decay process will generally be accelerated in bodies in sub-aerial contexts, particularly with open access to insect faunas. Different depositional and burial environments will lead to a difference in observed or expected results since neither environment is static (Wilson et al., 2007). In burial environments, there is a restriction of access to the remains from scavengers and insects who pose a major role in decomposition (Adlam and Simmons, 2007, Cross and Simmons, 2010, Simmons et al., 2010a, Simmons et al., 2010b), as well as restricting the effects of sub-aerial processes such as weathering, which can accelerate the decomposition and degradation of skeletal tissue itself (Tappen, 1969, Hill, 1976, Beherensmeyer, 1978, Tappen, 1994).

In the case of skeletal remains from the Dinaledi Chamber, analyses of surface condition, overall preservation, and trace actions by biotic modification agents has

suggested that the remains were introduced into the chamber as complete or largely complete bodies, which subsequently underwent *in situ* decomposition and skeletonisation, before being incorporated into the cave sediments (Dirks et al., 2015, Dirks et al., 2016). Much of the assemblage shows extensive modification of the surfaces of the bones by invertebrates (Dirks et al., 2015, Dirks et al., 2016), and mineral staining and patterns of fracturing and cracking arising as a result of fluctuations in soil moisture content and changing water levels in the Dinaledi Chamber over time (Dirks et al., 2015, Dirks et al., 2016, Randolph-Quinney et al., 2016).

This taphonomic scenario is reflected in the presence of bone elements usually and easily lost to winnowing, and partial or near-complete articulation of anatomical elements; the presence of these features lends strong credibility to the hypothesis that the remains were introduced into the chamber as complete or largely complete bodies. In general, there are three ways by which complete (or largely complete) skeletons can be preserved – quick burial in areas of rapid sedimentation, burial in places sheltered from transportation agents and forces, and processes leading to mummification (Lyman, 1994, Bristow et al., 2011). However, the remains contained within the sediments of the Dinaledi Chamber, whilst showing anatomical articulation in regional groups, do not appear as whole or complete bodies. As Figure 10 demonstrates, the extent of direct anatomical articulation is significant in pattern with regards to hands and feet, but limited in terms of overall completeness of whole skeletons. As Figure 10 demonstrates, whilst there is a broad dispersal of upper and lower limb elements within the limits of excavation, there is no direct anatomical association between the carpal bones of H1 and any preserved part of a radio-ulnar joint, or between F1 and the preserved parts of any tibio-talar joint. If hands and feet are internally articulated as units, why are they not articulated with their associated limbs? Why did the hand and foot preserve their anatomical association when the remainder of the limb is dispersed or perhaps not present?

To address such questions, we need to focus on human-specific patterns of manual and pedal element decomposition, rather than the use of non-human analogues. Much research has been conducted into the pattern and timing of disarticulation of different body parts during the skeletonisation processes, a sequence known as rank disarticulation (Lyman, 1994). However, many of these studies deal with rank disarticulation in artiodactyls with very different appendicular and locomotor morphology to hominins, such as okapi or domestic cow. In the artiodactyl skeleton the radio-carpal and tibio-tarsal joints tend to disassociate midway through the disarticulation sequence (reportedly covering stages 12 to 14 in a 30-stage decomposition sequence, with 1 being the first to anatomical region to disarticulate and 30 the last), with the carpal-metacarpal and tarsal-metatarsal joints disarticulating slightly later in the sequence (Lyman, 1994).

In contrast, cases of human decomposition and disarticulation have shown that the unprotected hands and feet often disarticulate early in the decomposition sequence, sometimes before the disarticulation of head from the neck (Roksandic, 2002). In cases of fluvial transport the order of disarticulation is the bones of the hands and wrists, bones of the feet and ankles, and mandible and cranium. In archaeological contexts the hip and the knee joint can become dislocated and disassociated, whereas the foot retains perfect anatomical articulation (Adlam and Simmons, 2007). In a summary of 20 forensic cases reported by Komar (2000) where whole or largely complete bodies (the majority skeletonised) were recovered from death scenes in Alberta, 75% of cases (*n* 15) presented with missing hands, although in two cases the hands were later recovered after being found separated from the body; in one of these cases the hand was still partially fleshed even though the rest of the individual was largely skeletonised. In only 25% of these cases (*n* 5) were the feet missing.

This pattern of disassociation of manual and pedal elements is most parsimoniously explained by intrinsic factors of the soft tissue anatomy of these

regions. For instance, in modern humans, the manual skeleton is highly flexible, with flexion, extension, abduction and adduction capable at the wrist (radio-carpal) joint being possible. The radio-carpal joint is a synovial ellipsoid joint, which articulates the distal end of the radius and its articular disc, with the scaphoid, lunate and triquetral bones. The joint capsule is fibrous, and reinforced by the dorsal and palmar radiocarpal, palmar ulnocarpal, and radial and ulnar collateral carpal ligaments, and extensor and flexor muscles the hand (Palastranga et al., 2006). Whilst this is a relatively stable configuration, the midcarpal joint which binds together the seven carpal bones, is much more strongly bound as a unit. This is a complex synovial joint system, reinforced by a series of short ligaments (the palmar and dorsal intercarpals, and the radial and ulnar collateral ligaments) assisted by the carpometacarpal and other ligaments which stabilise the metacarpal rays; the whole unit is bound transversely by the flexor retinaculum (transverse carpal ligament) which binds the region tightly from the hook of the hamate and the palmar surface of the pisiform, to the tubercle of the trapezium (Palastranga et al., 2006). As such, the hand as an anatomical unit is intrinsically less stable at the radio-carpal joint than in the midcarpal or carpometacarpal regions. A similar, though not entirely homologous pattern expresses in the ankle joint and foot. It is important to note that much of the 1550 elements making up the *H. naledi* assemblage were found disarticulated and highly fragmented, with H1 and F1 presenting some of the few semi-articulated anomalies within the chamber, and we suggest there are sound functional and taphonomic reasons why this is the case.

H1 was found semi-articulated, and the position of the reconstructed hand suggests that it was flexed (closed) or semi-closed during the process of skeletisation. The reconstruction of H1 as it lay *in situ* may suggest that the hand was positioned away from the rest of the body of this individual, potentially flat on the floor substrate, which would imply a supine position overall. This would ensure little or no movement of the hand during decomposition. This contrasts with bones of hands positioned in other than anterior palmar presentation which are generally subject to relatively more displacement as decomposition proceeds.

Alternatively, if H1 were positioned on or over the abdomen, as soft tissue of thorax decomposed, the disarticulated bones of the hand would have been subject to collapse into other areas of the body, most specifically the abdomen and pelvis (Roksandic, 2002). Spraying or spreading of the fingers, when observed from a forensic perspective, may be the result of the build-up of gases during the decomposition processes. This leaves empty spaces around a body, and thus the potential of movement of certain bones (Roksandic, 2002). This may serve as an indication for the movement of DP4 of H1, and the reason why the fifth digit was not found in semi-articulation with the rest of H1. It is important to note, however, that with the decomposition rate, disarticulation sequences of the body are highly dependent on the environment and micro environment (Roksandic, 2002).

Furthermore, the amplitude of movement away from original anatomical position will depend upon the position of the remains, as deposited, and the available space in which any movement can take place; such spaces can be created by the decomposition of surround soft tissues in cases of interment in sediment, and the amplitude of movement represents the extent to which a bone can move in any of the possible directions. Primary dispositions (especially burials) tend to place bones in a relatively stable position, and thus there will be little if any movement of individual bones or elements following the loss of soft tissue. As Roksandic (2002) has noted, if disposition occurs where bones are placed in an unstable position they will move in accordance with gravity and the shape of the surrounding space once soft tissue is lost.

Thus, the spatial disposition of H1 and F1 in relation to surrounding commingled elements creates an interesting and testable case study with regards to current models of localised decomposition, disarticulation and dispersal within the chamber. With reference to forensic case examples, the presence of anatomical association in H1 and F1 (and of the manual skeleton in particular) does not necessarily imply rapid incorporation into encapsulating sediments, but may instead be a reflection of the natural decomposition of whole body units in a small

enclosing space, whereby components more tightly bound by supporting muscles and ligaments may disarticulate as whole hands and feet from the wrist and ankle joints, but still maintain internal integrity as they are incorporated into sediments within the chamber. Such hypothetical patterns can be tested in future excavation efforts within the chamber, it is clear that patterns of differential decomposition expressed within the Dinaledi Chamber assemblage do not falsify or invalidate the hypothesis of deliberate body disposal by *Homo naledi*.

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FIGURES

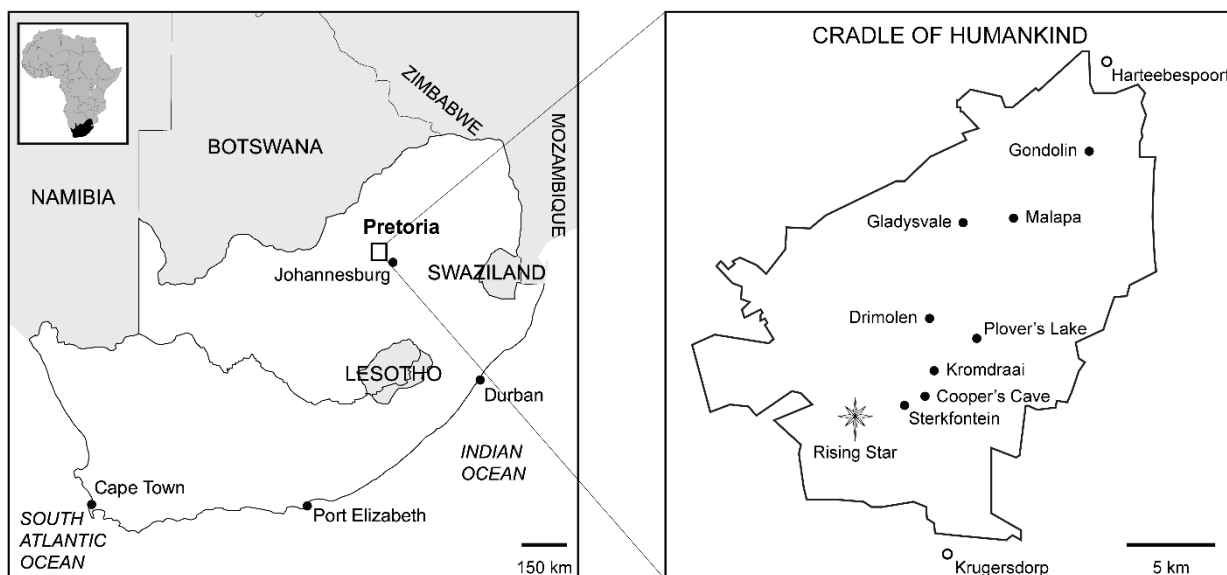


Figure 1. Location of the Rising Star Cave within the Cradle of Humankind, UNESCO World Heritage Site. Other major palaeontological sites are indicated.

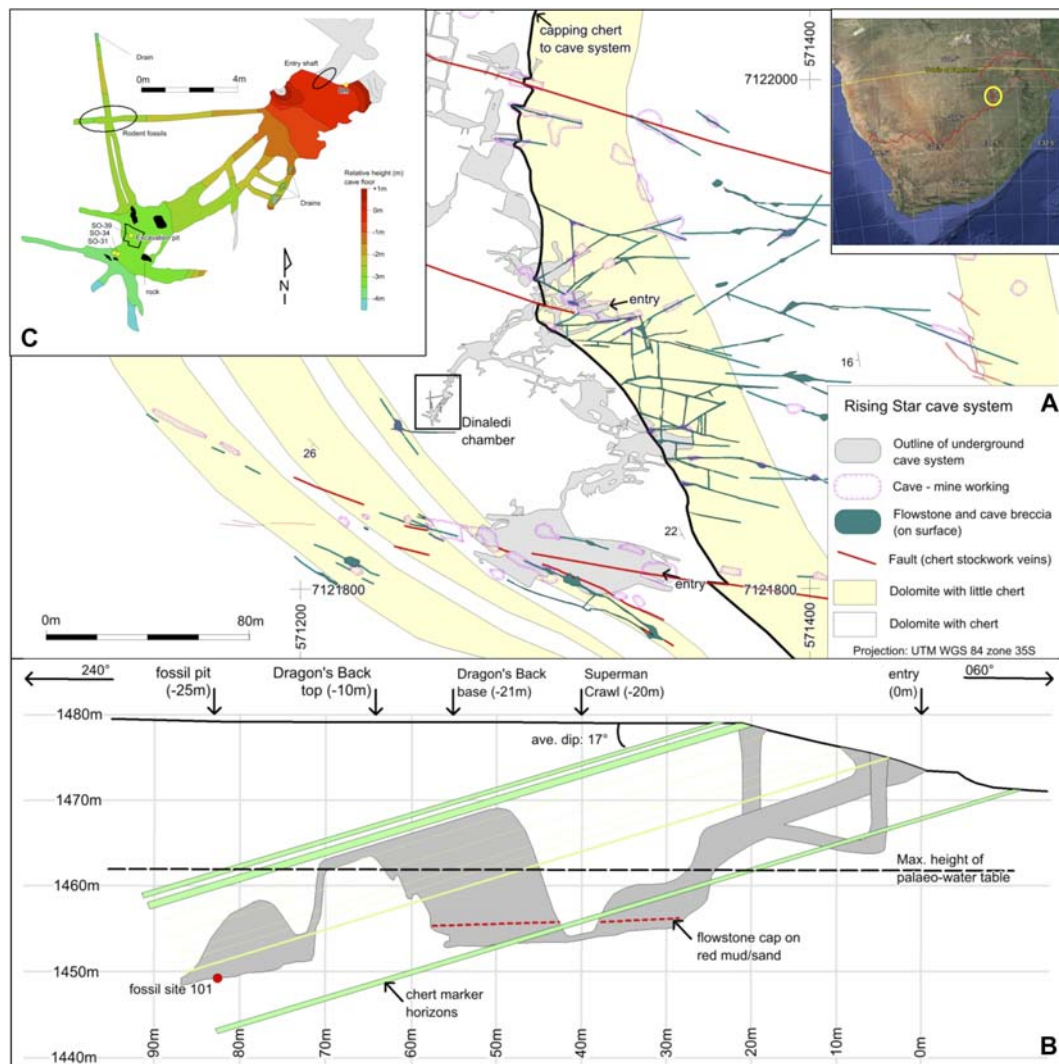


Figure 2. Geological map and cross-section of the Rising Star cave system. (A) Geological Map showing the distribution of chert-free dolomite and fracture systems controlling the cave. Inset shows the location of the Cradle of Humankind in southern Africa; (B) Northeast-Southwest, schematic cross section through the cave system, relative to several chert marker horizons; (C) Detailed map of the Dinaledi Chamber showing the orientation of the floor and the position of the excavation and sampling sites. Reused with permission of Dirks et al., (2015).

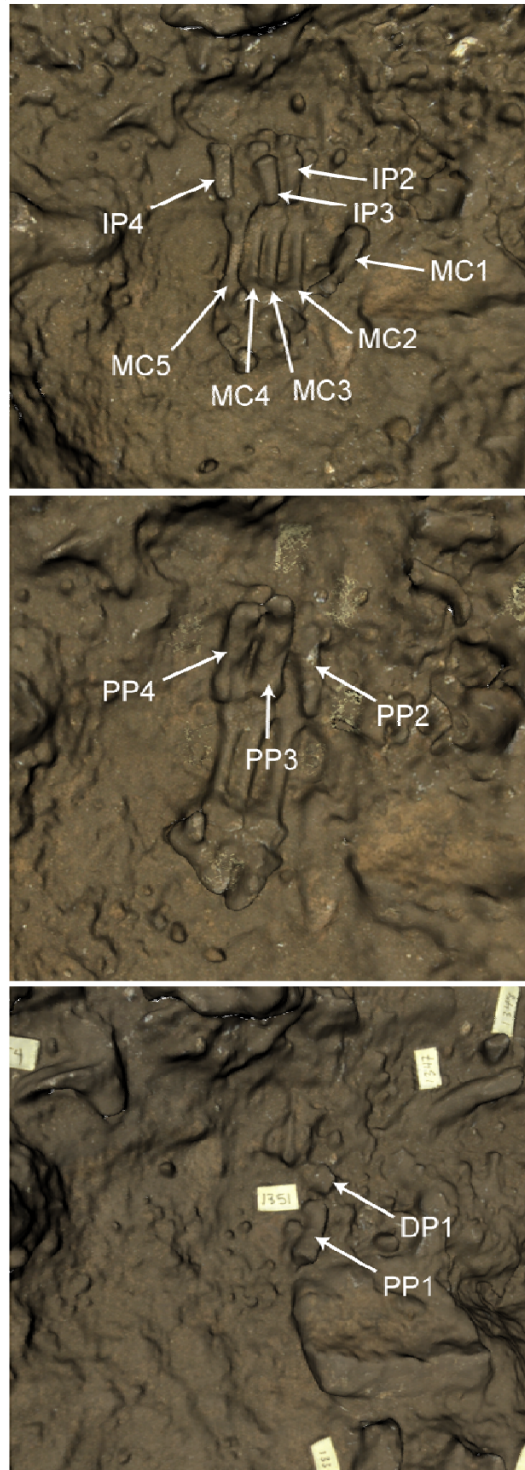


Figure 3. Consecutive *in situ* white light-source photogrammetry scans of Hand 1 (H1) from the Dinaledi Assemblage. Abbreviations: DP, distal phalanx; IP, intermediate phalanx; MC, metacarpal; PP, proximal phalanx.

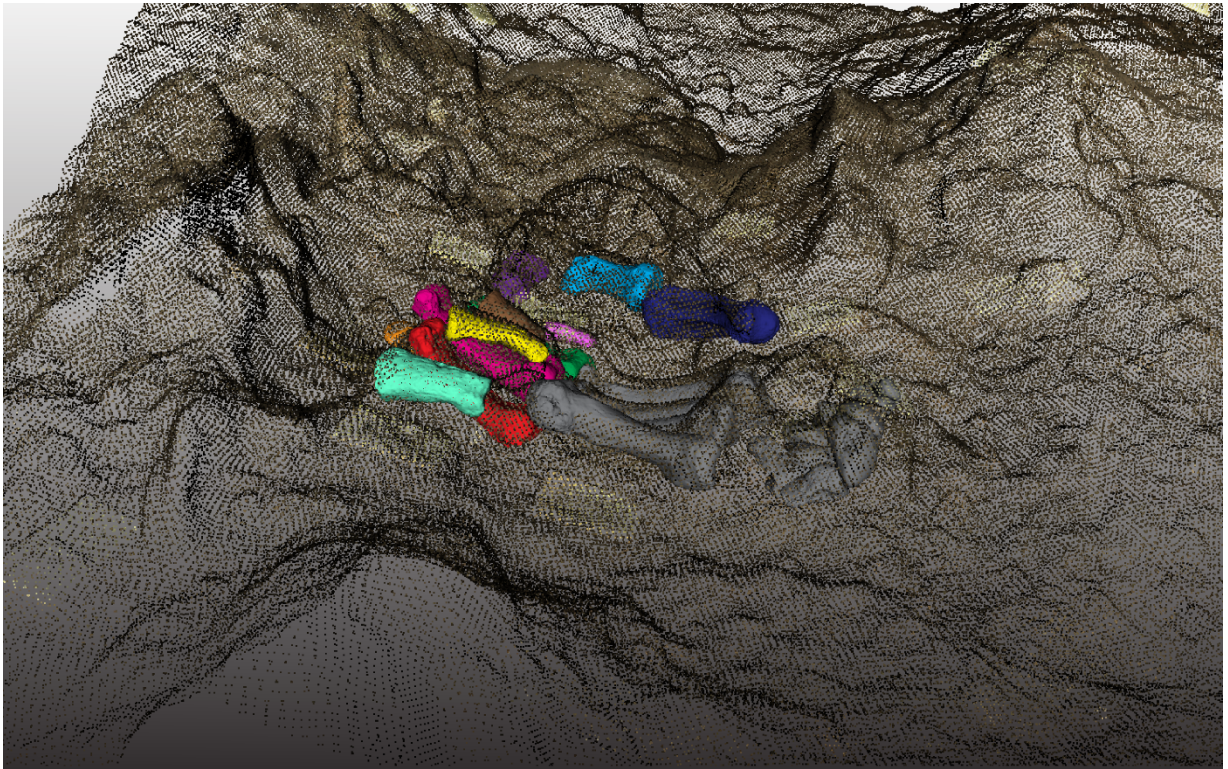


Figure 5. Three-dimensional recreation of the *in situ* position of the semi-articulated Hand 1 (H1) from the Dinaledi Assemblage. This figure is the combination of three white light-source photogrammetry scans (sediment) and accurately digitally positioned three-dimensional laser surface scans of H1.

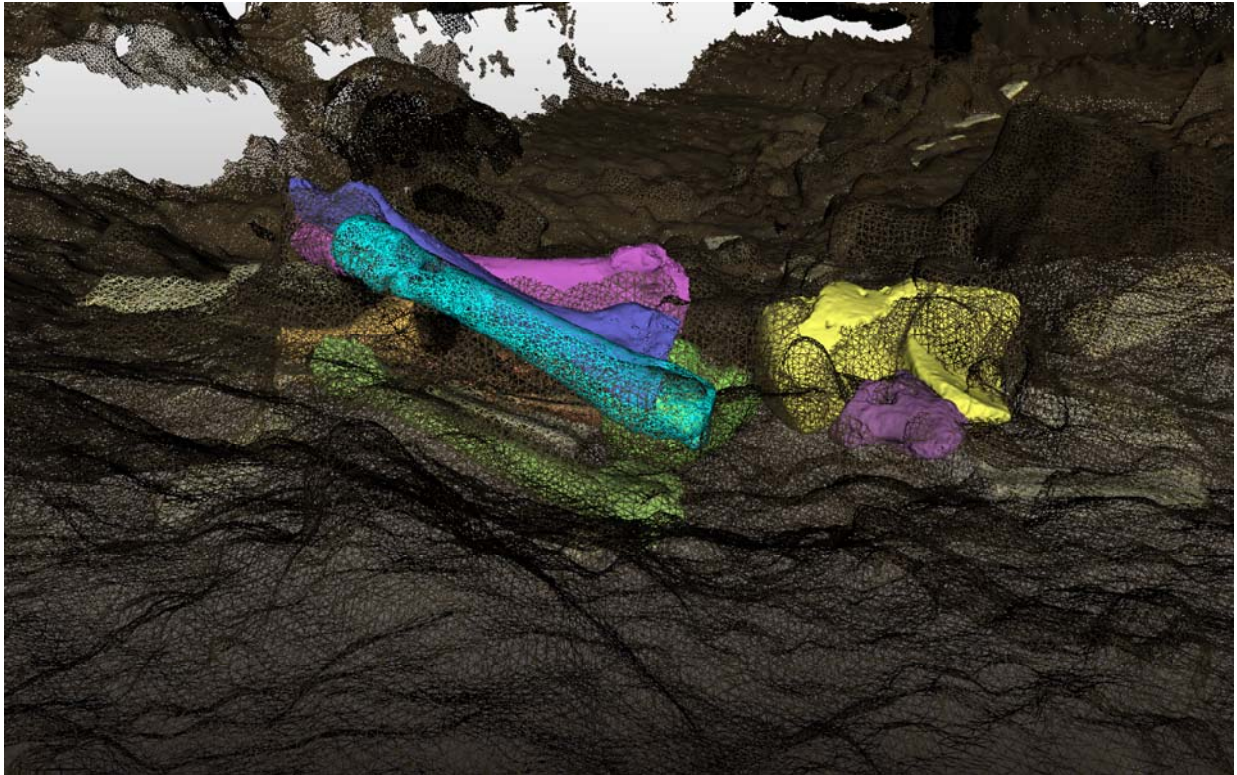


Figure 6. Three-dimensional recreation of the *in situ* position of the semi-articulated Foot 1 (F1) from the Dinaledi Assemblage. This figure is the combination of three white light-source photogrammetry scans (sediment) and accurately digitally positioned three-dimensional laser surface scans of F1.

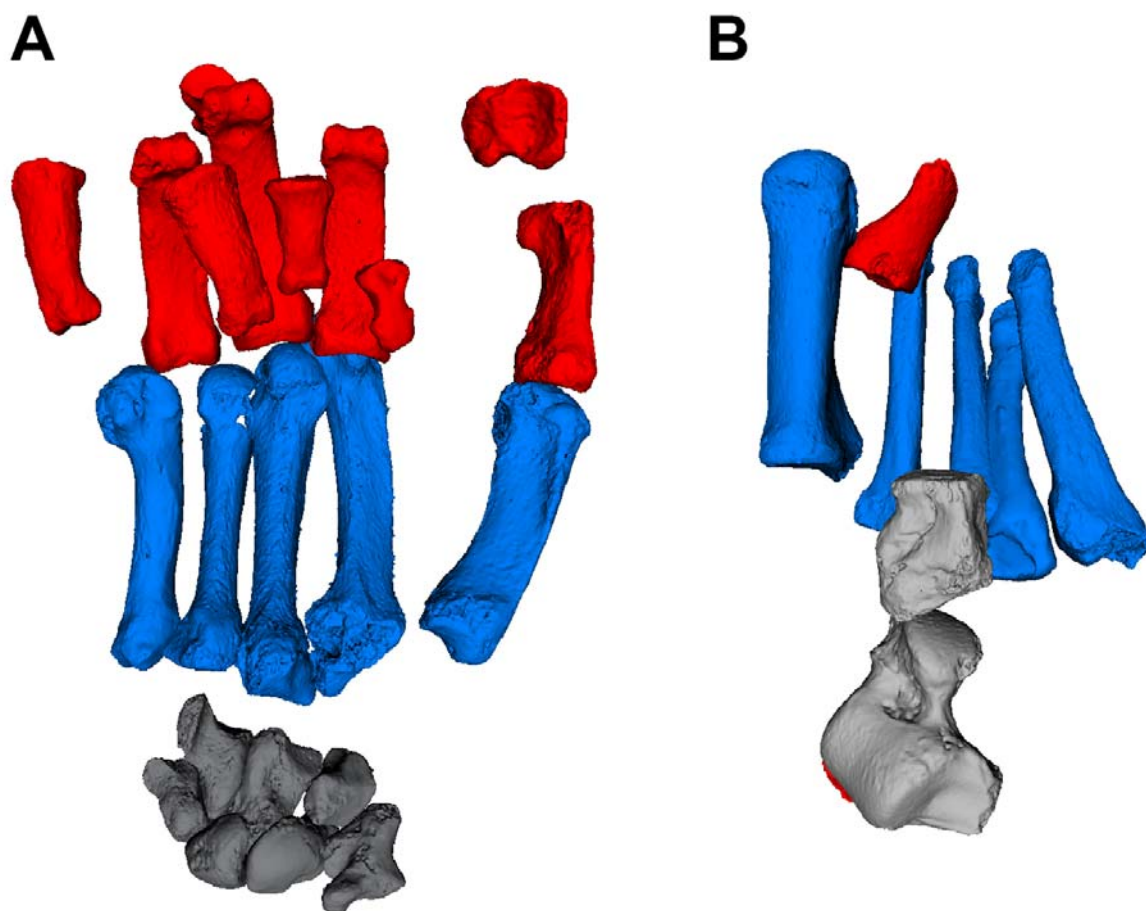


Figure 7. A) Digital reconstruction of the *in situ* position of the semi-articulated Hand 1 (H1), and B) Foot 1 (F1), from the Dinaledi Assemblage. Grey indicates carpals, blue - metacarpal rays, and red - phalangeal rays.

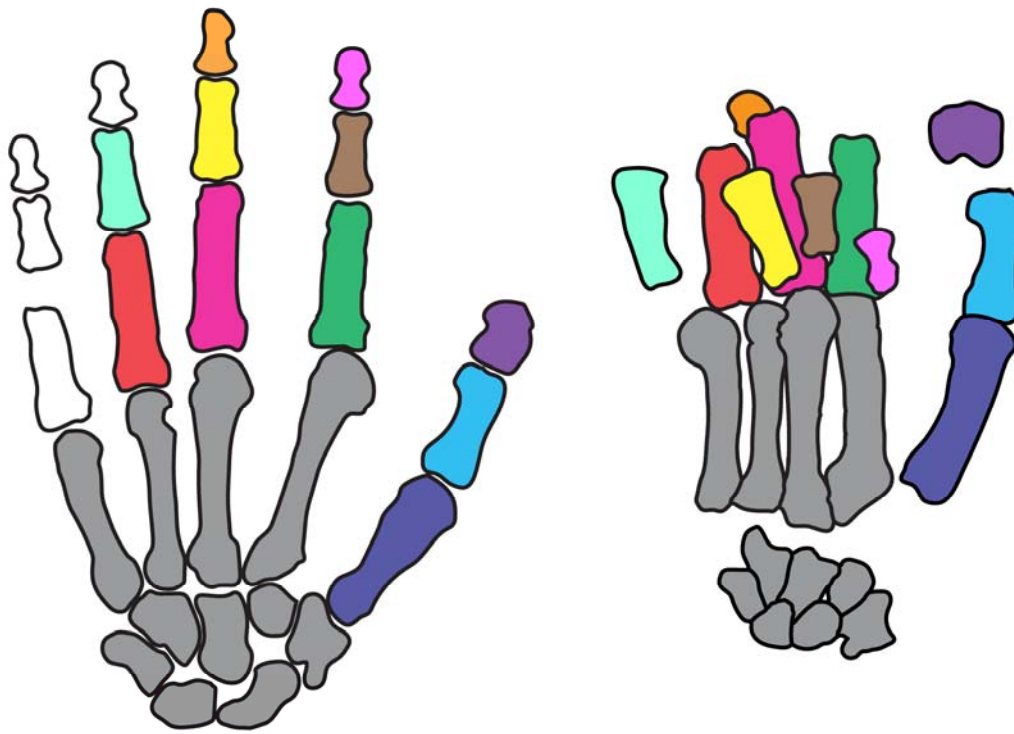


Figure 8. Displacement of the bones of the semi-articulated Hand 1 (H1) from the Dinaledi Assemblage. Left, normal palmer position of bones, and right, the *in situ* displacement of hand bones prior to excavation.

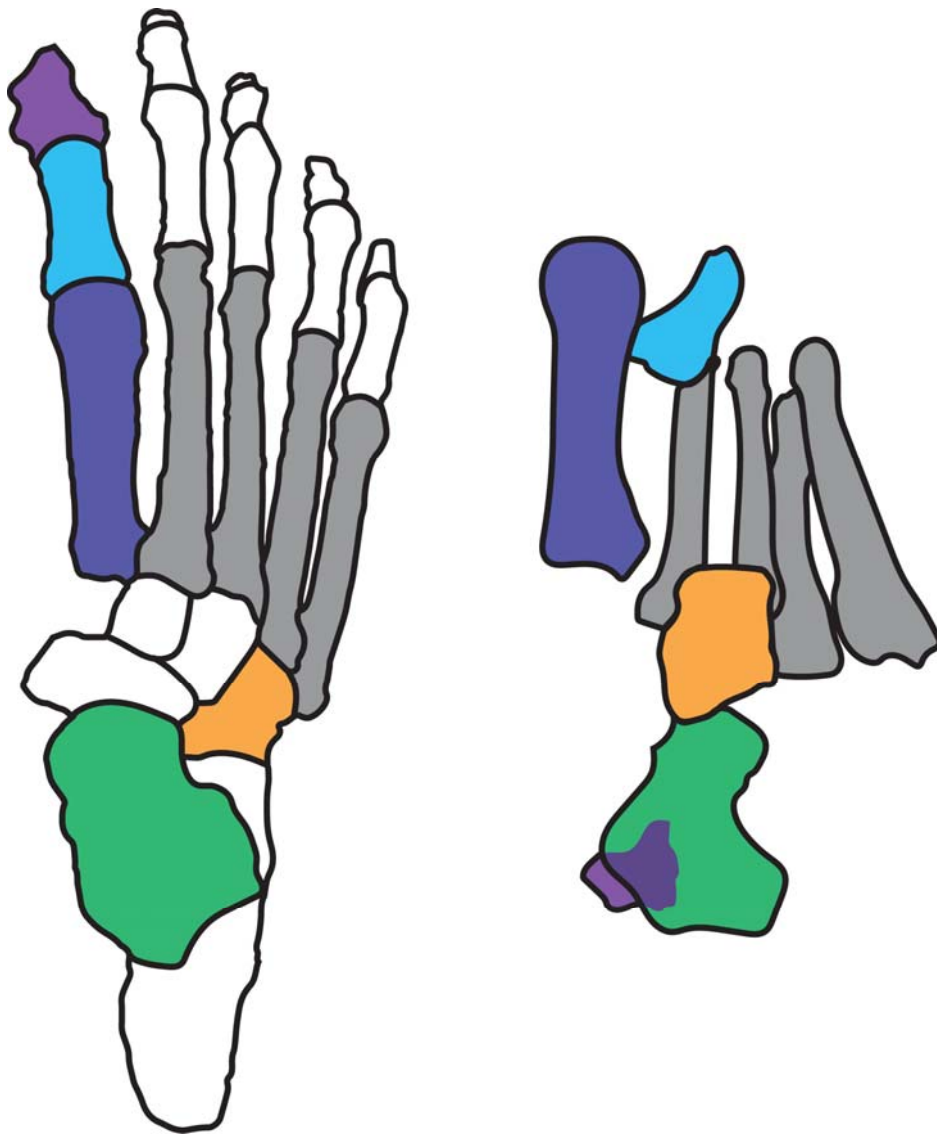


Figure 9. Displacement of the bones of the semi-articulated Foot 1 (F1) from the Dinaledi Assemblage. Left, normal anatomical position of bones, and right, the *in situ* displacement of foot bones prior to excavation.

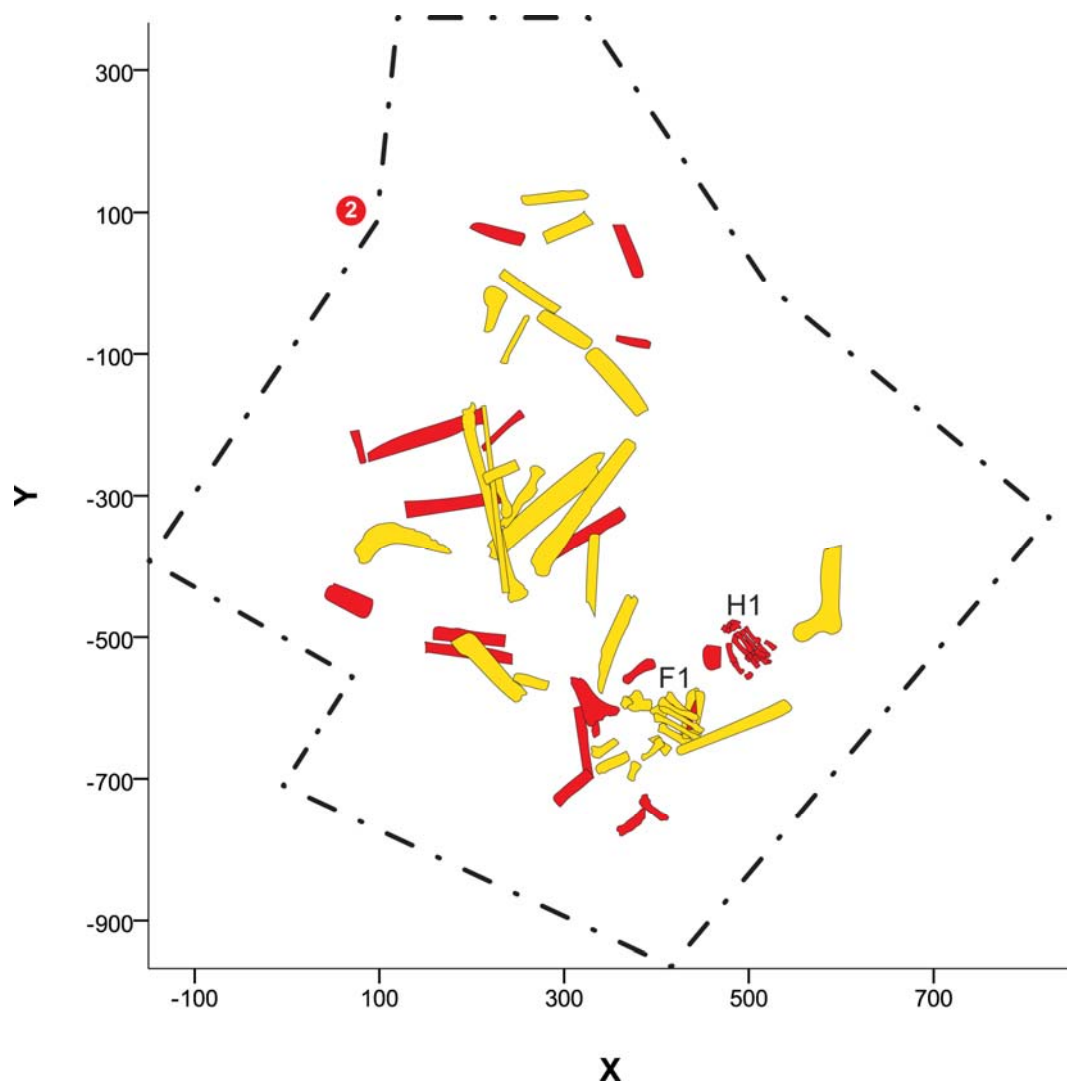


Figure 10. Two-dimensional distribution plot of lower limb (yellow) and upper limb (red) elements within the main excavation pit of the Dinaledi Chamber. The location of Hand 1 (H1) and Foot 1 (F1) is denoted. Location of the Pin 2 marker and the borders of the excavation pit are denoted. Axes are in mm.

TABLES

Anatomical group	Composition	Specimen numbers
Hand 1	Lunate Scaphoid Triquetral Trapezium Trapezoid Capitate Hamate 1 st to 5 th metacarpals Proximal digital phalanges 1 to 4 Intermediate digital phalanges 1-4 Distal digital phalanges 1-4 Proximal pollucial phalanx Distal pollucial phalanx	U.W. 101-1308 to 1311 U.W. 101-1318 to 1321 U.W. 101-1325 to 1329 U.W. 101-1351 U.W. 101-1464 U.W. 101-1721 to 1732
Foot 1	Talus Calcaneus Navicular Cuboid Lateral cuneiform 1 st to 5 th metatarsal Proximal hallucial phalanx Distal hallucial phalanx Sesamoid of flexor hallucis brevis	U.W. 101-1322 U.W. 101-1418 U.W. 101-1419 U.W. 101-1439 U.W. 101-1443 U.W. 101-1456 to 1458 U.W. 101-1551 U.W. 101-1553 U.W. 101-1562 U.W. 101-1698
Lower limb	Tibia (immature) Fibula (immature)	U.W. 101-1070 U.W. 101-1045
Thorax	10 th Thoracic vertebra 11 th Thoracic vertebra 11 th Rib	U.W. 101-855 U.W. 101-1733 U.W. 101-524

Table 1. Recognised articulated anatomical groups recovered from the Dinaledi Chamber to date.

Decomposition Stage	Description
Fresh stage	Begins with physiological death, and includes rigor, livor and algor mortis; continues until bloating of the carcass is visible.
Primary bloat stage	Accumulation of gases build up within the body; no body part disarticulation; hair and epidermis become loose; soil-skin interface turns grey; body gives off strong odour.
Secondary bloat stage	Body still bloated; disarticulation of limbs begins; purging of decomposition products through orifices or pre-existing trauma; soil-skin interface becomes black; body continues to give off strong odour.
Active decay stage	Deflation of the carcass begins; disarticulation of the limbs and head observed; muscle and integument still present; carcass becomes very wet; body continues to give off strong odour.
Advanced decay stage	Structural collapse of the abdomen and rib cage; most of the flesh is liquefied or gone; traces of skin, fat, and cartilage may remain; carcass is very wet; adipocere formation (saponification) may occur in some environments.
Skeletonisation	Flesh, skin, fat and cartilage have disappeared; some adipocere and connective tissue may remain.

Table 2. Recognised decompositional stages of the human body and the physical appearance of remains associated with each stage. Table modified from (Wilson et al., 2007, Bristow et al., 2011).

**CHAPTER SIX: SPATIAL TAPHONOMY OF THE *HOMO NALEDI*
ASSEMBLAGE FROM THE DINALEDI CHAMBER, RISING STAR
CAVE***

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Spatial taphonomy of the *Homo naledi* assemblage from the Dinaledi Chamber, Rising Star Cave

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ABSTRACT

The Dinaledi Chamber of the Rising Star Cave, has yielded over 1550 elements of *Homo naledi*, and is the largest single collection of fossil hominin material found on the African continent to date. Fossil recovery thus far have been limited in extent, and includes the collection of bone material from the accessible sediment surfaces of the chamber floor, and the controlled excavation of a restricted area of an *in situ* deposit in the central zone of the cave. The assemblage is commingled, and contains the remains of multiple adult and immature individuals. Although there are several clear examples of skeletal elements in anatomical articulation, none of these articulated units extend to whole limbs, and to date it has not generally been possible to individuate much of the commingled assemblage. As such, we have had to adopt multiple lines of evidence from analyses of spatial distribution and bone clustering in an attempt to understand both the extent of fossil dispersal within the cave, as well as the processes by which fossils may be winnowed or aggraded within the sediment profile of the chamber.

For the present study, we examined the spatial locations of 792 hominin bone specimens from the Dinaledi Chamber. Of these, 283 were recovered from the sediment surface across the chamber floor, while 509 specimens were recovered from within undisturbed floor sediments. A combination of registered white-light photogrammetry and high-resolution laser scans were used to collect three-dimensional data, providing an accurate location of each specimen. Subsequent analyses of spatial data comprised: **(1)** analysis of overall surface distribution and regions of apparent bone concentration; **(2)** statistical cluster analysis in both two and three-dimensions to characterize internal structure in spatial loci; **(3)** analysis of conjoins within the chamber to investigate up-slope or down-slope movement of fossils; and **(4)** the analysis of associated and articulated anatomical elements in order to elucidate the region on ingress into the chamber.

In summary, three main clusters of surface material were identified which show a concentration of fossils within the central region of the chamber, and a clear drop-

off in fossil density in both adjacent passages and up-slope towards the chamber entrance. In the excavated deposits, we identified clusters by body part which are best attributed to the decomposition and disarticulation of the anatomical regions of multiple individuals in a confined space, with limited winnowing of bones by size or element. A general downslope trend in the angular alignment of elements was noted, suggesting post-mortem movement of bones within their encapsulating matrix; the present distribution of bone may be most parsimoniously explained by downslope movement of floor sediment load. Intriguingly, clusters in the excavation pit may signal two separate depositional events, within what is now a palimpsest of commingled material. Further investigations in other subsurface parts of the chamber are needed in order to resolve issues regarding ingress of bodies into the chamber.

INTRODUCTION

The Dinaledi Chamber of the Rising Star cave system, South Africa, has yielded a dense assemblage of remains of an extinct hominin species, *Homo naledi*, with initial excavation uncovering remains attributable to a minimum of 15 individuals (Berger et al., 2015, Dirks et al., 2015). This assemblage has several unusual qualities compared to other cave deposits in South Africa: the unusually dense concentration of material within a spatially restricted environment, lack of mineralization of sedimentary matrix, the mono-specific nature of the assemblage, representation of nearly all regions and elements of the skeleton, and taphonomic and geological absence of aggrading processes such as carnivore accumulation, water-transport, or as a natural death trap (Dirks et al., 2015). Some of the taphonomic observations on the hominin material, such as the presence of articulated elements and the lack of carnivore modification, help to constrain the depositional circumstances (Dirks et al., 2015, Dirks et al., 2016). To attempt to further understand the depositional and post-depositional processes affecting the Dinaledi remains, we have undertaken an analysis of the three-dimensional spatial data of hominin material, both from the surface of the cave floor and from the excavation itself.

Spatial analyses of high-resolution data have provided insight into the behaviour, social organization and cognitive structures of past civilizations using a variety of methods and theoretical approaches (Seibert, 2006). Producing two-dimensional (2D) maps of three-dimensional (3D) objects found at a site is a common, but essential tool for understanding a site's context. With the development of 3D data collection methods, and improvements in tools and related software, 3D visualization analyses of such sites are now possible and practical. Many groups have experimented with structured light, laser scanning and photogrammetry of in-situ paleontological and archaeological sites and these techniques are becoming more common (McPherron et al., 2009, Bernatchez and Marean, 2011, Smith and Levy, 2012, Olson et al., 2013, Roosevelt et al., 2015, Stratford et al., 2016). Spatial analysis of high-resolution data is also becoming more common with software such as X-bones developed by Isaksen et al. (2007). The spatial recovery and recording of archaeological materials including bone, and the reconstruction of temporal and spatial relations, has been demonstrated by work done by Mainland et al. (2014) and Birkenfeld et al. (2015).

Here we report on the analyses of spatial data on hominin skeletal material to test taphonomic hypotheses concerning the formation and subsequent history of the Dinaledi Chamber fossil assemblage.

MATERIAL AND METHODS

General aspects of the Dinaledi Chamber

The Rising Star cave system is located within the Cradle of Humankind (CoH) World Heritage Site, just north-west of Johannesburg, South Africa. To date, two fossil-bearing deposits containing hominin material have been identified: the Dinaledi Chamber (Berger et al., 2015, Dirks et al., 2015) and the Lesedi Chamber (Hawks et al., 2017). Compared to many other hominin-bearing localities in the CoH, the Rising Star deposits are unusual for the dearth of non-hominin macrofaunal remains as well as the lack of mineralization of the mud-

clast sediments in which the fossils occur. Most other sites in the CoH contain hominin fossil remains encased in hard breccia, a consequence of the clastic karstic cemented deposits typical of the Malmani Subgroup (Eriksson et al., 2006). In addition, hominin fossil assemblages in these sites have largely been attributed to one of several taphonomic processes, including carnivore scavenging or other biotic agents of bone accumulation, natural death traps, or sediment mud flows (Brain, 1983, de Ruiter and Berger, 2000, Pickering et al., 2004, Gommery et al., 2008, Dirks et al., 2010, Bountalis and Kuhn, 2014). Spatial data from these sites has typically been of very low resolution because of the need to remove breccia *en bloc* for further preparation offsite.

A number of sediment-flowstone fill and removal cycles are evident throughout the Rising Star cave system, in the form of erosional remnants, fossiliferous sediment, breccia, and flowstone units (Dirks et al., 2015). The Dinaledi Chamber itself is filled exclusively by flowstone and fine-grained sediment, the product of two depositional facies (Facies 1 and 2) divided across three stratigraphic Units (1 – 3), which filled the chamber over time (Dirks et al., 2015). Unit 3 is considered to be the geologically youngest unit in the chamber, and is interpreted as having formed from the erosion products of the earlier Units 1 and 2. The hominin material was recovered from both surface and subsurface layers of Unit 3, with some articulated skeletal remains having been recovered from relatively deep (>10 cm) within the sediments (Dirks et al., 2015, Kruger et al., 2016). By contrast, the more shallow parts of Unit 3 sediments within the excavation area have greater fragmentation and are inferred to have been reworked by erosional processes and slumping of sediment downslope within the chamber. Unit 3 sediments were formerly much higher than at present, as is clear from the preservation of hanging remnants of this unit beneath flowstone ledges on the chamber wall. Hence, the taphonomy of the hominin bone-bearing Unit 3 must include the effects of sediment winnowing and compaction, gradual removal of material through floor drains, and some lateral movement driven by gravity and erosion downslope within the chamber (Dirks et al., 2015, Dirks et al., 2016).

Hominin bone material on the surface of the chamber floor may largely derive from these processes.

The Dinaledi Chamber excavations thus far have been limited in extent (Dirks et al., 2015). They have included the collection of bone material from most (but not all) of the surface of the chamber floor, and the excavation of a small area of approximately 0.8 square meters. The spatial distribution of hominin remains on the basis of this limited sampling may therefore not be representative of the site as a whole. The bone assemblage is commingled, the remains of multiple adult and immature individuals being present in the limited excavation area. Although there are several clear examples of elements in anatomical articulation *in situ* (Dirks et al., 2015, Randolph-Quinney, 2015, Kruger et al., 2016) none of these articulated units extend to whole limbs, and it is not generally possible to associate different parts of individual skeletons. Only in a few cases has it been possible to show anatomical connections between spatially separated elements; these cases are limited to post-mortem broken margins and ends with direct refits, and dental elements with clear evidence of association such as matching interproximal facets.

For the present study, we examined the spatial locations of 792 hominin bone specimens from the Dinaledi Chamber. Of these specimens, 283 were recovered from the sediment surface across the chamber floor (Table 1), while 509 specimens were recovered from within Unit 3 sediments by excavations in November 2013 and March 2014 (Table 2). Data collection and excavation protocols were the same for both field seasons.

Material collected from the surface near pins 10 and 14 were not included ($n = 28$) because the registration of these scans into the overall reference frame requires more fieldwork to establish contiguous relationships (Figure 1). Bone fragments smaller than 5 mm in diameter were excluded from analysis. We have also excluded a small number of specimens that were conjoined *in situ* and have since been reconstructed, as they would have been duplicated in the spatial analyses.

Data Collection

The constraints of the Rising Star cave and Dinaledi chamber affected both excavators and equipment and demanded an innovative approach to collecting high-resolution spatial data. These data are important for documenting spatial orientation, but can also be used for mapping and surveying. Methods used in this study are comprehensively presented in Kruger and colleagues (2016).

A combination of white-light surface scans and high-resolution laser scans were used to collect 3D data on the location on each specimen of the Dinaledi assemblage. All specimens, both on the surface of the chamber and in the excavation unit were scanned using white-light source photogrammetry *in situ* and prior to collection. By combining scans from the surface of the chamber, as well as the main excavation pit, a 3D record of all collected and excavated fossil material was created. Individual white-light source photogrammetry scans, taken during excavations, were converted to the E57 point cloud File Format for 3D Imaging Data Exchange (Huber, 2011). These .e57 point cloud data structures were aligned to the broader context of the Dinaledi Chamber [see Kruger et al. (2016)] using CloudCompare (Girardeau-Montaut, 2011). Each scan was aligned in CloudCompare by manually picking three or more reference points which were common to both the individual scan and the georeferenced Terrestrial Laser Scan (TLS) data collected from the Dinaledi Chamber. Reference points were a combination of fixed survey pins (15 in total) in the Dinaledi Chamber, together with permanent geological features of the chamber walls and floor that can be repeatedly identified in multiple scans. It is often convenient to refer to the locations of objects in terms of these reference points (for example, the excavation area includes Pin 2 and Pin 9 – Figure 1). As excavation has only been conducted in one area of the chamber, the remaining pin locations are useful in the present study only in reference to the material recorded and collected from the chamber surface.

Scans were aligned from the most recent (from the excavation during March 2014) to the oldest (November 2013). Once the scans were rotated, aligned and

scaled, fine registration was applied, to provide an optimum alignment. Once scans were accurately aligned, the 3D transformation was then applied and the individual scan's coordinate system were then updated to the global coordinates of the chamber, and thus any other scan's coordinates within the broader framework of the Dinaledi Chamber. This method of data collection provides a virtual snapshot of the excavations at any one point in time.

Individual bones and fossil fragments were then plotted, and their coordinates recorded by visualising the transformed .e57 point clouds in Autodesk's Recap 360 software. This was accomplished by using high-resolution white-light source photogrammetry scans, visualised in Artec Studio 10 Professional, in conjunction with the point cloud data, as a guide for placement of coordinate data (Figure 2). A surface resolution of approximately 0.5 mm and a three-dimensional point accuracy of approximately 0.1 mm ensured accurate placement of bone material into the global coordinate system. A centroid datum of these data, in the form of 3D points (x, y and z), were recorded for individual teeth, fragments and other small elements. In the case of long bones, a coordinate for the distal, centroid and proximal end of each bone or portion was recorded. Thus, when possible, three coordinates were recorded for each long bone, allowing for the directionality (strike and dip) of these bones to be attributed in spatial analysis in relation to the rest of the fossil assemblage.

Data Plotting

We chose to separate material into two subsets for analysis: "surface material" collected from the sediment surface across the floor of the chamber, and "excavated material" recovered from beneath the surface during excavations. The material collected from the surface of the chamber extends across a much larger area than the excavation unit. However, the excavation unit includes a much larger sample size and more extensive representation of skeletal elements than the chamber surface. We acknowledge that without further excavations, that the taphonomic processes affecting bone fragments on the chamber surface may have

been different from those affecting the spatial positions of fragments embedded within Unit 3 sediments.

Data were processed and visualised in 2D and 3D scatter plots using IBM's SPSS Statistics 24. Data were plotted by anatomical body region and include cranial, dental, lower limb, thorax, upper limb, and vertebral elements.

Cluster Analysis

A Two-Step Cluster Analysis was performed using IBM's SPSS Statistics 24. This analysis is an exploratory tool designed to reveal natural groupings (or clusters) within a dataset that would otherwise not be readily apparent. Hence, we used this algorithm to characterize underlying structures in the spatial locations of elements which may naturally cluster based on spatial association. The Two-Step algorithm automatically chooses the number of clusters most appropriate for the dataset, removing subjectivity in terms of cluster recognition. As the spatial data are continuous, we used Euclidean distance as a measure of association (Zhang et al., 1996).

RESULTS

Surface Material

Hominin remains occurred sporadically on the sediment surface within the Dinaledi Chamber prior to discovery and excavation. Spatial analysis of the recovery locations suggests three areas of concentration: between pin locations 1 & 2; 3 & 10; and 4 & 15 (Figure 1). A more limited amount of bone material was found between pins 3 & 12 (~ 6 specimens) and between 13 & 15 (~ 11 specimens). A single tooth was recovered from the area immediate to pin 5. The area between pins 4 & 15 yielded the highest concentration of surface bone material, consisting of 261 elements and fragments. The second most concentrated area for surface material was around pins 2 & 9, directly above the main excavation area of the chamber. Material recovered from the area around pin 10 was the third most dense area for surface material in the chamber (~ 25

specimens), followed by the area around pin 1 (~ 22 specimens). The densest cluster of material is at the area immediate to pin 9, whilst material around pins 4 & 15 is more spatially dispersed. A distribution of material, around the densest area within the chamber, by body part is presented in Figure 3A (see supplementary material 1).

Cluster Analysis was performed for the main concentration of surface material between pins 1, 2, 4, 9 and 15. The cluster analysis identifies three main clusters in this area (Figure 3B). Cluster 1 is the most dense, with the bone material, primarily cranial elements, being concentrated in a relatively small area. Cluster 2 has the highest concentration of all elements, although material is slightly more dispersed in this area, in relation to cluster 1. Cluster 3 presents no thoracic elements, and seems to be clustered against the cave wall and the single rock present at pin 1. The occurrence of two rocks within cluster 2 appears to have forced elements to be dispersed between the two rocks.

Excavated Material

Subsurface material were collected from the main excavation pit, an area the size of 685 cm, by 783 cm by ~15 cm. In such a high density area, cluster analysis was imperative, as bone distribution patterns were not immediately obvious. Spatial overprinting is a natural product of having a large number of specimens in an uneven distribution, in an area of approximately 1 square meter. Figure 4 is a two-dimensional distribution of bone material found in the excavation pit, defined by body part. In Figs. A – C two distinct groups are visible, one to the northwest of the pit and one to the southeast. These two groups (one to the northeast and one to the southeast) are not present for the distribution of thorax elements (Figure 4D).

A Cluster Analysis for the two dimensional distribution of material in the excavation pit (Figure 5) identified unique clusters for each body part excluding the thorax. For all material found in the pit, three clusters are visible (Figure 5A). Bone material in clusters 1 and 2 are scattered around the excavation pit. Cluster 3 is confined to the southeast section of the pit. Cranial and dental elements present

two clusters (Figure 5B), cluster 1 to the southeast and cluster 2 to the northwest of the pit. Upper limb material forms 2 clusters, cluster 1 to the northwest and centre, and a densely clustered cluster 2 to the southeast of the pit (Figure 5C). When comparing Figs. 5B – C, it is evident that there is an absence of upper limb material in the space that is occupied by cranial and dental material in the eastern section of the pit. Lower limb elements form three clusters, cluster 1 to the north, cluster 2 in the centre and south, and cluster 3 confined to the southeast of the pit. Lower limb elements in contrast to cranial and dental, and upper limb elements are underrepresented in the south area of the excavation pit. A more dense concentration of lower limb elements was found in the north of the excavation pit, compared to upper limb elements. Thoracic remains do not appear to cluster distinctly.

A Cluster Analysis for the three dimensional distribution of material in the pit (Figure 6; supplementary material 2) identifies three clusters on the basis of all body parts. Cluster 1 presents a dense vertical distributed cluster, whereas clusters 2 and 3 are more sporadic. Cluster 2 is confined to the bottom of the pit, with cluster 3 representing material in the northeast section of the excavation pit. Cranial and dental material form two clusters (Figure 6B), one to the east and one to the west of the excavation pit. Cluster 1 is more dense than cluster 2, both of which lack material in the lowest part of the pit. Similarly upper limb elements (Figure 6C) form 2 clusters, one in the east and one in the west of the pit, however, in contrast, these two clusters have bone material present in the lowest area of the pit. An absence of upper limb material is immediately noticeable in the very centre of the excavation pit, the same is true for lower limb elements (Figure 6D). Cluster 1 for lower limb elements is found in the lower east section, cluster 2 in the top half, and cluster 3 in the west, section of the excavation pit. A trend for the lower limb elements is evident, as material is found to be moving east, with a distinct absence of material in the centre of the pit. Again, thoracic remains do not appear to cluster.

A depth profile for the excavations (Figs. 7 – 8) identifies a number of long bones (among other bone material) and the orientation of the long axis of each of these elements relative to the excavation pit. Depth Profile 1 (-40 mm – -70 mm) does not show any trend in the directionality of bone material. As excavations get deeper within the excavation pit, a south, southeast directionality of bones becomes more evident. At Depth Profile 2 (-71 mm – -100 mm) long bone fragments within the centre and towards the south of the pit are mostly south, southeast directed. This trend is not reliably seen for Depth Profile 3 (-101 mm – -130 mm), however, Depth Profile 4 (-131 mm – -160 mm) exhibits this trend again. The relative location of Hand 1 (H1) (Berger et al., 2015, Kivell et al., 2015) and Foot 1 (F1) (Berger et al., 2015, Harcourt-Smith et al., 2015) are indicated in Figure 7. These semi-articulated elements represent the bulk of a limited number of articulated remains found in this assemblage. Having been found so close to each other within the pit (both by distance and depth), these two elements are both angled southeast within the deposit, following the overall trend.

DISCUSSION

Site Formation Processes

Mapping and recovery of bone material from the sediment surface of the Dinaledi Chamber is mostly complete. Most of the skeletal material on the sediment surface of the Dinaledi Chamber was out of primary depositional context, and was disturbed in a number of possible ways. Firstly, a number of bones were found on rock surfaces around the pin 4 area (Figure 9), above the sediment surface, and were in rough parallel alignment. These bones, mostly long bone shafts, were presumably placed on these rocks by unknown cavers prior to the discovery in 2013 by cavers working with the University of the Witwatersrand. A single molar found next to pin 5 also stands out in relation to the other remains on the surface of the chamber (Figure 10). It is possible that this molar may have been transported from elsewhere in the chamber. Alternatively, it may have been deposited in its location through sediment creep and slump, as the surface material seems largely unassociated. Figure 10 shows an example of conjoin specimens

which have moved considerably around the surface of the chamber. Movement of conjoin specimens between pins 1 & 4 may be the result of sediment creep as there is relative height of about half a metre between these two pins. Movement of conjoins specimens between pins 9 & 13 may also be subject to sediment creep and slump, as the area around Pin 13 is about half a metre lower relative to the area at Pin 9 (Figure 10).

The sediment surface of the Dinaledi Chamber is interrupted by a number of low rocky outcrops, which may extend to the rocky floor beneath the sediments. Where skeletal material on the surface of the chamber is most dense (i.e. between pin marks 4 and 15), it appears to be channelled near the borders of the rocks and the chamber walls. This is also true for skeletal material at Pin 1 (Figure 11). This can be explained by a number of possible scenarios. The rocks and chamber walls may constrain natural pathways for movement through the chamber and it is possible that earlier visits by cavers into the chamber may have dispersing bone material along these routes as they moved their way through the chamber. A second plausible explanation for this distribution is that slow sediment creep, movement of the underlying water table, or gravitational forces moving material down slope within this part of the chamber may have channelled material on the surface near rocks and walls (Figure 11).

The vast majority of surface material was recovered from the distal portion of the chamber, farthest from the only known entry shaft, 'the Chute', and roughly 4 m lower in elevation from the point of entry. Skeletal material is also present on the surface going into several extremely narrow passages radiating from the central part of the chamber. If sediment creep were the explanation for the occurrence of bone material so far down in the chamber, it does not account for the (albeit limited) amount of material found in these side passages.

The excavation area in the chamber is small and concentrated around pins 2 and 9. For this reason, we cannot yet test what relationship the surface scatter of bone material may have to the density of bone material within the sediment. The largest

number of surface elements were recovered from the area around pins 4 & 15. Under the hypothesis that fossil deposits within Unit 3 are correlated with the surface concentration of hominin skeletal material, we would predict that subsurface investigation in the region of pins 4 and 15 will reveal densely fossiliferous sediment.

Spatial analysis in the excavation pit area demonstrates a number of distinct groupings and clusters. In several of the clusters presented here, two separate groupings are identifiable, usually one in the northwest and one in the southeast of the pit. This may represent different individuals deposited temporally close together, but commingled and mixed as the sediment creeps within the deposit. The semi-articulated remains of H1 and F1 were recovered from relatively deep in the pit. Their preservation begs the question, why material recovered from the higher layers of the pit do not present articulated remains in this way. In the case of human burials, observations of skeletonization and disarticulation processes have shown that the hands and arms often disarticulate early on, sometimes before the disarticulation of head from the neck (Roksandic, 2002). H1 was found semi-articulated, and the position of the elements indicated that it was closed or semi-closed during the process of skeletonization. This is in contrast to most of the other 1550 elements making up the *H. naledi* assemblage, which were found disarticulated and fragmented. If H1 and F1 were deposited at the same time (perhaps because they belong to the same individual), they may have been protected from the processes occurring higher up, closer to the chamber's surface, where the unassociated and fragmentary elements were recovered. However, it is more than likely that H1 and F1 entered the chamber as intact units, covered with soft tissue, muscle and tendons. Otherwise, even limited sediment transportation would have dispersed the small elements of these anatomical regions, and they would not have remained articulated (Galloway, 1996, Pokines, 2013). The rate of decomposition however, is uncertain, as disarticulation sequences are highly dependent on the environment and micro environment (Roksandic, 2002).

Cranial and dental material in particular show a different spatial pattern from the postcranial body parts. This is possibly the result of some form of differential sorting, however further investigations in other subsurface parts of the chamber are needed to determine this.

The present spatial data give only limited information concerning the possible involvement of hominins in the formation of the skeletal assemblage. The excavation pit does show some patterning in the spatial distribution of different skeletal regions, but the most pertinent fact is that articulated material in primary depositional context is relatively lower in the excavation profile, while the more superficial parts of the excavated deposit contain more fragmented and disturbed material. The presence of articulated and semi-articulated remains lower in the deposit suggests that remains were present at this location, far from the entry chute, before their burial by sediment and possible subsequent reworking of parts of the deposit. More investigation will be necessary to determine whether the original depositional environment may have allowed elements to move down a talus from beneath the entry chute.

The differences between distributions of plate-like cranial fragments with sub-rounded postcranial fragments will become increasingly important when addressing further questions with regards to the transport of bone material within the Dinaledi Chamber. The intrinsic properties of bone will have an interrelating result with the taphonomic agent affecting it (Lyman, 1994). For example plate-like cranial material is less likely to survive this transport, than tubercular long bone. This may also account for the large number of long bone fragments preserved in this assemblage in relation to the lesser accounted for cranial elements.

The spatial patterning of surface skeletal material shows substantial accumulations in the area of the chamber far from the entry chute, and little evidence of hominin skeletal material beneath the chute itself. However, the area and sediments below the chute have not been excavated as yet. In addition, the

surface scatter of bone material may not correlate with the subsurface richness of the hominin deposit. Consequently, the present distribution of bone on the surface may be explained by the combined effects of sediment winnowing, slight downslope movement, and possibly some anthropogenic movement by cavers during the period before discovery. Alternatively, if material found on the surface today has resulted from in situ sediment winnowing from buried material, we might predict that the surface distribution does correlate with the subsurface density of hominin skeletal remains.

Dirks and colleagues (2015; 2016) have proposed that the hominin material in the Dinaledi Chamber resulted from the deliberate deposition of bodies over a period of time. If bodies were introduced into the present entry chute, we predict that the accumulation of hominin remains should be most dense in that part of the chamber, sloping away as a talus from that entry point. Excavations below the chute entrance should provide a test of this hypothesis. If dense hominin remains are not found in this area, then we must turn to alternative hypotheses. For example, it is possible that instead of dropping bodies down the Chute, the hominins entered the chamber, and placed bodies at the areas where high concentrations of surface material were recovered (between pins 4 & 15 and 1 & 2). This hypotheses would explain why pins 4 & 15 have the highest concentration of surface skeletal material. However, until more excavation is undertaken to investigate the subsurface density of fossils in these areas and other parts of the chamber, it is premature to interpret the surface clustering of skeletal material.

Future Excavation Strategy

A number of hypotheses surrounding the site formation processes in the Dinaledi chamber still need to be tested. To do this, excavation test pits need to be dug directly below the entry shaft of the Chute to determine the extent of bone material in this area. This will test the hypothesis that bodies were dropped down the entry crack from above. In addition, further excavations below the pin 4 would be advantageous to establish whether the concentration of surface material is

indicative of the subsurface density in this area. In addition, several key questions need to be addressed: 1. Why is there a lack of surface material found south of pins 1 & 6? 2. What is the reason for the lack of surface material within the central part of the chamber (between pins 8 & 10)? and 3. Is there also a concentration of subsurface material between pin 8 & 10 in the central part of the chamber? Finally, the identification of skeletal remains in the side passages at pins 12 & 13 may be able to address the possibility that material entered the chamber from another fissure other than the Chute, which is the only current entry point into the Dinaledi chamber.

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FIGURES

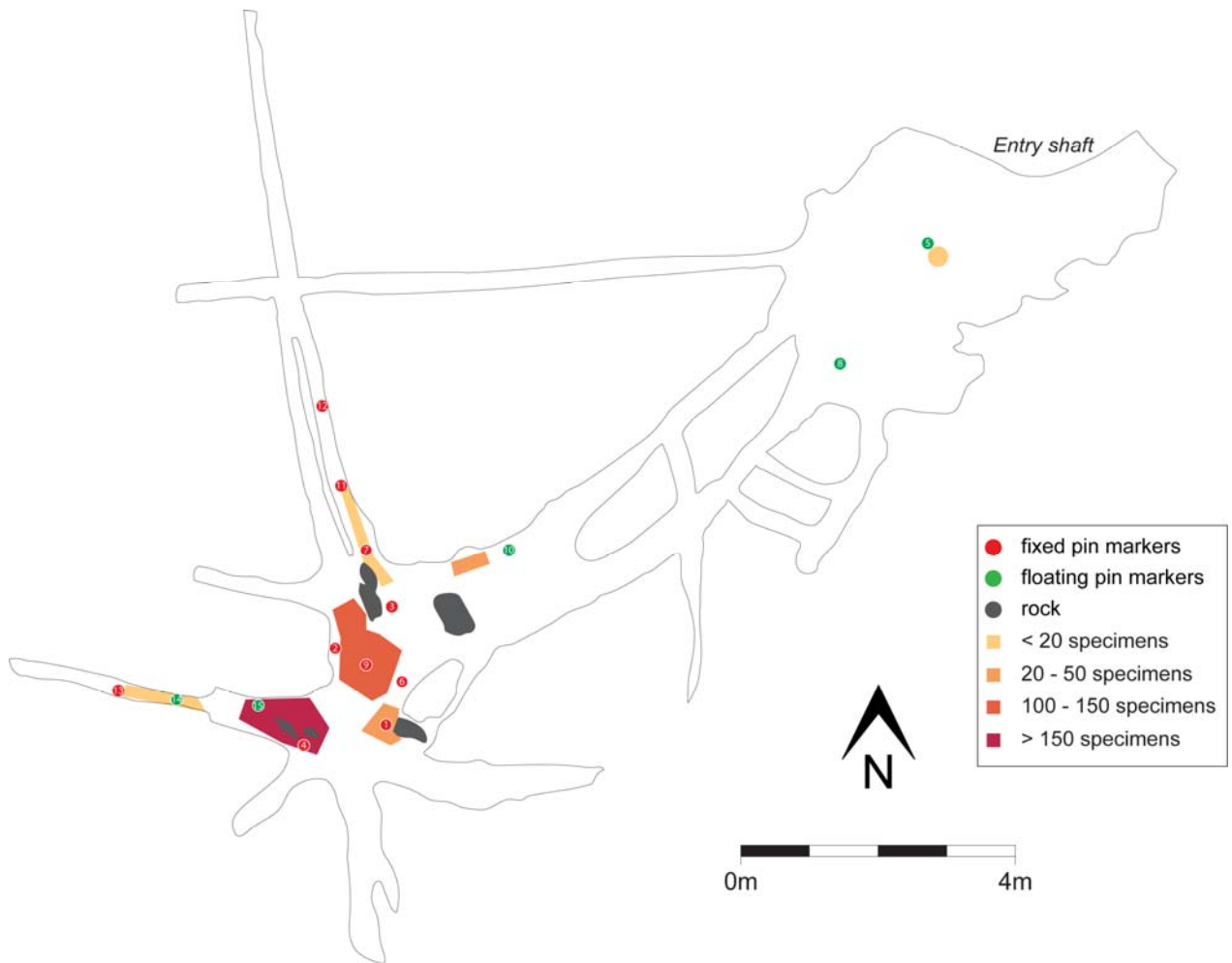


Figure 1: Map of the Dinaledi Chamber, Rising Star cave, depicting the spatial density of surface material found within the chamber.

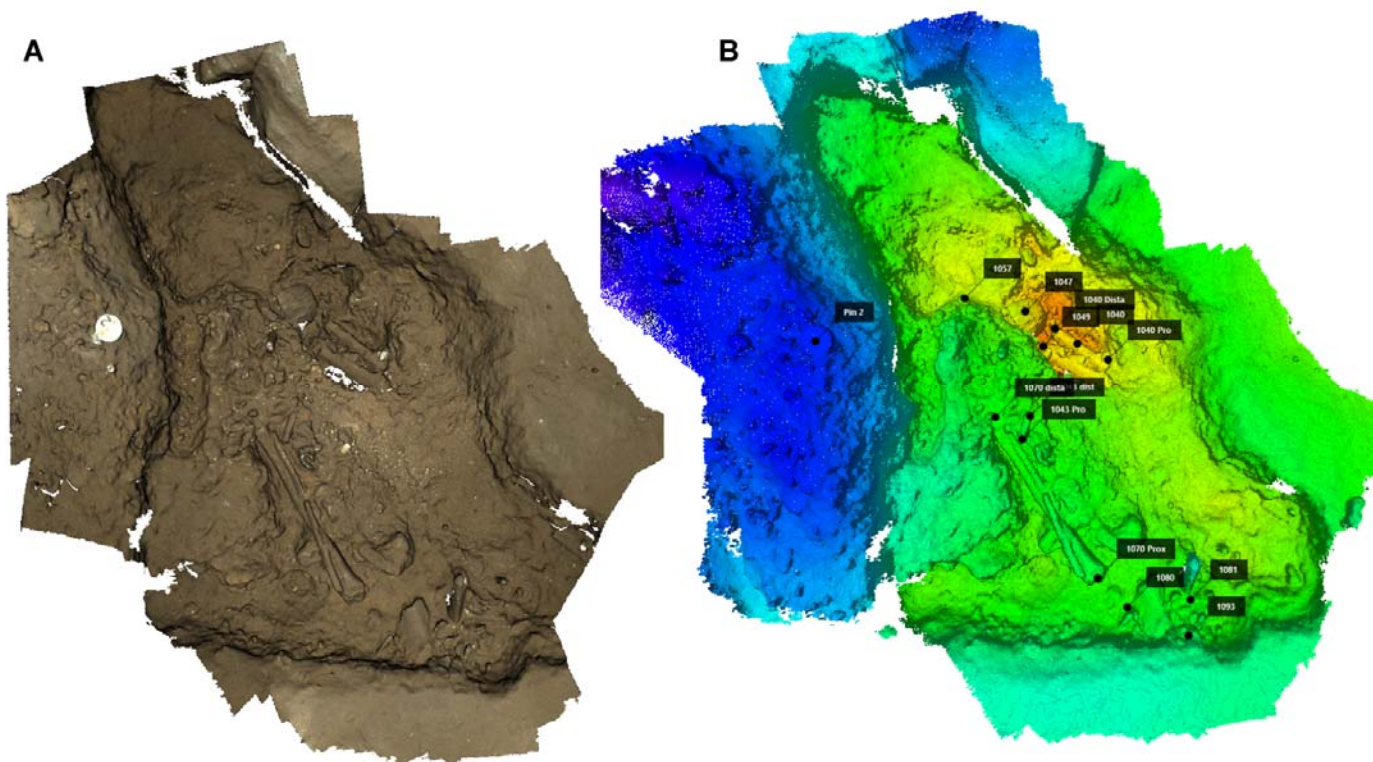


Figure 2: Example of spatial data collection of the Dinaledi assemblage: A) *in situ* three-dimensional white-light source photogrammetry scan of the excavation pit; with B) the corresponding point cloud data structure which spatial coordinates (x, y, and z) were plotted on.

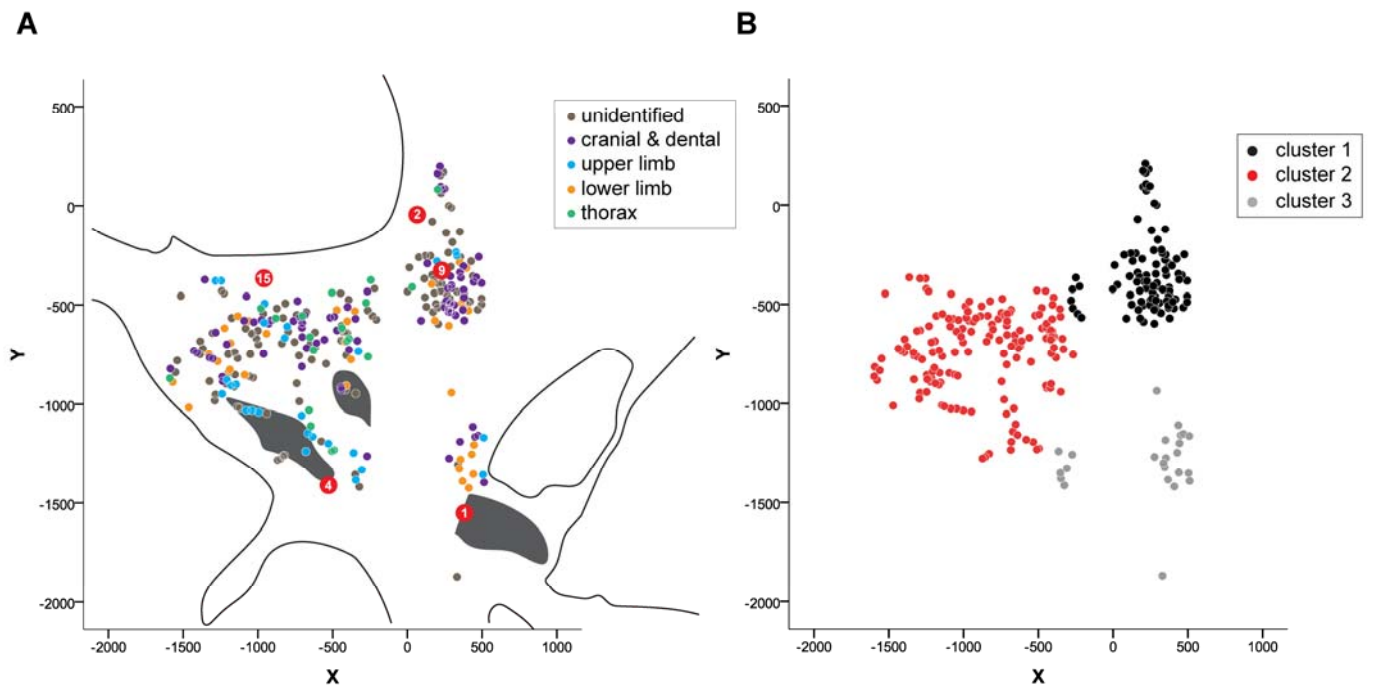


Figure 3: A) Expanded surface density map of the Dinaledi Chamber, Rising Star cave, by body part. B) TwoStep Cluster Analysis of the spatial data presented in A, showing three distinct natural clusters. Location pin markers are denoted in red. Axes are in mm.

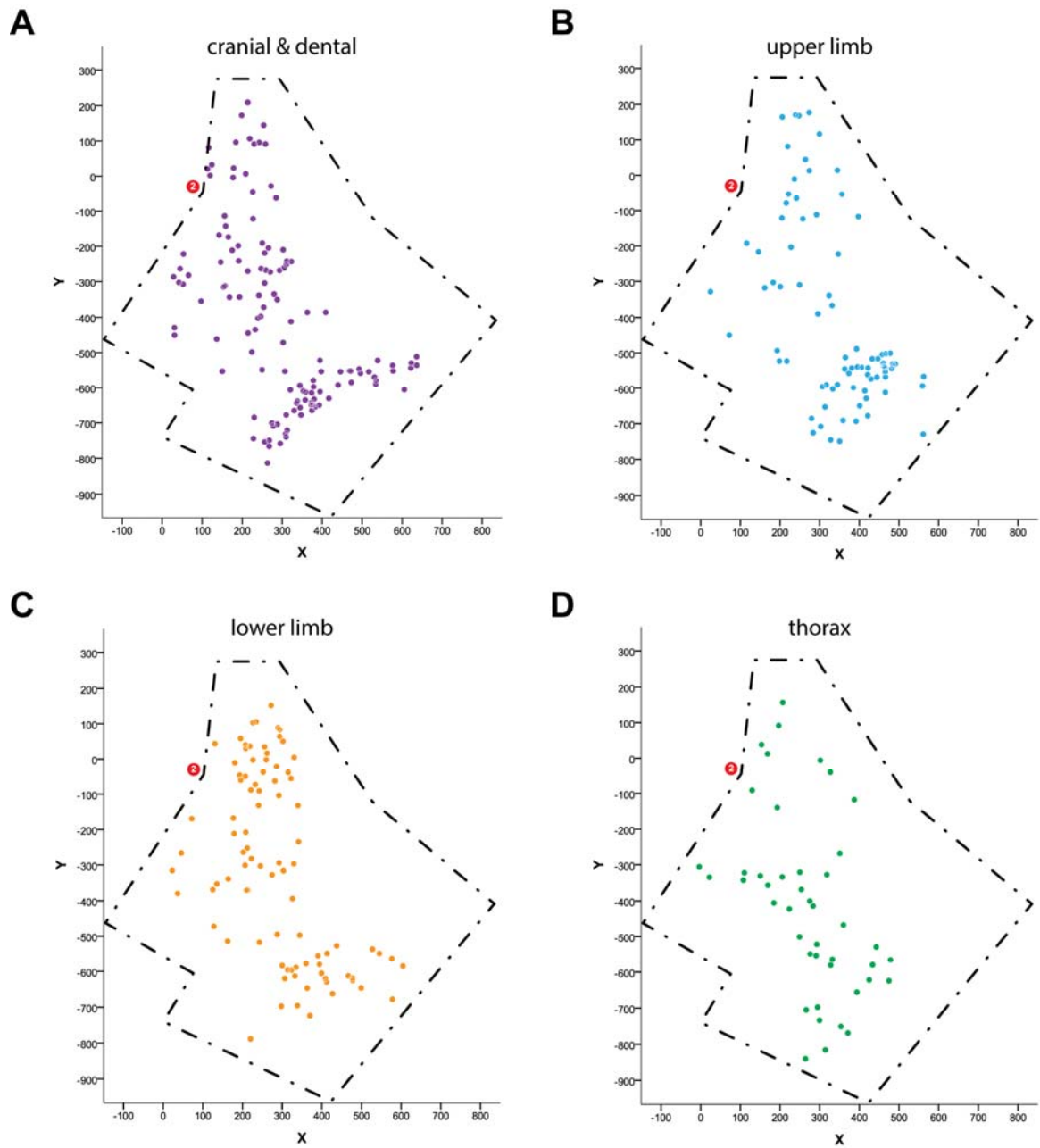


Figure 4: Plotted two-dimensional distribution map of subsurface material found in the main excavation pit of the Dinaledi Chamber, Rising Star cave, by body parts: A) cranial and dental; B) upper limb; C) lower limb; and D) thorax. Location of the Pin 2 marker and the borders of the excavation pit are denoted. Axes are in mm.

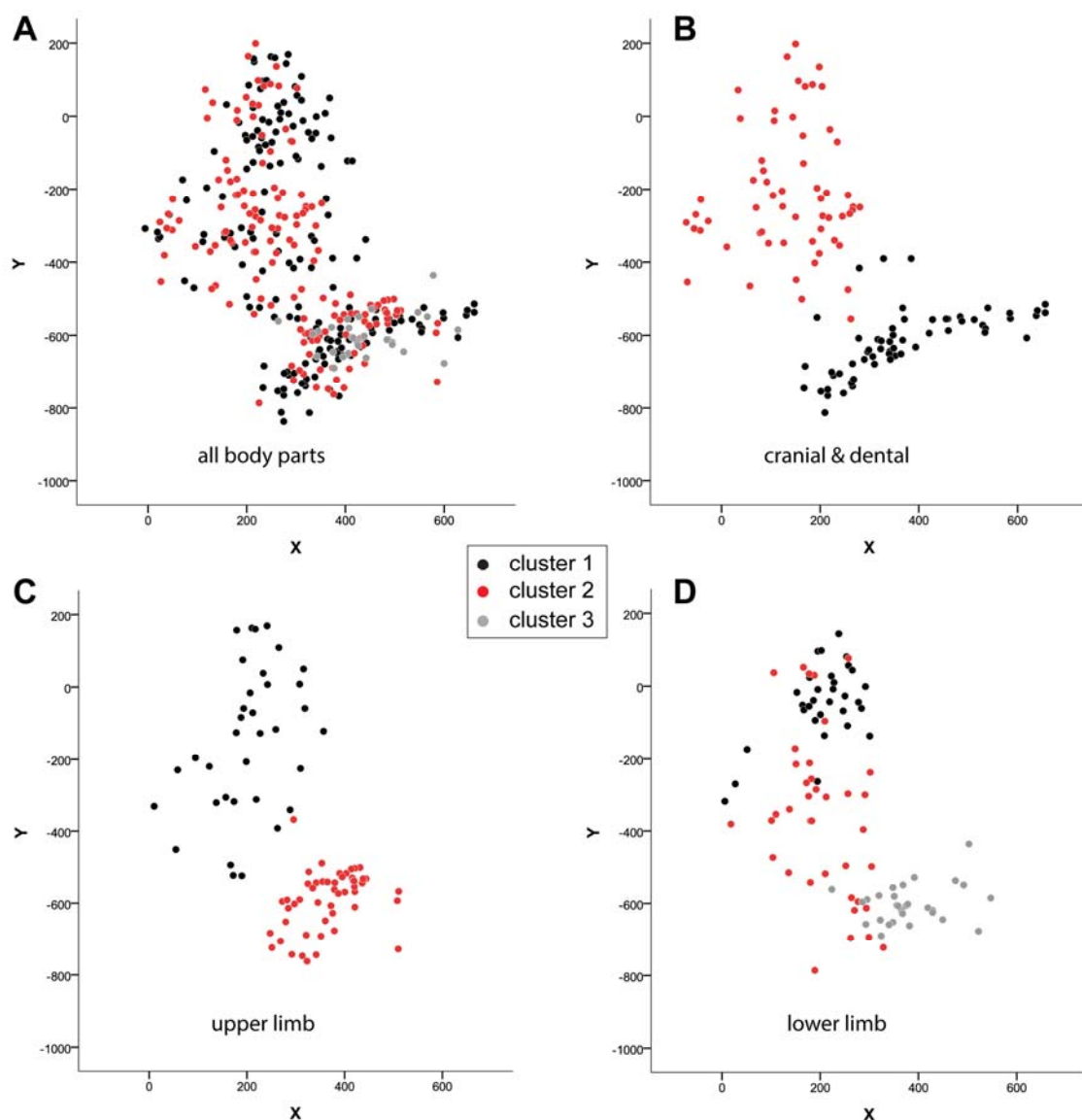


Figure 5: Two-dimensional TwoStep Cluster Analysis of subsurface material of the main excavation pit of the Dinaledi Chamber, Rising Star cave, depicting distinct natural clusters by body part: A) all body parts; B) cranial and dental; C) upper limb; and D) lower limb. Spatial data for the thorax do not cluster. Axes are in mm.

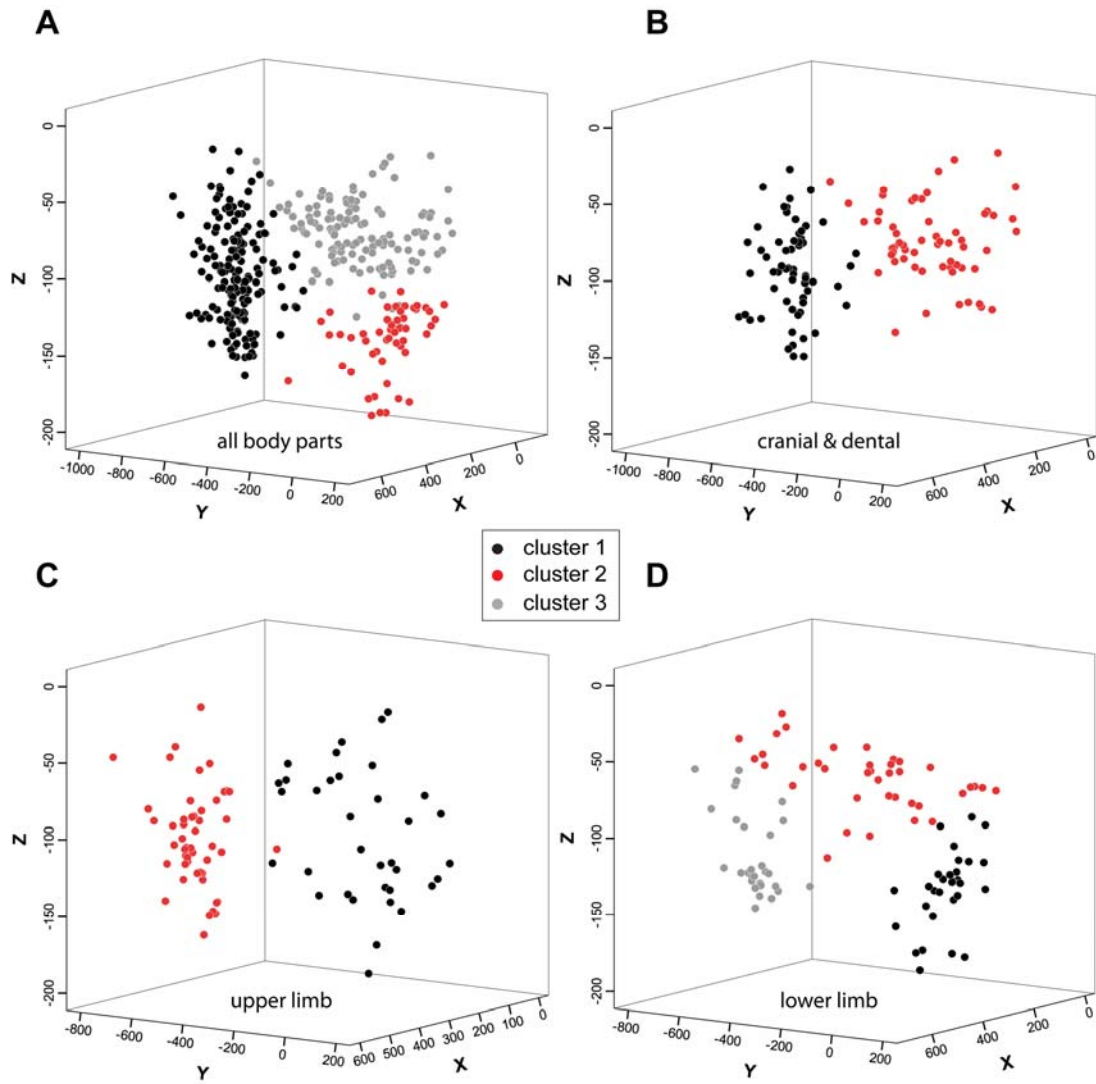


Figure 6: Three-dimensional TwoStep Cluster Analysis of subsurface material of the main excavation pit of the Dinaledi Chamber, Rising Star cave, depicting distinct natural clusters by body part: A) all body parts; B) cranial and dental; C) upper limb; and D) lower limb. Spatial data for the thorax do not cluster. Axes are in mm.

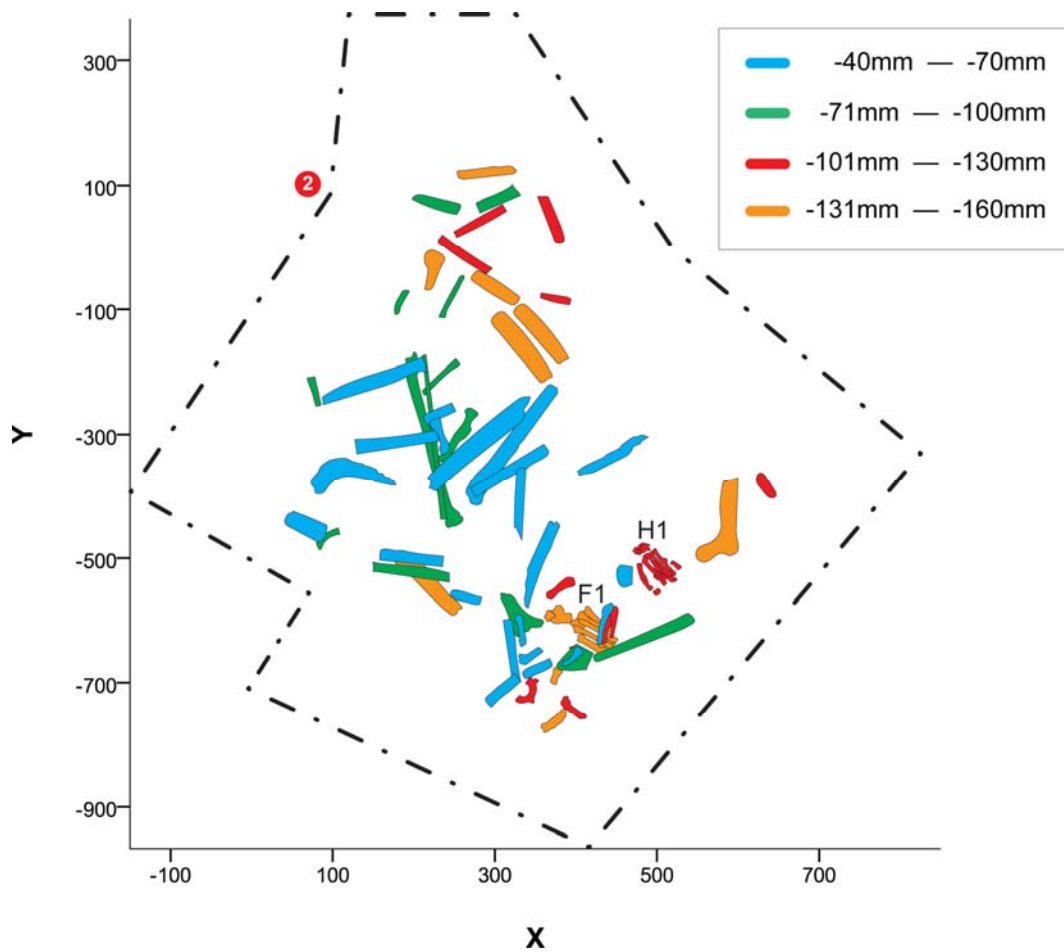


Figure 7: Two-dimensional depth profiles created from alignment spatial data of a number of long bones and other bone material found within the main excavation pit of the Dinaledi Chamber, Rising Star cave. The positions of Hand 1 (H1) and Foot 1 (F1) are noted. Location of the Pin 2 marker and the borders of the excavation pit are denoted. Axes are in mm.

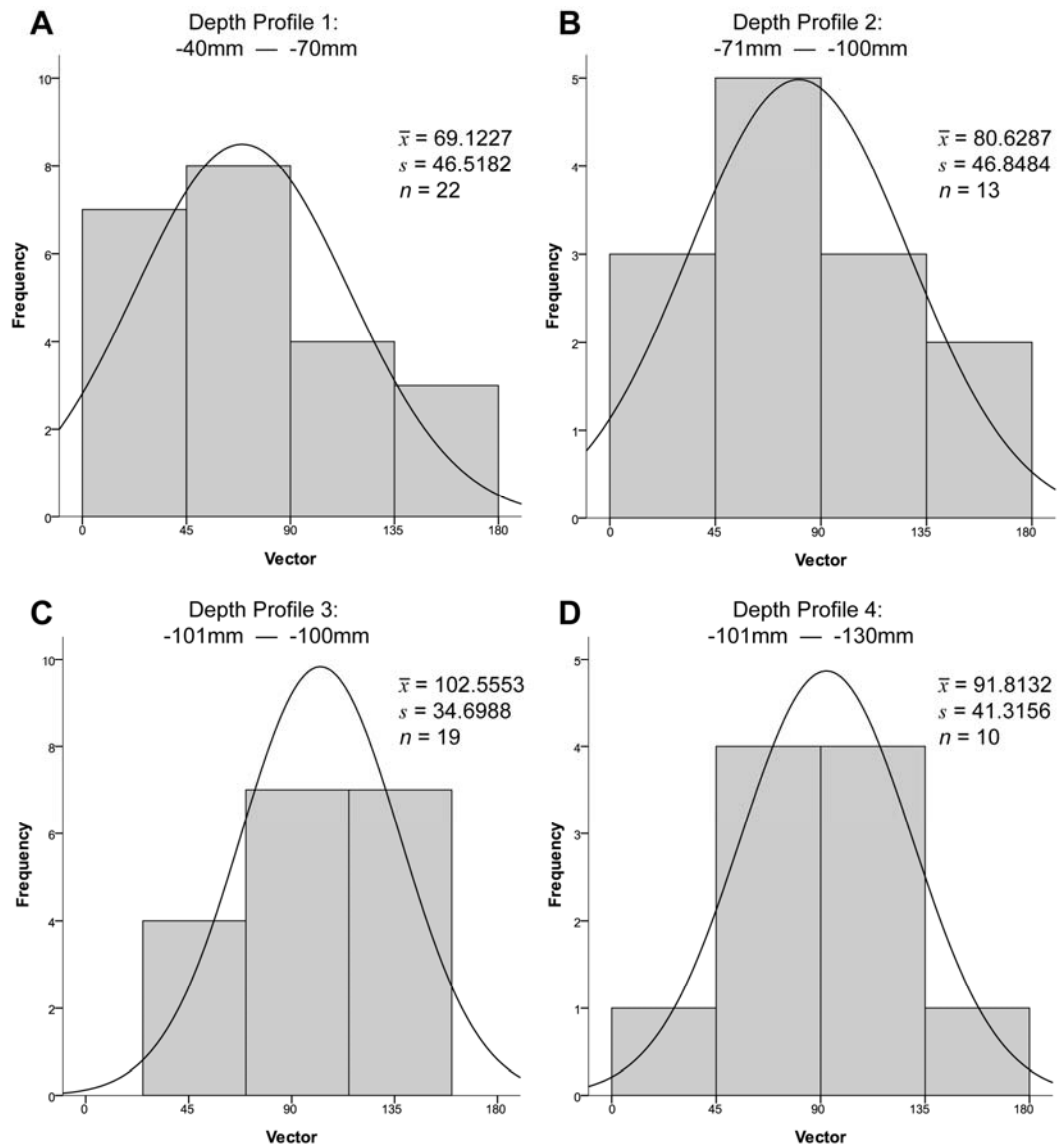


Figure 8: Depth profile groups from alignment spatial data of a number of long bones and other bone material found within the main excavation pit of the Dinaledi Chamber, Rising Star cave. The mean, standard deviation and sample number are presented for each depth profile group.

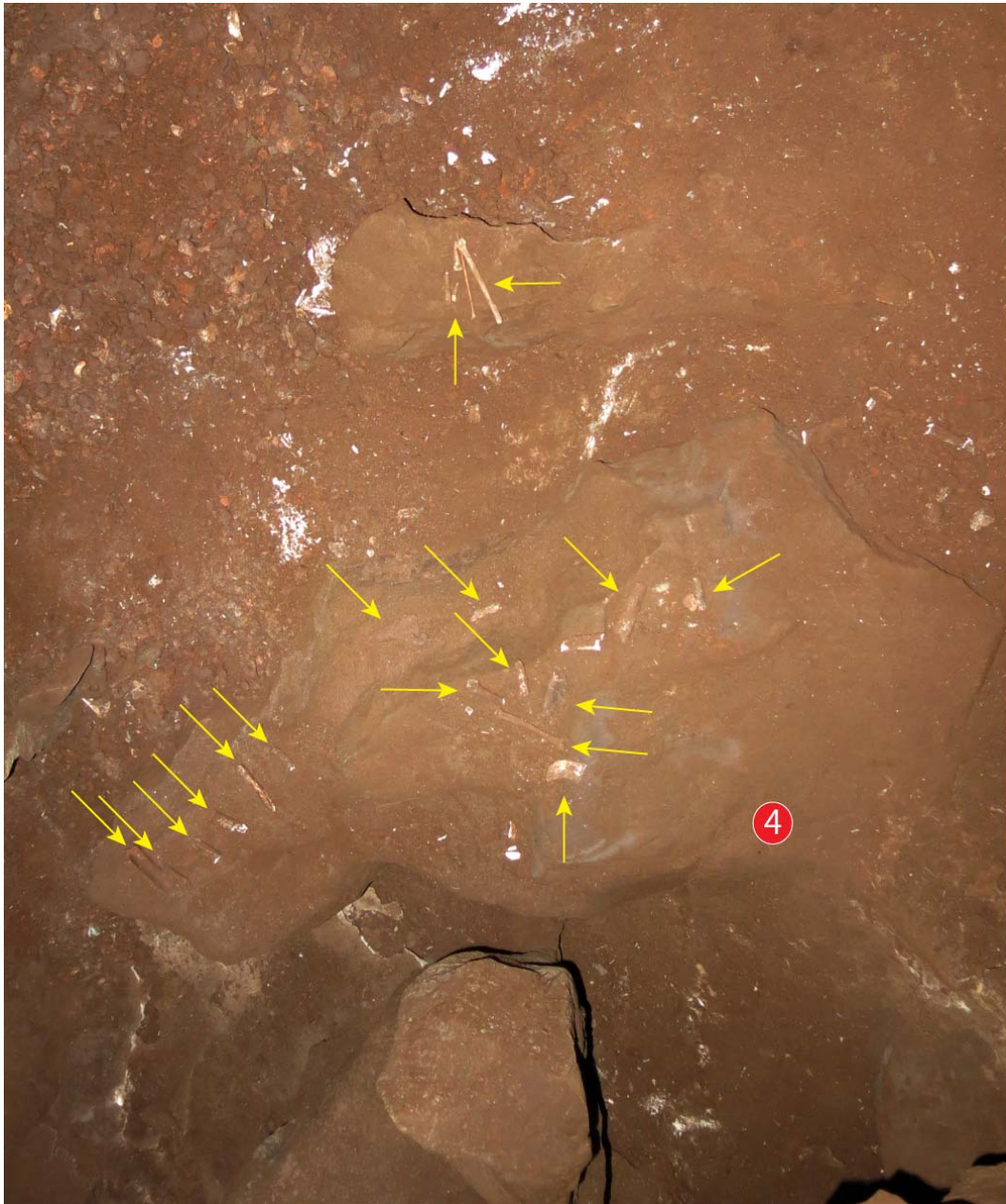


Figure 9: Surface material, including modern bird bones and hominin long bone fragments, arranged on rocks within the Dinaledi chamber by an unknown caver, prior to the discovery of this chamber by cavers from the University of the Witwatersrand.

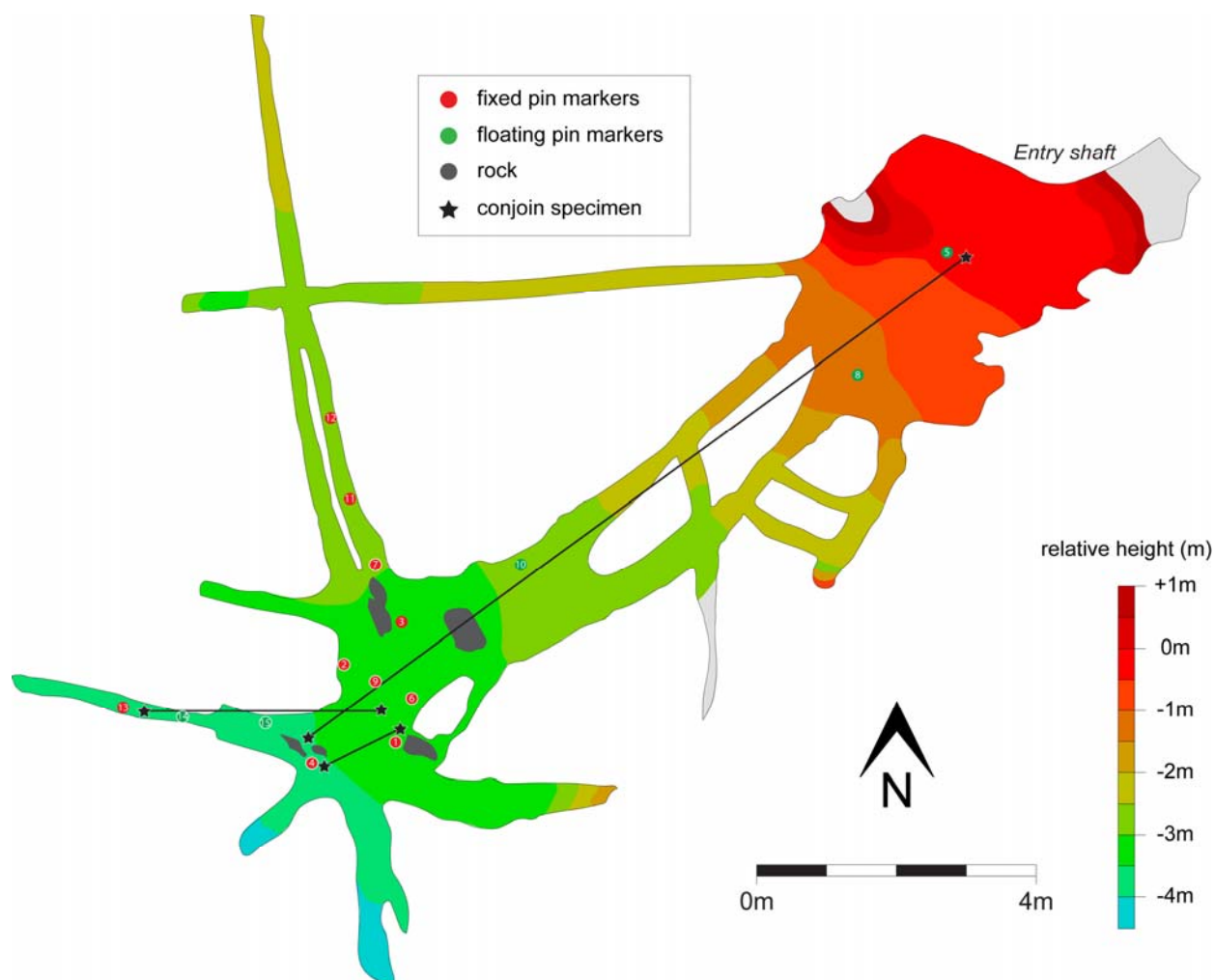


Figure 10: Conjoined specimens of *Homo naledi* from the Dinaledi Chamber of the Rising Star Cave. Note the almost 12 m distance between specimen UW-101-020 at Pin 5, and its associated conjoin at Pin 4. Relative height within the chamber is indicated.

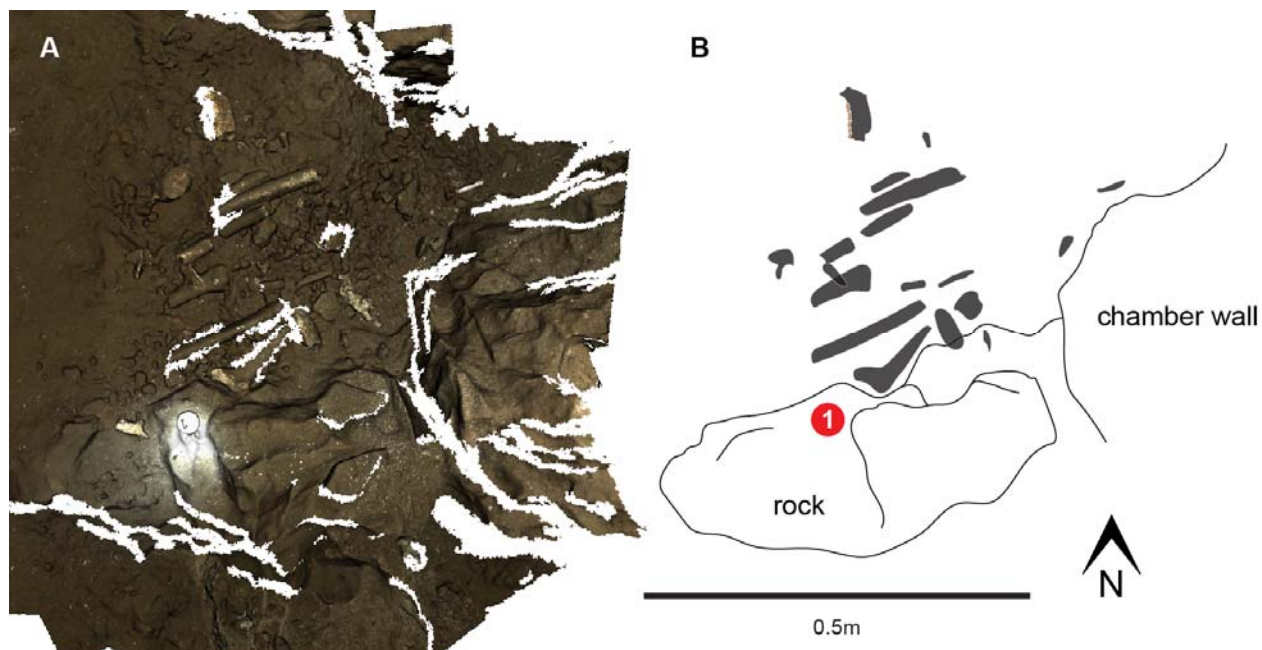


Figure 11. Surface material found at Pin 1 within the Dinaledi Chamber, Rising Star Cave. A) White light-source photogrammetry scan and B) illustration of a number of elements which have been pushed up to the rock and cave walls within this area, possibly the result of sediment creep and other geological processes which occurred in the chamber.

TABLES

Body Part	Number
Cranial	44
Dentition	34
Upper Limb	27
Lower Limb	35
Thorax	19
Unidentified / other	119
Immature	5
Number of specimens	278

Table 1. Number of surface specimens, by body part, used in the spatial analysis of surface specimens recovered from the Dinaledi Chamber, Rising Star Cave.

Body Part	Number
Cranial	71
Dentition	48
Upper Limb	87
Lower Limb	98
Thorax	46
Unidentified / other	148
Immature	15
Number of specimens	498

Table 2. Number of subsurface specimens, by body part, used in the spatial analysis of subsurface specimens recovered from the main excavation pit of Dinaledi Chamber, Rising Star Cave.

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CHAPTER EIGHT: LETTERS OF SUPPORT

Letters of Support for Chapter Two: *Homo naledi*, a New Species of the Genus *Homo* from the Dinaledi Chamber, South Africa

26 January 2017

RE: Support of stated contributions of PhD Candidate Ashley Kruger

To whom it may concern

As lead author and principle investigator of the *Homo naledi* projects, I am writing on behalf of all co-authors, and in support of the contributions made by Ashley Kruger to the paper published in *eLife*: “*Homo naledi*, A New Species of the Genus *Homo* from the Dinaledi Chamber, South Africa”. Ashley’s contributions to this work include the acquisition of data fundamental for this study, and analysis and interpretation of these data. These data included the acquisition of three-dimensional models, utilised in the analysis and interpretation presented in the aforementioned publication.

I fully support Ashley Kruger’s contributions.

Yours sincerely



Prof. Lee R Berger

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CHAPTER EIGHT: LETTERS OF SUPPORT CONTINUED

**Letters of Support for Chapter Three: Geological and Taphonomic Context
for the New Hominin Species *Homo naledi* from the Dinaledi Chamber,
South Africa**

26 January 2017

RE: Support of stated contributions of PhD Candidate Ashley Kruger

To whom it may concern

As corresponding author and principle investigator of the *Homo naledi* projects, I am writing on behalf of all co-authors, and in support of the contributions made by Ashley Kruger to the paper published in *eLife*: Geological and Taphonomic Context for the New Hominin Species *Homo naledi* from The Dinaledi Chamber, South Africa". Ashley's contributions included the analyses of spatial context and skeletal distribution patterns of the *Homo naledi* assemblage. These contributions aided the taphonomic analysis presented in this paper, and subsequently formed a crucial understanding of the site formation processes at the Rising Star site.

I fully support Ashley Kruger's contributions.

Yours sincerely



Prof. Lee R Berger

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CHAPTER EIGHT: LETTERS OF SUPPORT CONTINUED

Letters of Support for Chapter Four: Multimodal Spatial Mapping and Visualisation of Dinaledi Chamber and Rising Star Cave

02/03/2017

RE: Support of stated contributions of PhD Candidate Ashley Kruger

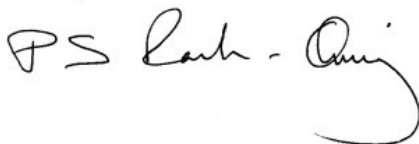
To whom it may concern:

As a co-author of the research paper entitled "Multimodal spatial mapping and visualisation of Dinaledi Chamber and Rising Star Cave", published in the *South African Journal of Science* (Kruger, A., Randolph-Quinney, P., Elliott, M. (2016) Multi-modal spatial mapping and visualisation of Dinaledi Chamber and Rising Star Cave. *South African Journal of Science*, 112.), I am writing to confirm the contributions made by PhD candidate, Ashley Kruger.

Ashley conceptualized and designed the study, undertook the primary research and analysis, wrote the original draft of the manuscript, and compiled the figures and tables for this paper. My part in the project involved, developing the original recovery protocols, supervising the student, as well as contributing to the writing and revision of subsequent drafts of the manuscript.

I hereby confirm and support Ashley Kruger's contributions.

Yours sincerely,



Dr Patrick Randolph-Quinney

28 February 2017

RE: Support of stated contributions of PhD Candidate Ashley Kruger

To whom it may concern:

As a co-author of the research paper entitled "Multimodal spatial mapping and visualisation of Dinaledi Chamber and Rising Star Cave", published in the South African Journal of Science (Kruger, A., Randolph-Quinney, P., Elliott, M. (2016) Multi-modal spatial mapping and visualisation of Dinaledi Chamber and Rising Star Cave. South African Journal of Science, 112.), I am writing to confirm the contributions made by PhD candidate, Ashley Kruger.

Ashley conceptualized and designed the study, undertook the primary research and analysis, wrote the original draft of the manuscript, and compiled the figures and tables for this paper. My part in the project involved providing primary material for analysis, supervising the in-field data collection, as well as contributing to the writing and revision of subsequent drafts of the manuscript.

I hereby confirm that Ashley Kruger's contributions were significant and are commensurate with first authorship of this work.

Sincerely,



Dr. Marina Elliott, PhD
Researcher, Exploration Sciences

and

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CHAPTER EIGHT: LETTERS OF SUPPORT CONTINUED

**Letters of Support for Chapter Five: Post-Mortem Disarticulation Patterns
in *Homo naledi*: Taphonomic Signatures of Differential Decomposition in the
Dinaledi Chamber, Rising Star Cave**



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02/03/2017

RE: Support of stated contributions of PhD Candidate Ashley Kruger

To whom it may concern:

As a co-author of the unsubmitted manuscript entitled "Post-mortem disarticulation patterns in *Homo naledi*: taphonomic signatures of differential decomposition in the Dinaledi Chamber, Rising Star Cave", I am writing to confirm the contributions made by PhD candidate, Ashley Kruger.

Ashley conceptualized and designed the study, undertook the primary research and analysis, wrote the original draft of the manuscript, and compiled the figures and tables for this paper. My part in the project involved, developing the original recovery protocols, supervising the student, aiding in the analyses and interpretation of data, as well as contributing to the writing and revision of subsequent drafts of the manuscript.

I hereby confirm and support Ashley Kruger's contributions.

Yours sincerely,

Dr Patrick Randolph-Quinney

28 February 2017

RE: Support of stated contributions of PhD Candidate Ashley Kruger

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As a co-author of the unsubmitted manuscript entitled “Post-mortem disarticulation patterns in *Homo naledi*: taphonomic signatures of differential decomposition in the Dinaledi Chamber, Rising Star Cave”, I am writing to confirm the contributions made by PhD candidate, Ashley Kruger.

Ashley conceptualized and designed the study, undertook the primary research and analysis, wrote the original draft of the manuscript, and compiled the figures and tables for this paper. My part in the project involved supervising the in-field data collection, as well as contributing to the writing and revisions of subsequent drafts of the manuscript.

Ashley Kruger’s contributions were significant and are commensurate with first authorship of this work.

Sincerely,



Dr. Marina Elliott, PhD
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John Hawks
Vilas-Borghesi Professor
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March 10, 2017

RE: Support of stated contributions of PhD Candidate Ashley Kruger

To whom it may concern:

As co-author of the unsubmitted manuscript entitled “Post-mortem disarticulation patterns in *Homo naledi*: taphonomic signatures of differential decomposition in the Dinaledi Chamber, Rising Star Cave” I am writing on behalf of, and in support of the contributions made by Ashley Kruger.

Ashley wrote the original draft of the manuscript, undertook the research and analysis, and compiled the figures. I contributed to the second draft of the manuscript, and provided interpretation of the results.

I fully support Ashley Kruger’s contributions.

Sincerely,

John Hawks

28 February 2017

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To whom it may concern

As co-author of the unsubmitted manuscript entitled "Post-mortem disarticulation patterns in *Homo naledi*: taphonomic signatures of differential decomposition in the Dinaledi Chamber, Rising Star Cave" I am writing on behalf of, and in support of the contributions made by Ashley Kruger.

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I fully support Ashley Kruger's contributions.

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CHAPTER EIGHT: LETTERS OF SUPPORT CONTINUED

**Letters of Support for Chapter Six: Spatial Taphonomy of the *Homo naledi*
Assemblage from the Dinaledi Chamber, Rising Star Cave**



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02/03/2017

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Ashley conceptualized and designed the study, undertook the primary research and analysis, wrote the original draft of the manuscript, and compiled the figures and tables for this paper. My part in the project involved, developing the original recovery protocols, supervising the student, helping with the interpretation of the data, as well as contributing to the writing and revision of subsequent drafts of the manuscript.

I hereby confirm and support Ashley Kruger's contributions.

Yours sincerely,

Dr Patrick Randolph-Quinney

28 February 2017

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To whom it may concern:

As a co-author of the unsubmitted manuscript entitled “Spatial taphonomy of the *Homo naledi* assemblage from the Dinaledi Chamber, Rising Star Cave” I am writing on behalf of, and in support of, the contributions made by Ashley Kruger.

Ashley conceptualized and designed the project, undertook the primary research and analysis, wrote the original draft of the manuscript, and compiled the figures and tables for this paper. My part in the project involved providing data for the analyses, supervising the in-field data collection, as well as contributing to the writing and revision of subsequent drafts of the manuscript.

I confirm that Ashley Kruger’s contributions were significant and are in keeping with his being the first author of this work.

Sincerely,



Dr. Marina Elliott, PhD
Researcher, Exploration Sciences

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March 10, 2017

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As co-author of the unsubmitted manuscript entitled “Spatial taphonomy of the Homo naledi assemblage from the Dinaledi Chamber, Rising Star Cave” I am writing on behalf of, and in support of the contributions made by Ashley Kruger.

Ashley wrote the original draft of the manuscript, undertook the research and analysis, and compiled the figures. I contributed to the second draft of the manuscript, provided data for the analysis, and provided interpretation on the results.

I fully support Ashley Kruger’s contributions.

Sincerely,

John Hawks

28 February 2017

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CHAPTER NINE: SUPPLEMENTAL MATERIAL

Supplemental Material to Chapter Two: *Homo naledi*, a New Species of the Genus *Homo* from the Dinaledi Chamber, South Africa

Supplementary File 1

Supplementary File 2

(Click the supplementary file above or see attachments to this PDF)

CHAPTER NINE: SUPPLEMENTAL MATERIAL CONTINUED

Supplemental Material to Chapter Three: Geological and Taphonomic Context for the New Hominin Species *Homo naledi* from the Dinaledi Chamber, South Africa

Supplementary File 1

Supplementary File 2

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CHAPTER NINE: SUPPLEMENTAL MATERIAL CONTINUED

Supplemental Material to Chapter Six: Spatial Taphonomy of the *Homo naledi* Assemblage from the Dinaledi Chamber, Rising Star Cave

Supplementary File 1

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Supplementary File 3

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