The first hominin from the early Pleistocene paleocave of Haasgat, South Africa

AB Leece[1,2], Anthony D.T. Kegley[3], Rodrigo S. Lacruz[4], Andy I.R. Herries[1,5], Jason Hemingway[6], Lazarus Kgasi[7], Stephany Potze[7] and Justin W. Adams[2]

[1] The Australian Archaeomagnetism Laboratory, Department of Archaeology and History, La Trobe University, Bundoora, Victoria, Australia
[2] Department of Anatomy and Developmental Biology, Monash University, Melbourne, Victoria, Australia
[3] Department of Biomedical Sciences, Grand Valley State University, Allendale, MI, United States of America
[4] Department of Basic Science and Craniofacial Biology, New York University, New York, NY, United States of America
[5] Centre for Anthropological Research, University of Johannesburg, Johannesburg, Gauteng, South Africa
[6] School of Anatomical Sciences, Faculty of Health Sciences, University of the Witwatersrand, Johannesburg, South Africa
[7] Plio-Pleistocene Section, Department of Vertebrates, Ditsong National Museum of Natural History, Pretoria, South Africa

Corresponding author
Justin W. Adams,
justin.adams@monash.edu

ABSTRACT

Haasgat is a primate-rich fossil locality in the northeastern part of the Fossil Hominid Sites of South Africa UNESCO World Heritage Site. Here we report the first hominin identified from Haasgat, a partial maxillary molar (HGT 500), that was recovered from an *ex situ* calcified sediment block sampled from the locality. The *in situ* fossil bearing deposits of the Haasgat paleokarstic deposits are estimated to date to slightly older than 1.95 Ma based on magnetobiostratigraphy. This places the hominin specimen at a critical time period in South Africa that marks the last occurrence of *Australopithecus* around 1.98 Ma and the first evidence of *Paranthropus* and *Homo* in the region between ~2.0 and 1.8 Ma. A comprehensive morphological evaluation of the Haasgat hominin molar was conducted against the current South African catalogue of hominin dental remains and imaging analyses using micro-CT, electron and confocal microscopy. The preserved occlusal morphology is most similar to *Australopithecus africanus* or early *Homo* specimens but different from *Paranthropus*. Occlusal linear enamel thickness measured from micro-CT scans provides an average of ~2.0 mm consistent with *Australopithecus* and early *Homo*. Analysis of the enamel microstructure suggests an estimated periodicity of 7–9 days. Hunter–Schreger bands appear long and straight as in some *Paranthropus*, but contrast with this genus in the short shape of the striae of Retzius. Taken together, these data suggests that the maxillary fragment recovered from Haasgat best fits within the *Australopithecus*—early *Homo* hypodigms to the exclusion of the genus *Paranthropus*. At ~1.95 Ma this specimen would either represent another example of late occurring *Australopithecus* or one of the earliest examples of *Homo* in the region. While the identification of this first hominin specimen from Haasgat is not unexpected given the composition of other South African penecontemporaneous site deposits, it represents one of the few hominin localities in the topographically-distinct northern World Heritage Site. When coupled with the substantial differences

in the mammalian faunal communities between the northern localities (e.g., Haasgat, Gondolin) and well-sampled Bloubank Valley sites (e.g., Sterkfontein, Swartkrans, Kromdraai), the recovery of the HGT 500 specimen highlights the potential for further research at the Haasgat locality for understanding the distribution and interactions of hominin populations across the landscape, ecosystems and fossil mammalian communities of early Pleistocene South Africa. Such contextual data from sites like Haasgat is critical for understanding the transition in hominin representation at ∼2 Ma sites in the region from *Australopithecus* to *Paranthropus* and early *Homo*.

INTRODUCTION

The Haasgat fossil site is a paleokarstic deposit consisting of a large cave passage completely in-filled with calcified cave sediments and interstratified speleothem, the latter of which was largely removed by lime mining at the turn of the 20th century. This mining activity also generated a large talus slope outside the cave consisting of fossil bearing paleocaves sediment blocks that have yielded the Haasgat *ex situ* faunal assemblage (HGD; *Keyser, 1991*; *Keyser & Martini, 1991*; *McKee & Keyser, 1994*; *Plug & Keyser, 1994*; *Adams, 2012*). The Haasgat primate community is unique relative to that reported from most Bloubank Valley sites (e.g., Sterkfontein, Swartkrans, Cooper's, Kromdraai), with the most demographically diverse and potentially oldest sample of the basal *Papio* species, *Papio angusticeps,* in the African fossil record (*Freedman, 1957*; *Gilbert et al., 2015*). Haasgat is also the only site currently documenting multiple fossil colobine species (*Cercopithecoides haasgati, Cercopithecoides williamsi, Cercopithecoides* sp.) in South Africa (*McKee & Keyser, 1994*; *McKee, Von Mayer & Kuykendall, 2011*; *Kegley, Hemingway & Adams, 2011*; *Adams, 2012*; *Adams et al., 2015*). The overall mammalian faunal assemblage is also unusual in the low representation of Order Carnivora, as well as the recovery of primitive alcelaphins/ovibovins and a high proportion of extremely large klipspringers (*Oreotragus* sp.) that are more similar to those from the Makapansgat Member 3 deposits (3.03–2.58 Ma; *Herries et al, 2013*) than those recovered from the nearby Gondolin GD 2 deposits (∼1.8 Ma; *Herries et al., 2006*; *Adams, 2010*; *Adams, 2012*). Despite this rich and regionally-unique faunal community established through the *ex situ* HGD assemblage, no hominins were recovered during the first phases of paleontological sampling at Haasgat. This paper provides a comprehensive morphological and dental microstructure analysis of the first hominin specimen, a partial maxillary molar (HGT 500; Fig. 2), that was recovered from a calcified *ex situ* dumpsite block collected in 2011 from the site.

The unique nature of the fossil assemblage may also reflect the fact that the site is formed within the Eccles Formation of the Malmani dolomite in the northern sector of the Hominid Fossil Sites of South Africa UNESCO World Heritage Site (known locally as the Cradle of Humankind or 'Cradle'; Fig. 1: ∼50 km north-northwest of
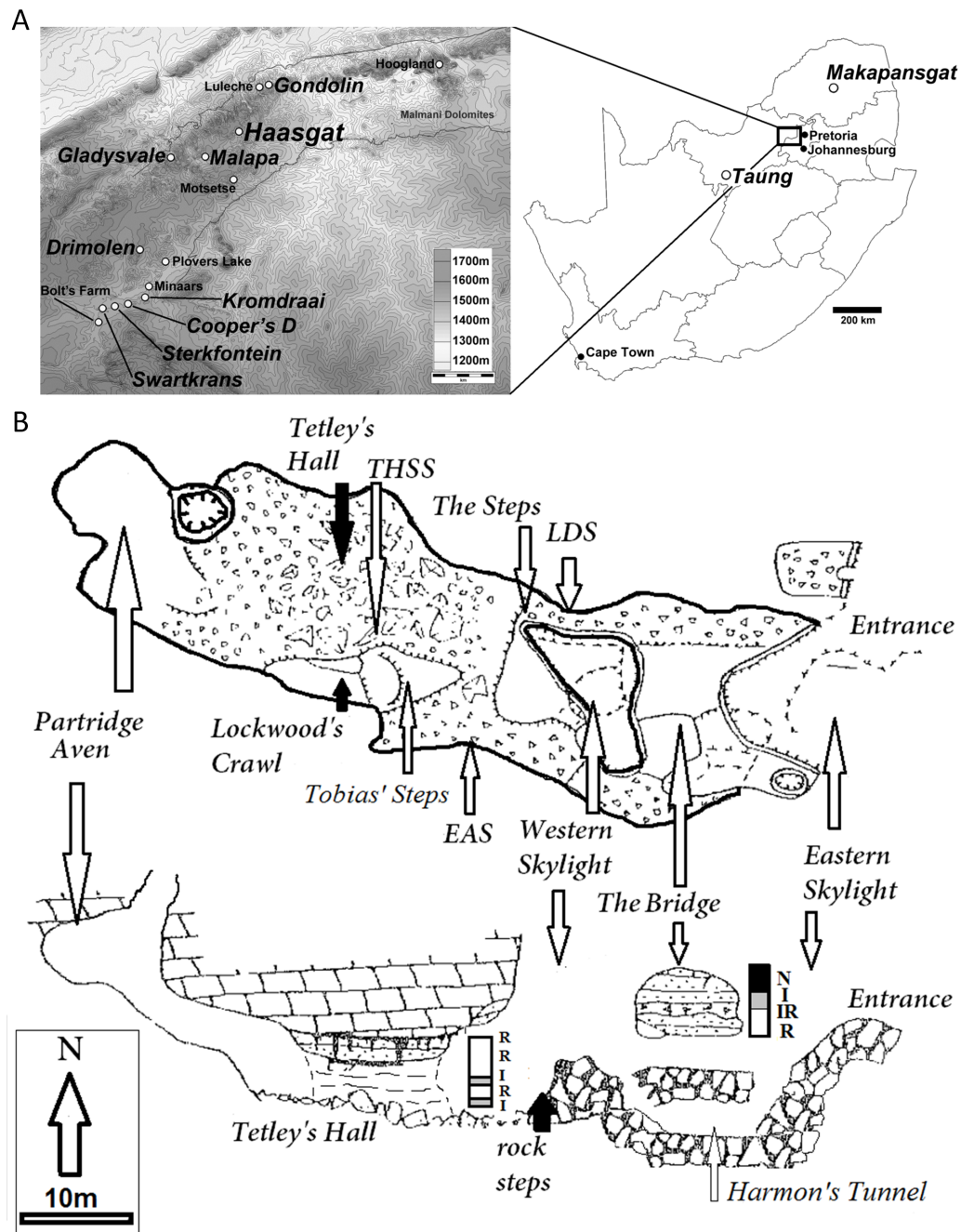
Figure 1 Location and site plan of the Haasgat paleocave system. (A) topographic contour map indicating the position of Haasgat relative to other South African late Pliocene and early Pleistocene sites and location of these sites within South Africa. (B) plan and section views of the excavated Haasgat paleocave system. Scale bars as indicated.

Johannesburg in Gauteng Province). This high topographic setting, with upland plateaus and deeply incised valleys is quite distinct from the southern area of the Cradle and the Bloubank Valley, from which the majority of the Plio-Pleistocene paleontological data has been recovered (Sterkfontein, Swartkrans, Kromdraai, Cooper's). This landscape is
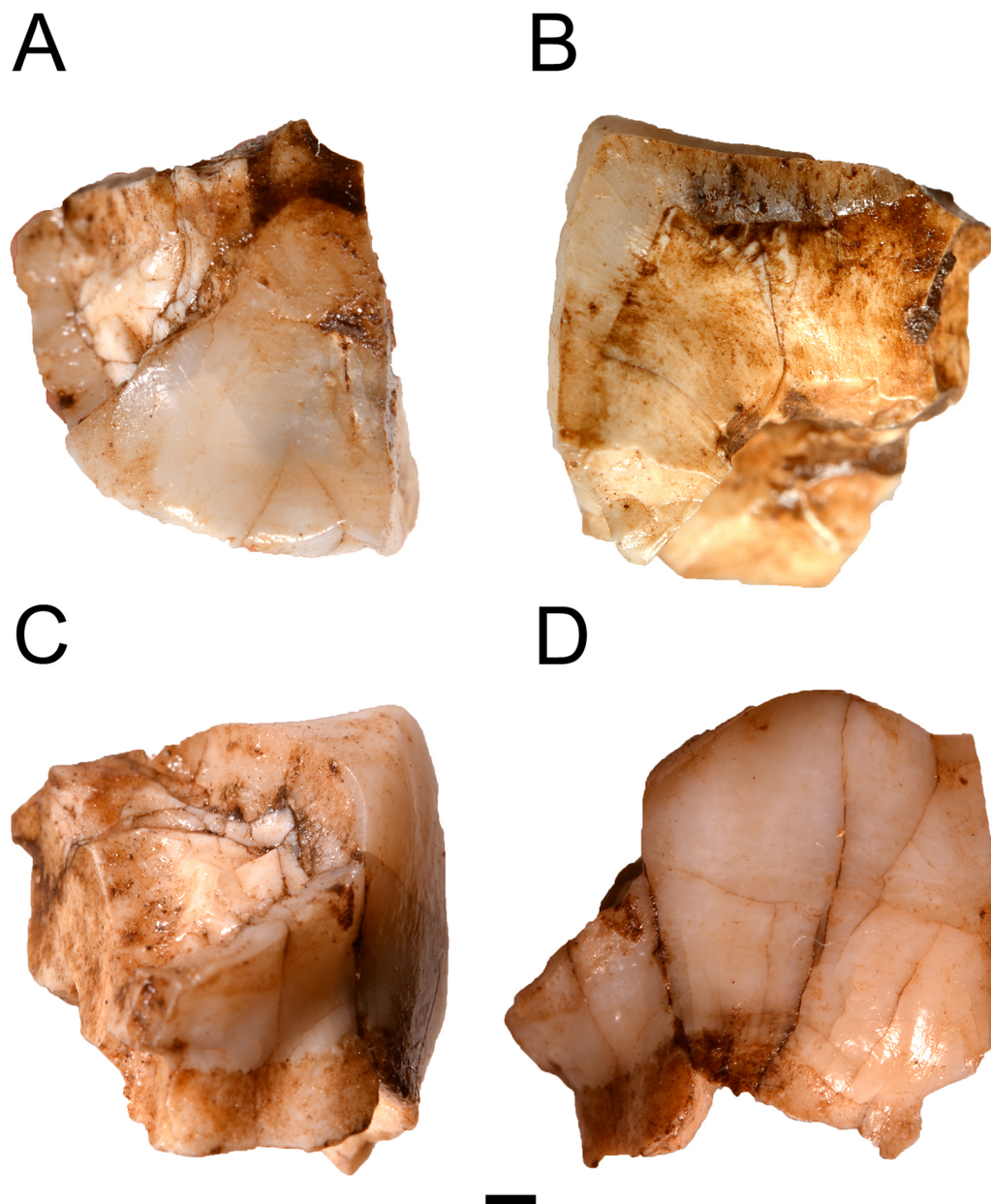
Figure 2 The HGT 500 Hominini gen. et sp. indet. molar. (A) occlusal view; (B) mesial view; (C) distal view; (D) buccal view. Scale bar equals 1 mm.

indicative of highly variable erosional processes during the Neogene and reflected in the variable paleohabitats and mammalian community composition between sites across the region (*Vrba, 1976*; *Brain, 1981*; *Reed, 1996*; *Avery, 2001*; *Adams & Conroy, 2005*; *Adams et al., 2010*; *Bailey, Reynolds & King, 2011*; *Adams, 2012*; *Adams, Kegley & Krigbaum, 2013*). These differences are further reflected in reconstructions that suggest the local environments during deposition were both mesic and rugged as evidenced by trace geochemical analysis (*Herries et al., 2014*) and the dominance of C3-consuming and/or broken terrain adapted species in the *ex situ* HGD faunal assemblage (*Adams, Kegley & Krigbaum, 2013*).

Unlike the Bloubank Valley caves, Haasgat does not suffer from major phases of karstification that have caused the mixing of fossils from different aged deposits (*Reynolds, Clarke & Kuman, 2007*; *Herries & Adams, 2013*). While two phases of cave formation occurred at Haasgat, the later sediment fill is distinct (uncalcified, greyish-brown) from the older (calcified, reddish-brown) paleocave sediments (*Herries & Adams, 2013*; *Herries et al., 2014*). Given similarities with *in situ* excavated material, the *ex situ* derived fauna is considered a reliable temporal indicator of both the *ex situ* and *in situ* fossil assemblages. Only recently have comprehensive geological, geochemical and paleobiological analyses been undertaken alongside the first excavations into the rich *in situ* sediment deposits (*Kegley, Hemingway & Adams, 2011*; *Adams, 2012*; *Adams, Kegley & Krigbaum, 2013*; *Herries et al., 2014*; *Adams et al., 2015*; J Adams, 2016, unpublished data). The recent recovery of *P. angusticeps*, *C. haasgati*, and *C. williamsi* craniodental remains from the first *in situ* excavations (*Adams et al., 2015*; J Adams, 2016, unpublished data) confirms data from the *ex situ* assemblage and has also established the occurrence of partial skeletons within the deposits. These *in situ* sediments have been dated to slightly older than 1.95 Ma based on the occurrence of *in situ* *Equus* material (thus <2.3 Ma) within the walls of the deposit as well as a magnetic reversal correlated to the base of the Olduvai SubChron in the upper portion of the sediment sequence (*Herries et al., 2014*). As such, the site covers a critical time period in the South Africa fossil record with the extinction of *Australopithecus* by ~2 Ma (*Au. africanus* at the end of Sterkfontein Member 4 deposition and *Au. sediba* from Malapa) and the first occurrence of *Paranthropus*, early *Homo*, and the first mode 1 stone tools by 1.8 Ma (*Herries et al., 2010*; *Herries & Shaw, 2011*; *Pickering et al., 2011a*; *Pickering et al., 2011b*; *Herries & Adams, 2013*).

MATERIALS AND METHODS

The HGT 500 specimen was processed from an *ex situ* block recovered from the calcified sediment dumpsite in 2011. The original ~10 cm × ~25 cm reddish siltstone calcified block (HGT 11-50) is consistent with deposits occurring in the reversed polarity deposits at the rear of the paleocave system. The block was processed using a 5% acetic acid solution and stabilized with the thermoplastic resin Paraloid[TM] B-72 (Dow Chemical Co., USA) following protocols of the fossil preparation lab at the Plio-Pleistocene Section, Ditsong National Museum of Natural History, Pretoria (the repository institution of Haasgat fossil specimens collected since 2009; all assigned a 'HGT' prefix to identify them relative to the previously collected, *ex situ* HGD fossils from the site curated with the Council for Geosciences, Pretoria). The HGT 500 specimen is one of only three identifiable macromammalian craniodental specimens recovered from the block, with the other two representing an indeterminate Class II (*sensu Brain, 1981*: Table 1) bovid central cavity (Family Bovidae, Order Cetartiodactyla; HGT 557) and a partial hyrax (*Procavia* sp.; Family Procaviidae, Order Hyracoidea) molar (HGT 558). One partial right coracoid (HGT 554) and one right distal humerus (HGT 560) are likely derived from a single indeterminate avian. The remaining 58 fossils recovered from the block consist of: six <1 cm indeterminate taxon enamel fragments, one partial indeterminate epiphysis, and indeterminate element

Table 1 South African hominin specimens used in comparative analysis of HGT 500.

Species	Locality	Specimen
Paranthropus robustus	Drimolen	DNH 44, 47, 84, 107, 108
	Kromdraai B	KB 5222, 5383, TM 1536, 1517, 1601c, 1603
	Swartkrans Member 1HR	SK 13, 14, 31, 36, 41, 42, 46, 47, 48, 52, 57, 62, 83, 98, 102, 829, 831, 832, 833, 834, 835, 836, 838, 849, 870, 872, 3975, 3977, 25605
		SKW 11, 14, 3114
Australopithecus africanus	Sterkfontein Member 4 (Type Site)	STS 1, 2, 8, 19, 12, 17, 19[a], 21, 22, 23, 24, 32,
		37, 43, 52, 53, 54, 57, 71, 72, 1881, 3009
		TM 1512, 1561
	Sterkfontein Member 5c (West Pit)	SE 255, 1508
	Makapansgat Limeworks	MLD 11/30
	Sterkfontein	STW 151[b]
Australopithecus sediba	Malapa	MH 1
Homo erectus (sensu lato)	Swartkrans Member 1HR	SK 27
South African Early *Homo*	Drimolen	DNH 35, 67/70/71, 83
	Swartkrans Member 1HR	SK 874
	Swartkrans Member 2	SKX 267
	Kromdraai B	KB 5223[c]

Notes.

These materials are curated at the Ditsong National Museum of Natural History in Pretoria, South Africa and at the Evolutionary Studies Institute, University of Witwatersrand in Johannesburg, South Africa (Table 1).

[a]*Ahern (1998)* and *Lockwood & Tobias (2002)*; Argued to represent early *Homo* by *Kimbel & Rak (1993)*.

[b]Unknown provenience; Recently published as "Indeterminate Hominin" (*Smith et al., 2015*).

[c]Originally assigned to *Paranthropus* (*Grine, 1982*) but recently ascribed to *Homo* (*Braga & Thackeray, 2003*).

diaphyseal fragments (1–2 cm: 32, 2–3 cm: 17, 3–4 cm: 2). All assessable elements record minimal evidence of cortical exfoliation from environmental exposure (Weathering Stage 0: 7, Stage 1: 9, Stage 2: 3; *sensu Behrensmeyer, 1978*), porcupine gnawing is evident on at least two indeterminate diaphyseal specimens (HGT 568 and HGT 576; possibly HGT 756), and possible carnivore-induced gnawing on two elements (HGT 568 and HGT 575). Although a further 24 fossiliferous *ex situ* calcified blocks were collected from across the exposed surface of the HGD dumpsite during the same field season, processing of these blocks did not yield fossil specimens that can be confidently associated with those from HGT 11-50 (J Adams, 2016, unpublished data).

Direct morphological comparison

The specimens used in comparative analysis included craniodental remains attributed to *Paranthropus robustus, Australopithecus africanus, Australopithecus sediba,* South African early *Homo*, and *Homo habilis* (Table 1).

Specimen imaging
MicroCT

Preparation of the HGT 500 for analysis included removal of residual Paraloid[TM] , which allowed a naturally-fractured section of the crown to separate (this section was rejoined after
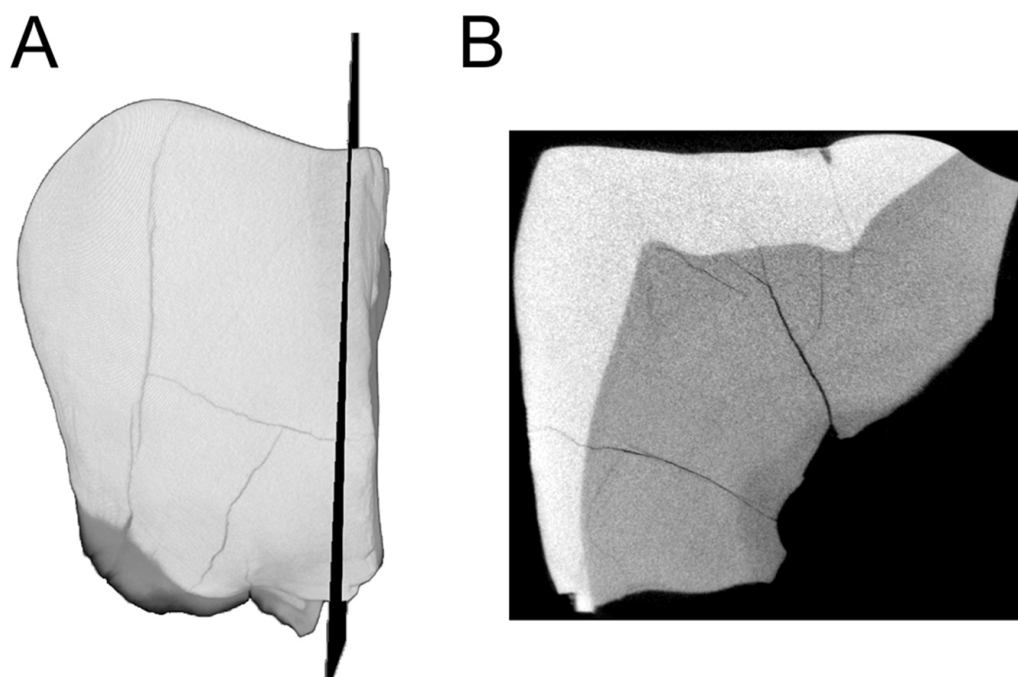
Figure 3 **MicroCT derived surface render of the HGT 500.** (A) mesial view of the specimen demonstrating the section plane used for evaluating enamel thickness. (B) section plane through the molar demonstrating enamel thickness and morphology of the EDJ and dentin horns.

scanning was completed). This larger portion of HGT 500 was scanned and reconstructed on a SCANCO microCT 50 (SCANCO Medical, Brüttisellen, Switzerland) housed at the Institute for Genetic Medicine, University of Southern California. Acquisition settings were: 70 kVp, 200 uA, 750 ms exposure, 750 projections, 10 micron isotropic resolution (FOV: 15.1×15.1×10.58 mm, Grid: 1,510×1,510×1,058). The resulting microCT TIFF stack is openly available for download through Morphosource (10.17602/M2/M8952) as part of the Ditsong National Museum of Natural History Digital Archive (*Adams et al., 2015*). Images were converted to DICOM format (NEMA Standard PS3) and imported into AMIRA$^{©}$ 5.4.0 (FEI^{TM} Visualization Sciences Group, Hillsboro, OR, USA) for volume/surface rendering and measurement. Linear measurements (in millimetres) of enamel thickness were taken from the enamel dentine-junction to the outer-most enamel surface from virtual sections in various planes following a similar methodology to *Grine & Martin (1988)*. Given the wear on this specimen, the linear measurements are not exactly taken at the true occlusal plane (to the cusp tip). No attempts were made to estimate the loss of enamel. Instead, the thickness represents a point between the occlusal and lateral enamel, also recorded by *Grine & Martin (1988)* in the specimens described therein. Virtual cross-sections were aligned perpendicular to a horizontal plane using the cemento-enamel junction as a reference and passing near the dentine horn (Fig. 3A).

Portable confocal microscopy

A portable confocal scanning optical microscope was used to analyze the enamel microstructure using $10\times$ and $20\times$ objective lenses following previously described methods (*Bromage et al., 2007*; *Lacruz et al., 2008*).

RESULTS

Comparative morphological description

The HGT 500 specimen is a partial molar preserving one complete cusp, small portions of two additional cusps, and very minimal root structures below the cemento-enamel junction (Fig. 2). Due to the incomplete nature of this specimen, crown and root measurements could not be taken for the purposes of comparison. The overall occlusal shape of the remaining cusp is indicative of a left maxillary molar, as it does not demonstrate the smaller, more closely-packed cusps seen in mandibular molars (*Grine, 1984*).

Following this positioning the preserved cusps represent a complete metacone and portions of the paracone, protocone, and metaconule. The metacone is complete from the cervical margin to the occlusal margin and the premetacrista and postmetacrista through the trigone basin are visible on the occlusal surface. The paracone is broken along the coronal plane with only a distal portion preserved showing the postparacrista from the cervical margin to the trigone basin. The mediodistal portion of the protocone is preserved at the trigone basin. The buccal-most portion of the metaconule is preserved along the cervical margin and does not reach the occlusal surface. The crown displays a significant flaring at the cemento-enamel junction on the distal face while the buccal face is very straight, running vertically to the occlusal surface. The lack of bulbous lateral faces is distinct from the morphological suite observed in *Paranthropus robustus* and is more suggestive of *Australopithecus* or *Homo*. Minor torsion in the preserved state of this smaller fragment makes it appear to protrude further than it would have prior to deposition.

The occlusal surface preserves a portion of a dentine exposure. It has been estimated that this exposure would have occupied the majority of the absent protocone. This level of wear indicates moderate to heavy attrition. A shallow groove is visible between the metacone and remaining paracone. This is distinctly different from the deeply incised buccal groove seen in *P. robustus* and is instead more similar to those seen in both *Australopithecus africanus* and *Australopithecus sediba* (*Grine, 1984*; *Berger et al., 2010*).

The lack of a distal interproximal facet on the preserved surface of this specimen may indicate that it represents either an M^3 or an M^2 lacking this facet with the M^3 not yet in occlusion. The absence of this feature may eliminate the possibility of the specimen representing an M^1 given that the advanced wear would imply that the M^2 would have been in occlusion. Alternatively, it is possible the portion of the distal face expected to show an interproximal wear facet has not preserved.

The linear enamel thickness measured along three planes of the larger fragment provided an average of 2.03 mm (range 1.99 mm–2.13 mm) in the occlusal area (Fig. 3). This linear enamel thickness average is inconsistent with values previously reported for *P. robustus* M^2, and instead falls within the upper boundary of enamel thickness for early South African

Table 2 Enamel thickness of South African hominin species by element.

Species	M1 Mean	M1 Min-Max	M2 Mean	M2 Min-Max	M3 Mean	M3 Min-Max	Species Mean
Australopithecus africanus[a]							1.63
Max	1.59	–	–	–	1.67	–	
Mand	1.68	1.31–2.05	1.36	1.23–1.49	1.33	0.98–1.60	
Paranthropus robustus[a]							2.03
Max	2.04	1.68–2.39	–	–	1.78	1.37–2.03	
Mand	1.85	1.35–2.33	1.56	–			
Early *Homo*[b]							–
Max	–	–	2.2	–	–	–	
Mand	1.77	–	–	–	–	–	

Notes.
[a]Data from *Olejniczak et al. (2008)*.
[b]Data from *Smith et al. (2015)*.

Homo M^2 (Table 2). However, if HGT 500 represents either an M^1 or an M^3, it would result in an enamel thickness outside the range of early South African *Homo* and instead within the range of *A. africanus* (Table 2).

Enamel microstructure

Analysis of the perikymata packing pattern along the cervical portion of the tooth revealed relatively packed perikymata (Fig. 4A). Enamel microstructural details (Hunter–Schreger bands, striae of Retzius shape, cross striations) were observed more clearly on the naturally broken surface. Hunter–Schreger bands appeared long and straight (Fig. 4B). Confocal microscopy revealed striae of Retzius in places along the lateral and cervical portion of the enamel but appeared faint at the occlusal enamel. Where visible, the overall shape of the striae tend to be short and not curving rapidly toward the occlusal portion of the enamel (Fig. 4B). Limited data were obtained on cross striation length as these were only visible in a few areas of the mid-to-outer lateral enamel. In those areas, cross striations measured on average ∼4.1 μm. Although the striae periodicity could not be clearly determined, a range of 7–9 days was obtained by measuring cross striations in the vicinity and applying this measurement to the distance between two adjacent striae, an approach similar to that described in *Lacruz, Ramirez-Rozzi & Bromage (2006)* (Figs. 4B and 4C).

DISCUSSION

The suite of micro- and macro- morphological features preserved on the HGT 500 specimen allows attribution to the Tribe Hominini (*sensu Wood & Richmond, 2000*) and is inconsistent with the genus *Paranthropus* in several key respects. The limits of the preserved anatomy, however, preclude a definitive generic or species attribution. The occlusal linear enamel thickness of ∼2.0 mm is beyond reported enamel thickness for large-bodied cercopithecoid primates (e.g., *Theropithecus*; *Swindler & Beynon, 1993*), at the lower end of values assigned to *P. robustus* (*Grine, 1984*) and most consistent with the reported range for *A. africanus* and early *Homo* (Table 2). The 7–9 day striae of Retzius
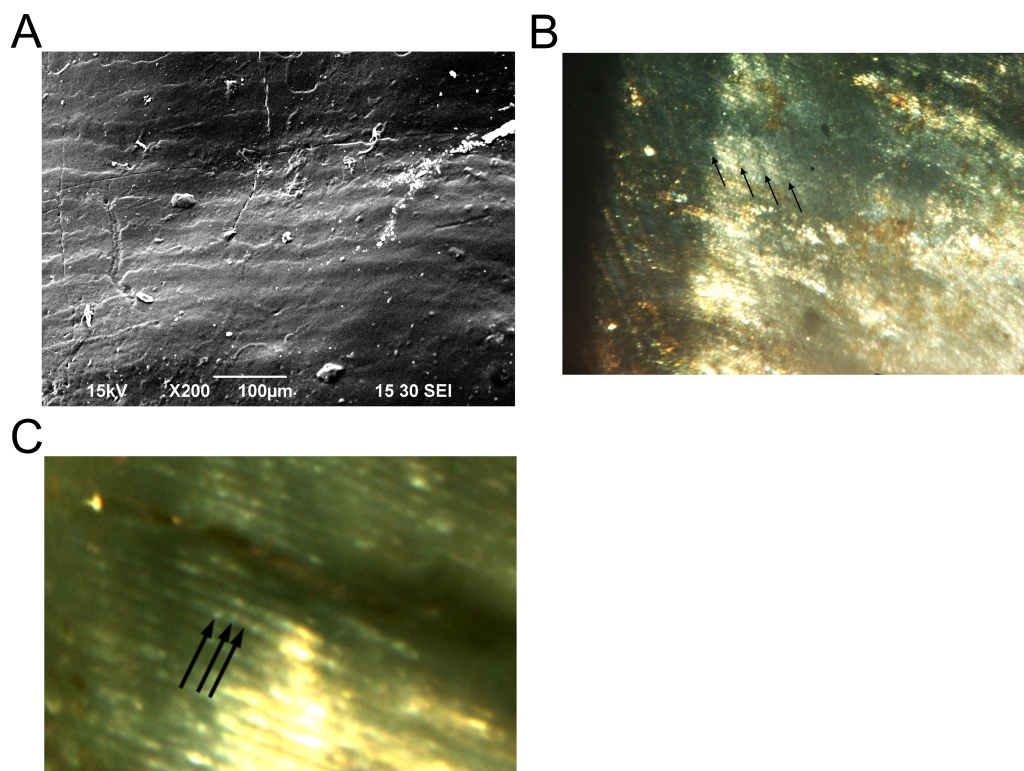
Figure 4 **Enamel microstructure and microwear analyses of the HGT 500 specimen.** (A) SEM image of the cervical portion of the molar demonstrating perikymata packing; (B) confocal microscopy (CM) image of the lateral aspect of the naturally broken enamel surface of the HGT 500 specimen demonstrating the shape of the striae of Retzius (arrows); (C) CM image of the same exposed enamel region as (B) with visible cross striations (arrows). Scale bars as indicated.

periodicity is consistent with the 6–9 day range evinced by *Australopithecus* and early *Homo* specimens (australopiths: ∼7 days, early *Homo*: ∼9 days (*Lacruz et al., 2008*); *A. africanus*: ∼8.5 days, early South African *Homo*: just above 7 days (*Smith et al., 2015*)) to the exclusion of other large-bodied primates (*Bromage et al., 2009*). Long and straight Hunter–Schreger bands are visible on the naturally broken surface; however these features can be quite variable as they are affected by the plane of the examined section (*Ramirez-Rozzi, 1998*). The bands on the HGT 500 specimen are comparable to some of these features described for *Paranthropus* (*Beynon & Wood, 1986*; *Ramirez-Rozzi, 1993*), but are also seen in some specimens of east African *Australopithecus* and some early *Homo* (*Beynon & Wood, 1986*; *Lacruz & Ramirez-Rozzi, 2010*; *Lacruz et al., 2012*). Within the HGT 500 specimen, we observed tight packing of the perikymata on the cervical portion of the tooth. Tightly packed perikymata are observed in specimens assigned to *Australopithecus* and early *Homo* (*Lacruz, Ramirez-Rozzi & Bromage, 2006*) and differ from that described for *Paranthropus* molars where the perikymata are widely spaced (*Dean et al., 1993*). The portions of the striae of Retzius that are visible also suggest that the striae were not long; contrasting with the long striae described for East and South African *Paranthropus* species (*Beynon & Wood, 1986*; *Ramirez-Rozzi, 1993*; *Lacruz, Ramirez-Rozzi & Bromage, 2006*).

Irrespective of a more specific allocation of the specimen, the recovery of HGT 500 from the already primate-rich Haasgat locality is not unexpected given the taxonomically-diverse South African *Australopithecus* and *Homo* community proposed during the time period (between 2.3 and 1.95 Ma; but likely closer to 1.95 Ma) encompassed by the Haasgat *in situ* paleocave deposits. *Australopithecus africanus* is ubiquitous on the South African landscape from approximately 3.0–2.6 Ma (Makapansgat Limeworks and Taung) until ~2.0 Ma (Sterkfontein Member 4; *Herries et al., 2010*; *Herries & Adams, 2013*), and the genus persists in the South African record later into the Pleistocene than in eastern Africa via *Australopithecus sediba* dated to approximately 1.98 Ma (Malapa; *Pickering et al., 2011a*). As such, if HGT 500 is *Australopithecus* then this is entirely in keeping with what we know about its temporal range and only slightly extends its geographic range to the north and east from Malapa. The oldest known fossils attributed to early *Homo* in South Africa are from the Swartkrans Member 1 deposits and date to between 2.3 and 1.8 Ma (*Pickering et al., 2011b*), although it has been suggested that the deposits date to between 2.0 and 1.8 Ma (and likely closer to 1.8 Ma; *Herries & Adams, 2013*). As *Grine (2013)* has also pointed out, it is perhaps unlikely that Swartkrans is as old as 2.3 Ma based on the age of *Australopithecus* bearing deposits at Sterkfontein, as there remains little evidence to suggest that early *Homo* and *Paranthropus* overlapped in the region contemporaneously with *Australopithecus*. At Sterkfontein the >2 Ma Member 4 deposits are generally considered to contain only *Australopithecus*. Although *Kimbel & Rak (1993)* have argued for the inclusion of Sts 19 in early *Homo*, this has been challenged by both *Ahern (1998)* and *Lockwood & Tobias (2002)*. Early *Homo* fossils have also been recovered from Drimolen (*Moggi-Cecchi et al., 2010*), however the age of the deposits at the site remains only broadly established (between 2.0 and 1.4 Ma; *Herries & Adams, 2013*).

Ultimately, the significance of the HGT 500 specimen lies with the continued expansion of known hominin localities into the topographically and paleoecologically unique regions of South Africa outside the Bloubank Valley paleocave systems. Despite the limited geographic area encompassed by the Fossil Hominid Sites of South Africa World Heritage Site there are substantial differences in landscape topography and reconstructed mammalian paleocommunities between the southwestern Bloubank Valley sites (e.g., Sterkfontein, Swartkrans, Kromdraai, Bolt's Farm, Cooper's) and the few fossil localities, like Haasgat, that have been identified to the north or east of this well-sampled region (e.g., Gondolin, Gladysvale, Malapa, Motsetse, Hoogland). The northeastern World Heritage Site area is within the Skurweberg mountain range defined by sharp topographic relief due to differential erosion of the less chert-rich Monte Cristo dolomites in the southern region relative to the more chert-rich Eccles Formation dolomites in the northern region. This somewhat mirrors the higher topographic relief surrounding the Makapansgat site ~250 km to the northwest of the Bloubank Valley sites. Faunal data from the Gondolin GD 2 deposits (*Adams & Conroy, 2005*; *Adams, 2006*) and Haasgat (*Adams, 2012*; *Herries et al., 2014*), that lie ~4 km from each other, support the presence of a proto-Skurweberg range before 2 Ma, while cosmogenic nuclide exposure dating of quartz near Malapa (*Dirks et al., 2010*) also indicates substantial differential erosion of the region since the early Pleistocene that may have radically reshaped the topography from an upland plateau to

the modern mountainous topography. Although there are similarities between the Haasgat and Gondolin faunal assemblages that underlies a regional paleoecological interpretation of locally rocky and broken terrain by 2 Ma, there are also substantial differences in the current faunal samples; ranging from significant metric differences between the Haasgat HGD and Gondolin GD 2 klipspringer (*Oreotragus* sp.) populations (*Adams, 2012*), to the proportions of cercopithecoids (with Gondolin GD 2 lacking any non-hominin primates; *Adams & Conroy, 2005*), and hominin representation (with Gondolin recording two isolated *ex situ* hominin teeth, only one of which has been specifically attributed to *Paranthropus robustus*; *Menter et al., 1999*; *Grine et al., 2012*; *Herries & Adams, 2013*). Establishing Haasgat as one of few hominin-bearing localities in this unique region affords more insight into the range of South African paleohabitats hominin populations occupied and the early Pleistocene paleocommunities that hominin populations interacted with; particularly critical in establishing the larger ecological context of the major hominin lineage transitions occurring ∼2 Ma.

CONCLUSION

All of the South African sites from which these hominin species have been recovered are, for the most part, in an extremely constrained geographical range that would have presented similar adaptive pressures on early Pleistocene hominin populations. This is reflected in the considerable overlap across South African hominin species in stable isotope values (*Lee-Thorp et al., 2010*), morphological features associated with dietary adaptation such as enamel thickness (*Smith et al., 2015*) or dental crown metrics (*Moggi-Cecchi et al., 2010*), and retention of shared dental development patterns (*Dean et al., 1993*; *Dean et al., 2001*; *Dean, 2010*; *Smith et al., 2015*). These factors, when combined with the incomplete state of the HGT 500 specimen, contribute to the non-diagnostic nature of HGT 500 for taxonomic attribution. This first recovery of hominin material at Haasgat reinforces the potential for development of the ∼1.95 Ma site deposits to address outstanding paleoanthropological and paleontological research questions about hominin, primate, faunal and paleoecological variability outside the Bloubank Valley in the poorly-sampled northeastern Malmani dolomites that range between Malapa and Gondolin (*Adams & Conroy, 2005*; *Herries et al., 2006*; *Adams et al., 2007*; *Berger et al., 2010*; *Adams, 2012*; *Grine et al., 2012*; *Adams, Kegley & Krigbaum, 2013*; *Gilbert et al., 2015*).

ACKNOWLEDGEMENTS

We would like to thank Phil Tetley, Glyn French and the entire Kalkheuvel West community for their support of our continued research at Haasgat. This discovery was made possible by permission from the South African Heritage Resources Administration (SAHRA) to excavate the Haasgat locality. We also wish to thank the Council for Geosciences (Pretoria, South Africa), the Ditsong National Museum of Natural History, and the Evolutionary Studies Institute at the University of the Witwatersrand for access to comparative specimens. Finally, we would like to thank Christopher Dean, Bernard Wood, and Matt Skinner for

their constructive input during our initial analyses; as well as Kaye Reed and two anonymous reviewers on an earlier version of this publication.

Funding

This discovery was made possible by funding provided to JWA and ADTK through the National Science Foundation (BSC 0962564) and the Leakey Foundation. AIRH additionally received funding for Haasgat research from the Australian Research Council Future Fellowship (FT120100399). The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

Grant Disclosures

The following grant information was disclosed by the authors:
National Science Foundation: BSC 0962564.
Leakey Foundation.
Australian Research Council Future Fellowship: FT120100399.

Competing Interests

The authors declare there are no competing interests.

Author Contributions

- AB Leece conceived and designed the experiments, performed the experiments, analyzed the data, wrote the paper, prepared figures and/or tables, reviewed drafts of the paper.
- Anthony D.T. Kegley conceived and designed the experiments, performed the experiments, analyzed the data, wrote the paper, reviewed drafts of the paper.
- Rodrigo S. Lacruz and Justin W. Adams conceived and designed the experiments, performed the experiments, analyzed the data, contributed reagents/materials/analysis tools, wrote the paper, prepared figures and/or tables, reviewed drafts of the paper.
- Andy I.R. Herries analyzed the data, contributed reagents/materials/analysis tools, wrote the paper, reviewed drafts of the paper.
- Jason Hemingway performed the experiments, analyzed the data, wrote the paper, reviewed drafts of the paper.
- Lazarus Kgasi and Stephany Potze contributed reagents/materials/analysis tools, wrote the paper, reviewed drafts of the paper, excavation, fossil preparation and curation.

Data Availability

MorphoSource (www.morphosource.org), accession ID: M7737-8952; 10.17602/M2/M8952;

http://ezid.cdlib.org/id/doi:10.17602/M2/M8952.

REFERENCES

Adams JW. 2006. Taphonomy and paleoecology of the Gondolin Plio-Pleistocene cave site, South Africa. D. Phil. Thesis, Washington University, St. Louis.

Adams JW. 2010. Taphonomy of the Gondolin GD 2 *in situ* deposits and its bearing on interpretations of South African Plio-Pleistocene karstic fossil assemblages. *Journal of Taphonomy* **8**:81–116.

Adams JW. 2012. A revised listing of fossil mammals from the Haasgat cave system *ex situ* deposits (HGD), South Africa. *Palaeontologia Electronica* **15(3)**:1–88.

Adams JW, Conroy GC. 2005. Plio-Pleistocene faunal remains from the Gondolin GD 2 *in situ* assemblage, North West Province, South Africa. In: Lieberman D, Smith RJ, Kelley J, eds. *Interpreting the past: essays on human, primate and mammal evolution in honor of David Pillbeam.* Boston: Brill Academic Publishers, 243–261.

Adams JW, Herries AIR, Conroy GC, Kuykendall KL. 2007. Taphonomy of a South African cave: geological and hydrological influences on the GD 1 fossil assemblage at Gondolin, a Plio-Pleistocene paleocave system in the Northwest Province, South Africa. *Quaternary Science Reviews* **26**:2526–2543 DOI 10.1016/j.quascirev.2007.05.006.

Adams JW, Herries AIR, Hemingway J, Kegley ADT, Kgasi L, Hopley P, Reade H, Potze S, Thackeray JF. 2010. Initial fossil discoveries from Hoogland, a new Pliocene primate-bearing karstic system in Gauteng Province, South Africa. *Journal of Human Evolution* **59**:685–691 DOI 10.1016/j.jhevol.2010.07.021.

Adams JW, Kegley ADT, Krigbaum JT. 2013. New faunal stable carbon isotope data from the Haasgat HGD fossil assemblage, South Africa, including the first reported values for *Papio angusticeps* and *Cercopithecoides haasgati*. *Journal of Human Evolution* **64**:693–698 DOI 10.1016/j.jhevol.2013.02.009.

Adams JW, Olah A, McCurry M, Tallman M, Kegley ADT, Potze S, Kgasi L, Herries AIR. 2015. Newly discovered *in situ* primates and mammals from the early Pleistocene Haasgat deposits, South Africa. *American Journal of Physical Anthropology* **156**:66.

Ahern JCM. 1998. Underestimating intraspecific variation: the problem with excluding Sts 19 from *Austalopithecus africanus*. *American Journal of Physical Anthropology* **105**:462–480.

Avery D. 2001. The Plio-Pleistocene vegetation and climate of Sterkfontein and Swartkrans, South Africa, based on micromammals. *Journal of Human Evolution* **41**:113–132 DOI 10.1006/jhev.2001.0483.

Bailey GN, Reynolds SC, King GCP. 2011. Landscapes of human evolution: models and methods of tectonic geomorphology and the reconstruction of hominin landscapes. *Journal of Human Evolution* **60**:257–280 DOI 10.1016/j.jhevol.2010.01.004.

Behrensmeyer AK. 1978. Taphonomic and ecologic information from bone weathering. *Paleobiology* **4**:150–162.

Berger LR, De Ruiter DJ, Churchill S, Schmid P, Carlson K, Dirks P, Kibii J. 2010. *Australopithecus sediba*: a new species of *Homo*-like australopith from South Africa. *Science* **328**:195–204 DOI 10.1126/science.1184944.

Beynon A, Wood B. 1986. Variations in enamel thickness and structure in east African hominids. *American Journal of Physical Anthropology* **70**:177–193 DOI 10.1002/ajpa.1330700205.

Braga J, Thackeray JF. 2003. Early *Homo* at Kromdraai B: probabilistic and morphological analysis of the lower dentition. *Comptes Rendus Palevol* **2**:269–279.

Brain C. 1981. *The hunters or the hunted? An introduction to African cave taphonomy*. Chicago: University of Chicago Press.

Bromage TG, Lacruz RS, Hogg R, Goldman HM, McFarlin SC, Warshaw J, Dirks W, Perez-Ochoa A, Smolyar I, Enlow DH, Boyde A. 2009. Lamellar bone is an incremental tissue reconciling enamel rhythms, body size, and organismal life history. *Calcified Tissue International* **84**:388–404 DOI 10.1007/s00223-009-9221-2.

Bromage T, Lacruz R, Perez-Ochoa A, Boyde A. 2007. Portable confocal scanning optical microscopy of *Australopithecus africanus* enamel structure. In: Bailey S, Hublin J, eds. *Dental perspectives on human evolution*. New York: Springer Verlag, 193–209.

Dean MC. 2010. Retrieving chronological age from dental remains of early fossil hominins to reconstruct human growth in the past. *Philosophical Transactions of the Royal Society B* **365**:3397–3410 DOI 10.1098/rstb.2010.0052.

Dean MC, Beynon AD, Thackeray JF, Macho GA. 1993. Histological reconstruction of dental development and age at death of a juvenile *Paranthropus robustus* specimen, SK 63, from Swartkrans, South Africa. *American Journal of Physical Anthropology* **91**:401–419 DOI 10.1002/ajpa.1330910402.

Dean MC, Leakey MG, Reid D, Schrenk F, Schwartz GT, Stringer C, Walker A. 2001. Growth processes in teeth distinguish modern humans from *Homo erectus* and earlier hominins. *Nature* **414**:628–631 DOI 10.1038/414628a.

Dirks P, Kibii J, Kuhn B, Steininger C, Churchill S, Kramers J, Pickering R, Farber D, Merlaux A, Herries AIR, King G, Berger LR. 2010. Geological setting and age of *Australopithecus sediba* from southern Africa. *Science* **328**:205–208 DOI 10.1126/science.1184950.

Freedman L. 1957. The fossil Cercopithecoidea of South Africa. *Annals of the Transvaal Museum* **23**:121–262.

Gilbert C, Steininger C, Kibii J, Berger LR. 2015. *Papio* cranium from the hominin-bearing site of Malapa: implications for the evolution of modern baboon cranial morphology and South African Plio-Pleistocene biochronology. *PLoS ONE* **10**:e0133361 DOI 10.1371/journal.pone.0133361.

Grine FE. 1982. A new juvenile hominid (Mammalia: Primates) from Member 3, Kromdraai Formation, Transvaal, South Africa. *Annals of the Transvaal Museum* **33**:165–239.

Grine FE. 1984. The deciduous dentition of the Kalahari San, the South African Negro and the South African Plio-Pleistocene hominids. D. Phil. Thesis, University of the Witwatersrand.

Grine FE. 2013. The alpha taxonomy of *Australopithecus africanus*. In: *The paleobiology of Australopithecus*. Springer Netherlands, 73–104.

Grine FE, Jacobs R, Reed KE, Plavcan JM. 2012. The enigmatic molar from Gondolin, South Africa: implications for *Paranthropus* paleobiology. *Journal of Human Evolution* **63**:597–609 DOI 10.1016/j.jhevol.2012.06.005.

Grine FE, Martin L. 1988. Enamel thickness and development in *Australopithecus* and *Paranthropus*. In: Grine FE, ed. *Evolutionary history of the "robust" australopithecines*. New York: A. de Gruyter, 3–42.

Herries AIR, Adams JW. 2013. Clarifying the context and dating of the Gondolin hominin tooth and the age range of *Paranthropus* in South Africa: a comment on Grine et al (2012). *Journal of Human Evolution* **65**:676–681 DOI 10.1016/j.jhevol.2013.06.007.

Herries AIR, Adams JW, Kuykendall KL, Shaw J. 2006. Speleology and magnetobiostratigraphic chronology of the Gondolin hominin paleocave, South Africa. *Journal of Human Evolution* **51**:617–631 DOI 10.1016/j.jhevol.2006.07.007.

Herries AIR, Hopley P, Adams JW, Curnoe D, Maslin M. 2010. Geochronology and palaeonvironments of southern African hominin localities—a reply to Wrangham et al (2009) 'Shallow-water habitats as sources of fallback foods for hominins'. *American Journal of Physical Anthropology* **143**:640–646 DOI 10.1002/ajpa.21389.

Herries AIR, Kappen P, Kegley ADT, Paterson D, Howard D, deJonge M, Potze S, Adams JW. 2014. Palaeomagnetic and synchrotron analysis of >1.95 Ma fossil-bearing palaeokarst at Haasgat, South Africa. *South African Journal of Science* **110**: 12pp.

Herries AIR, Pickering R, Adams JW, Curnoe D, Warr G, Latham A, Shaw J. 2013. A multi-disciplinary perspective on the age of *Australopithecus* in southern Africa. In: Leakey L, Reed KE, eds. *Paleoecology of Australopithecus. Vertebrate Paleobiology and Paleoanthropology Series*, New York: Springer Verlag, 21–40.

Herries AIR, Shaw J. 2011. Palaeomagnetic analysis of the Sterkfontein paleocave deposits: implications for the age of the hominin fossils and stone tool industries. *Journal of Human Evolution* **60**:523–539 DOI 10.1016/j.jhevol.2010.09.001.

Kegley ADT, Hemingway J, Adams JW. 2011. Odontometric analysis of the reanalyzed and expanded Cercopithecoides sample from the Haasgat fossil assemblage, Cradle of Humankind, South Africa. *American Journal of Physical Anthropology* **144**:183.

Keyser AW. 1991. The palaeontology of Haasgat: a preliminary account. *Palaeontologia Africana* **28**:29–33.

Keyser AW, Martini J. 1991. Haasgat: a new Plio-Pleistocene fossil occurrence. In: Heine K, ed. *Palaeoecology of Africa*. Rotterdam: A.A. Balkema, 119–129.

Kimbel WH, Rak Y. 1993. The importance of species taxa in palaeoanthropology and an argument for the phylogenetic concept of the species category. In: Kimbel WH, Martin LB, eds. *Species, species concepts, and primate evolution.* New York: Plenum Press, 461–484.

Lacruz RS, Dean MC, Ramirez-Rozzi FV, Bromage TG. 2008. Megadontia, striae periodicity and patterns of enamel secretion in Plio-Pleistocene fossil hominins. *Journal of Anatomy* **213**:148–158 DOI 10.1111/j.1469-7580.2008.00938.x.

Lacruz RS, Ramirez-Rozzi FV. 2010. Molar crown development in *Australopithecus afarensis. Journal of Human Evolution* **58**:210–206.

Lacruz RS, Ramirez-Rozzi FV, Bromage TG. 2006. Variation in emamel development of South African fossil hominids. *Journal of Human Evolution* **51**:580–590 DOI 10.1016/j.jhevol.2006.05.007.

Lacruz RS, Ramirez-Rozzi FV, Wood BA, Bromage TG. 2012. Cusp and crown areas in early *Australopithecus. American Journal of Physical Anthropology* **148**:632–640 DOI 10.1002/ajpa.22089.

Lee-Thorp JA, Sponheimer M, Passey BH, De Ruiter DJ, Cerling TE. 2010. Stable isotopes in fossil hominin tooth enamel suggest a fundamental dietary shift in the Pliocene. *Philosophical Transactions of the Royal Society B* **265**:3389–3396.

Lockwood CA, Tobias PV. 2002. Morphology and affinities of new hominin cranial remains from Member 4 of the Sterkfontein Formation, Gauteng Province, South Africa. *Journal of Human Evolution* **42**:389–450 DOI 10.1006/jhev.2001.0532.

McKee J, Keyser AW. 1994. Craniodental remains of *Papio angusticeps* from the Haasgat cave site, South Africa. *International Journal of Primatology* **15**:823–841 DOI 10.1007/BF02736070.

McKee J, Von Mayer A, Kuykendall K. 2011. New species of *Cercopithecoides* from Haasgat, North West Province, South Africa. *Journal of Human Evolution* **60**:83–93 DOI 10.1016/j.jhevol.2010.08.002.

Menter C, Kuykendall KL, Keyser AW, Conroy GC. 1999. First record of hominid teeth from the Plio-Pleistocene site of Gondolin, South Africa. *Journal of Human Evolution* **37**:299–307 DOI 10.1006/jhev.1999.0329.

Moggi-Cecchi J, Menter C, Boccone S, Keyser A. 2010. Early hominin dental remains from the Plio-Pleistocene site of Drimolen, South Africa. *Journal of Human Evolution* **58**:374–405 DOI 10.1016/j.jhevol.2010.01.006.

Olejniczak AJ, Smith TM, Skinner MM, Grine FE, Feeney RNM, Thackeray JF, Hublin J-J. 2008. Three-dimensional molar enamel distribution and thickness in *Australopithecus* and *Paranthropus. Biology Letters* **4**:406–410.

Pickering R, Dirks P, Jinnah Z, De Ruiter DJ, Churchill S, Herries AIR, Woodhead J, Hellstrom J, Berger LR. 2011a. *Australopithecus sediba* at 1.977 Ma and implications for the origins of the Genus *Homo. Science* **333**:1421–1423 DOI 10.1126/science.1203697.

Pickering R, Kramers J, Hancox P, De Ruiter DJ, Woodhead J. 2011b. Contemporary flowstone development links early hominin bearing cave deposits in South Africa. *Earth and Planetary Science Letters* **306**:23–32 DOI 10.1016/j.epsl.2011.03.019.

Plug I, Keyser AW. 1994. Haasgat Cave, a Pleistocene site in the central Transvaal: geomorphological, faunal and taphonomic considerations. *Annals of the Transvaal Museum* **36**:139–145.

Ramirez-Rozzi FV. 1993. Tooth development in east African *Paranthropus*. *Journal of Human Evolution* **24**:429–454 DOI 10.1006/jhev.1993.1030.

Ramirez-Rozzi FV. 1998. Can enamel microstructure be used to establish the presence of different species of Plio-Pleistocene hominids from Omo, Ethiopia? *Journal of Human Evolution* **35**:543–576.

Reed KE. 1996. The paleoecology of Makapansgat and other African Plio-Pleistocene hominid localities. D. Phil. Thesis, State University of New York Stony Brook.

Reynolds SC, Clarke RJ, Kuman K. 2007. The view from Lincoln Cave: mid- to late Pleistocene fossil deposits from Sterkfontein hominid site, South Africa. *Journal of Human Evolution* **53**:260–271 DOI 10.1016/j.jhevol.2007.02.004.

Smith TM, Tafforeau P, Le Cabec A, Bonnin A, Houssaye A, Pouech J, Moggi-Cecchi J, Manthi F, Ward C, Makaremi M, Menter C. 2015. Dental ontogeny in Pliocene and early Pleistocene hominins. *PLoS ONE* **10**(**2**):e0118118 DOI 10.1371/journal.pone.0118118.

Swindler DR, Beynon AD. 1993. The development and microstructure of the dentition of *Theropithecus*. In: Jablonski NG, ed. *Theropithecus: the rise and fall of a primate genus*. Cambridge: Cambridge University Press, 351–382.

Vrba E. 1976. The fossil Bovidae of Sterkfontein, Swartkrans and Kromdraai. *Transvaal Museum Memoirs* **21**:1–166.

Wood B, Richmond B. 2000. Human evolution: taxonomy and paleobiology. *Journal of Anatomy* **196**:19–60 DOI 10.1046/j.1469-7580.2000.19710019.x.