Microtomographic Archive of Hominin Fossils from the Swartkrans Formation, South Africa (1948–1967)

MATTHEW M. SKINNER*
School of Anthropology and Conservation, University of Kent, Canterbury CT2 7NR, UNITED KINGDOM; and, Max Planck Institute for Evolutionary Anthropology, Leipzig, GERMANY; matthew_skinner@eva.mpg.de

MYKOLAS D. IMBRASAS
Max Planck Institute for Evolutionary Anthropology, Leipzig, GERMANY; mykolas_imbrasas@eva.mpg.de

ROBERT M.G. MARTIN
Department of Anthropology, University of Toronto, Toronto M5S 2S2, CANADA; rob.martin@mail.utoronto.ca

MIRRIAM TAWANE
Ditsong National Museum of Natural History, Pretoria 0001, SOUTH AFRICA; tawane@ditsong.org.za

JEAN-JACQUES HUBLIN
Chaire de Paléoanthropologie, CIRB (UMR 724 – U1050), Collège de France, Paris, FRANCE; and, Max Planck Institute for Evolutionary Anthropology, Leipzig, GERMANY; jean-jacques.hublin@ecollege-de-france.fr

TRAVIS RAYNE PICKERING
Department of Anthropology, University of Wisconsin-Madison, Madison, WI, 53706, USA; and, Evolutionary Studies Institute, University of the Witwatersrand, Johannesburg 2050, SOUTH AFRICA; travis.pickering@wisc.edu

DARRYL J. DE RUITER
Department of Anthropology, Texas A&M University, College Station, TX 77843, USA; and, Centre for the Study of the Deep Human Journey, University of the Witwatersrand, Johannesburg 2050, SOUTH AFRICA; deruiter@tamu.edu

*corresponding author: Matthew M. Skinner; matthew_skinner@eva.mpg.de

submitted: 15 May 2023; revised: 4 December 2023; accepted: 23 February 2024

Handling Editor in Chief: Karen Rosenberg

ABSTRACT

Since initial excavations in 1948, the site of Swartkrans, located in the 'Cradle of Humankind,' South Africa, has yielded hundreds of fossil hominin specimens belonging to species of *Paranthropus*, *Homo*, and possibly *Australopithecus*. Here we provide an updated catalogue of material excavated between 1948–1967 from Swartkrans (SK prefix) with additional information about associations between specimens and preserved anatomy. In particular, we employ microtomography to comprehensively catalogue the preserved dental remains, including unerupted teeth. Information about the internal preservation provided here and via the website (https://human-fossil-record.org) will facilitate research applications for access to the original CT volumes from the relevant curatorial institution.

INTRODUCTION

Since excavations began there in 1948, Swartkrans has yielded hundreds of hominin fossils originally attributed to both *Paranthropus crassidens* (Broom 1949), now referred to as *Paranthropus robustus* or *Australopithecus robustus*, and *Telanthropus capensis* (Broom and Robinson 1949a), now referred to as *Homo erectus* (Robinson 1961), *Homo ergaster*, or *Homo* sp. (Grine 2004). Most recently, Clarke (2017) has also argued for the presence of late *Australopithecus* cf. *africanus* in the Swartkrans hominin sample. Here we announce the availability of a research archive of high-resolution microtomographic (microCT) scans of hominin fossils from the site of Swartkrans that were excavated between 1948–1967 (i.e., those having the SK prefix) via an open access archive (https://human-fossil-record.org). Additionally, 1) we clarify previous uncertainties about specimen

accession numbers, 2) confirm which teeth are preserved in all gnathic specimens, and 3) provide current information about the stratigraphic context of each specimen.

1948–1967 SWARTKRANS FOSSIL SAMPLE

The Swartkrans cave complex sits at an altitude of 1480m on the southeastern aspect of Swartkrans Hill, 40km northwest of Johannesburg in Gauteng Province, South Africa (Brain 1981). There have been five main periods of research at Swartkrans. Robert Broom began excavating the site in 1948 and, along with John Robinson, continued this work until his death in 1951. Subsequently, Robinson took up the Swartkrans excavations until 1953. C.K. Brain resumed excavations at the site in 1965, spending seven years sorting through breccia dumps produced from earlier lime-mining activities, and then another seven years systematically clearing the natural overburden and exposing the extent of the cave system. This was followed by a seven-year excavation of *in situ* fossiliferous deposits within the cave, when the presently accepted stratigraphy, with five separate depositional members of the Swartkrans Formation, was finally established (Brain 1993). The Swartkrans Paleoanthropology Research Project (SPRP) began current excavations at the site in 2005, under the direction of T.R. Pickering. As one of its research foci, the SPRP continues to refine the stratigraphy and absolute dating of the Swartkrans Formation (e.g., Gibbon et al. 2014; Kuman et al. 2021; Sutton et al. 2009).

Early Pleistocene hominin remains have been recovered from four of Swartkrans' recognized stratigraphic units. One of these units, the 'Talus Cone Deposit' (Sutton et al. 2009), awaits planned recodification of the Swartkrans Formation for its formal inclusion in that system. Moreover, as a more recently recognized stratum, it does not figure into the current discussion of remains recovered 1948–1967. The latter is also true for Member 3, a 0.96±0.09 Ma stratum (Gibbon et al. 2014) that has yielded fossils of *P. robustus*, as well as stone and bone tools, and debated evidence indicating that its contemporary hominins controlled fire.

Of the two remaining, relevant members, Member 1 is the oldest and consists of two distinct parts—the Hanging Remnant (HR), which is an unsupported mass of fossiliferous breccia on the north wall of the cave, and the Lower Bank (LB), a largely uncalcified body that rests on a boulder-choked portion of the cave floor. There have been various approaches to date Member 1, including biostratigraphy, (e.g., Churcher and Watson 1993; Vrba 1985), a combination of uranium series and electron spin resonance techniques (Curnoe et al. 2001), and uranium-lead dating (e.g., Balter et al. 2008). Of the last approach, Pickering et al. (2011) have provided the most precise age estimates, two of which derive from a flowstone that caps the HR, and thus, the entire Member 1 sequence (see Pickering et al. 2012 for stratigraphic justifications). These Member 1 capping dates of 1.71±0.07 Ma and 1.80±0.005 Ma overlap in their error margins. A third date of 2.249±0.077 Ma (Pickering et al. 2011) derives from a flowstone that underlies the LB, and thus, also the entire Member 1 sequence (see Pickering et al. 2012 for stratigraphic justifications). A more precise absolute date of 2.22±0.09 Ma for a large portion of the LB was generated using the isochron method for burial dating (Kuman et al. 2021).

Member 2 consists of variously calcified sediment that has been deposited in an erosional space that is up to 5 meters high between the HR and the LB. Direct radiometric dates are not yet available for Member 2, but based on its stratigraphic position between the older Member 1 and younger Member 3, it is between ~1.8 – ~1.0 Ma. Both rather outdated faunal estimates (e.g., Vrba 1985) and rather suspect uranium-lead dates (Balter et al. 2008) for the member conform to this broad range provided by the absolute dates of bracketing members discussed above. Member 1 and Member 2 have both yielded hominin fossils attributed to *Paranthropus* and *Homo* (e.g., Broom 1949; Broom and Robinson 1949a, 1950a,b, 1952; Clarke 1977; Clarke et al. 1970, Grine 1989; Grine and Daegling 1993; Pickering et al. 2012, 2016), as well as abundant archaeological traces created by one or more of these hominin taxa (e.g., Brain 1993; Brain et al. 1988; Kuman et al. 2018; Pickering et al. 2008). Clarke (2017) has also argued for the presence of *Australopithecus* in Member 1.

The specimens included in this study derive from excavations of Member 1 and 2 from 1948–1967 and tend to have an SK prefix. In 1968, the University of the Witwatersrand purchased the property on which Swartkrans resides, and the numbering system was changed to the prefix SKW. When *in situ* excavations commenced in 1979, the prefix assigned to specimens was altered to SKX. SWT designation refers to specimens recovered by the Swartkrans Paleoanthropological Research Project (SPRP) and that have been recovered since 2005 (Pickering et al. 2012). The Swartkrans numbering system is therefore based on individual phases of excavation (prefix), and when they were entered into the fossil accession catalogue (number). Several fossils were initially numbered SK 14XXX when they were discovered in the 1960s and some of these were renumbered as SKW XX in 1968 after the University of the Witwatersrand purchased the Swartkrans property (e.g., SK 14129a was changed to SKW 33 [Brain 1981]). Regarding letter designations at the end of accession numbers (e.g., SK 21a or 74c), they typically indicate the order in which fossils were extracted from a particular block of breccia. It does not necessarily indicate that they belong to the same individual or are associated at all; it was simply a means of recording numerous fossils coming from the same block. For example, SK 1587a and 1587b were recovered from the same block of breccia, and turned out to be from the same individual, while other specimens such as SK 846a and 846b were recovered from the same block but do not represent the same individual.

MICROTOMOGRAPHIC ARCHIVE

In 2006 and 2010 portable microCT scanners were brought to the Ditsong National Museum of Natural History (DNMNH) by the Department of Human Evolution, Max Planck Institute for Evolutionary Anthropology. In collabo-

ration with the DNMNH, an archive of microCT scans was created of the majority of fossil hominin specimens for the purpose of research and curation. Here we present visual representations of these CT scans (as well as photographs of the few SK specimens that were not CT scanned) and provide updated morphological details of the dentognathic remains. In particular, we clarify which teeth (including fragmented crowns and roots) are present, including those that are unerupted, for relevant specimens. In a number of cases, this is the first time the presence of these unerupted teeth has been reported. Visualizations of the CT volumes and images of surface models are available via the human-fossil-record.org online archive. Researchers interested in the original microCT scans can apply for access through the submission of an application to the DNMNH. The online, open access archive that is at the center of this collaborative research initiative is a companion to a similar archive published for the material from Kromdraai (Skinner et al. 2013).

CT SCANNING

Fossil specimens were scanned on either a BIR Actis 300/225 FP or SkyScan 1172 microtomographic scanner with a resultant isometric voxel size between ~15–100 microns. Complete scan parameters for each specimen are provided with the associated image stack. In the figures of this manuscript, as well as in the online CT archive, there are 2D images of surface renderings of each specimen (the CT archive contains multiple images of standard anatomical positions). These images were produced as screenshots (with an associated scale) in Avizo 6.3 (Visualization Sciences Group, www.vsg3d.com) of an isosurface of each specimen. This surface is based on a threshold level that was chosen manually to best represent the surface of the specimen. However, due to variation in radiopacity throughout skeletal tissues, preservative materials, and 'noise' in the CT volumes due to X-ray attenuation from the density of some specimens, some regions of a few models are poorly surfaced. As such, we do not consider images in this article to be appropriate for data collection (e.g., measurements) for research purposes. Researchers are encouraged to apply to the DNMNH through standard application procedures (including the application form that can be found at human-fossil-record.org) to acquire their own copies of the CT data and generate surface models appropriate for their particular research questions.

SPECIMENS

Table 1 presents a list of the specimens that are included in this archive. It is organized by accession number and contains a list of preserved teeth/roots and postcranial fossils, as well as information about associations between specimens. For dental specimens, the basis for tooth type is included using the follow code: 1 – specimen is *in situ* within a mandible or maxilla making the attribution certain; 2 – the attribution is based on an association with one or more other dental specimens making the attribution likely but not necessarily certain; 3 – the attribution is based on morphological evaluation of the crown and roots making the attribution uncertain. CT-based images of a number of specimens are not provided in this publication as they were unavailable for scanning. We have provided digital photographs of these specimens were possible (denoted by a small camera icon in the figure). There are a number of associations between specimens that have been noted by previous researchers through their work on the collection. In some cases, this has resulted in specimens being physically glued together, while in other cases the association is a hypothesis based on a number of potential factors including geological context, patina of the fossils, morphological similarities, and/or the degree of attrition in the case of teeth. When specimens have been glued together, we list all the original accession numbers but separate them with a '/'. Accession numbers of specimens that are informally associated are combined with a '+'. In all occlusal images of teeth mesial is towards the top and distal is towards the bottom of the figure. We have provided at least one citation for each specimen (typically an early publication in which it is included) and often this is one of the three catalogue-type publications that includes material from Swartkrans: Robinson (1956), Tobias et al. (1977), and Brain (1981). In many cases, this is the only time these specimens have been published (often without photographs) and we hope that this publication and the availability of the associated microCT will result in new research on these neglected specimens.

- **SK 1** – a complete left mandibular molar with good root preservation, slight wear but no dentine exposure, and some fractures (Figure 1). Robinson (1956) lists this specimen as a LM_2.
- **SK 2** – a right maxillary incisor with some wear and dentine exposure on the occlusal surface and the tip missing from the root apex (see Figure 1). Robinson (1956) lists this specimen as a RI^1.
- **SK 3 + SK 4 + SK 40** – two associated upper central incisors and a canine (see Figure 1). SK 3 is a right maxillary incisor that Robinson (1956) originally listed as a RI^2, but Clarke (1990) identiied, based on interproximal facets and its similarity to SK 40, as a RI^1. SK 40 is a left maxillary incisor that Robinson (1956) listed as a LI^1. SK 4 is considered a R^C and is associated to SK 3 and SK 40 by Brain (1981).
- **SK 5** – a left mandibular molar with the roots embedded in breccia (see Figure 1). Robinson (1956) lists this specimen as a LM_2.
- **SK 6 + SK 100** – an associated mandible and isolated tooth. SK 6 consists of a left hemi-mandible of an adolescent with P_3-M_3, a fragment of the right corpus with P_4-M_1, and isolated RM_2 and RM_3 (Figure 2). SK 100 is a RP_3 that is considered the antimere of the LP_3 in SK 6. The combined SK 6 and SK 100 mandible has been suggested to be associated with the SK 13 + SK 14 maxilla (Tobias et al. 1977), but we have chosen not to make this a formal association in this paper.
- **SK 7 + SK 9** – two associated mandibular premolars (see Figure 1). SK 7 is identified by Robinson (1956) as a

TABLE 1. SWARTKRANS SAMPLE INCLUDED IN THE STUDY.

Accession	Anatomy	Basis[1]	Association	Figure
SK 1	LM_2	3		1
SK 2	RI^1	3		1
SK 3	RI^1	2	SK 4 + SK 40	1
SK 4	R^C	3	SK 3 + SK 40	1
SK 5	LM_2	3		1
SK 6	mandible, LP_3-M_3, RP_4-M_3	1	SK 100; possibly SK 13/14	2
SK 7	RP_4	3	SK 9	1
SK 9	LP_4	3	SK 7	1
SK 10/SK 1648	mandible, LP_4-M_3, RM_1-M_2	1	Possibly SK 11	3
SK 11	maxilla LI^2, LP^3-M^3, RP^3-M^2	1	Possibly SK 10/SK 1648	3
SK 12a	maxilla, LI^2, LP^3-M^1, RP^3-M^2	1	SK 12b	4
SK 12b	mandible, LP_3-M_3, RP_3-M_3	1	SK 12a	4
SK 13/14	maxilla, LP^3-M^3, RP^3-M^3	1	Possibly SK 6 + SK 100	2
SK 15	mandible, LM_1-M_3, RM_2-M_3	1	SK 18a + SK 18b + SK 43	5
SK 16/1591	LM^1-M^2	2	SK 17	5
SK 17	RM^1	3	SK 16.1591 (DNMNH records)	5
SK 18a	LP_3	3	SK 15 + SK 18b + SK 43	5
SK 18b	proximal radius, left	n/a	SK 15 + SK18a + SK 43	5
SK 19	RM_2	3		5
SK 20	LM_1	3		5
SK 21/SK 3913	maxilla, LI^2-M^2	1	SK 21a	6
SK 21a	LM^3	3	SK 21/SK 3913	6
SK 22	RM_3	3	SK 880	6
SK 23	mandible, LI_1-M_3, RI_1-M_3	1		7
SK 24	LP^3	3		8
SK 25	mandible, LP_4-M_2, RP_4-M_2	1	SK 832	7
SK 27	cranium, LI^2, Ldm^2, LP^4-M^1, R^C-P^3, RM^2	1		9
SK 28	LP^4	3		8
SK 29	R_C	3		8
SK 30	LP_3	3		8
SK 31	RM^3	3		8
SK 32	RP^4	3		8
SK 33	RP^3	3		8
SK 34	mandible, LP_4-M_3, RI_1-M_3	1		10
SK 35	LM^1	3		8

TABLE 1. SWARTKRANS SAMPLE INCLUDED IN THE STUDY (continued).

Accession	Anatomy	Basis[1]	Association	Figure
SK 36	RM^3	3		8
SK 37	mandible, LM_{1-3}	1		8
SK 38	R^C	3		8
SK 39	RP^4	3		8
SK 40	LI^1	2	SK 3 + SK 4	1
SK 41	LM^3	3		8
SK 42	RM^2	3		8
SK 43	RP_4	3	SK 15 + SK 18a + SK 18b	5
SK 44	RP^3	3		8
SK 45	mandible, RM_1-M_2	1	SK 847	31
SK 46	cranium, LP^4-M^3, RP^3-M^3	1		11
SK 47	cranium, LM^{2-3}, RP^4-M^3	1		12
SK 48	cranium, L^C-M^3, R^C-M^2	1		13
SK 49	cranium, LP^3-M^3, RP^3-M^3	1		14
SK 50	os coxae, right	n/a		15
SK 52	cranium, LI^2, LP^3-M^1, RI^2, RP^3-M^1, RM^3	1	SKW 18	16
SK 54	calotte	n/a		17
SK 55a	maxilla, LI^1-M^2, Ldm^2, RI^1-P^3, Rdm^2	1	SK 1589 + SK 55b + SK 14250	18
SK 55b	mandible, L_C-P_3, Ldm_2, LM_1-M_2, Rdm_2, RP_4-M_3	1	SK 14250 + SK 55a + SK 1589	18
SK 57	maxilla, LI^2, LP^3-M^3 and RP^4-M^2	1		19
SK 61	mandible, Ldi_1-dm_2, Rdi_1-dm_2, LI_1-LP_4 and RI_1-M_1	1		19
SK 62	mandible, Ldi_1-dm_2, LM_1, Rd_C-dm_2, LI_1-M_2 and RI_1-P_4	1		19
SK 63	mandible, Ld_C-Ldm_2, Rd_C-Rdm_2, LI_2-M_2 and RI_1-M_2	1	SK 89 + SK 90 + SK 91	20
SK 64	mandible, Rdm_1-dm_2, RP_3, RM_1	1		20
SK 65	maxilla, LI^1-P^4	1	SK 65a + SK 67 + SK 74c	21
SK 65a	R^C	2	SK 65 + SK 67 + SK 74c	21
SK 66	maxilla, Rd^C-dm^2, RI^1-P^3	1		21
SK 67	RI^1	2	SK 65 + SK 65a + SK 74c	21
SK 68	LI^1	3		21
SK 69	LI^1	2	SK 73	21
SK 70	LI^2	3		21
SK 71	RI^2	3		21

TABLE 1. SWARTKRANS SAMPLE INCLUDED IN THE STUDY (continued).

Accession	Anatomy	Basis[1]	Association	Figure
SK 72	LP_3	3		21
SK 73	RI^1	2	SK 69	21
SK 74a	mandible, LP_3-M_2 and RI_2, RP_3-M_2	1		22
SK 74b	RI_1	3		21
SK 74c	RP^4	2	SK 65 + SK 65a + SK 67	21
SK 75	RM_3	2	SK 843 + 846a; possibly SK 105 + SK 826a + SKW 33	22
SK 79	cranium, LP^3-M^3, RP^3-M^3	1		23
SK 80				
SK 81	mandible, L_C-M_3, R_C-M_3	1		23
SK 82	femur, right	n/a		24
SK 83	cranium, LI^1-M^3 and RI^1-M^3; Rd^C? or Rdi^2?	1		24
SK 84	first metacarpal, left	n/a		25
SK 85	fourth metacarpal, left	n/a		25
SK 85a	R^C	2	SK 93	25
SK 86	L^C	3		25
SK 87	R_C	3		25
SK 88	LP_4	3		25
SK 89a	LM^1	2	SK 90 + SK 91 + SK 63	20
SK 90	Ldm^2	2	SK 89 + SK 91 + SK 63	20
SK 91	Rdm^1	2	SK 90 + SK 91 + SK 63	20
SK92	R^C	3		25
SK 93	L^C	2	SK 85a	25
SK 94	R_C	3		25
SK 95	L^C	3		25
SK 96	mandible, Ldm_1, L_C, LP_3	1		25
SK 97	femur, right	n/a		26
SK 98	LM^2	3		25
SK 99	LP^4	3		25
SK 100	RP_3	2	SK 6	2
SK 101	LP^3	3		26
SK 102	LM^1	2	SK 838a	26
SK 104	RM_1	3		26

TABLE 1. SWARTKRANS SAMPLE INCLUDED IN THE STUDY (continued).

Accession	Anatomy	Basis[1]	Association	Figure
SK 105	LM^3	2	SK 826a2 + SKW 33; possibly SK 75 + SK 843 + SK 846a	26
SK 438	mandible, Ldm_2, LM_1	1		27
SK 820	mandibular canine	3		n/a
SK 821	cranium, LP^3	1		27
SK 822	LP^3	3		26
SK 823	RP^3	3		27
SK 824	LP^4	3		27
SK 825	LP^4	3		27
SK 826a1	maxilla, ULP^3-M^1	1	SK 877/SKW 31	28
SK 826a2	LM^2	2	SK 105 + SKW 33; possibly SK 75 + SK 843 + SK 846a	26
SK 826b/SK 828	LP_4-M_1	2		27
SK 827	LP_4	3		27
SK 829	LM^1	3		27
SK 830	LP_4	3		27
SK 831	RP_3	3		27
SK 831a	maxilla, LM^2-M^3	1		28
SK 832	LM^1	3	SK 25	7
SK 833	LM^1	3		27
SK 834	RM^2	3		27
SK 835	LM^3	3		27
SK 836	LM^3	3		27
SK 837	RM^2	3		28
SK 838a	maxilla, Rdm^2, RP^4, RM^1	1	SK 102	26
SK 838b	LM_1	3		28
SK 839	maxilla, Rdi^1, Rdm^1-dm^2, RI^1-I^2, RM^1, Ldi^1, LI^1, LI^2?, LM^1	1	SK 852	29
SK 840	LM_3	2	SK 855	28
SK 841a	mandible, Ldm_2, LM_1	1		28
SK 841b	LM_3	3		28
SK 842	Ldm_2	2	SK 869	28
SK 843	mandible, LM_1-M_3	1	SK 75 + SK 846a; possibly SK 105 + SK 826a + SKW 33	22
SK 844	mandible, LM_2-M_3	1		30

TABLE 1. SWARTKRANS SAMPLE INCLUDED IN THE STUDY (continued).

Accession	Anatomy	Basis[1]	Association	Figure
SK 845/SK 14251	maxilla, LI^2-M^2, RP^3-M^1	1		30
SK 846a	RM_1	2	SK 75 + SK 843; possibly SK 105 + SK 826a + SKW 33	22
SK 847	cranium, LI^2, LP^3, RP^3-P^4, LM^2-M^3 (includes SK 80 maxilla and isolated RP^4)	1	SK 45	31
SK 848	temporal with incus, malleus, and stapes	n/a		32
SK 849	RM^1	3		32
SK 850	mandibular premolar	3		28
SK 851	RM_3	3		32
SK 852	mandible, Ldm_1-dm_2, LI_1-M_1, Rdc, Rdm_1-dm_2, RP_3, RM_1	1	SK 839	29
SK 853	lumbar vertebra	n/a		33
SK 854	cervical vertebra (C2)	n/a		33
SK 855	RM_3	2	SK 840	28
SK 856	RP^4, $RM^{1/2}$	3		32
SK 857	RP_3	3		32
SK 858/SK 861/SK 883	mandible, LI_1-M_2, RI_1-M_3	1		33
SK 859	cranium	n/a		34
SK 862	mandible, RP_4-M_3	1		35
SK 863	molar?	3		35
SK 864	mandibular molar?	3		35
SK 865	molar?	3		35
SK 866	tooth fragment	3		35
SK 867	maxillary premolar	3		36
SK 868	RM^2-M^3	3		36
SK 869	mandible, Ldm_1, LP_3	1	SK 842	28
SK 870	LM^3	3		36
SK 871	LM_3	3		36
SK 872	LM^1	3		36
SK 873	incisor	3		36
SK 874	tooth fragment	3		36
SK 875	tooth fragment	3		n/a
SK 876	mandible, Lc-M_3, RI_2-M_3	1		37
SK 877/SKW 31	maxilla, URP^4-M^2	1	SK 826a1	28

TABLE 1. SWARTKRANS SAMPLE INCLUDED IN THE STUDY (continued).

Accession	Anatomy	Basis[1]	Association	Figure
SK 878	Cranial fragments and two partial tooth crowns	3		36
SK 879	temporals, left and right, long bone fragments	n/a		37
SK 880	LM_3	3	SK 22	6
SK 881	maxilla, LP^3-P^4, fragmentary $M^{1?}$	1	SK 882	38
SK 882	left partial maxillary molar	3	SK 881	38
SK 884	fragments of mastoid and L_C	3		38
SK 885	LM_3	3		36
SK 1425a/SK 2635	L^C-M^3	1		38
SK 1512/SK 1592	maxilla, two left molars, RP^4-M^3, RI^2?	1		39
SK 1514	mandible, M_1-M_2	2		39
SK 1524	LM^3	3		n/a
SK 1585	endocast	n/a		40
SK 1586	mandible, LP_4-M_3 and RI_2-M_3, 3 anterior tooth roots	1		40
SK 1587a	mandible, LI_2, LP_3-M_2	1	SK 1587b	39
SK 1587b	RM_2	2	SK 1587a	39
SK 1588	mandible, R_C-M_2	1		40
SK 1589	RP^4	3	SK 55a + SK 55b + SK 14250	18
SK 1590	maxilla, RI^2-M^1, LP_4-LM_2, femoral head, os coxa	1		41
SK 1592	RP^4-M^3	1		42
SK 1593	RP_3	3		42
SK 1594	RM_1	3		42
SK 1595	maxilla, LI^1-I^2, LM^1 and Ldm^2	1		42
SK 1596	maxillary canine	3		42
SK 1813	first metatarsal, right	n/a		42
SK 1896	distal femur, right	n/a		42
SK 2147	Ldm^1	3		n/a
SK 2223	fragmentary tooth crown	3		n/a
SK 2381	zygomatic	n/a		43
SK 2598	Distal humerus	n/a		n/a
SK 3121	femur, right	n/a		43
SK 3155b	os coxae, right	n/a		43

TABLE 1. SWARTKRANS SAMPLE INCLUDED IN THE STUDY (continued).

Accession	Anatomy	Basis[1]	Association	Figure
SK 3974	RM_1	3		43
SK 3975	LM^3	3		43
SK 3976	LM_2	3		43
SK 3977	RM^3	3		43
SK 3978	mandible, Ldm_1-dm_2, Rdm_1-dm_2, RI_2-RP_3, LI_1-LP_3, LM_1	1		43
SK 3981a	T12 vertebra	n/a	SK 3981b	44
SK 3981b	L5 vertebra	n/a	SK 3981a	44
SK 6934	incisor crown	3		n/a
SK 14000	molar fragment	3		44
SK 14001	LP_3	3		44
SK 14003	RM_1-M_3	1		44
SK 14024	partial femoral head	n/a		45
SK 14115	fragmentary tooth	3		45
SK 14132	fragmentary tooth	3		45
SK 14133	maxilla, LP^4-M^1	1		45
SK 14246	mandible, anterior tooth roots	3		45
SK 14248	cranial fragment	n/a		n/a
SK 14249	maxillary fragments?	n/a		n/a
SK 14250	mandibular fragments in breccia	n/a	SK 55b + SK 55a + SK 1589	18
SK 24600	distal humerus, left	n/a		46
SK 24601	proximal radius, left	n/a		46
SK 24605	maxillary molar	3		n/a
SK 24606	maxillary molar	3		n/a
SK 24607	root fragment	3		n/a
SK 24613	tooth fragment	3		n/a
SK 24626	LP_3-P_4	1		45
SK 24627	Root and crown fragments of multiple teeth	3		n/a
SK 24628	maxillary molar crown fragment	3		45
SK 24629	LM^1	3		45
SK 24630	LP^4	2	SK 24631	45
SK 24631	LP^3	2	SK 24630	45
SK 24632	maxillary molar fragment	3		n/a
SK 24633	RM^2	3		45
SK 24653	maxillary premolar	3		n/a

TABLE 1. SWARTKRANS SAMPLE INCLUDED IN THE STUDY (continued).

Accession	Anatomy	Basis[1]	Association	Figure
SK 24660	mandible	3		n/a
SK 24661	maxillary canine	3		n/a
SK 24662	maxillary molar	3		n/a
SK 42207	maxillary incisor	3		n/a
SKW 18	basicranium, right incus, stapes and malleus	N/A	SK 52	16
SKW 33	RM^1-M^2	2	SK 105 + SK 826a2; possibly SK 75 + SK 843 + SK 846a	26

[1]Tooth type basis: 1 – specimen is *in situ* within a mandible or maxilla making the attribution certain; 2 – the attribution is based on an association with one or more other dental specimens making the attribution likely but not necessarily certain; 3 – the attribution is based on morphological evaluation of the crown and roots making the attribution uncertain.

RP_4 with very little wear and well-preserved roots. SK 9 is identified by Robinson (1956) as a LP_4 with very little wear and some enamel broken off at the cervix. Tobias et al. (1977) identify SK 7 and SK 9 as antimeres.

- **SK 10/SK 1648** – two mandibular fragments whose anatomical connection (Figure 3) was determined by Clarke (1990). SK 10 is a portion of mandibular corpus that Tobias et al. (1977) list as containing LM_2-M_3. They list SK 1648 as containing LP_4-M_1 and RM_1-M_2. No scan of this specimen was available for this publication. Tobias et al. (1977) and Brain (1981) suggest that it is probably the same individual as SK 11 but we have chosen not to make this a formal association.
- **SK 11** – a maxilla of an adult preserving much of the lower face and with L^C-M^3 and RP^3-M^2 (see Figure 3). Tobias et al. (1977) and Brain (1981) suggest that it is probably the same individual as SK 10/SK 1648 but we have chosen not to make this a formal association. Plaster has been added to adhere the various parts of the specimen together (particularly on the palate and right maxilla superior to the teeth).
- **SK 12a + SK 12b** – an associated maxilla (SK 12a) and mandible (SK 12b) with markedly worn teeth (Figure 4). The maxilla preserves roots and/crowns of LI^2, LP^3-M^1, RP^3-M^2 (Brain 1981). The mandible preserves roots and/or crowns of L_C-M_3, R_C-M_3. The left condyle, coronoid process, and mandibular angle of SK 12b have been reconstructed from plaster.
- **SK 13/SK 14** – a maxilla preserving the middle and lower face and containing LP^3-M^1, M^3 and RP^3-M^3 (SK 13). Clarke (1990) identified the LM^2 (SK 14) and attached it to the palate (see Figure 2). It has been suggested that this specimen is probably the same individual as SK 6 and SK 100 (Tobias et al. 1977) but we have chosen not to make this a formal association. Plaster has been added to parts of the maxilla during the reconstruction and preservation process, particularly on the posterior surface and to hold the erupting RM^3.
- **SK 15 + SK 18a + SK 18b + SK 43** – an associated mandible, two isolated teeth, and a proximal radius (Figure 5). SK 15 is a mandible containing RM_2-M_3 and LM_1-M_3. It is the holotype of *Telanthropus capensis* (Broom and Robinson 1949a), was later reassigned to *Homo erectus* by Robinson (1961), and has recently been attributed to *Paranthropus* by Zanolli and colleagues (2022). The right alveolar margin from the RM_2 to the ascending ramus has been reconstructed with plaster. SK 18a is a mandibular premolar that Broom and Robinson (1952) consider to be a LP_3. It is associated with SK 15 (Broom and Robinson 1949a) and is generally considered *Homo* (Grine 2005); however, Davies et al. (2019) found similarities in the morphology of the enamel-dentine junction with *Paranthropus*. SK 18b is the proximal end of a left radius that is associated with SK 15 and SK 18a based on its spatial association within the deposits (Broom and Robinson 1949a, 1952). SK 43 is a worn mandibular right premolar in two fragments. Tobias et al. (1977) and Brain (1981) list this specimen as a mandibular RP_4 and indicate that it is associated with SK 15 and SK 18a.
- **SK 16/SK 1591 + SK 17** – an associated partial maxilla and isolated tooth (see Figure 5) whose association was determined by Clarke (1990). SK 16 is a left maxillary molar that was listed as a LM^3 by Robinson (1956) presumably based on the tapering of the distal crown and the lack of a distal interproximal facet. However, Clarke (1990) established its direct articulation with the distal alveolus behind the molar in SK 1591 (as well as the matching interproximal facets). Thus, if SK 1591 is a LM^1 as suggested by Clarke (1990), then SK 16 is a LM^2. SK 17 is a strong antimeric match with SK 1591 based on morphology and level of attrition and is thus also considered a RM^1 (as noted by Robinson 1956).
- **SK 19** – a right mandibular molar embedded in breccia

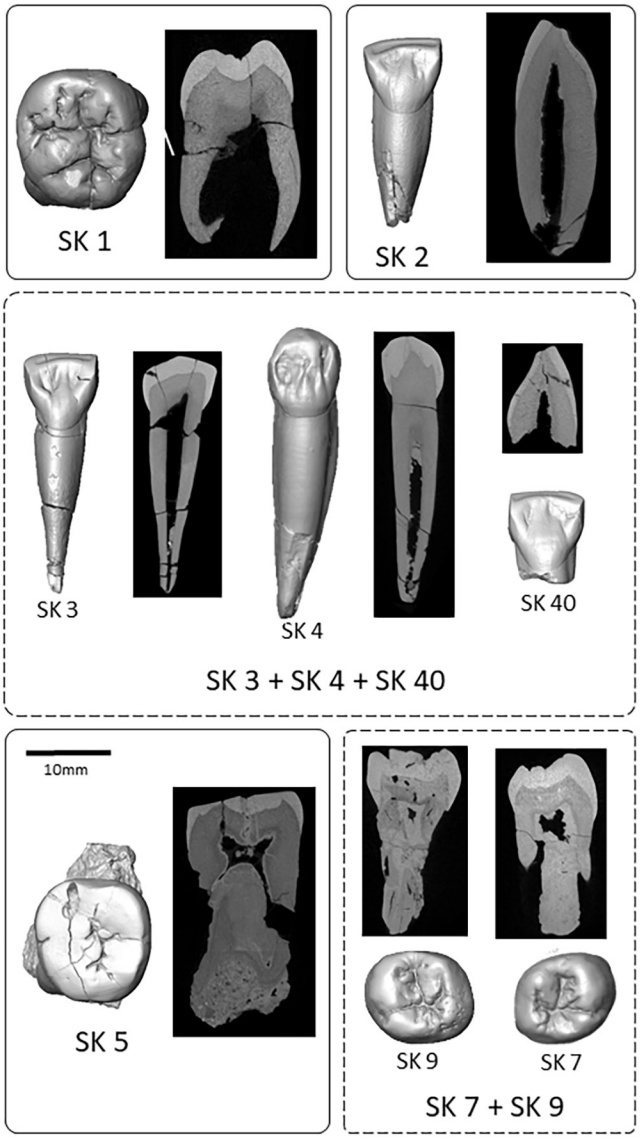

Figure 1. SK 1, SK 2, SK 3 + SK 4 + SK 40, SK 5, SK 7 + SK 9. In this and all subsequent figures, specimens are represented by digital surface renderings derived from the CT scans and a representative cross-section (not to scale) through the CT volume. In cases where specimens were not CT scanned, digital photographs are provided and identified with a camera icon. Specimens surrounded by a dotted line, rather than a solid line, identify sets of specimens that have been formally associated either in previous publications or in this publication (see text descriptions for further detail.

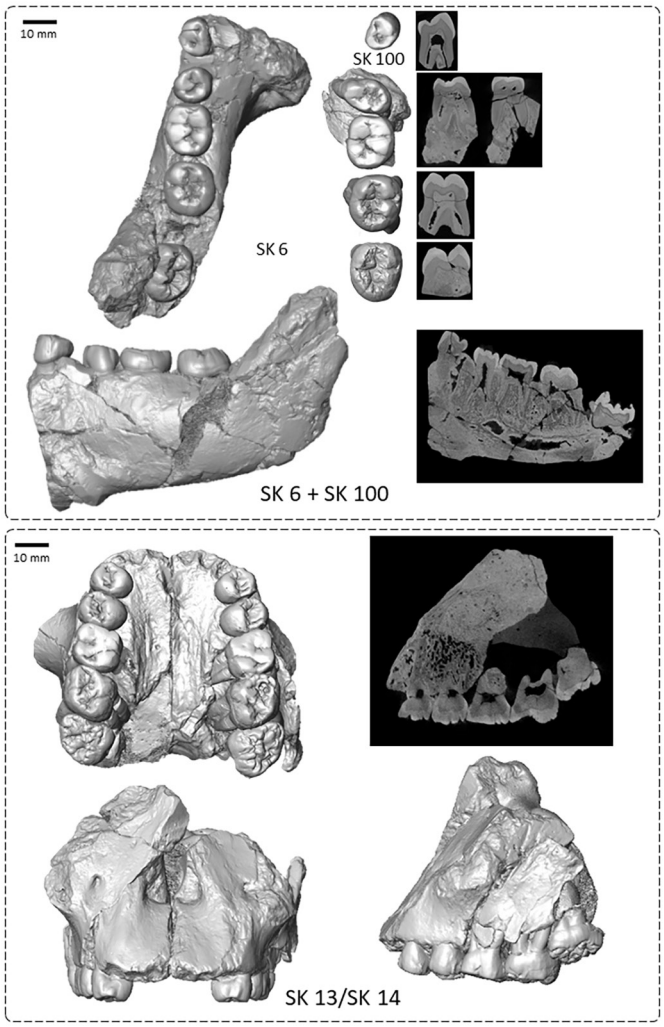

Figure 2. SK 6 + SK 100, SK 13/SK 14.

(see Figure 5). There is a large portion of enamel missing along the lingual and distal faces of the crown that has exposed the dentine. The crown is unworn, but it is difficult to tell from the degree of noise in the CT scan if the roots are broken off or developing. Based on its morphology, Tobias et al. (1977) list this specimen as a RM_2.

- **SK 20** – a worn left mandibular molar with moderate dentine exposure on the cusps and with fragments of enamel missing from the mesiobuccal and distolingual corners of the crown (see Figure 5). Tobias et al. (1977) lists this specimen is listed as a LM_1.
- **SK 21/SK 3913 + SK 21a** – an associated maxilla and isolated tooth. SK 21 is a fragmented left portion of a maxilla (with some adhering breccia) containing roots and/or crowns of LI^2-M^2 (Figure 6). Enamel crowns are heavily worn and the LI^2 (not noted in Tobias et al. 1977) is represented only by a small fragment of root. Tobias et al. (1977) include a LM^3 with SK 21 but this molar is currently identified as SK 21a in the collections and in Brain (1981). SK 3913 is a small maxilla fragment preserving approximately half of the crown and half of the root of the left canine, plus half of the crown and most of the root of the left lateral incisor (de Ruiter in press), which can be refit to SK 21 (as we have done virtually in Figure 6).
- **SK 22 + SK 880** – an associated antimeric set of mandibular molars (Tobias et al. 1977; association not noted in Brain 1981). SK 22 is a right mandibular molar that Robinson (1956) lists as a RM_3 (see Figure 6). SK 880 is

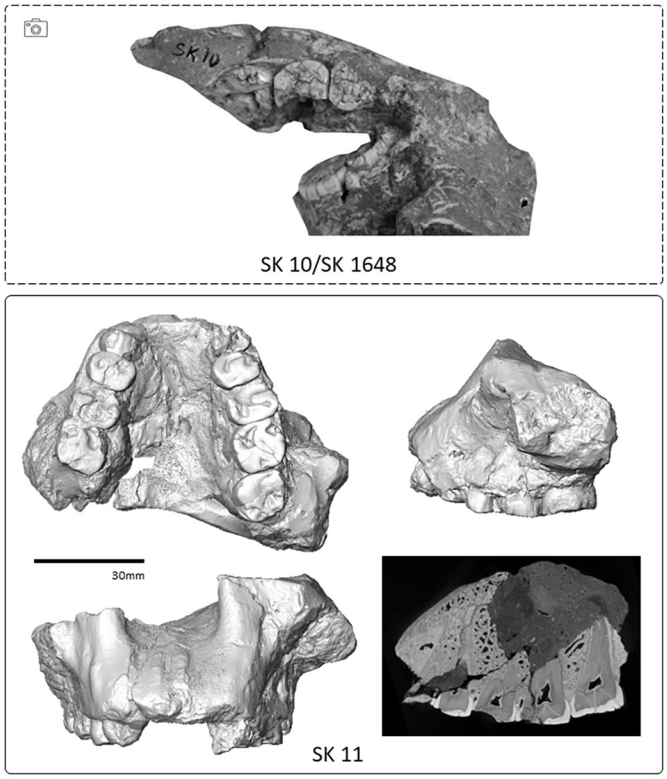

Figure 3. SK 10/SK 1648, SK 11.

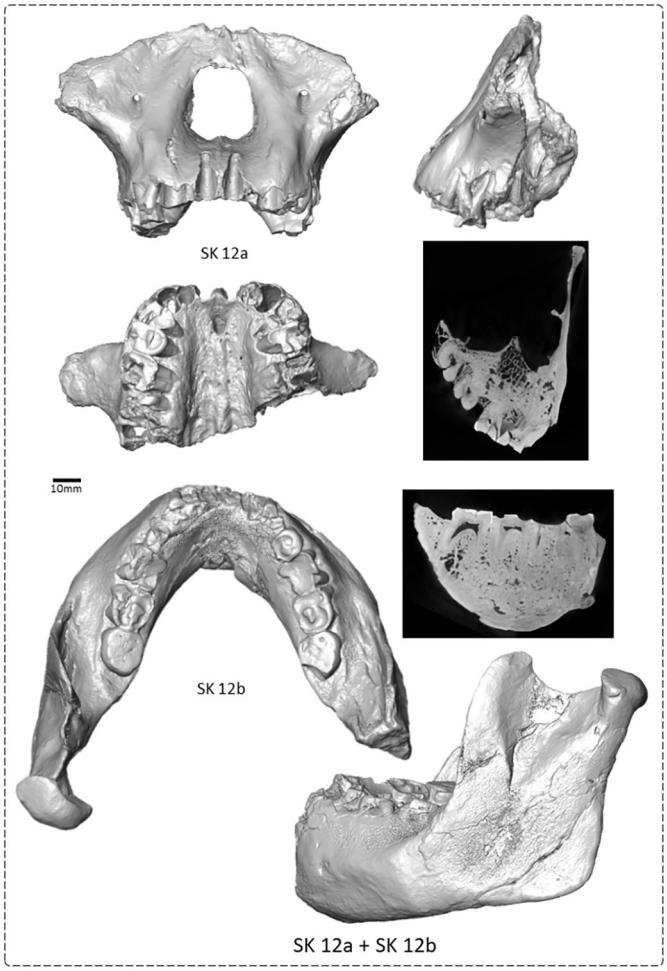

Figure 4. SK 12a + SK 12b.

a left mandibular molar that Tobias et al. (1977) lists as a LM_3. The roots are missing from the scan. Note that Tobias et al. (1977: 142) list SK 880 as "SK 880 a + b" and as a "lt M3 associated with two very broken dents"; we assume that SK 880b referred to the two fragments (not imaged here).

- **SK 23** – a well-preserved mandible (Figure 7) with RI_1-M_3, LI_1-M_3 (Brain 1981).
- **SK 24** – a complete left maxillary premolar with only slight wear, and fractures throughout both the crown and roots (Figure 8). Based on its morphology, Robinson (1956) lists the specimen as a LP^3.
- **SK 25 + SK 832** – an associated mandible and isolated maxillary molar crown (see Figure 7). SK 25 is a mandible containing LP_4-M_2 and RP_4-M_3. The unerupted right third molar was not previously noted by Tobias et al. (1977) or Brain (1981). Brain (1981) suggest this specimen is probably the same individual as SK 832, which is listed as a LM^1 by Robinson (1956).
- **SK 27** – a crushed and fragmented cranium containing roots and/or crowns of Ldm^2, LI^2, LP^4-M^2 and Rdm^2, RI^1-R^C, RM^1 (Figure 9). The Rdm^2, R^C, roots of the RI^1, RI^2, and the unerupted LM^2 were not noted by Brain (1981). Isolated teeth that were removed from the maxilla (Brain 1981) include a LP^3, L^C, and RM^2.
- **SK 28** – a complete and slightly worn left maxillary premolar with fractures in both the crown and roots (see Figure 8). Robinson (1956) lists this specimen as a LP^4, however, Plummer (2021) found strong evidence from the EDJ morphology of this crown indicating it is more likely a LP^3.
- **SK 29** – a R_C (Robinson 1956) that was not scanned for this publication (see Figure 8).
- **SK 30** – a moderately worn left mandibular premolar with near complete roots (see Figure 8). Robinson (1956) lists this specimen as a LP_3.
- **SK 31** – a slightly worn right maxillary molar with some fractures in the crown and roots, and some reparative filler (see Figure 8). Robinson (1956) lists this specimen as a RM^3.
- **SK 32** – a maxillary premolar with multiple fractures in the roots and crown, and chips of enamel missing from the distal and lingual faces of the crown (see Figure 8). Robinson (1956) lists this specimen as a RP^4.
- **SK 33** – a slightly worn maxillary premolar with multiple fractures in the roots and crown, with the distobuccal root missing (see Figure 8). Robinson (1956) and Wood and Engleman (1988) list this specimen as a RP^3.
- **SK 34** – a mandible of an adult in two halves (Figure 10) containing LP_4-M_3 and LI_1, RI_1-M_3 (Brain 1981). Plaster has been used inside the body of the corpus during the reconstruction and preservation process.
- **SK 35** – an isolated molar fragment that Brain (1981)

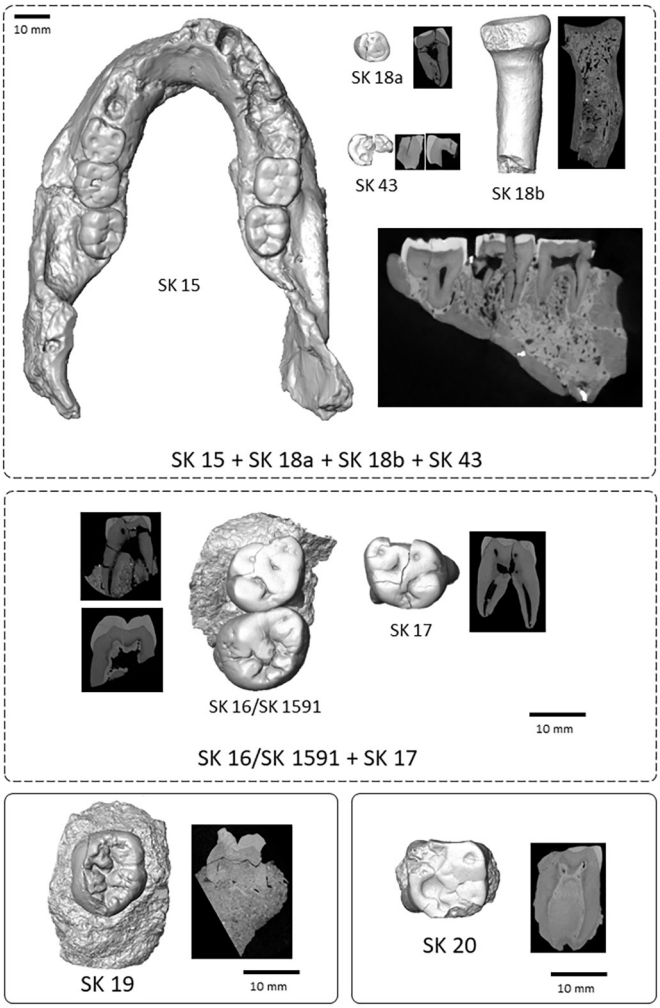

Figure 5. SK 15 + SK 18a + SK 18b + SK 43, SK 16/SK 1591 + SK 17, SK 19, SK 20.

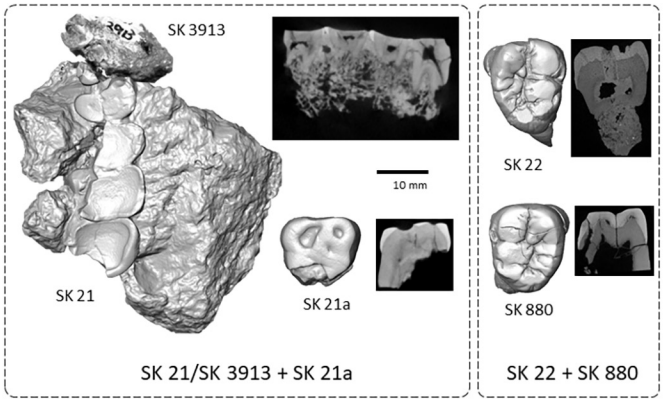

Figure 6. SK 21/SK 3913 + SK 21a, SK 22 + SK 880. Note that SK 3913 is represented in the figure by a digital photograph that we have placed adjacent to the digital surface model of SK 21.

identifies as a LM^1 (see Figure 8). It was not scanned for this publication.

- **SK 36** – a slightly worn right maxillary molar with multiple fractures in the crown and roots and some adhering breccia (see Figure 8). The enamel-dentine junction and coronal dentine is poorly preserved. Based on its morphology, Robinson (1956) lists this specimen as a RM^3.
- **SK 37** – a fragmentary left mandibular fragment containing LM_1-M_3 (see Figure 8). The LM_1 consists only of the distal end of the crown and the LM_3 only preserves a mesial fragment of the unerupted and developing crown. Robinson (1956) identified the complete molar as a LM_2 and by extension that identifies the mesial and distal crown fragments. The CT scan is limited to the crown of the LM_2 and LM_1 fragment.
- **SK 38** – listed as a R^C by Brain (1981). It was not scanned for this publication (see Figure 8).
- **SK 39** – a fragmented maxillary premolar (see Figure 8) that Tobias et al. (1977) list as a RP^4.
- **SK 41** – a worn left maxillary molar (see Figure 8); Robinson (1956) lists this specimen as a LM^3.
- **SK 42** – a worn and fragmented right maxillary molar (see Figure 8) that Tobias et al. (1977) list as a RM^2 (there is also a faint distal interproximal facet).
- **SK 44** – a worn maxillary premolar with some dentine exposure and broken root apices (see Figure 8). Tobias et al. (1977) list this specimen as an 'abnormal' RP^3.
- **SK 46** – a partial cranium with the left half of the brain-

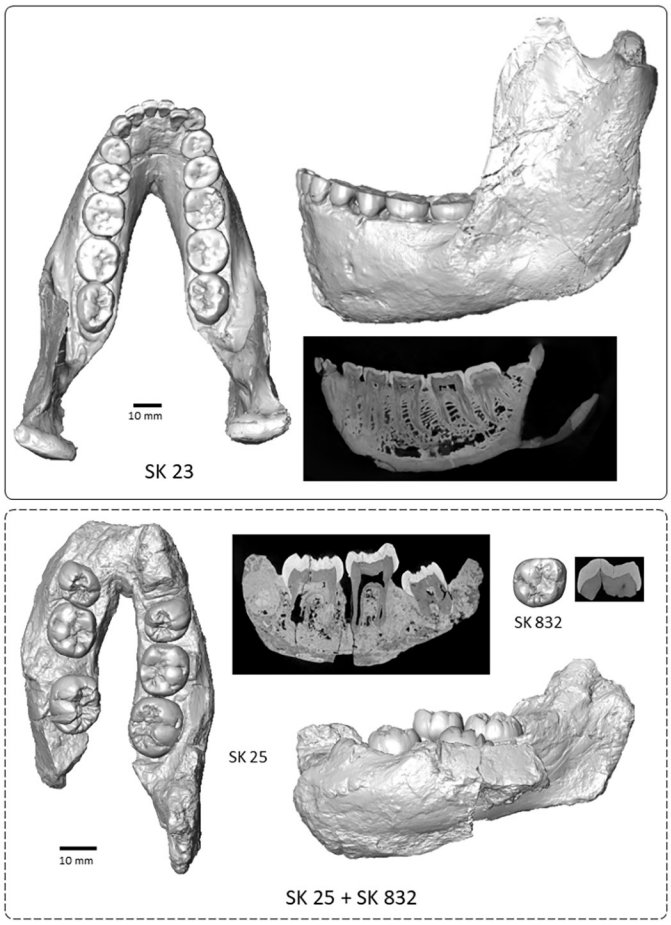

Figure 7. SK 23, SK 25 + SK 832.

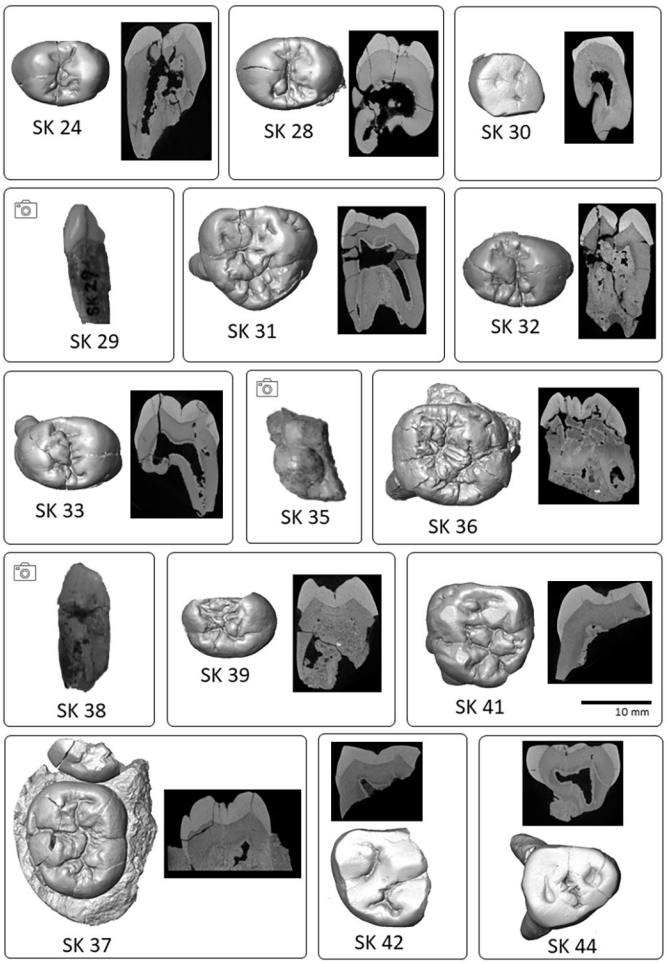

Figure 8. SK 24, SK 28, SK 29, SK 30, SK 31, SK 32, SK 33, SK 35, SK 36, SK 37, SK 38, SK 39, SK 41, SK 42, SK 44.

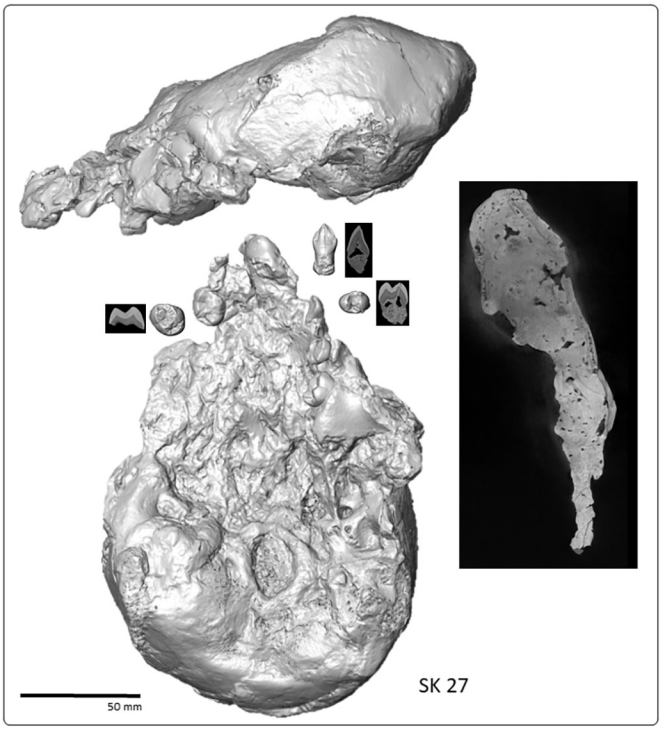

Figure 9. SK 27.

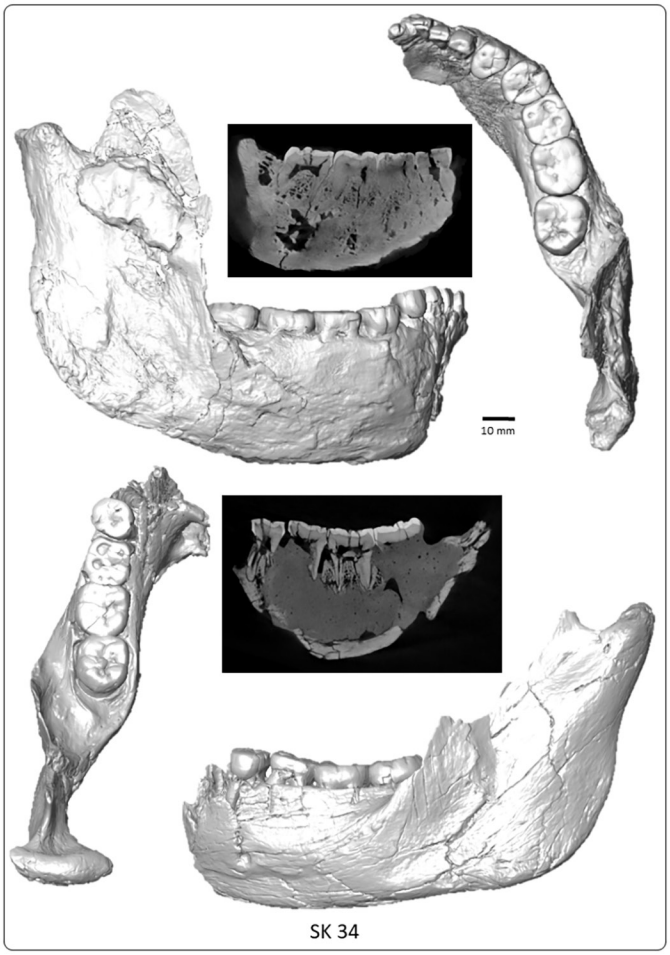

Figure 10. SK 34.

case (Figure 11), a portion of the left upper face, and the maxilla containing crowns/roots of LP^4-M^3 and RI^1 (root only), RP^3-M^3 (Brain 1981).

- **SK 47** – a fragmented and crushed cranium preserving parts of the neurocranium, the cranial base, and maxilla (Figure 12). The maxilla contains a developing dentition that includes LM^1-M^2 and RP^4-M^3 (Brain 1981). The alveolar sockets of the anterior teeth are partially preserved.
- **SK 48** – a cranium containing crown/roots of L^C-M^3 and R^C-M^2. L^C-P^4 are only preserved as roots or partial roots (Figure 13). The crowns of the RP^4-M^2 were originally accessioned as SKW 7 and their direct association with SK 48 was determined by Clarke (1990). Plaster has been added into and above the palate as part of the reconstruction and preservation process.
- **SK 49** – a fragmented and crushed cranium (Figure 14) containing LP^3-M^3 and RP^3-M^3 (Brain 1981).
- **SK 50** – a partial right os coxae (Figure 15) including the ischium and ilium (Brain 1981).
- **SK 52 + SKW 18** – two associated parts of the same cranium (Clarke 1990). SK 52 preserves parts of the right temporal, right orbit and zygomatic, and the maxilla

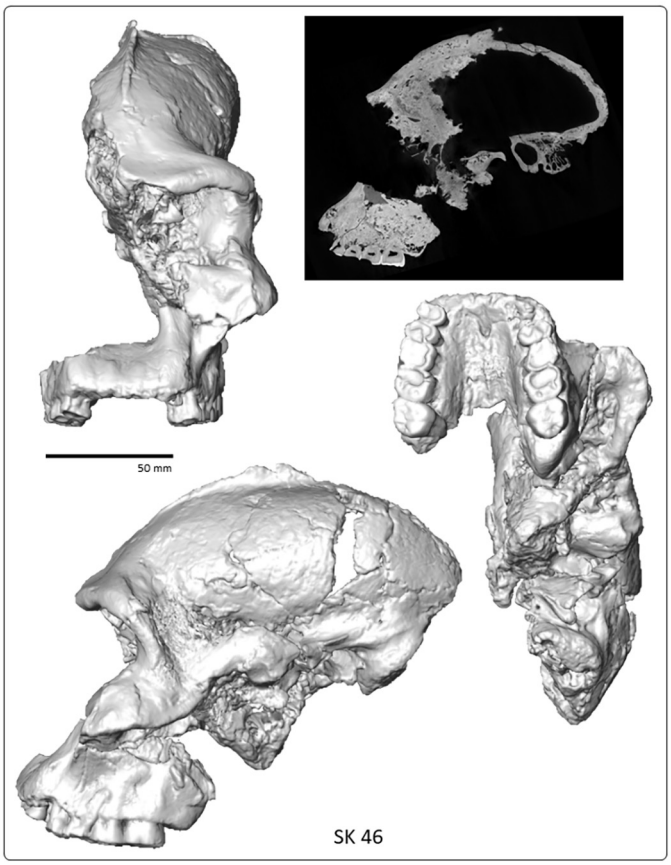

Figure 11. SK 46.

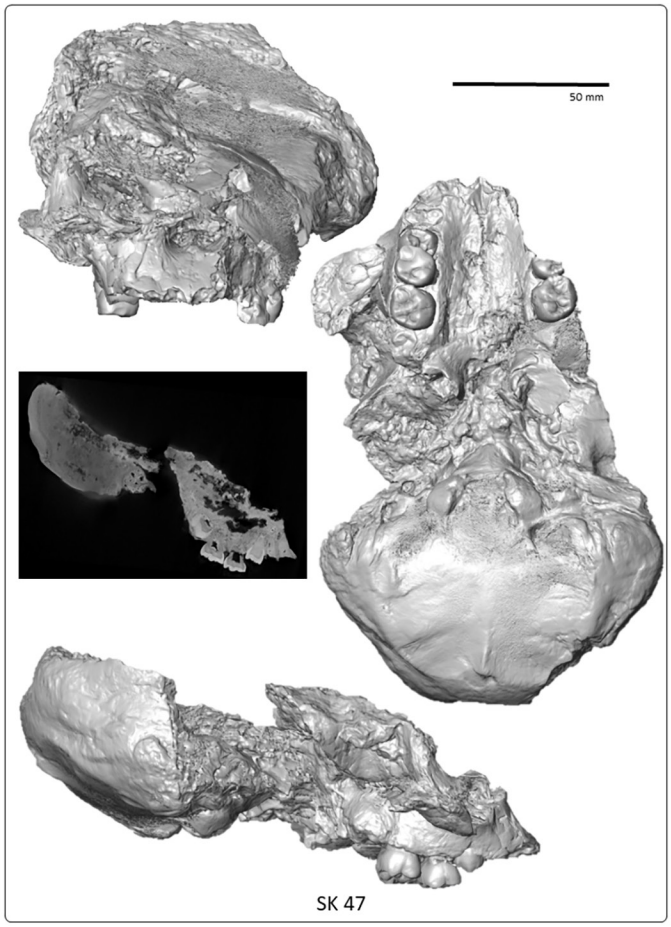

Figure 12. SK 47.

(Figure 16). The maxilla contains RI^2, RP^3-M^1, RM^3 and LI^2, LP^3-M^1. SKW 18 is a partial cranium preserving parts of the occipital, temporals (petrous portion of the right temporal is isolated and scanned separately) and right parietal (de Ruiter et al. 2006). It also preserves the right incus, stapes, and malleus.

- **SK 54** – a fragmented and crushed calvaria (Figure 17) that includes a separate fragment of the temporal-zygomatic (Brain 1981).
- **SK 55a + SK 1589 + SK 55b + SK 14250** – an associated partial maxilla and mandible. SK 55a is a maxilla containing Ldm^2, LI^1-M^2 and Rdm^2, RI^1-P^3 (Figure 18). Clarke (1990) determined its association with SK 1589 (RP^4). SK 55b is a mandible containing Ldm_2, L_C-M_2 and Rdm_2, RM_1-M_3. Clarke (1990) determined its association with SK 14250, which consists of mandibular fragments in breccia (not scanned).
- **SK 57** – a crushed and fragmented maxilla (Figure 19) containing LI^2, LP^3-M^3 and RP^4-M^2 (Brain 1981). Our identification of the displaced tooth located mesially to the RM^1 as the RP^4 is based its location and the degree of splay in the buccal roots, which resembles that of the LP^4.
- **SK 61** – a mandible containing Ldi_1-dm_2 and Rdi_1-dm_2 (see Figure 19). Unerupted permanent teeth include LI_1-LP_4 and RI_1-M_1 (Brain 1981; Conroy and Vannier 1991).
- **SK 62** – a mandible containing Ldi_2-dm_2 and Rd_C-dm_2 (see Figure 19). Unerupted permanent teeth include LI_1-M_2 and RI_1-P_4 (Brain 1981; Conroy and Vannier 1991).
- **SK 63 + SK 89a + SK 90 + SK 91** – an associated mandible and isolated maxillary teeth (Brain 1981). SK 63 is a mandible in two halves containing Ld_C-dm_2 and Rd_C-dm_2 (Figure 20). Unerupted permanent teeth include LI_2-M_2 and RI_1-M_2 (Conroy and Vannier 1991). According to Robinson (1956) and Brain (1981), SK 89a includes a RM^1 and a LM^1. Only the LM^1 has been CT scanned and included here and currently the RM^1 that was originally part of SK 89a is not in the museum collections. SK 90 is a worn left maxillary deciduous molar that is listed as a Ldm^2 molar by Robinson (1956). SK 91 is a worn right maxillary deciduous molar that is listed as a Rdm^1 by Robinson (1956).
- **SK 64** – a hemi-mandible containing Rdm_1-dm_2 (see Figure 20). It also contains a developing RP_3 and RM_1 that were noted by Conroy and Vannier (1991).
- **SK 65 + SK 65a + SK 67 + SK 74c** – a partial maxilla (Figure 21) combining a number of associated teeth (Brain 1981; Clarke 1977). SK 65 is a left partial maxilla containing LI^1-P^4. SK 65a is a R^C, SK 67 is a RI^1, and SK 74c is a RP^4.

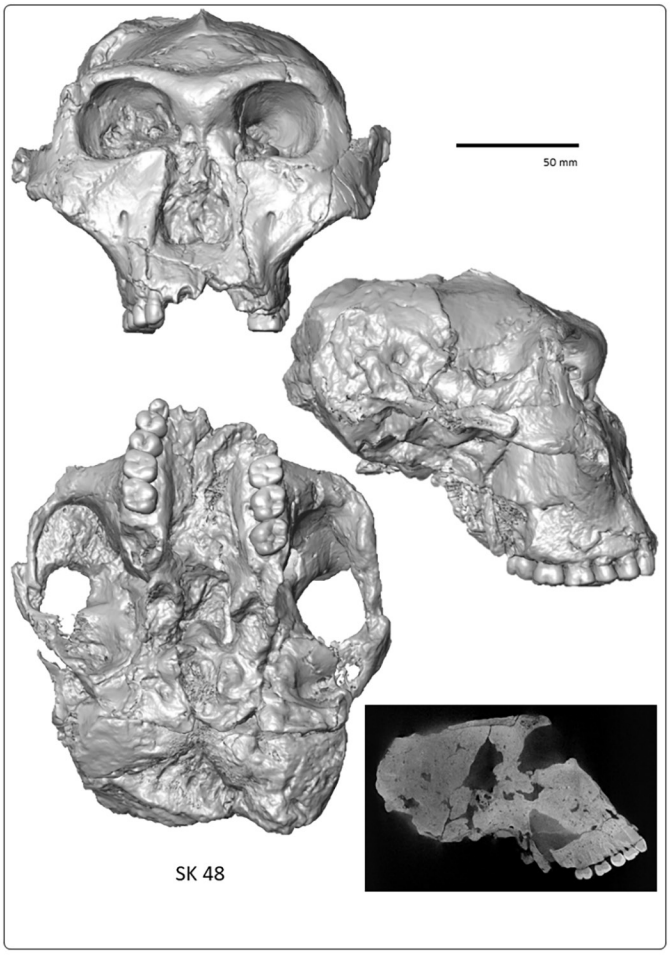

Figure 13. SK 48.

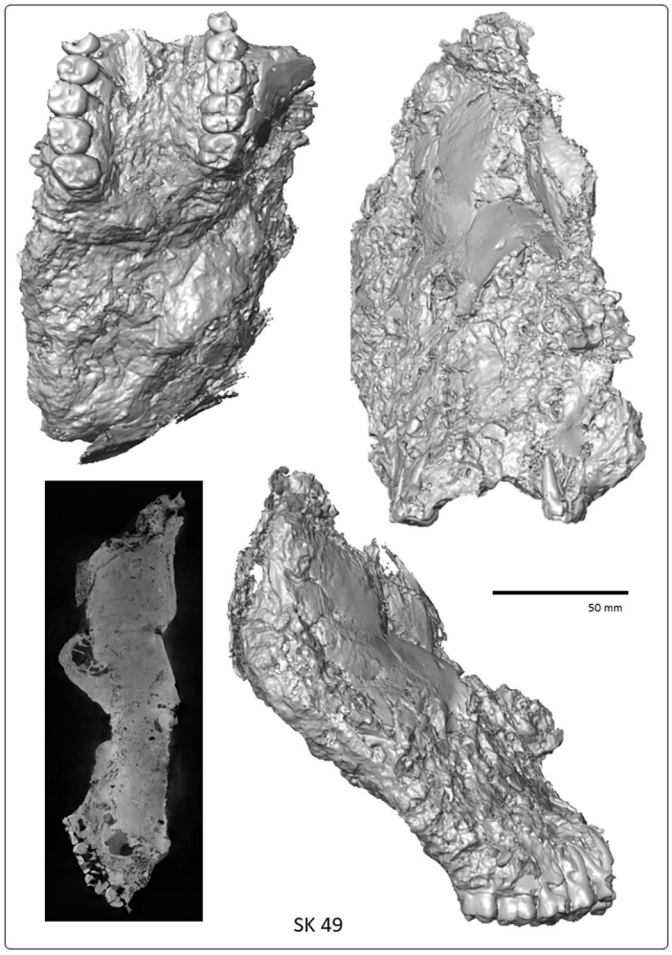

Figure 14. SK 49.

- **SK 66** – a right maxilla (see Figure 21) containing roots of Rd^{C}-dm^{2} (note the root of the Rd^{C} is double). Unerupted permanent teeth include RI^{1}-RP^{3} (Brain 1981).
- **SK 68** – an unworn left maxillary incisor (see Figure 21) that Robinson (1956) lists as a LI^{1}.
- **SK 69 + SK 73** – two associated maxillary incisors (Brain 1981). SK 69 is considered a LI^{1} and SK 73 is considered a RI^{1} (Robinson 1956). SK 69 was not scalled for this publication (see Figure 21).
- **SK 70** – a maxillary incisor that Brain (1981) identifies as a LI^{2} (see Figure 21). It was not scanned for this publication.
- **SK 71** – a maxillary incisor that Brain (1981) identifies as a RI^{2} (see Figure 21). It was not scanned for this publication.
- **SK 72** – a complete, but worn, left mandibular premolar (see Figure 21) that Robinson (1956) lists as a LP_{3}.
- **SK 74a** – a mandible containing poorly preserved crowns/roots of LP_{3}-M_{2} and RI_{2}, RP_{3}-M_{2} (Figure 22). It has been suggested that this specimen exhibits a mental eminence (Broom and Robinson 1950b; Tobias et al. 1977; Brain 1981).
- **SK 74b** – a right mandibular incisor that Robinson (1956) lists as a RI_{1} (see Figure 21). Tobias et al. (1977) note that this specimen is not associated with either SK 74a or SK 74c.
- **SK 75 + SK 843 + SK 846a** – an associated left partial hemi-mandible (see Figure 22) and two isolated teeth (Brain 1981; Tobias et al. 1977). SK 75 is a developing RM_{3} that is considered the antimere of the unerupted LM_{3} in SK 843 (note that Brain 1981 did not recognize

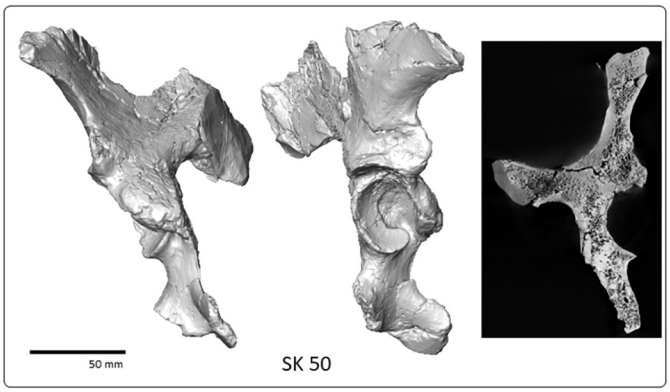

Figure 15. SK 50.

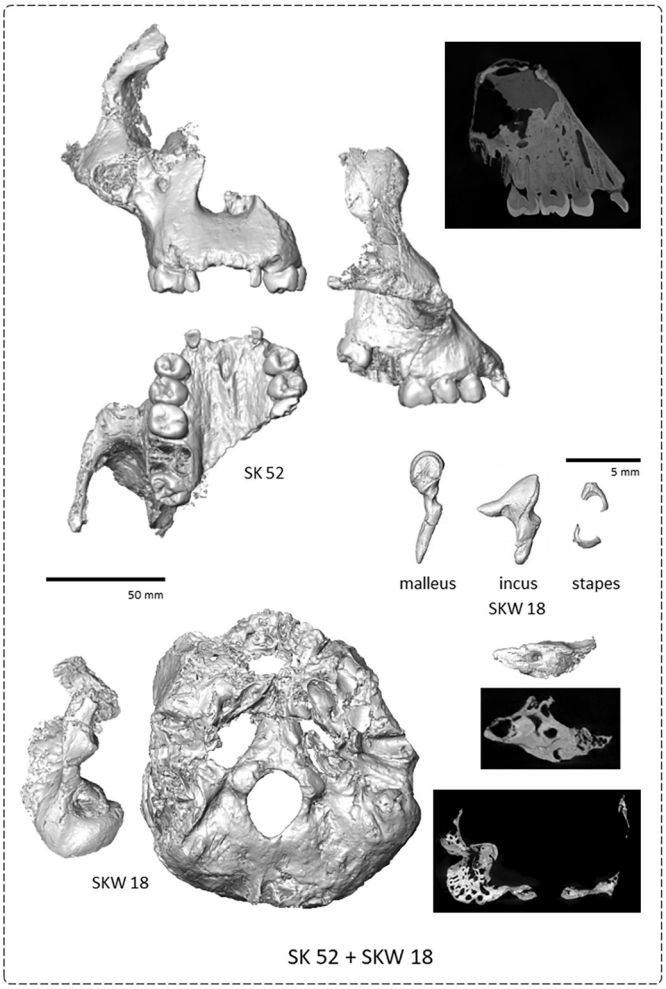

Figure 16. SK 52 + SKW 18.

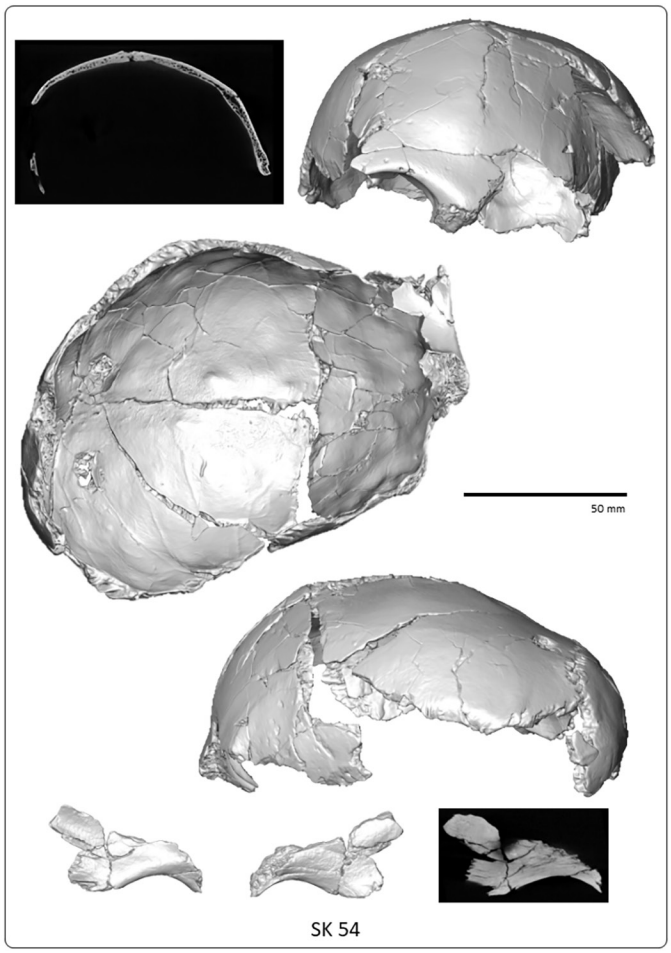

Figure 17. SK 54.

SK 75 as being associated with SK 843 but it is listed as being the same individual by Tobias et al. 1977). SK 843 is a partial left hemi-mandible containing LM_1-M_3. SK 846a is a RM_1 that is considered the antimere of the LM_1 in SK 843. Tobias et al. (1977) suggest this composite specimen is probably associated with the composite maxillary specimen SK 105 + SK 826a + SKW 33 (see below).

- **SK 79** – a crushed and fragmented cranium (Figure 23) preserving much of the face and palate and containing LP^3-M^3 and RP^3-M^3 (Brain 1981).
- **SK 81** – a mandible (see Figure 23) containing L_C-M_3 and R_C-M_3. Tobias et al. (1977) do not list this specimen as a mandible and only identify it as LP_4-M_1. Brain (1981) does not list the L_C but includes a RI_2 that is only represented by the alveolar socket.
- **SK 82** – the proximal portion of a right femur (Napier 1964). The internal structure is in fair condition, though there are some repairs that have been made obscuring some of the internal structure (Figure 24).
- **SK 83** – a damaged cranium containing LI^1-M^3 and RI^1-M^3 (see Figure 24). There is also a supernumerary right lateral incisor sitting lingually and between the R^C and RI^2 (Ripamonti et al. 1999). It is unclear why the R^C-M^2 are not listed in either Brain (1981) or Tobias et al. (1977).
- **SK 84** – a left first metacarpal (Broom and Robinson 1949b; Napier 1959). This accession number is also assigned to a maxillary canine by Robinson (1956) but it is assumed this is a typographical error and is referring to another specimen (Figure 25).
- **SK 85** – a left fourth metacarpal (Napier 1959). This specimen has fractures and there is some precipitated crystallized mineral in the internal structure of the metacarpal head (see Figure 25).
- **SK 85a + SK 93** – an associated set of antimeric maxillary canines (Brain 1981). SK 85a is an unworn R^C with a broken and fractured root (see Figure 25). SK 93 is an unworn L^C with a broken and fractured root.
- **SK 86** – a tooth listed as a L^C by Brain (1981) and was not scanned for this publication (see Figure 25).
- **SK 87** – an unworn R_C (see Figure 25) with a broken root (Robinson 1956).
- **SK 88** – This specimen is an unworn left mandibular premolar with some fractures and broken roots (see Figure 25). Brain (1981) lists this specimen as a LP_4.
- **SK 92** – a tooth listed as a R^C by Brain (1981) and was not scanned for this publication (see Figure 25).

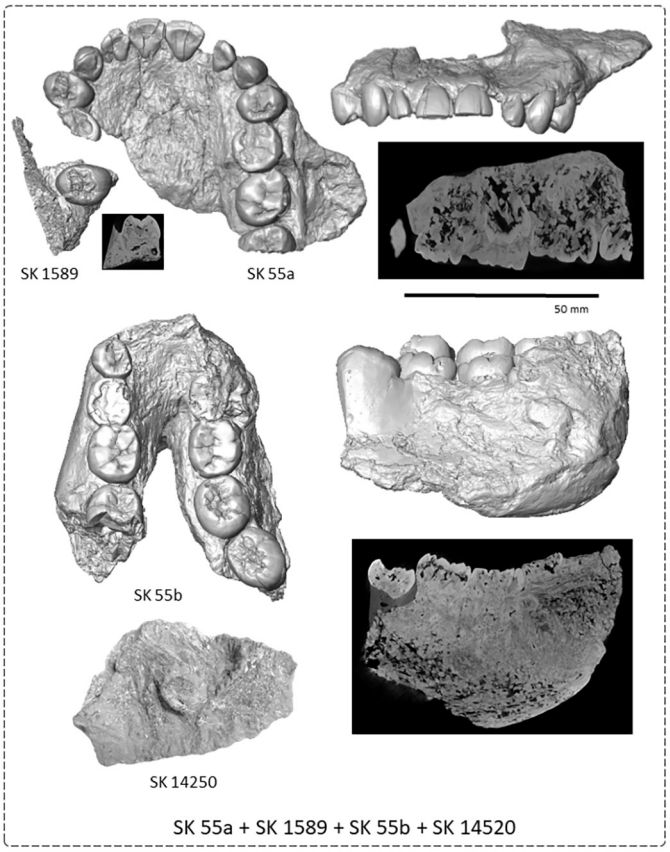

Figure 18. SK 55a + SK 1589 + SK 55b + SK 14250.

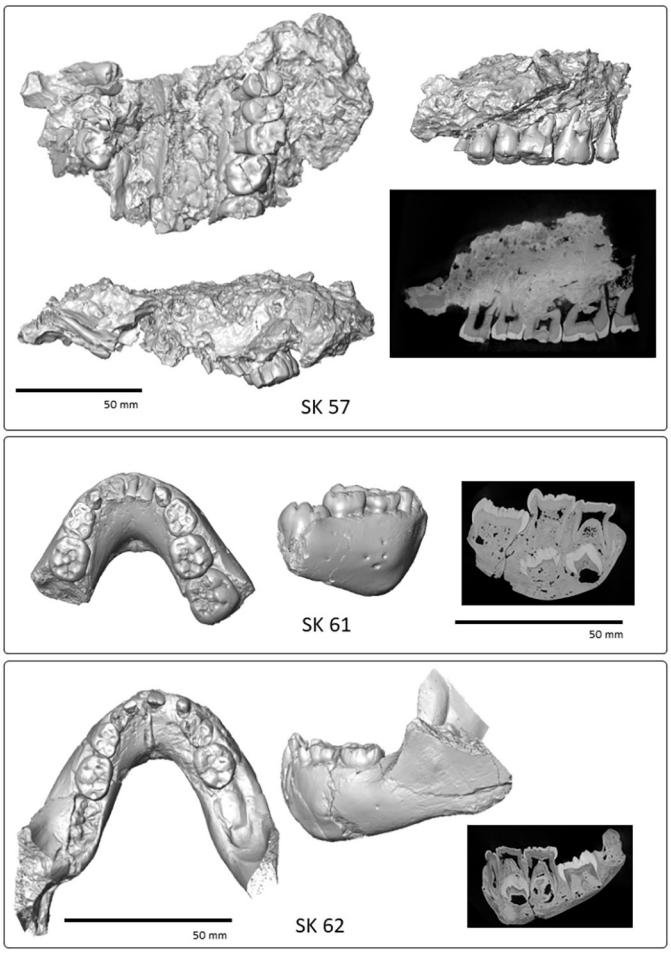

Figure 19. SK 57, SK 61, SK 62.

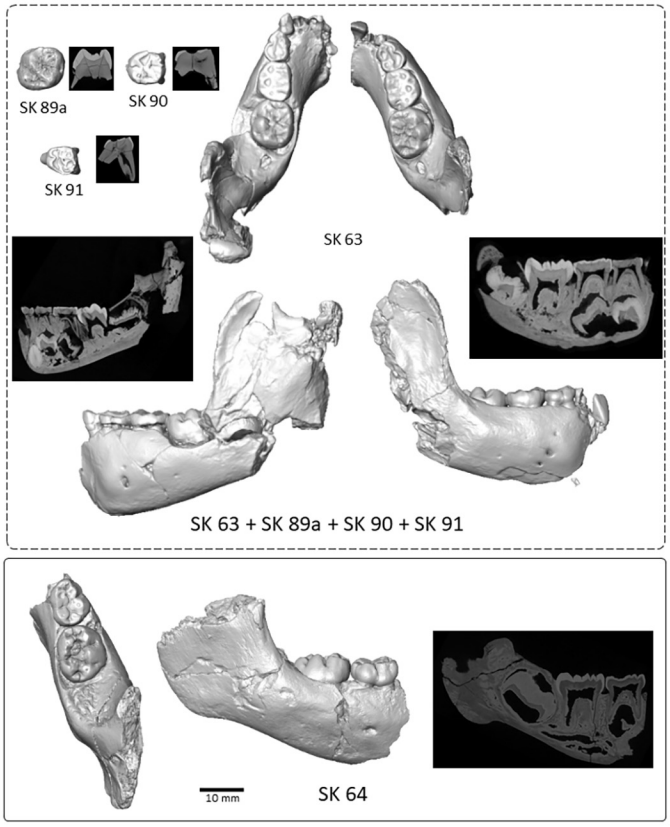

Figure 20. SK 63 + SK 89a + SK 90 + SK 91, SK 64.

- **SK 94** – a tooth listed as a R_C by Brain (1981) and was not scanned for this publication (see Figure 25).
- **SK 95** – a tooth listed as a L^C by Brain (1981) and was not scanned for this publication (see Figure 25).
- **SK 96** – a fragment of a mandible (see Figure 25) containing roots of Ldm_1, isolated and developing L_C and LP_3, and a separate mandibular fragment (Tobias et al. 1977).
- **SK 97** – the proximal portion of a right femur (Figure 26) of an adult (Napier 1964).
- **SK 98** – an unworn left maxillary molar (see Figure 25) that Robinson (1956) lists as a LM^2.
- **SK 99** – an unworn maxillary left premolar (see Figure 25) that Robinson (1956) lists as a LP^4.
- **SK 101** – an unworn left maxillary developing premolar (see Figure 26) that Tobias et al. (1977) lists as a LP^3.
- **SK 102 + SK 838a** – an associated maxilla fragment with teeth and an isolated tooth (see Figure 26). SK 102 is a slightly worn left maxillary molar with broken roots, and a mesial wear facet. Robinson (1956) lists this specimen as a LM^1. SK 838a is a partial right maxilla embedded in breccia that contains Rdm^2, RM^1, and RP^4 (note that the developing RP^4 was not noted by Tobias et al. 1977). The scan includes all the teeth but not all the adhering breccia. This specimen is not associated

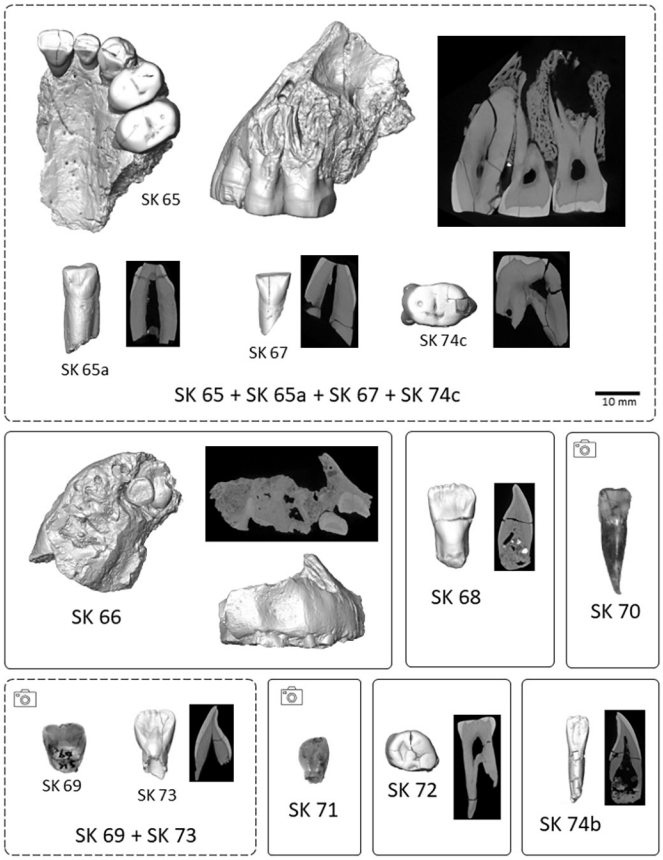

Figure 21. SK 65 + SK 65a + SK 67 + SK 74c, SK 66, SK 68, SK 69 + SK 73, SK 70, SK 71, SK 72, SK 74b.

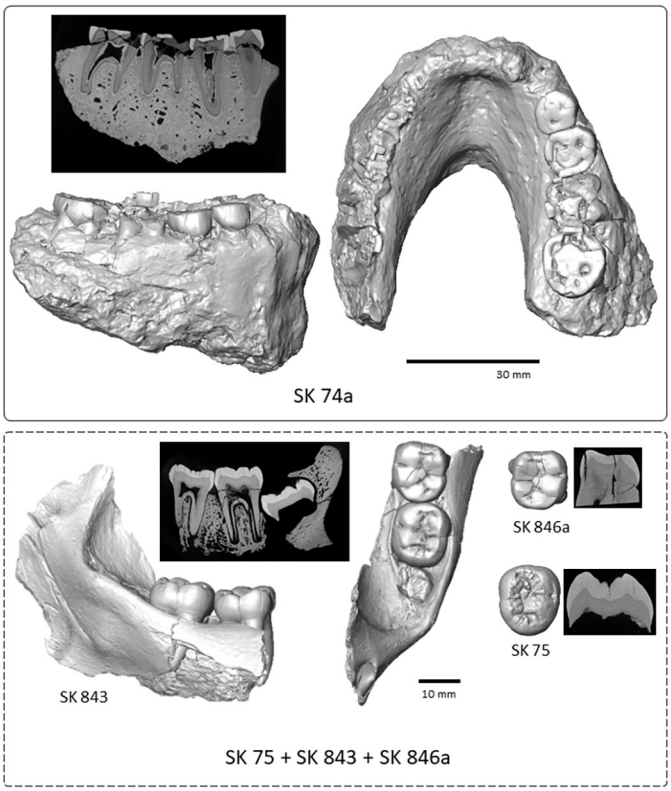

Figure 22. SK 74a, SK 75 + SK 843 + SK 846a.

with SK 838b (Tobias et al. 1977). The RM^1 is considered the antimere of SK 102 (LM^1) and is the basis for their association (Brain 1981).

- **SK 104** – an unworn right mandibular molar (see Figure 26) that Robinson (1956) lists as a RM_1 and this is consistent with the analysis of the enamel-dentine junction morphology (Skinner et al. 2008).
- **SK 105 + SK 826a2 + SKW 33** – an associated set of four isolated teeth. SK 105 is a developing maxillary molar that Robinson (1956) lists as a LM^3 (see Figure 26). SK 826a2 is an isolated maxillary molar that is identified as a LM^2 based on its morphology and its presumed antimeric status with SKW 33. Robinson (1956) also identifies this tooth (listed as SK 826 by him) as a LM^2. SKW 33 (formerly SK 14129a) is a fragment of molar identified as a RM^1 and more complete molar identified as an RM^2. Tobias et al. (1977) make the association between these two specimens, as well as SK 105 (LM^3). Additionally, they indicate this set of three maxillary molars could be the same individual as SK 75 + SK 843 + SK 46a (see Figure 22). The degree of wear among the teeth is consistent with this association and the degree of development and coloration of SK 105 is, indeed, a good match for SK 75. It is not clear that either Tobias et al. (1977) or Brain (1981) lists the molar identified here (and in the museum collections) as SK 826a2.
- **SK 438** –a left hemi-mandible (Figure 27) containing a Ldm_2 and a LM_1 (note the developing LM_1 crown was not noted by Tobias et al. 1977 or Brain 1981).
- **SK 820** – a mandibular canine that was "removed from its crypt" (Robinson 1956: 46). It is listed as a canine by Tobias et al. (1977) but is not listed by Brain (1981). It was not in the collection during scanning for this project and its location remains uncertain, so no image is provided in this publication.
- **SK 821** – a partial left maxillary premolar in situ (see Figure 27), and a portion of the alveolus of the mesial tooth (Tobias et al. 1977). Robinson (1956) lists this specimen as a LP^3 and this is consistent with the single, mesially positioned alveolar socket that would have contained the L^C. CT scan is restricted to the tooth and does not contain the whole maxillary portion.
- **SK 822** – a left maxillary premolar (see Figure 26) that Robinson (1956) lists as a LP^3.
- **SK 823** – a right maxillary premolar (see Figure 27) that Robinson (1956) lists as a RP^3. A portion of the buccal root is missing from the scan.
- **SK 824** – a developing left maxillary premolar (see Figure 27) that Robinson (1956) lists as a LP^4.
- **SK 825** – an unworn left maxillary premolar (see Figure 27) that was crown complete but with only a few millimeters of root formation (roots embedded in breccia and with a small fragment of maxillary alveolus that is not included in the scan). Robinson (1956) lists this tooth as a LP^4.

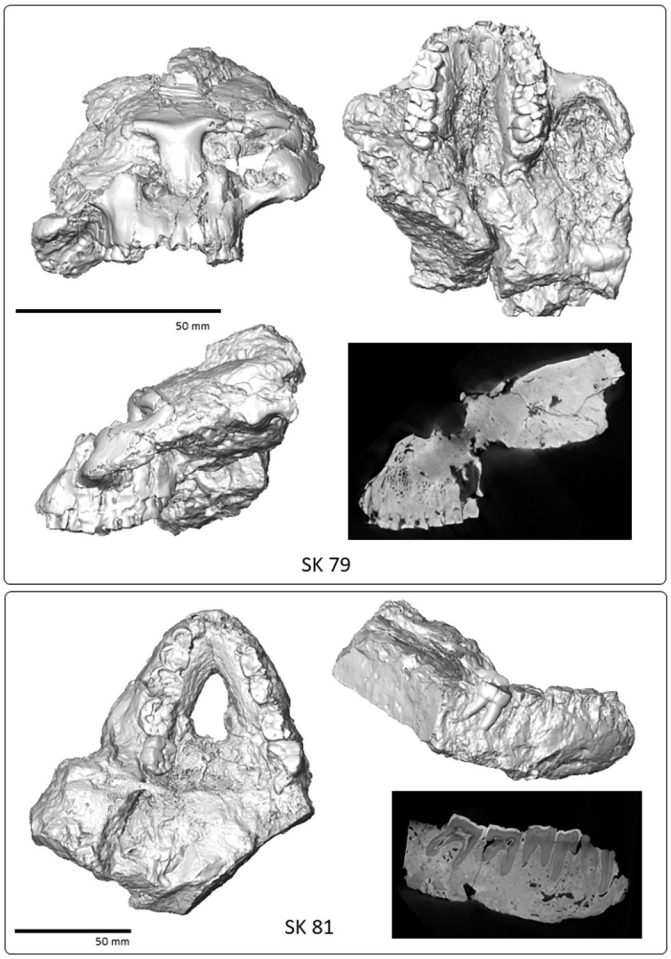

Figure 23. SK 79, SK 81.

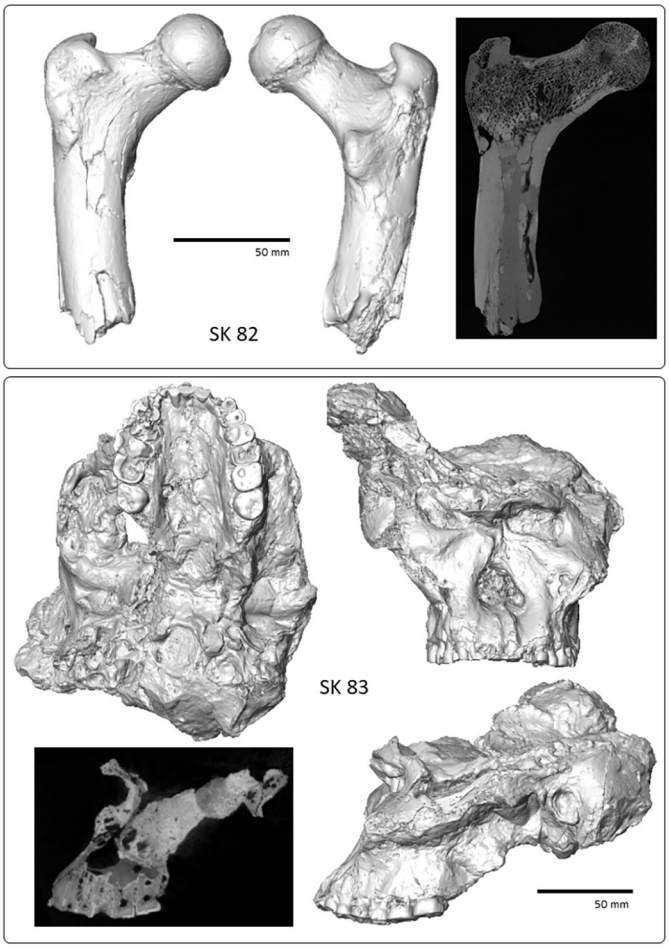

Figure 24. SK 82, SK 83.

- **SK 826a1 + SK 877/SKW 31** – associated right and left halves of a maxilla (Figure 28). SK 826a1 is a left partial maxilla containing LP^3-M^1 (not scanned for this publication). Both Brain (1981) and Tobias et al. (1977) list this specimen under the accession number SK 826a but the museum currently identifies it as SK 826a1. SK 877 is a right partial maxilla containing URP^4-M^2 (note the RM^2 crown is only partial). There is a small maxillary fragment included in this specimen (not scanned). SKW 31 is the distobuccal portion of the RM^2 (formerly SK 14080 as listed by Tobias et al. 1977 who also incorrectly list it as a *left* M^2) that articulates with the mesiolingual portion of the RM^2 in SK 877 and they are glued together in the collection. Brain (1981) also incorrectly identifies SKW 31 as being a left, rather than right, M^2. Brain (1981) associates the SK 826a + SK 877/SKW 31 maxillary specimen with SK 843 + SK 846a, however, this is not possible given the markedly different levels of wear on the mandibular dentition of the latter.
- **SK 826b/SK 828** – an associated fragment of hemimandible and an isolated tooth (according to museum records the association was identified by M. Wolpoff). SK 826b is a slightly worn LP_4 that fits onto the preserved alveolar socket of the SK 828 mandibular fragment that contains LM_1 (see Figure 27).
- **SK 827** – a left mandibular premolar (see Figure 27) that Robinson (1956) lists as a LP_4.
- **SK 829** – a maxillary molar (see Figure 27) that was listed as a LM^1 by Brain (1981).
- **SK 830** – a left mandibular premolar (see Figure 27) that Robinson (1956) lists as a LP_4.
- **SK 831** – a right mandibular premolar (see Figure 27) that Robinson (1956) lists as a RP_3. Unfortunately, the apical portions of the roots were not included in the CT scan. This specimen is not associated with SK 831a (Tobias et al. 1977).
- **SK 831a** – a fragmented portion of a maxilla containing LM^2-M^3 (see Figure 28). Note that Robinson (1956: 87) illustrates the LM^3 incorrectly in the maxillary second molar figure (although the reported linear dimensions of the crown seem to match with the correct crown).
- **SK 833** – a left maxillary molar (see Figure 27) that Tobias et al. (1977) list as a LM^1.
- **SK 834** – a right maxillary molar (see Figure 27) that Robinson (1956) lists as a RM^2.
- **SK 835** – a left maxillary molar that Robinson (1956) lists as a LM^3 (see Figure 27). The apical portions of the roots are missing from the scan. There are a few small

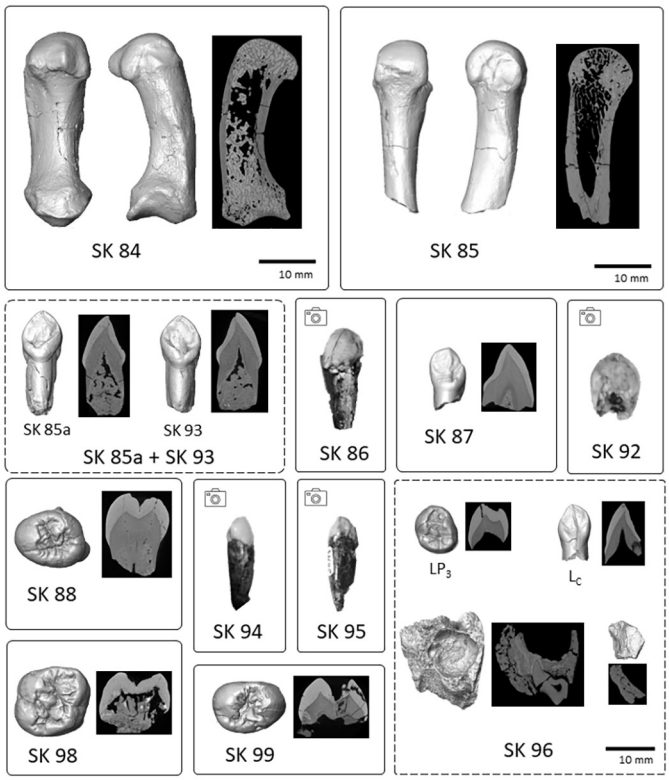

Figure 25. SK 84, SK 85, SK 85a + SK 93, SK 86, SK 87, SK 88, SK 92, SK 94, SK 95, SK 96, SK 98, SK 99.

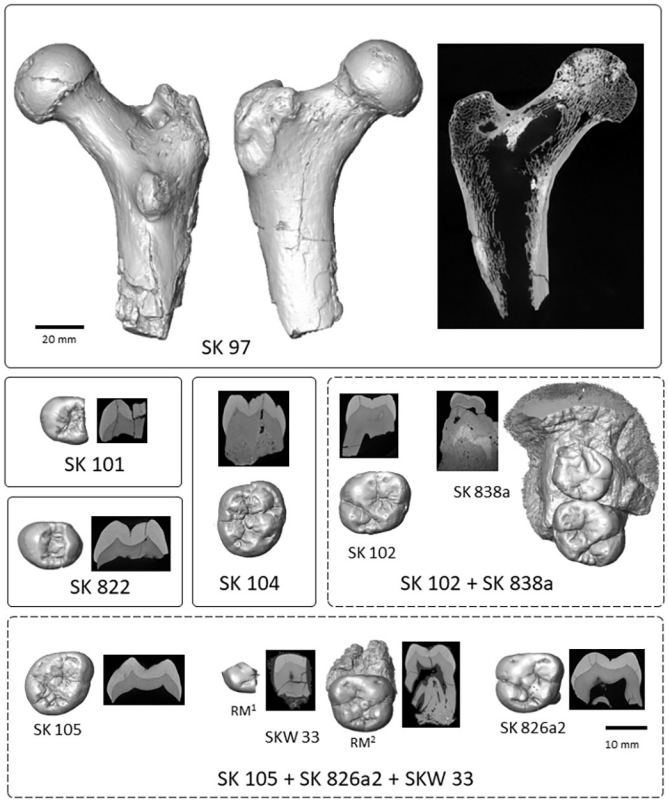

Figure 26. SK 97, SK 101, SK 102 + SK 838a, SK 104, SK 105 + SK 826a2 + SKW 33, SK 822.

osseous fragments associated with this specimen that were not scanned.

- **SK 836** – a left maxillary molar (see Figure 27). The lingual portion of the crown has been broken off and has been restored with plaster. The lingual roots are partially broken off and the preserved apical portion is missing from the scan. Robinson (1956) lists this tooth as a LM^3.
- **SK 837** – a right maxillary molar embedded in breccia (see Figure 28) that Robinson (1956) lists as a RM^2. The apical portion of this specimen is missing from the scan.
- **SK 838b** – a left mandibular molar with some preserved alveolar bone between the roots (see Figure 28). Robinson (1956) lists this tooth as a LM_1 (note that Robinson referred to the molar as SK 838 not SK 838b). It is not associated with SK 838a (Tobias et al. 1977).
- **SK 839 + SK 852** – an associated maxilla and mandible (Figure 29). SK 839 is a set of associated maxillary teeth including Rdi^1, Rdm^1, Rdm^2, RI^1-I^2, RM^1 and Ldi^1, LI^1, LM^1 (Grine 1981). Grine (1981) identified the crushed tooth as the LI^2, however, the groove on the lingual face does not match that of the RI^2, so we think the identity of this tooth should be investigated further. Note the deciduous incisors have some adhering maxillary bone and the permanent incisors were not listed in either Tobias et al. (1997) or Brain (1981). SK 852 is a partial mandible with some isolated anterior teeth. Preserved teeth (including those developing) include Ldm_1-dm_2, LI_1-M_1

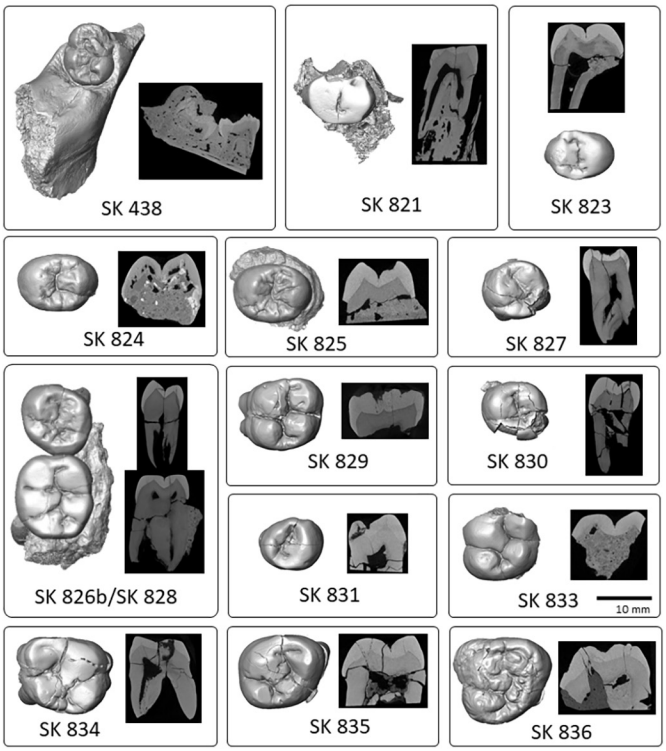

Figure 27. SK 438, SK 821, SK 823, SK 824, SK 825, SK 826b/SK 828, SK 827, SK 829, SK 830, SK 831, SK 833, SK 834, SK 835, SK 836.

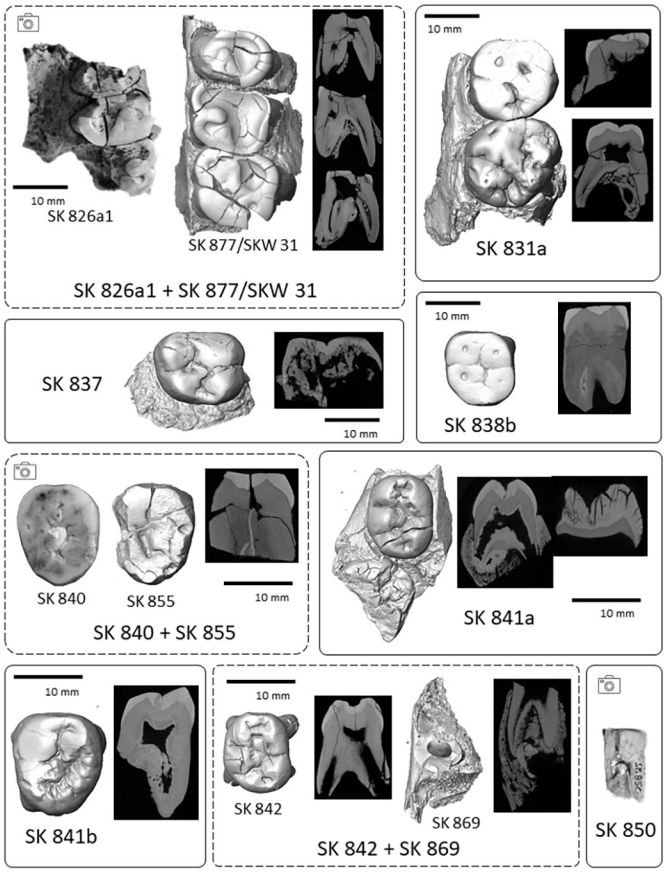

Figure 28. SK 826a1 + SK 877/SKW 31, SK 831a, SK 837, SK 838b, SK 840 + SK 855, SK 841a, SK 841b, SK 842 + SK 869, SK 850.

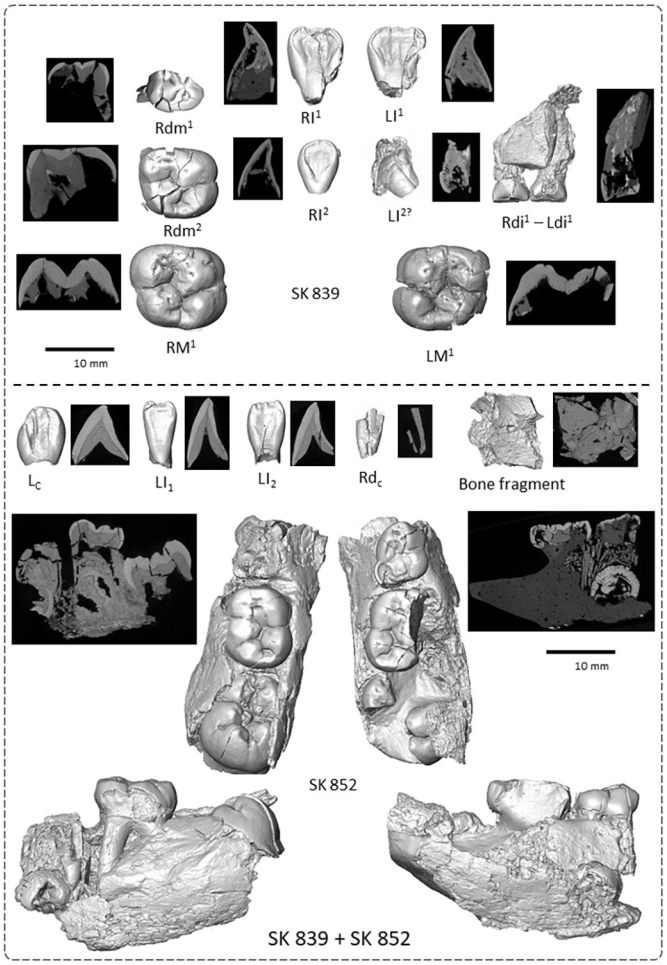

Figure 29. SK 839 + SK 852.

and Rdm_1-dm_2, RP_3 and RM_1. There is an apical root fragment present which, based on similarities in the fractures at the apex, is likely from the Rd_c described and figured in Grine (1981); however, the crown is absent. There is also an unidentified bone fragment that could be part of the mandibular corpus. Tobias et al. (1977) did not identify the LI_1-L_C or the unerupted premolars. Grine (1981) associated these two dentitions together based on matching occlusal wear facets of the deciduous molars.

- **SK 840 + SK 855** – an associated set of mandibular molars. SK 840 is a mandibular molar that was identified by Brain (1981) as a LM_3 (see Figure 28). It was not scanned for this publication. SK 855 is a worn and fragmented right mandibular molar with a broken lingual side of the crown and broken roots. Tobias et al. (1977) list this specimen as a RM_3 and as the likely antimere of SK 840 (LM_3).
- **SK 841a** – a partial hemi-mandible containing Ldm_2 and a partial developing LM_1 (see Figure 28). There is no evidence of a developing LP_4. This specimen is not associated with SK 841b (Tobias et al. 1977).
- **SK 841b** – a left mandibular molar (see Figure 28); Robinson (1956) lists this tooth as a LM_3. This specimen is not associated with SK 841a (Tobias et al. 1977).
- **SK 842 + SK 869** – a partial mandible and isolated tooth (see Figure 28) whose association was determined by Clarke (1990). SK 842 is an isolated Ldm_2 and SK 869 is a partial hemi-mandible containing the broken roots of the Ldm_1 and the developing LP_3 (note that the LP_3 was not previously reported by Tobias et al. 1977 or Brain 1981).
- **SK 844** – a left hemi-mandible (Figure 30) containing LM_2-M_3 (Tobias et al. 1977).
- **SK 845/SK 14251** –a partial maxilla that connects to a tooth embedded in a breccia block (Clarke 1990). SK 845 preserves much of the palate and contains RP^3-M^1 and LI^2-M^2 (Tobias et al. 1977). The RM^1 crown consists only of a small mesial fragment but the roots that can be seen in the CT scan indicate that another, more distally placed, crown fragment is likely part of the half of the RM^2 (see Figure 30). SK 14251 is a tooth crown fragment in a large breccia block that directly connects (Clarke 1990) to the RM^2 fragment of SK 845. Clarke (1990) lists the tooth in SK 14251 as a crushed M^3, however, we think it is more likely the antimere of the LM^2 given cusp morphology similarities in the distal half of the crown and similar levels of wear.
- **SK 847 + SK 45** – an associated partial cranium and

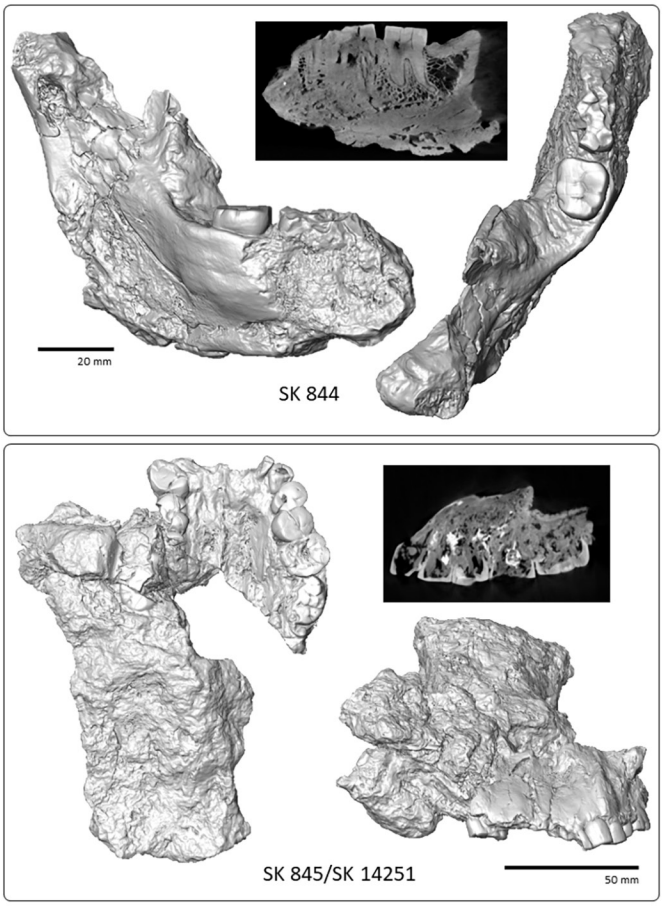

Figure 30. SK 844, SK 845/SK 14251.

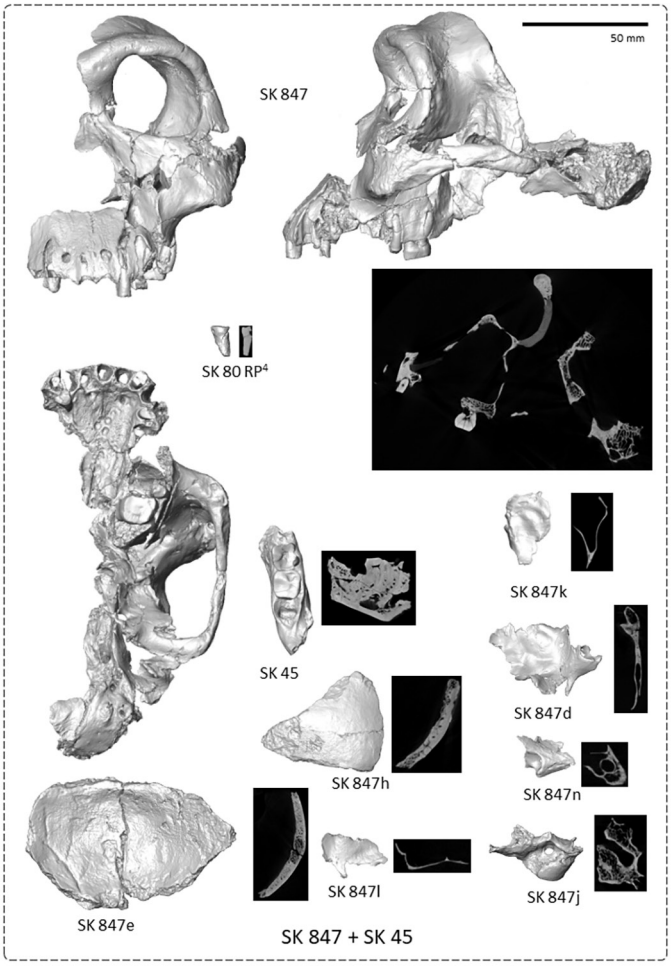

Figure 31. SK 847 + SK 45.

mandible fragment (Figure 31). SK 847 is a partial cranium that includes the distobuccal root of the LM^2 and the crown and roots of the LM^3, and a number of other cranial fragments (SK 847d, e, h, j, k, and l). SK 846b is most of the left temporal that is attached to the SK 847 cranium (Clarke et al. 1970). SK 80 is a partial maxilla containing the lingual root of LP^3, the lingual and mesiobuccal root of the RP^3, and the root of the LI^2. The direct connection between SK 80 and SK 847 was determined by Clarke et al. (1970). SK 847, SK 846b, and the SK 80 maxilla are glued together and referred to in the literature as SK 847 (Clarke and Howell 1972). There is an isolated partial crown/root fragment, still accessioned as SK 80 in the collections, which Clarke et al. (1970) identify as a RP^4. We have identified it as SK 80 in Figure 31. Clarke (1977) identifies a number of fragments that are not part of SK 847, including SK 847f, g, i, and m. SK 45 is a fragment of right hemi-mandible containing RM_1-M_2, and the alveolus of the third molar. Based on levels of dental attrition and overall morphology Clarke et al. (1970) associate SK 45 and SK 847.

- **SK 848** – a cranial fragment consisting of partial right temporal and the stapes, incus, and malleus (Figure 32).
- **SK 849** – a right maxillary molar (see Figure 32) that Tobias et al. (1977) list as a RM^1.
- **SK 850** – a partial isolated tooth that Tobias et al. (1977) identify as a mandibular third premolar (see Figure 28). It was not scanned for this publication.
- **SK 851** – a right mandibular molar (see Figure 32) that Tobias et al. (1977) list as a RM_3. The scan excludes a small portion of the preserved broken roots.
- **SK 853** – a lumbar vertebra (Brain 1981) that was not scanned for this publication (Figure 33).
- **SK 854** – an axis vertebra (C2) (see Figure 33) with some damage to the left superior and inferior articular surfaces, odontoid process, and the spinous process (Brain 1981).
- **SK 856** –a left maxillary premolar and a left maxillary molar (see Figure 32) embedded in breccia. Both Tobias et al. (1977) and Brain (1981) list the premolar as a P^4, while the former lists the molar as either a LM^1 or LM^2 and the latter lists it as a LM^1.
- **SK 857** – a right mandibular premolar (see Figure 32) that Robinson (1956) lists as a RP_3.
- **SK 858/SK 861/SK 883** – a fragmentary mandible originally recovered as three separately accessioned pieces (Brain 1981). SK 858 comprises the anterior portion and includes RI_1-RM_2, a corner of the crown of RM_3, LI_1-LP_4, and parts of LM_1-M_2 (see Figure 33). SK 861 includes

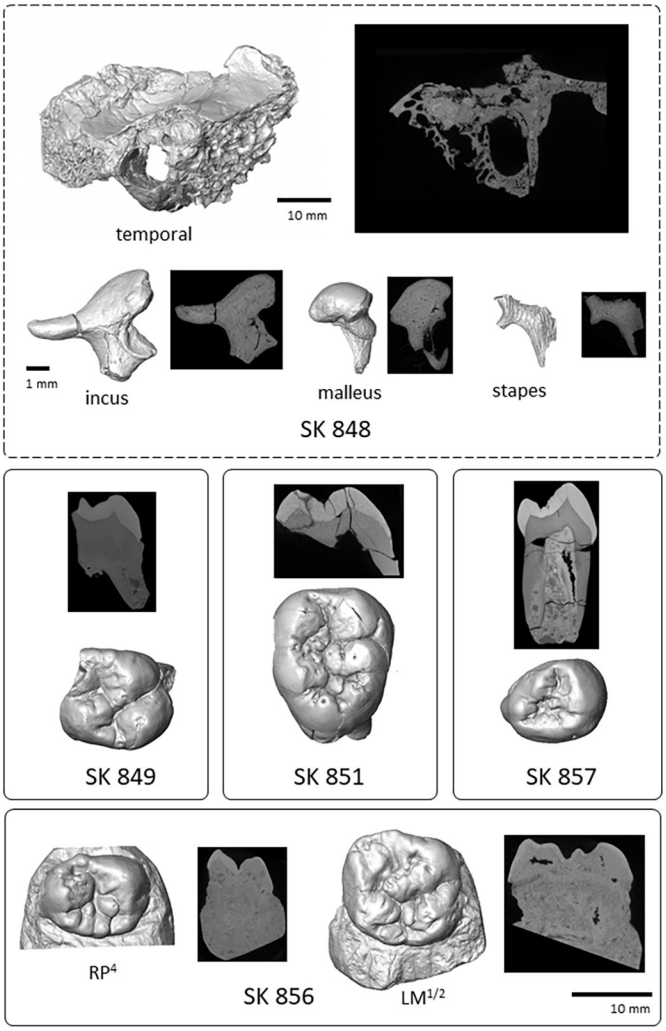

Figure 32. SK 848, SK 849, SK 851, SK 856, SK 857.

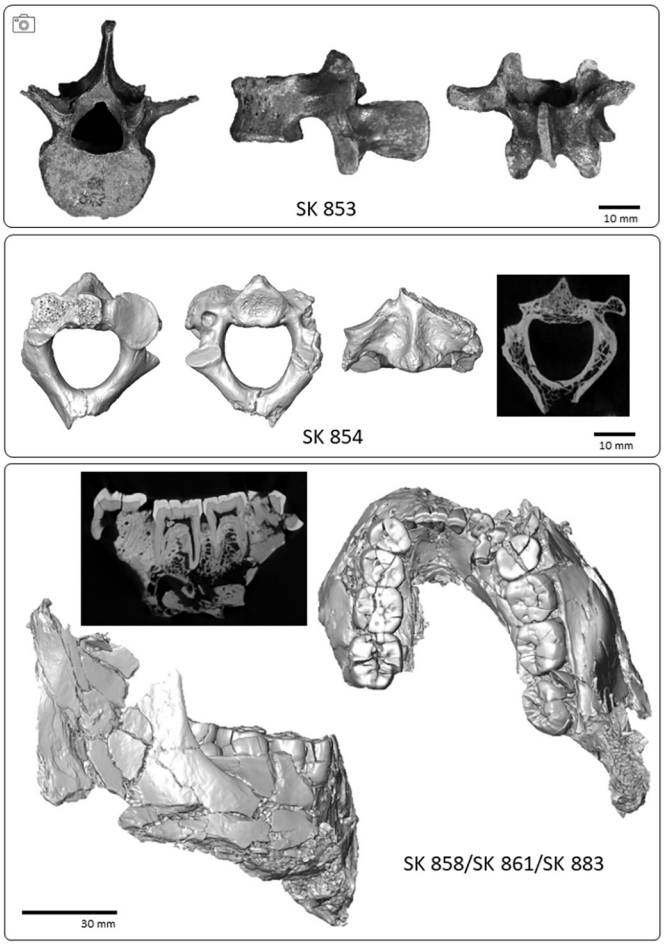

Figure 33. SK 853, SK 854, SK 858/SK 861/SK 883.

parts of the buccal potions of LM_1-M_2. SK 883 includes most of the RM_3 and the ascending ramus. There is a small, detached fragment associated with this specimen that was not scanned as part of this publication.

- **SK 859** – a partial calvaria (Figure 34) including the occipital and fragments of the left and right parietal bones, as well as a vertebral fragment and three smaller cranial fragments (Brain 1981).
- **SK 862** – a partial right hemi-mandible (Figure 35) containing roots and/or crowns of RP_4-M_3 (Brain 1981). It was not scanned for this publication.
- **SK 863** – an isolated molar fragment (Brain 1981; Tobias et al. 1977) in a block of breccia (see Figure 35). It was not scanned for this publication.
- **SK 864** – a partial molar in a block of breccia that Brain (1981) identifies as possibly a mandibular first molar (see Figure 35). It was not scanned for this publication.
- **SK 865** – a crushed tooth with some adhering bone and breccia that Brain (1981) identifies as a molar (see Figure 35). It was not scanned for this publication.
- **SK 866** – a fragmentary tooth (see Figure 35) in a small piece of breccia (Tobias et al. 1977). It was not scanned for this publication.
- **SK 867** – a maxillary premolar with some adhering breccia (Figure 36). Tobias et al. (1977) and Brain (1981) list this specimen as a maxillary third premolar, but neither comment on the siding of the tooth. We interpret it as from the right side.
- **SK 868** – two partial tooth crowns embedded in breccia that Brain (1981) identifies as RM^2-M^3 (see Figure 36). They were not scanned for this publication.
- **SK 870** – a left maxillary molar (see Figure 36) that Brain (1981) lists as a LM^3.
- **SK 871** – a left mandibular molar crown (see Figure 36) that Brain (1981) lists as a LM_3.
- **SK 872** – a left maxillary molar (see Figure 36) that Brain (1981) lists as a LM^1.
- **SK 873** – the root and part of the crown of an anterior tooth (see Figure 36) that Tobias et al. (1977) identify as an incisor. It was not scanned for this publication.
- **SK 874** – a crown fragment in breccia (see Figure 36). It is not identified to tooth position by Brain (1981) or Tobias et al. (1997) but could be part of a molar or premolar crown. It was not scanned for this publication.
- **SK 875** – a fragment of tooth (Brain 1981) that was not scanned or photographed for this publication.
- **SK 876** – a mandible (Figure 37) containing L_C-LM_3 and

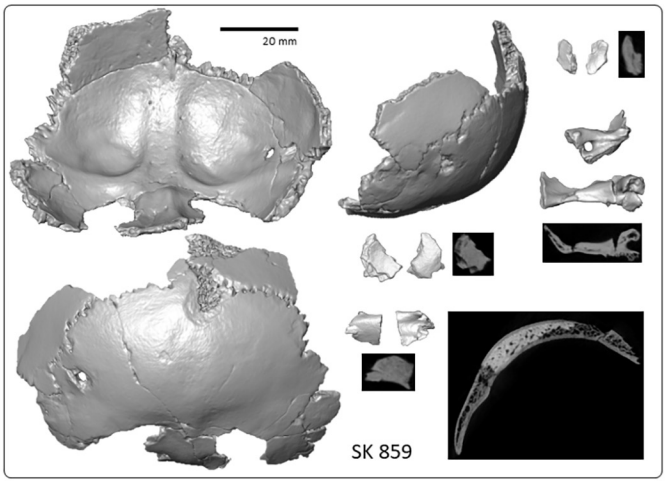

Figure 34. SK 859.

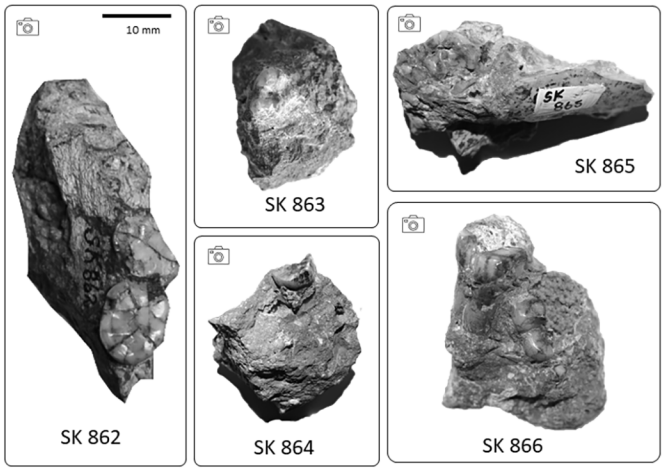

Figure 35. SK 862, SK 863, SK 864, SK 865, SK 866.

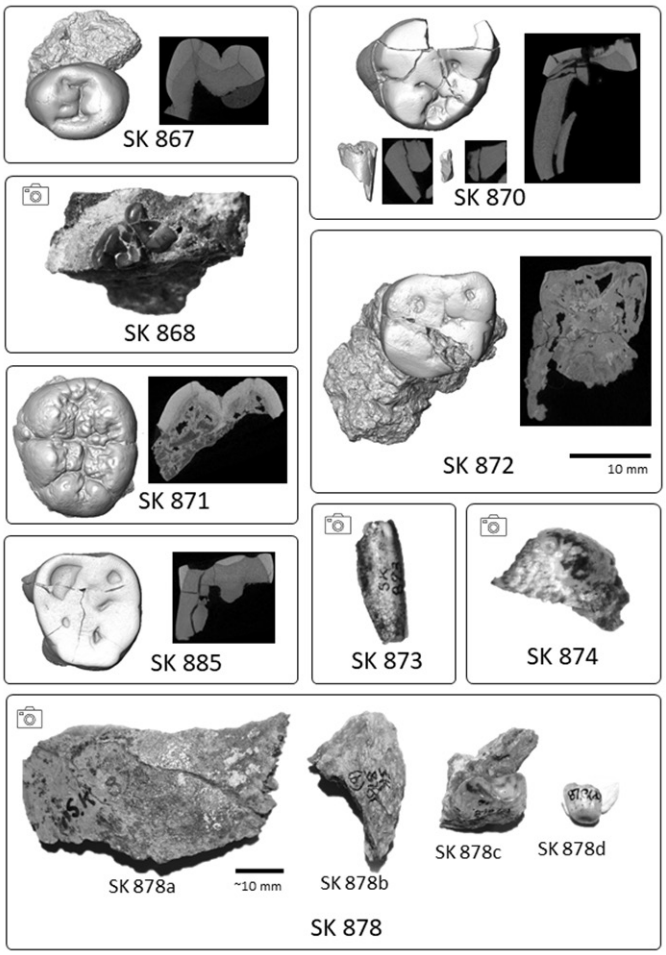

Figure 36. SK 867, SK 868, SK 870, SK 871, SK 872, SK 873, SK 874, SK 878, SK 885.

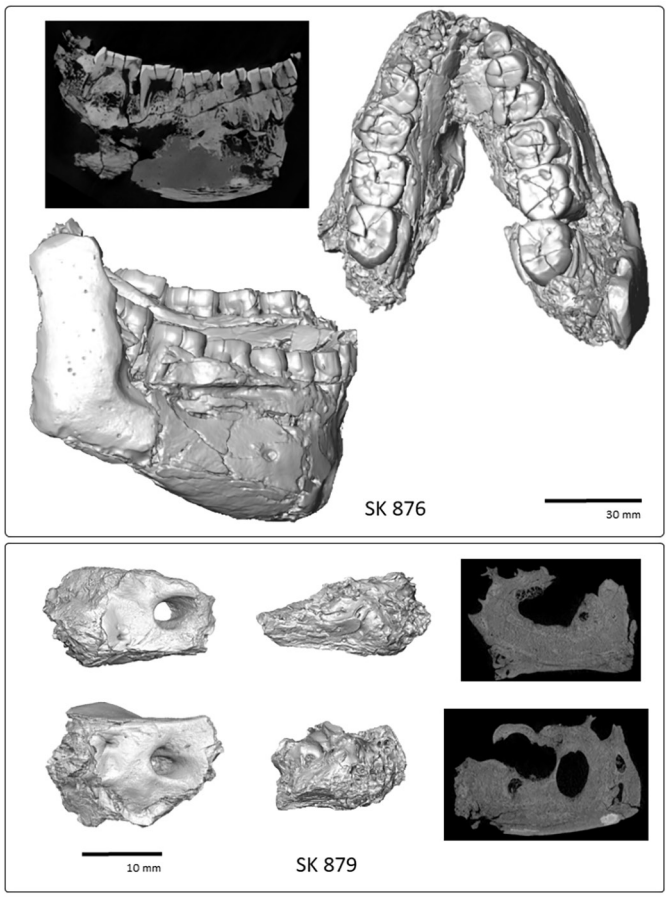

Figure 37. SK 876, SK 879.

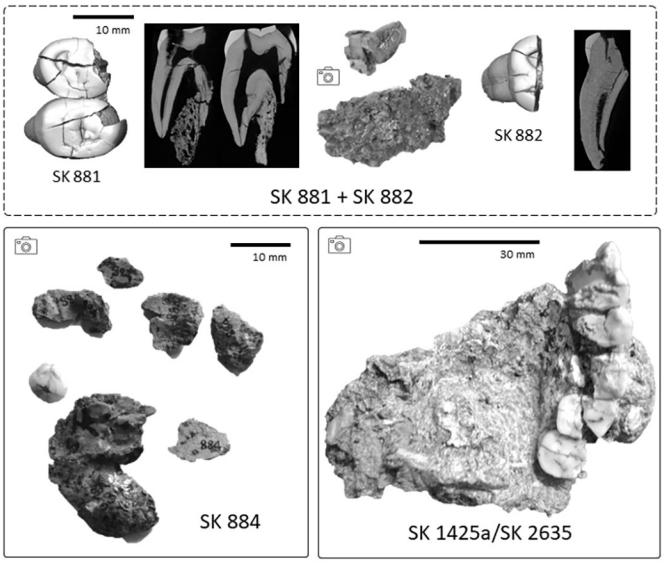

Figure 38. SK 881 + SK 882, SK 884, SK 1425a/SK 2635.

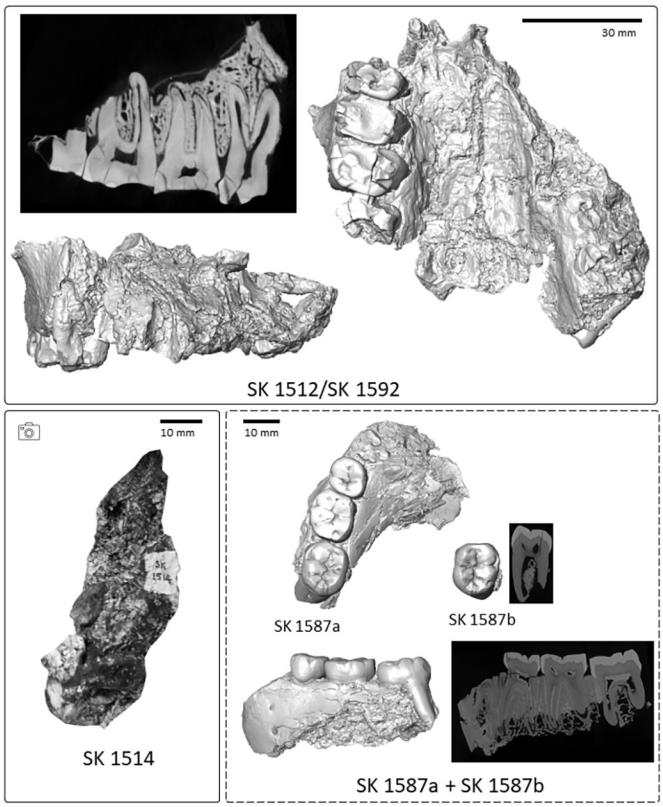

Figure 39. SK 1512/SK 1592, SK 1514, SK 1587a + SK 1587b.

RI_2-M_3 (Brain 1981). Plaster has been added with the corpus and along the right ascending ramus as part of the reconstruction and preservation process.

- **SK 878** – two cranial fragments and two dental fragments (Tobias et al. 1977). SK 878a and SK 878b are cranial fragments, SK 878c and SK 878d are partial tooth crowns (see Figure 36). None were scanned for this publication.
- **SK 879** – a number of cranial bone fragments including portions of a left and right temporals, as well as some long bone fragments (see Figure 37). Only the temporals have been scanned and imaged for this publication. Both Tobias et al. (1977) and Brain (1981) note associated dental fragments, but these were sacrificed for isotopic sampling in the 1980s (DNMNH records).
- **SK 881 + SK 882** – isolated teeth and some bone fragments (Figure 38) that were associated by Brain (1981) and Tobias et al. (1977). SK 881 is a fragment of a maxilla containing LP^3-P^4. Tobias et al. (1977) included a fragmentary LM^1 in SK 881, but it is not clear if the tooth fragment photographed in Figure 38 is this tooth. There is also a piece of breccia containing bone fragments associated with this specimen that was not scanned for this publication. SK 882 is the worn lingual half of a left maxillary molar with dentine exposure on the protocone and hypocone. Tobias et al. (1977) list this specimen as a left maxillary molar, but neither they nor Brain (1981) speculate as to its metameric position.
- **SK 884** – fragments of mastoid region and a tooth (see Figure 38). The tooth is listed as a L_C by Brain (1981). None were scanned for this publication.
- **SK 885** – a left mandibular molar (see Figure 36) that Brain (1981) lists as a LM_3.
- **SK 1425a/SK 2635** – a palate comprised of two pieces whose fit was determined by Clarke (1990). SK 1425a is a palate with partial LM^1-M^3 and some broken premolar roots (see Figure 38). SK 2635 is two premolar crowns (originally published in Clarke 1977) that fit onto the broken premolar roots of SK 1425a. Clarke (1990) also was able to fit a partial L^C crown onto the LP^3 via the interproximal facet. It was not scanned for this publication.
- **SK 1512/SK 1592** – a palate comprised of two pieces whose fit was determined by Clarke (1990). SK 1512 is the posterior left portion of the palate (Figure 39) and contains the roots of two molars; due to distortion and poor preservation it is unclear whether these are the LM^1-M^2 or LM^2-M^3. Additionally, there is a partial crown and root distal to these molars, but based on its morphology it is likely a fragment of an anterior tooth. The preserved enamel cusp has little wear and thus it is unclear whether it belongs to this palate. SK 1592 is the remaining palate and contains RP^4-M^3 and a root that possibly belongs to the RI^2.
- **SK 1514** – a fragmented hemi-mandible (see Figure 39) containing the crowns of M_1 and M_2 (Brain 1981). It was not scanned for this publication.
- **SK 1524** – a maxillary molar that Brain (1981) identifies as a LM^3. It was not scanned or photographed for this publication.
- **SK 1585** – the right half of an endocranial cast (Figure 40) that is described in Holloway (1972).
- **SK 1586** – a mandible containing LP_4-M_3 and RI_2-M_3 (see Figure 40). There are three displaced roots of unidentified anterior teeth left of midline. Tobias et al.

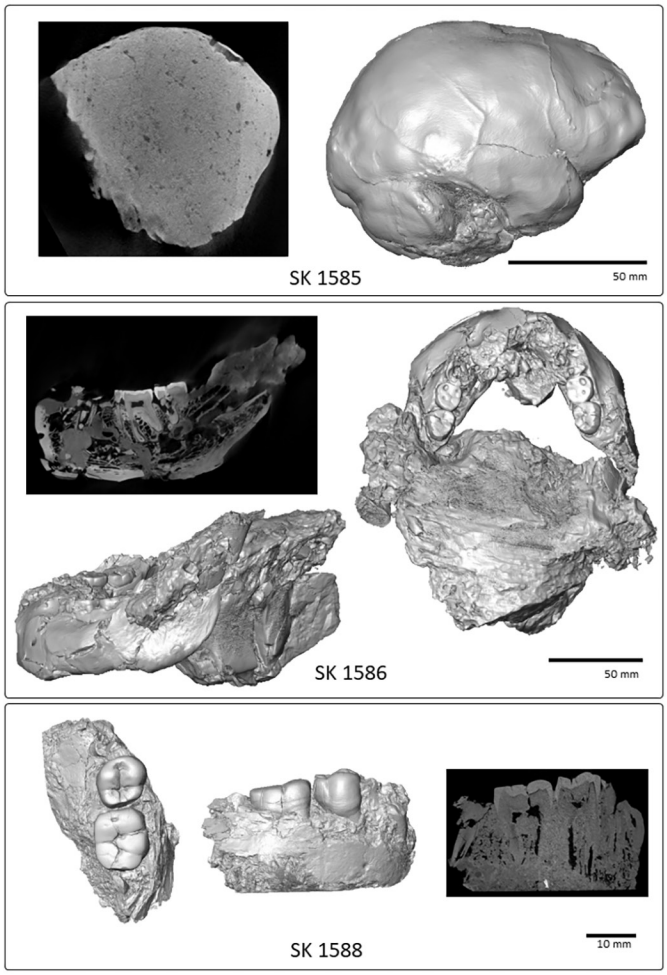

Figure 40. SK 1585, SK 1586, SK 1588.

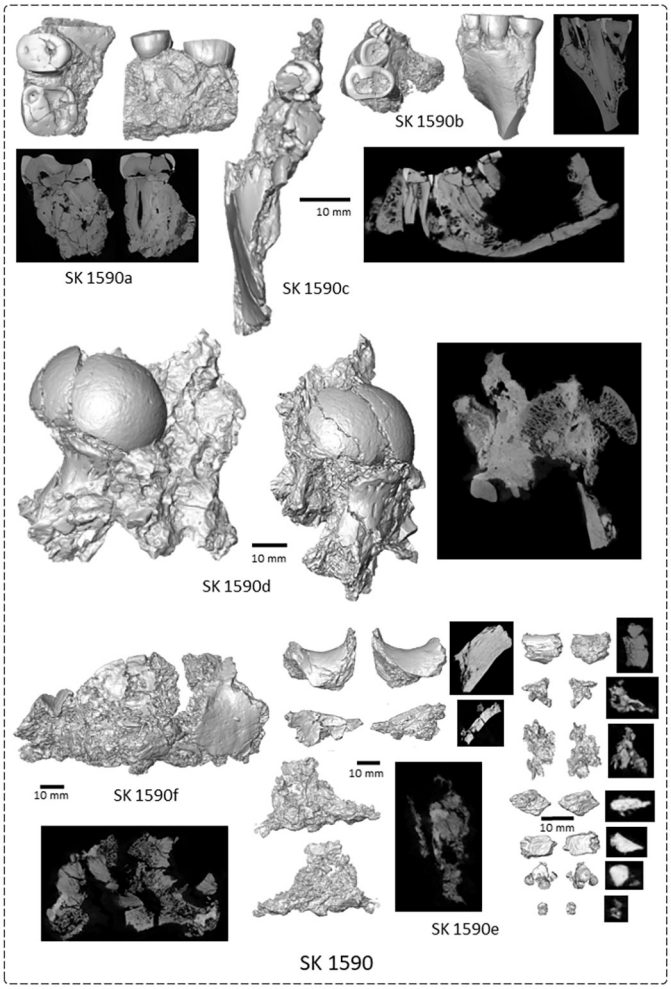

Figure 41. SK 1590.

(1977) do not note a LP_4 but list the RI_1-I_2 and LI_1 being present, though it is difficult to match tooth fragments to particular teeth.

- **SK 1587a + SK 1587b** – a partial mandible and isolated mandibular molar (see Figure 39). SK 1587a is a left mandible fragment containing LI_2, LP_3-M_2. SK 1587b is considered a LM_2 based on its antimeric status with the RM_2 in SK 1587a (Brain 1981).
- **SK 1588** – a right hemi-mandible (see Figure 40) containing R_C-M_2 (note that Brain 1970 mistakenly lists this specimen as a left hemi-mandible).
- **SK 1590** – a set of associated craniodental and postcranial fossils (Figure 41). SK 1590a consists of the right portion of a maxilla containing RP^4 and RM^1. SK 1590b consists of the right portion of a maxilla containing RI^2-RP^3. Brain (1981) and Tobias et al. (1977) do not say what teeth are contained in the SK 1590c hemi-mandible fragment, but they appear to be the fragmented LP_4-LM_2. SK 1590d consists of a highly fragmented femoral head and neck. SK 1590e and SK 1590f are various fragments of an os coxae.
- **SK 1592** – a partial maxilla (Figure 42) with RP^4-M^3 (Brain 1981). It was not scanned or photographed for this publication.
- **SK 1593** – a right mandibular premolar that Brain (1970) lists as a RP_3 (see Figure 42).
- **SK 1594** – a tooth crown in breccia (see Figure 42) that is listed as the buccal half of the RM_1 by Brain (1981). It was not scanned for this publication.
- **SK 1595** – fragments of maxilla with associated teeth (see Figure 42). Grine (1981) provides a comprehensive description and images of the specimen that includes partial crowns of LI^1-I^2, LM^1 and Ldm^2. It was not scanned for this publication.
- **SK 1596** – an isolated tooth (see Figure 42) identified by Brain (1981) as maxillary canine. It was not scanned for this publication.
- **SK 1813** – a first right metatarsal (Susman and de Ruiter 2004) that preserves the remnant of the proximal growth plate (see Figure 42).
- **SK 1896** – This specimen (see Figure 42) is the fragmented distal end of a right femur (Susman et al. 2001).
- **SK 2147** – This specimen is a partial tooth crown that was described and identified by Grine (1981) as a Ldm^1. It was not scanned or photographed for this publication.
- **SK 2223** – a fragmentary tooth crown, parts of which

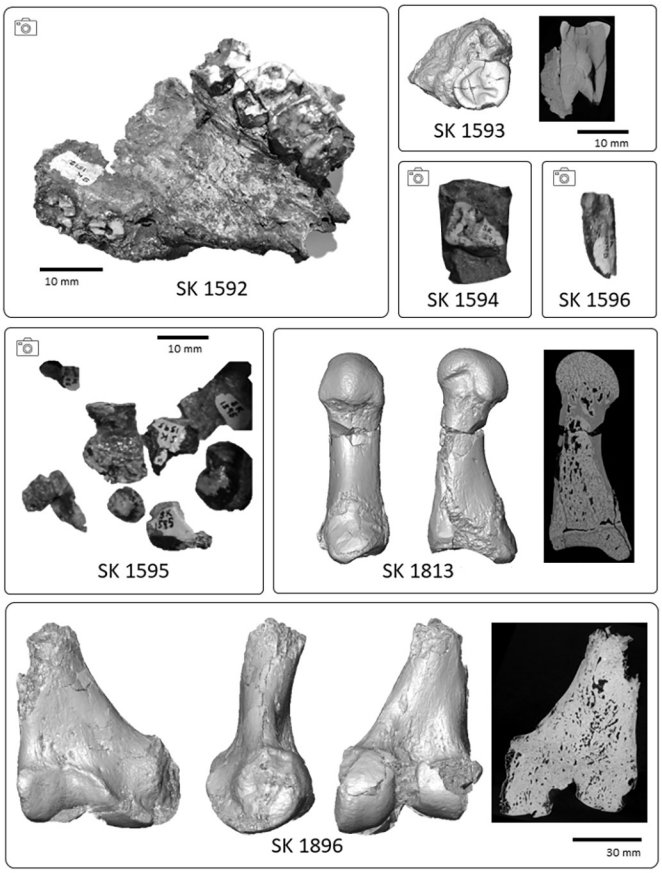

Figure 42. SK 1592, SK 1593, SK 1594, SK 1595, SK 1596, SK 1813, SK 1896.

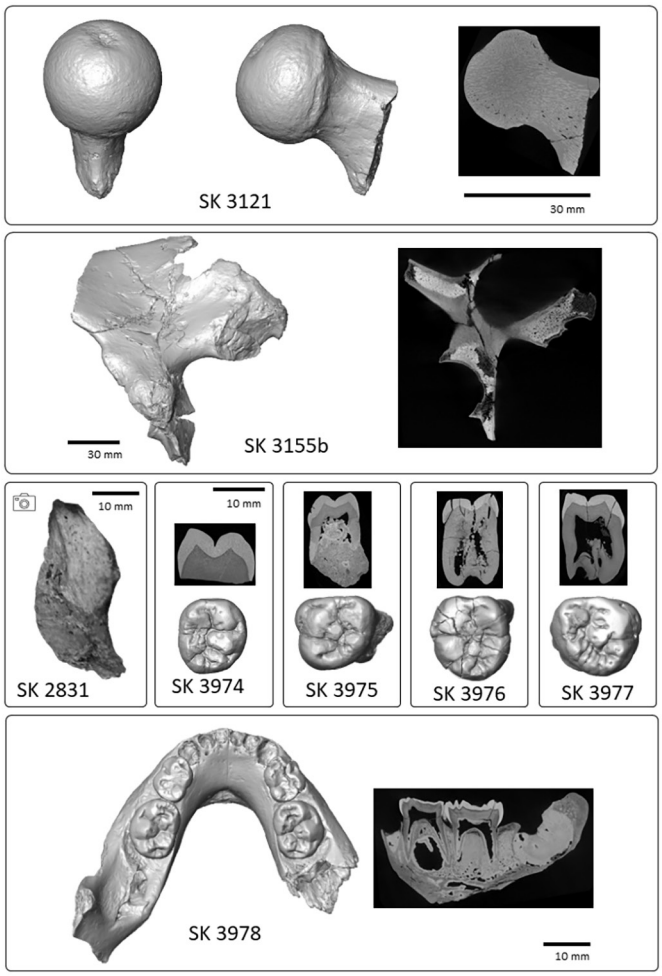

Figure 43. SK 2381, SK 3121, SK 3155b, SK 3974, SK 3975, SK 3976, SK 3977, SK 3978

are partially embedded in breccia (DNMNH records, unpublished). It was not scanned or photographed for this publication.

- **SK 2598** – a partial distal end of a humerus (Susman et al. 2001). It was not scanned or photographed for this publication.
- **SK 2831** – a partial zygomatic that Clarke (1977) determined was not part of SK 847 and that its previously assigned accession number, SK 847g, should no longer be used (Figure 43). It was not scanned for this publication.
- **SK 3121** – the head and neck of a right femur (see Figure 43) that was described by Susman et al. (2001).
- **SK 3155b** – a right innominate (see Figure 43) that preserves a partial ilium and acetabulum (Brain et al. 1974; McHenry 1975).
- **SK 3974** – a right mandibular molar (see Figure 43) that Brain (1981) lists as a RM_1.
- **SK 3975** – a left maxillary molar (see Figure 43) that Brain (1981) lists as a LM^3.
- **SK 3976** – a left mandibular molar (see Figure 43) that Brain (1981) lists as a LM_2.
- **SK 3977** – a right maxillary molar (see Figure 43) that Brain (1981) lists as a RM^3.
- **SK 3978** – a mandibular corpus (see Figure 43) of an infant containing Rdm_1-dm_2 and Ldm_1-dm_2 (Brain 1981; Conroy and Vannier 1991). Also present are the unerupted and developing RI_2-RP_3 and LI_1-LP_3 and LM_1.
- **SK 3981a + SK 3981b** – a set of associated vertebrae. Robinson (1970) identifies SK 3981a as a twelfth thoracic vertebra (Figure 44) and SK 3981b is a first lumbar vertebra.
- **SK 6934** – an incisor crown (DNMNH records, de Ruiter 2024) that was not scanned or photographed for this publication.
- **SK 14000** – a tooth crown in a piece of breccia (see Figure 44) that is identified as an upper molar fragment by Tobias et al. (1977) and as a tooth fragment by Brain (1981). It was not scanned for this publication.
- **SK 14001** – a left premolar that Brain (1981) lists as a LP^3 (see Figure 44). However, Skinner (2024) identifies it as a LP_3 based on the morphology of the enamel-dentine junction.
- **SK 14003** – a crushed face (see Figure 44) preserving three molars (likely RM_1-M_3) and an originally unnumbered crushed calvaria that were associated by Clarke (1990). It was not scanned for this publication.
- **SK 14024** – a fragmented half of the head of a femur

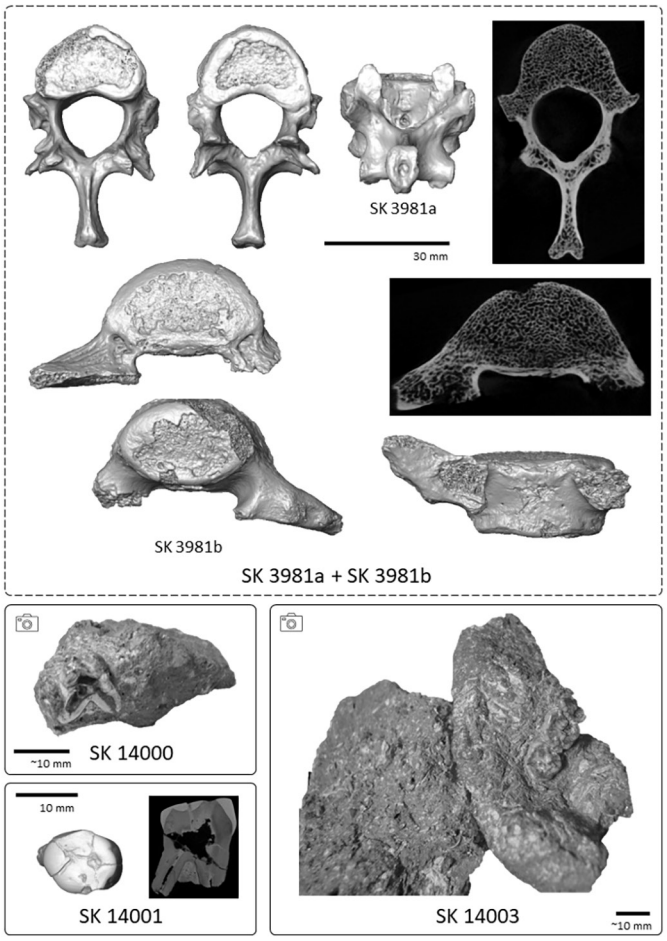

Figure 44. SK 3981a + SK 3981b, SK 14000, SK 14001, SK 14003.

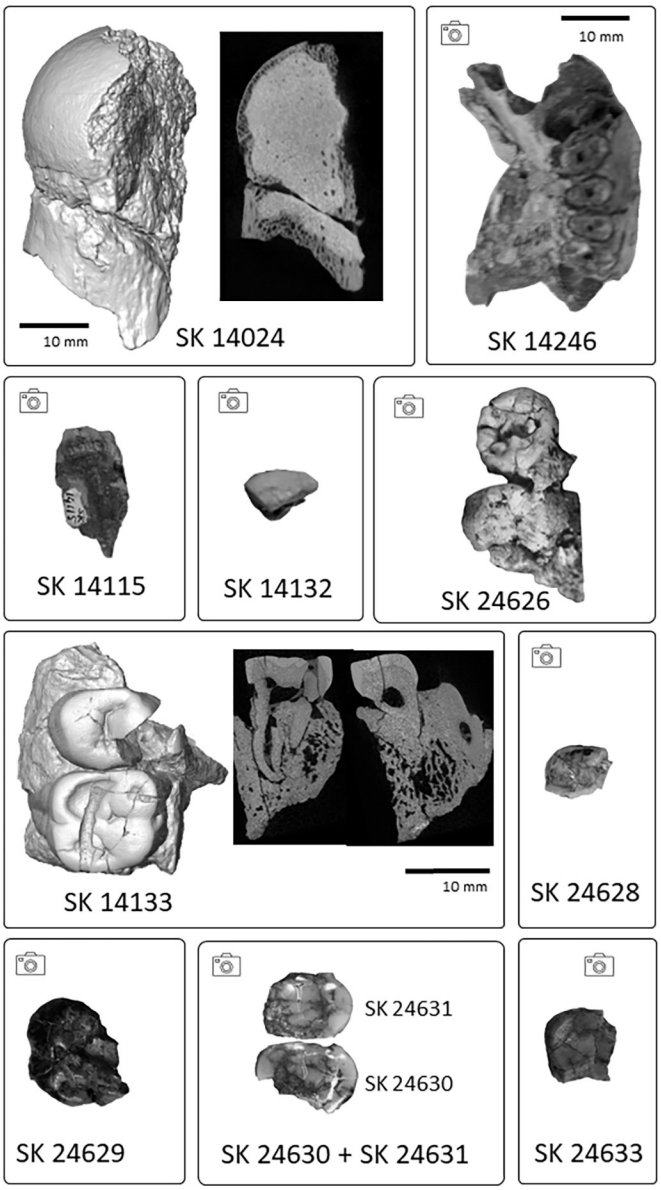

Figure 45. SK 14024, SK 14246, SK 14115, SK 14132, SK 14133, SK 24626, SK 24628, SK 24629, SK 24630 + SK 24631, SK 24633.

(Figure 45) that has not been described to our knowledge (unpublished).

- **SK 14115** – a fragmentary, isolated tooth (see Figure 45) that was not scanned for this publication (unpublished).
- **SK 14132** – an isolated tooth fragment (see Figure 45) that was not scanned for this publication (Grine and Strait 1994).
- **SK 14133** – a partial left palate (see Figure 45) containing LP^4-M^1 (Grine and Strait 1994).
- **SK 14246** – the symphysis portion of a mandible (see Figure 45) that was not scanned for this publication (de Ruiter 2024).
- **SK 14248** – a cranial fragment (DNMNH records) that was not scanned or photographed for this publication (unpublished).
- **SK 14249** – fragments of bone (possibly from a maxilla) in a block of breccia (DNMNH records). It was not scanned or photographed for this publication (unpublished).
- **SK 24600** – the distal end of a left humerus (Figure 46) described by Susman et al. (2001).
- **SK 24601** – the proximal end of a left radius (see Figure 46) described by Susman et al. (2001).
- **SK 24605** – a maxillary molar that is currently being described by de Ruiter (2024) and was not scanned or photographed for this publication.
- **SK 24606** – a maxillary molar that is currently being described by de Ruiter (2024) and was not scanned or photographed for this publication.
- **SK 24607** – a root fragment that is currently being described by de Ruiter (2024) and was not scanned or photographed for this publication.
- **SK 24613** – a tooth fragment that is currently being described by de Ruiter (2024) and was not scanned or photographed for this publication.
- **SK 24626** – a LP_3-P_4 (see Figure 45) that were described by de Ruiter (2004).
- **SK 24627** – five root and enamel crown fragments rep-

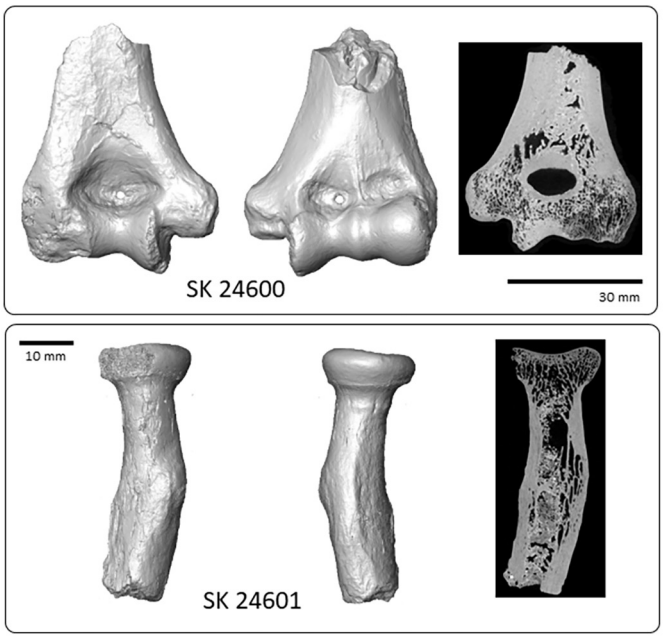

Figure 46. SK 24600, SK 24601.

resenting at least two teeth that were described by de Ruiter (2004). It was not scanned or photographed for this publication.

- **SK 24628** – a fragment of a maxillary molar crown (see Figure 45) described by de Ruiter (2004).
- **SK 24629** – a fragmentary LM^1 (see Figure 45) described by de Ruiter (2004).
- **SK 24630 + SK 24631** – two maxillary premolars described by de Ruiter (2004). SK 24630 is a LP^4 and SK 24631 is a LP^3 (see Figure 45). Their association is based on their recovery from a small piece of breccia in near anatomical position, their similar relative degree of wear, and their patina.
- **SK 24632** – a fragmentary maxillary molar that was described by de Ruiter (2004). It was not scanned or photographed for this publication.
- **SK 24633** –a partial crown of a RM^2 (see Figure 45) that was described by de Ruiter (2004).
- **SK 24653** – a maxillary premolar that is currently being described by de Ruiter (2024). It was not scanned or photographed for this publication.
- **SK 24660** – a mandible that is currently being described by de Ruiter (2024). It was not scanned or photographed for this publication.
- **SK 24661** – a maxillary canine that is currently being described by de Ruiter (2024). It was not scanned or photographed for this publication.
- **SK 24662** – a maxillary molar that is currently being described by de Ruiter (2024). It was not scanned or photographed for this publication.
- **SK 42207** – a maxillary incisor that is currently being described by de Ruiter (2024s). It was not scanned or photographed for this publication.

DISCUSSION

In this study we have provided a current catalogue of hominin fossils from Swartkrans that were excavated between 1948 and 1967. In particular, we provide a comprehensive update of the teeth that are preserved in each specimen including those that were not identified in their initial descriptions. We also have summarized associations between specimens that have been published in various independent articles. By providing visual documentation of the internal structure of each CT scanned fossil (both here in the figures, but also as image stacks on human-fossil-record.org) researchers will be able to evaluate the appropriateness of particular fossils for prospective research projects. Human-fossil-record.org, in collaboration with the Ditsong National Museum of Natural History, also provides researchers with the ability to remotely apply for access to the CT scans of these fossils for research and education.

Many crania and mandibles from Swartkrans are distorted due to fracturing and/or plastic deformation. This is unfortunate as it reduces the degree to which they can contribute to characterizing craniodental morphology, neuroanatomy, and masticatory behavior in *P. robustus* and early *Homo*. Mandibles such as SK 12b, SK 15, SK 23, SK 34, SK 55b, SK 858/SK 861/SK 883, and SK 1586 all have the potential to be virtually reconstructed using modern techniques, which utilize dental wear facets, chewing mechanics, dental arcade shape, and occlusal contact patterns (e.g., Kullmer et al. 2013; Spoor et al. 2015). Similarly, crania such as SK 27, SK 47, SK 49, SK 79, and SK 83 all preserve morphology of the neurocranium, basicranium, and face that perhaps could be studied if modern digital reconstruction approaches were applied (e.g., Grine et al. 2010; Gunz et al. 2009, 2012, 2020). The CT database presented here will help make these reconstruction projects possible for future researchers.

In general, the preservation of internal bone and tooth structure is very good in the Swartkrans fossils; particularly with regards to the level of radiographic contrast between more dense tissues like enamel compared to less dense tissues like dentine or bone. That said, taphonomic processes have impacted the fossils to varying degrees. In addition to the fragmentation and plastic deformation noted above, many of the fossils have an infilling of dense material that seems to uniformly coat internal bone surfaces (e.g., SK 6: see Figure 2, SK 84: see Figure 25). This could be precipitated calcium carbonate and may thus provide some information about the post-depositional environment that different fossils have been in. It could be fruitful to compare variation in infillings from different members and/or locations in the Swartkrans Cave system.

Several fossils also show considerable damage to their internal structure which includes both bone tissues and dental tissues. This can include what appears to be erosion and fragmentation of tissues as well as demineralization of enamel. One of the most striking examples of this is SK 55a (see Figure 18), which exhibits damage to the dentine and underside of the enamel cap as well as the internal alveolar

bone surrounding the teeth. Additional examples include SK 36 (see Figure 8), SK 98 (see Figure 25), SK 824 (see Figure 27), SK 837 (see Figure 28), and SK 856 (see Figure 32). This appears similar to the damage to dental tissues of the KB 5223 teeth from Kromdraai (Skinner et al. 2013). It remains to be determined whether the acid treatments that were often used to remove breccia from fossils curated at the DNMNH caused this damage, but it seems like a possible cause as protective coatings could only be applied to the external surfaces of the fossils during repeated acid bath treatments.

CONCLUSION

We have presented the results of a collaborative project to produce high resolution CT scans of the SK hominin fossils from the site of Swartkrans. We provide a comprehensive summary of preserved teeth in the dental remains, which should guide future research projects on taxonomy, development, and functional morphology. We also provide visual information on the preservation of internal structure of both craniodental and postcranial elements. This publication serves as a citable document associated with an online, open-access archive (human-fossil-record.org) of the CT scans for each specimen, which can be accessed via a research application to the DNMNH.

ACKNOWLEDGEMENTS

All of the fossils included in this study can be accessed following the relevant procedures of the Ditsong National Museum of Natural History. We would like to acknowledge the considerable contributions that Bob Brain made to the recovery and analysis of the Swartkrans fossil collections. We would also like to thank Ron Clarke for particularly important correspondence regarding the history and organization of the Swartkrans hominin assemblage. For technical assistance we thank Heiko Temming, Patrik Schoenfield, Collin Moore, Tracy Kivell, and Adam Sylvester. We would also thank Zachary Cofran for his insightful comments on previous drafts of this manuscript. This project has received funding from the European Research Council (ERC) under the European Union's Horizon 2020 research and innovation programme (grant agreement No. 819960). It is also supported by the Max Planck Society.

DATA AVAILABILITY STATEMENT

All of the data associated with this manuscript are available through human-fossil-record.org and/or the Ditsong National Museum of Natural History. Data access requires following the relevant procedures of the Ditsong National Museum of Natural History.

REFERENCES

Balter, V., Blichert-Toft, J., Braga, J., Telouk, P., Thackeray, F., Albarède, F., 2008. U-Pb dating of fossil enamel from the Swartkrans Pleistocene hominid site, South Africa. Earth Planet. Sci. Lett. 267, 236–246.

Brain, C.K., 1967. The Transvaal Museum's fossil project at Swartkrans. S. Afr. J. Sci. 63, 378–384.

Brain, C.K., 1970. New finds at the Swartkrans australopithecine site. Nature 225, 1112–1119.

Brain, C.K., 1981. The Hunters or the Hunted?: An Introduction to African Cave Taphonomy. The University of Chicago Press, Chicago.

Brain, C.K., 1993. Swartkrans: A Cave's Chronicle of Early Man. Transvaal Museum Monograph No. 8, Transvaal Museum, Pretoria.

Brain, C.K., Sillen, A., 1988. Evidence from the Swartkrans cave for the earliest use of fire. Nature 336, 464–466.

Brain, C.K., Vrba, E.S., Robinson, J.T., 1974. A new hominid innominate bone from Swartkrans. Anns. Transv. Mus. 29, 55–63.

Broom, R., 1949. Another new type of fossil ape-man. Nature 163, 57.

Broom, R., Robinson, J.T., 1949a. A new type of fossil man. Nature 164, 322–323.

Broom, R., Robinson, J.T., 1949b. Thumb of the Swartkrans ape-man. Nature 164, 841–842.

Broom, R., Robinson, J.T., 1950a. Note on the skull of the Swartkrans ape-man *Paranthropus* crassidens. Am. J. Phys. Anthropol. 8, 295–300.

Broom, R., Robinson, J.T., 1950b. Man contemporaneous with the Swartkrans ape-man. Am. J. Phys. Anthropol. 8, 151–156.

Broom, R., Robinson, J.T., 1952. Swartkrans Ape-Man: *Paranthropus crassidens*. Transvaal Museum, Pretoria.

Churcher, C.S., Watson, V., 1993. Additional fossil equidae from Swartkrans. In: Brain, C.K. (Ed.), Swartkrans: a Cave's Chronicle of Early Man. Transvaal Museum, Pretoria, pp. 137–150.

Clarke, R.J., 1977. A juvenile cranium and some adult teeth of early *Homo* from Swartkrans, Transvaal. S. Afr. J. Sci. 73, 46-49.

Clarke, R.J., 1990. Observations on some restored hominid specimens in the Transvaal Museum, Pretoria. In Sperber, G.H. (Ed.) From Apes to Angels: Essays in Anthropology in Honour of Phillip V. Tobias. Wiley-Liss Inc, Hoboken, NJ, pp. 135–151.

Clarke, R.J., 2017. *Homo habilis*: the inside story. In: Sahnouni, M., Semaw, S., Garaizar, J.R. (Eds.), Proceedings of the II Meeting of African Prehistory. Centro Nacional de Investigacion sobre la Evolucion Humana, Burgos, pp. 25–51.

Clarke, R.J., Howell, F.C., 1972. Affinities of the Swartkrans 847 hominid cranium. Am. J. Phys. Anthropol. 37, 319–336.

Clarke, R.J., Howell, F.C., Brain, C.K., 1970. More evidence of an advanced hominid at Swartkrans. Nature 225, 1219–1222.

Curnoe, D., Grün, R., Taylor, L., Thackeray, F., 2001. Direct

ESR dating of a Pliocene hominin from Swartkrans. J. Hum. Evol. 40, 379–391.
Davies, T.W., Delezene, L.K., Gunz, P., Hublin, J.J., Skinner, M.M., 2019. Endostructural morphology in hominoid mandibular third premolars: Geometric morphometric analysis of dentine crown shape. J. Hum. Evol. 133, 198–213.
de Ruiter, D.J., 2004. Undescribed hominin fossils from the Transvaal Museum faunal collections. Ann. Trans. Mus. 41, 29–40.
de Ruiter, D.J., 2024. Undescribed hominin cranio-dental remains from Swartkrans Cave, South Africa. Ann. Dit. Mus. Nat. Hist. 11.
de Ruiter, D.J., Steininger, C.M., Berger, L.R., 2006. A cranial base of *Australopithecus robustus* from the hanging remnant of Swartkrans, South Africa. Am. J. Phys. Anthropol. 130, 435–444.
Gibbon, R.J., Pickering, T.R., Sutton, M.B., Heaton, J.L., Kuman, K., Clarke, R.J., Brain, C.K., Granger, D.E., 2014. Cosmogenic nuclide burial dating of hominin-bearing Pleistocene cave deposits at Swartkrans, South Africa. Quat. Geochronol. 24, 10–15.
Grine, F.E., 1981. Description of some juvenile hominid specimens from Swartkrans, Transvaal. Ann. S. Afr. Mus. 86, 43–71.
Grine, F.E., 1989. New hominid fossils from the Swartkrans formation (1979-1986 excavations): craniodental specimens. Am. J. Phys. Anthropol. 79, 409–449.
Grine, F.E., 2004. Description and preliminary analysis of new hominid craniodental fossil from the Swartkrans formation. In: Brain, C.K. (Ed.), A Cave's Chronicle of Early Man. Transvaal Museum, Pretoria, pp. 75–116.
Grine, F.E., 2005. Early *Homo* at Swartkrans, South Africa: a review of the evidence and an evaluation of recently proposed morphs. S. Afr. J. Sci. 101, 43–52.
Grine, F.E., Daegling, D.J., 1993. New mandible of *Paranthropus robustus* from Member 1, Swartkrans formation, South Africa. J. Hum. Evol. 24, 319–333.
Grine, F.E., P Gunz, P., Betti-Nash, L., Neubauer, S., Morris, A.G., 2010. Reconstruction of the late Pleistocene human skull from Hofmeyr, South Africa. J. Hum. Evol. 59, 1–15.
Grine, F.E., Strait, D.S., 1994. New hominid fossils from Member 1 "Hanging Remnant", Swartkrans Formation, South Africa. J. Hum. Evol. 26, 57–75.
Gunz, P., Kozakowski, S., Neubauer, S., Le Cabec, A., Kullmer, O., Benazzi, S., Hublin, J-J., Begun, D.R., 2020. Skull reconstruction of the late Miocene ape *Rudapithecus hungaricus* from Rudabánya, Hungary. J. Hum. Evol. 138, 102687.
Gunz, P., Mitteroecker, P., Neubauer, S., Weber, G.W., Bookstein, F.L., 2009. Principles for the virtual reconstruction of hominin crania. J. Hum. Evol. 57, 48–62.
Gunz, P., Neubauer, S., Golovanova, L., Doronichev, V., Maureille, B., Hublin, J-J., 2012. A uniquely modern human pattern of endocranial development. Insights from a new cranial reconstruction of the Neandertal newborn from Mezmaiskaya. J. Hum. Evol. 62, 300–313.
Holloway, R.L., 1972. New australopithecine endocast, SK 1585, from Swartkrans, South Africa. Am. J. Phys. Anthropol. 37, 173–185.
Kullmer, O., Benazzi, S., Schulz, D., Gunz, P., Kordos, L., DR Begun, D.R., 2013. Dental arch restoration using tooth macrowear patterns with application to *Rudapithecus hungaricus*, from the late Miocene of Rudabánya, Hungary. J. Hum. Evol. 64, 151–160.
Kuman, K., Granger, D.E., Gibbon, R.J., Pickering, T.R., Caruana, M.V., Bruxelles, L., Clarke, R.J., Heaton, J.L., Stratford, D., Brain, C.K., 2021. A new absolute date from Swartkrans Cave for the oldest occurrences of *Paranthropus robustus* and Oldowan stone tools in South Africa. J. Hum. Evol. 156, 10300.
Kuman, K., Sutton, M., Pickering, T.R., Heaton, J.L., 2018. The Oldowan industry from Swartkrans cave, South Africa, and its relevance for the African Oldowan. J. Hum. Evol. 123, 52–69.
McHenry, H.M., 1975. Biomechanical interpretation of the early hominid hip. J. Hum. Evol. 4, 343–355.
Napier, J.R., 1959. Fossil metacarpals from Swartkrans. Fossil Mammals Afr. 17, 1–18.
Napier, J.R., 1964. The evolution of bipedal walking in the hominids. Arch. Biol. (Liège) 75(Suppl.), 673–708.
Pickering, T.R., Egeland, C.P., Domínguez-Rodrigo, M., Brain, C.K., Schnell, A.G., 2008. Testing the "shift in the balance of power" hypothesis at Swartkrans, South Africa: hominid cave use and subsistence behavior in the Early Pleistocene. J. Anthropol. Archaeol. 27, 30–45.
Pickering, T.R., Heaton, J.L., Clarke, R.J., Sutton, M.B., Brain, C.K., Kuman, K., 2012. New hominid fossils from Member 1 of the Swartkrans formation, South Africa. J. Hum. Evol. 62, 618–628.
Pickering, R., Kramers, J.D., Hancox, P.J., de Ruiter, D.J., Woodhead, J.D., 2011. Contemporary flowstone development links early hominin bearing cave deposits in South Africa. Earth Planet. Sci. Lett. 306, 23–32.
Pickering, T.R., Heaton, J.L., Sutton, M.B., Clarke, R.J., Kuman, K., Hutton Senjem, J., Brain, C.K., 2016. New early Pleistocene hominin teeth from the Swartkrans formation, South Africa. J. Hum. Evol. 100, 1–15.
Plummer, W.P., 2021. The Enamel-Dentine Junction of the Upper Premolars of *Homo naledi* and Other Hominins: A Morphometric Study. M.Sc. Dissertation, University of Kent.
Ripamonti, U., Petit, J., Thackeray, J., 1999. A supernumerary tooth in a 1.7 million-year-old *Australopithecus robustus* from Swartkrans, South Africa. Eur. J. Oral Sci. 107, 317–321.
Robinson, J.T., 1956. The Dentition of the Australopithecinae. Transvaal Museum, Pretoria.
Robinson, J.T., 1961. The australopithecines and their bearing on the origin of man and of stone tool-making. S. Afr. J. Sci. 57, 3–13.
Robinson, J.T., 1970. New finds at the Swartkrans australopithecine site (cont'd): two new early hominid vertebrae from Swartkrans. Nature 225, 1217–1219.
Skinner, M.M., Kivell, T.L., Potze, S., Hublin, J.-J., 2013. Mi-

crotomographic archive of fossil hominin specimens from Kromdraai B, South Africa. J. Hum. Evol. 64, 434–447.

Skinner, M.M., 2014. An image atlas of mandibular postcanine tooth crowns attributed to *Paranthropus.* In: Constantino P.J., Reed, K.E., Wood, B.A. (Eds.), Paleobiology of *Paranthropus*: The Forgotten Lineage(s). Springer, Cham.

Spoor, F., Gunz, P., Neubauer, S., Stelzer, S., Scott, N., Kwekason, A., Dean, M.C., 2015. Reconstructed *Homo habilis* type OH 7 suggests deep-rooted species diversity in early *Homo.* Nature 519, 83–86

Susman, R.L., de Ruiter, D.J., 2004. New hominin first metatarsal (SK 1813) from Swartkrans. J. Hum. Evol. 47, 171–181.

Susman, R.L., de Ruiter, D., Brain, C.K., 2001. Recently identified postcranial remains of *Paranthropus* and early *Homo* from Swartkrans Cave, South Africa. J. Hum. Evol. 41, 607–629.

Sutton, M.B., Pickering, T.R., Pickering, R., Brain, C.K., Clarke, R.J., Heaton, J.L., Kuman, K., 2009. Newly discovered fossil- and artifact-bearing deposits, uranium-series ages, and Plio-Pleistocene hominids at Swartkrans Cave, South Africa. J. Hum. Evol. 57, 688–696.

Tobias, P.V., Copley, K., Brain, C.K., 1977. South Africa. In: Oakley, K.P., Campbell, B.G., Molleson, T.I. (Eds.), Catalogue of Fossil Hominids. Trustees of the British Museum (Natural History), London, pp. 95–151.

Vrba, E.S., 1985. Early hominids in southern Africa: updated observations on chronological and ecological background. In: Tobias, P.V. (Ed.), Hominid Evolution: Past, Present and Future. Alan R. Liss, New York, pp. 195–200.

Wood, B.A., Engleman, C.A., 1988. Analysis of the dental morphology of Plio-Pleistocene hominids. V. Maxillary postcanine tooth morphology. J. Anat. 161, 1–35.

Zanolli, C.M, Davies, T.W., Joannes-Boyau, R., Beaudet, A., Bruxelles, L., de Beer, F., Hoffman, J., Hublin, J-J., Jakata, K., Kgasi, L., Kullmer, O., Macchiarelli, R., Pan, L., Schrenk, F., Santos, F., Stratford, D., Tawane, M., Thackeray, F., Xing, S., Zipfel, B., Skinner, M.M., 2022. Novel dental data challenge the ubiquitous presence of *Homo* in the Cradle of Humankind. Proc. Nat. Acad. Sci. U.S.A. 119, e2111212119.