



News and Views

Genetic data and radiocarbon dating question Plovers Lake as a Middle Stone Age hominin-bearing site

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ABSTRACT

We have sampled five out of the eleven previously identified human specimens and some faunal remains from the Plovers Lake site in the Cradle of Humankind, South Africa, for ancient DNA. We were successful in obtaining positive results for three of the human individuals and three ‘buffalo’ teeth. Based on ages obtained for flowstone and one bovid tooth, the site was interpreted previously as a hominin-bearing Middle Stone Age site of more than 60 000 years old. Our work, however, revealed that not all the material accumulated during the Pleistocene. Instead, the sampled humans and bovinds most likely represent a Bantu-speaking Iron Age population (mtDNA haplogroup L3d) and their Nguni cattle. Newly obtained radiocarbon dates confirmed that these remains are probably no older than the last 500 years bp. This study demonstrates the usefulness of inter-disciplinary investigation into the human past, and the depositional and stratigraphic complexities that researchers in the Cradle of Humankind need to contend with before interpreting their assemblages.

1. Introduction

Since the presence of human remains at Plovers Lake on the trans-Vaal Highveld in the Fossil Hominids UNESCO World Heritage Site in South Africa (a.k.a., the Cradle of Humankind) was published in this journal (de Ruiter et al., 2008), it became widely known as a hominin-bearing site (e.g., Backwell et al., 2012; Dusseldorp et al., 2013; Wadley, 2013; Grine, 2016). All the reported human remains (i.e., several isolated teeth and postcranial pieces [Grine, 2016]) were from a perceived in situ context, capped and underlain by flowstone dated to the late-Pleistocene designated as FBU1 (de Ruiter et al., 2008; Supplementary Online Material (SOM) Fig. S1). Here we provide the full list of human remains from Plovers Lake (Table 1), and reveal the results obtained from DNA analyses, and direct C14 dating and isotope analyses on some of this material, and its implications for the site.

2. Previous age estimates for Plovers Lake

Work on Plovers Lake Farm was initiated by Francis Thackeray who published a preliminary list of fauna, extracted from a few breccia blocks (Thackeray and Warson, 1994), six of which were extinct. It was suggested that the presence of *Metridiochoerus andrewsi* (an extinct suid) and *Mus minutoides* (a rodent) indicate an age of ~1 Ma. No artefacts were associated directly with the fauna, but weathered Middle Stone Age (MSA) artefacts were recovered from the excavated overburden (Thackeray and Warson, 1994).

During 2002–2004, teams from the University of the Witwatersrand (South Africa) and Duke University (USA) excavated at a second location on the farm, ~100 m northeast of the Thackeray exploration. Here, the fossiliferous deposit was described as located inside an existing cave, some of which (FBU1) was thought to be in situ, sandwiched between flowstone layers (de Ruiter et al., 2008: fig. 3; SOM Fig. S1). An isochron ESR date of 75.6 ± 5.6 ka, produced from a bovid tooth from FBU1, was announced at a conference (Skinner et al., 2005), and “U-series dating provided an estimate of 62.9 ± 1.3 ka for Flowstone I, while Flowstone II is dated at 88.7 ± 1.6 ka” (de Ruiter et al., 2008: 1103). An associated stone tool assemblage purportedly characteristic of the MSA (but as yet unpublished) was announced. It was also claimed that all the fauna

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Table 1
Human remains from Plovers Lake represented in the catalogue of the repository at the University of the Witwatersrand, with our unique numbers for specimens sampled in the context of our study.

Specimen ID	Anatomical position	Sedimentary context	Our unique number	DNA successful/not successful (also see Table 2 and SOM Table S1)	C14 dating
PV1385	Indeterminate	FBU1		Not sampled	Not sampled
PV1947	Long bone fragment	FBU1	plo004	Not successful	Not sampled
PV3701	Tooth: Right P4	FBU1		Not sampled	Not sampled
PV3702	Tooth: Right M1	FBU1		Not sampled	Not sampled
PV3703	Tooth: Right M2	FBU1	plo003	Not successful	Not sampled
PV12780	Long bone fragment	FBU1	plo001	Successful	Yes (see Section 4)
PV13000	Tibial shaft fragment	FBU1	plo005	Successful	Not sampled
PV14000 A/B	Tibial shaft fragments	FBU1	plo002	Successful	Yes (see Section 4)
PV16500	Maxilla fragment	FBU1		Not sampled	Not sampled
PV17507	Indeterminate	FBU1		Not sampled	Not sampled
PV/ST3	Fragmentary teeth	FBU1		Not sampled	Not sampled

(from both the PDU and FBU1 contexts, see SOM Fig. S1) accumulated during the Late Pleistocene MSA (de Ruiter et al., 2008), roughly between MIS 5a/5b and MIS 3 (Lombard et al., 2012 for cultural sequence; also see; Brophy et al., 2014; Grine, 2016). Plovers Lake hence became known as a hominin-bearing MSA site in the Cradle of Humankind.

3. Preliminary genetic data from the Plovers Lake humans and bovinds

In the context of an ongoing, long-term project aimed at reconstructing the Stone Age population history of southern Africa from a cross-disciplinary context (e.g., Lombard et al., 2013; Schlebusch et al., 2013, 2017), we were permitted to take small samples to investigate DNA preservation on a few teeth identified as buffalo from PDU, and hominin fragments from FBU1 at Plovers Lake in 2014 (SOM Fig. S1; SAHRA sampling and export permits ID 1934 and ID 1935). We needed to prove success for the faunal material, before analyses could start on human material. In 2015, our initial investigation showed that three of the 'buffalo' samples gave reasonable DNA yields, where ~3% of the sequences mapped to the *Bos* genome – the evolutionary closest high-quality reference genome available. We observed typical ancient-DNA damage patterns, indicating that the samples are old, not current. Interestingly, though, our results provided a match to cattle mitochondrial-DNA (mtDNA), which first arrived in southern Africa <2 ka (e.g., Russell and Lander, 2015). Thus, although we were successful with the extraction of DNA from Plovers Lake bovinds, our results presented a challenge for the interpretation of the site. Consequently, we were permitted to proceed with work on the human samples.

By 2016, we obtained low, but workable levels of DNA in two human samples (plo001 and plo002; Tables 1 and 2, Fig. 1), from the presumed in situ FBU1 MSA deposits. The DNA-sequence data had all the characteristics of being old and reasonably uncontaminated (Table 2). Yet, our preliminary observations indicated that the mtDNA haplogroups are more consistent with current-day populations from West and East Africa than with that of southern

African hunter-gatherers. Considering that the deposit was thought to be >60 ka, our initial results indicated either a mixed deposit, or provided completely new population-distribution information based on mtDNA for southern Africa.

Because the samples were thought to fall outside of the C14 range, we did not directly date them before genetic analysis. Yet, due to the potential scientific impact of our results, we requested additional samples of two human (plo001 and plo002) and one bovid (pla004) specimens for C14 dating (SAHRA permit ID 2262). Our hypothesis was that young C14 dates will confirm a mixed/more recent deposit, with the potential to add knowledge about the timing and genetic affiliation of Iron Age farmers on the Highveld north of the Vaal River. On the other hand, C14 dates of >46,000 bp combined with the DNA results, would be revolutionary in terms of human history in Africa.

4. Results from C14 dating, associated stable isotope analyses, and further DNA analyses

The human remains were AMS-dated and calibrated using the High Probability Density Range Method (HPD) (Bronk Ramsey, 2009) and SHCAL13 (Hogg et al., 2013) to respectively 534–454 calBP (plo001; Beta-476777, 480 ± 30 bp) and 504–326 calBP (plo002; Beta-476776, 420 ± 30 bp), and the bovid tooth to 276–post 0 calBP (pla004; Beta-476778, 160 ± 30 bp) (Table 2). These dates fit well with the more recent origin inferred from our preliminary genetic results. We also obtained separate isotope ratio mass spectrometer (IRMS) measures of stable carbon ($\delta^{13}\text{C}$ was -9.7‰ for plo001, -10.5‰ for plo002 and -7.0‰ for pla004) and nitrogen isotopes ($\delta^{15}\text{N}$ was 10.2‰ for plo001, 10.1‰ for plo002 and 5.8‰ for pla004) from Beta Analytic (Table 2). The enriched carbon values, together with the relatively low nitrogen values are similar to those obtained from Iron Age farmers from the central trans-Vaal Highveld (Lee-Thorp et al., 1993).

We retrieved further mtDNA data from three human and three bovid samples using a shotgun sequencing approach (Fig. 1; SOM Sections 2, 3 and 4). The bovid samples had 29X, 9.8X and 2.7X

Table 2
Data generated from three human samples previously associated with the Middle Stone Age at Plovers Lake with contamination estimates using two methods (i.e., Green et al., 2008 and Fu et al., 2014, also see SOM Section 3 and SOM Table S2).

Sample ID	Accession no.	Age cal BP (95.4%)	MT coverage	MT haplogroup	Isotope values $\delta^{13}\text{C}/\delta^{15}\text{N}$ (‰)	Contamination estimate in percent (Green et al./Fu et al.)		
						Point estimate	Lower end CI	High end CI
plo001	PV12780	534–454	6.6x	L3d1a1a1	–9.7/10.2	0.0/2.4	0.0/0.5	22.1/56.8
plo002	PV14000A/PV14000B	504–326	27.0x	L3d1a1a1	–10.5/10.1	5.9/1.3	0.9/0.2	10.9/28.4
plo005	PV13000	na	14.3x	nd	na	29.5/16.3	19.4/3.7	39.6/75.5

nd = not determined, but the data points to L3, and na = not analyzed.

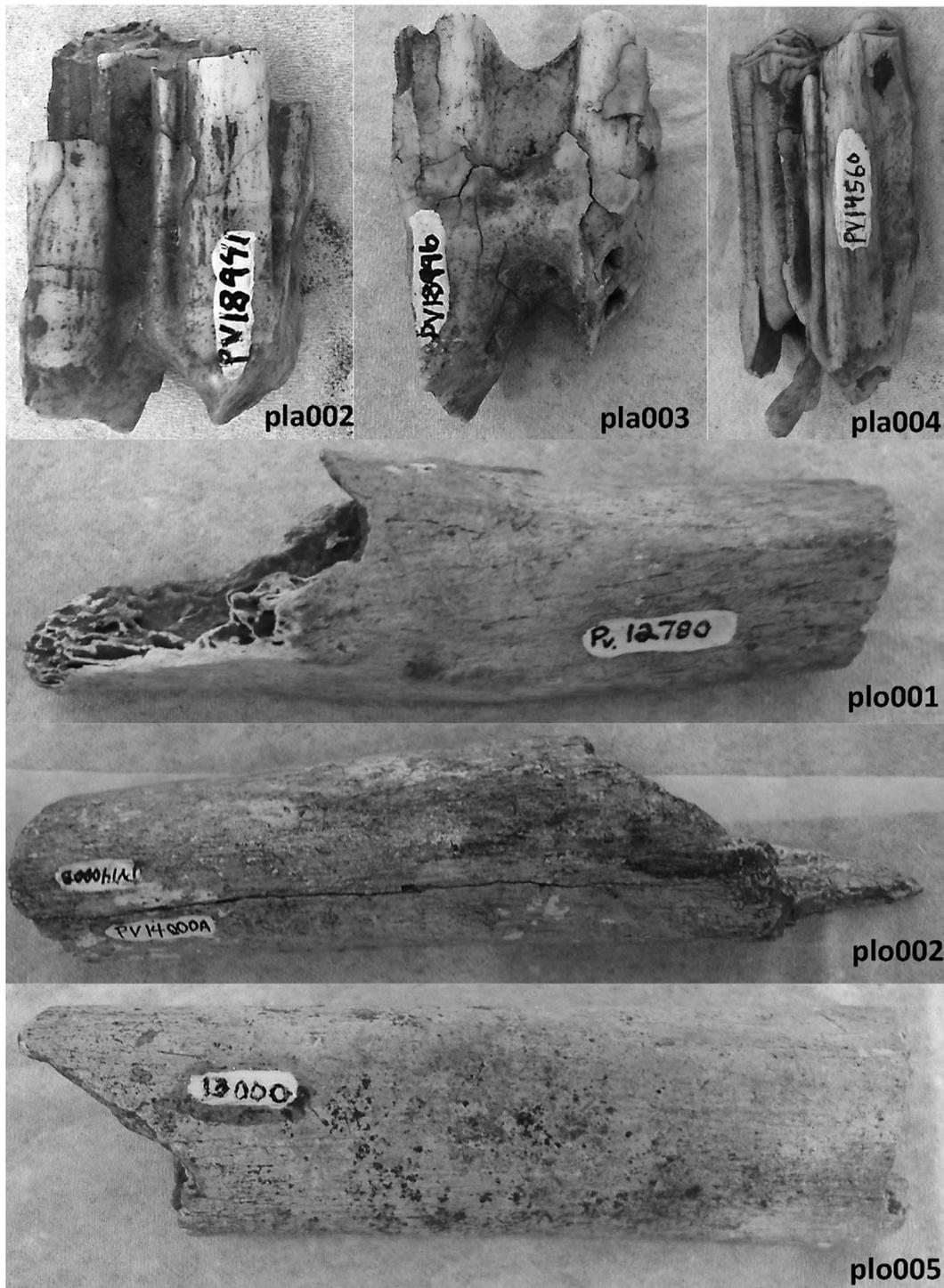


Figure 1. Bone fragments from Plovers Lake for which we were able to extract and analyse or partially analyse mtDNA. In the top row are bovid teeth/tooth fragments from the PDU layer, and the three pieces below are human post-cranial remains from the FBU1 layer.

mitochondrial coverage and the sequence reads showed increased deamination at the ends of the fragments (Sawyer et al., 2012) (SOM Section 4, SOM Fig. S2). Phylogenetic analyses showed that none of the samples clustered with *Syncerus caffer* (Cape buffalo). Instead, they fall within the *Bos taurus* portion of the tree (Fig. 2), specifically within *B. taurus* haplogroup T1b (SOM Section 4, SOM Table S7 and S8, Fig. S3), the most common haplogroup among South African Nguni cattle (Horsburgh et al., 2013). Nguni cattle

was also the breed that best matched two of the ancient samples using a BLAST search (pla003 and pla004; SOM Section 4).

We were able to generate mtDNA data ranging in coverage from 6.6x to 27.0x for three of the human samples (Table 2, Fig. 1; SOM Section 3), displaying typical characteristics of ancient DNA (Sawyer et al., 2012) (Fig. 3; SOM Section 3), and low contamination (Table 2; SOM Section 3, SOM Table S2) (Green et al., 2008; Fu et al., 2014). We further filtered the sequence data to only retain DNA

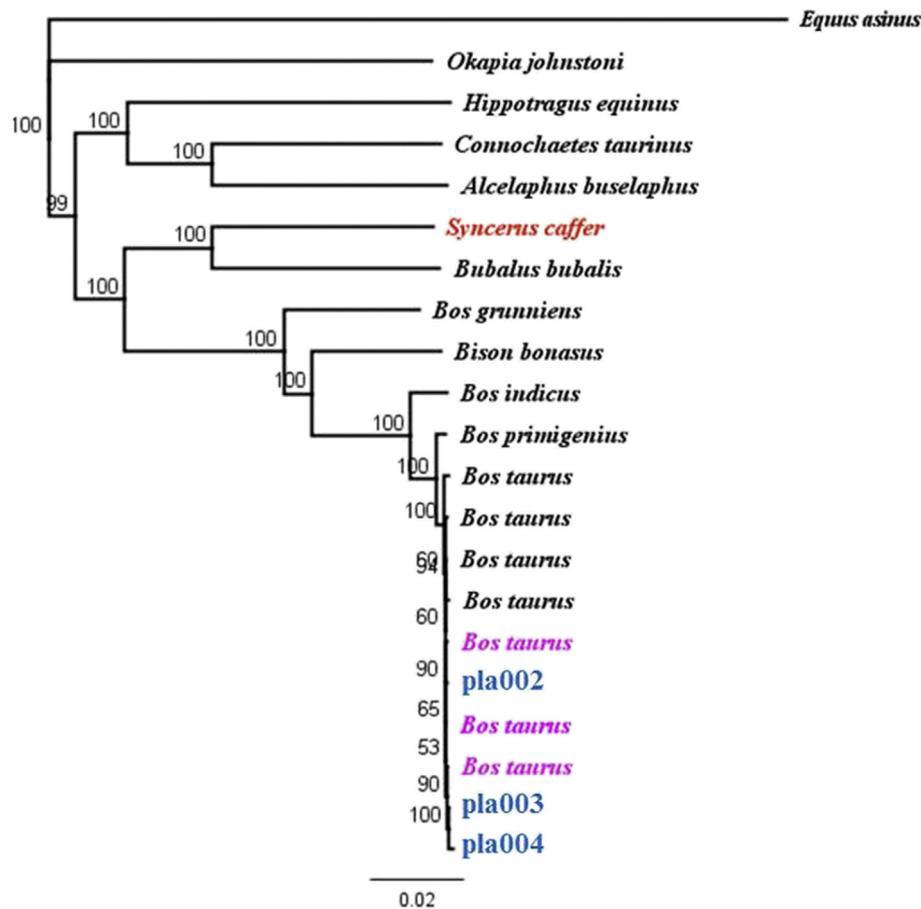


Figure 2. Neighbour-joining tree for mtDNA, including the Plovers Lake bovid samples (pla002, pla003, pla004 in blue on on-line version), *Syncerus caffer*, to which they were originally identified (red in on-line version), *Bos taurus* samples belonging to haplogroup T1 (pink in on-line version), (and the other species from SOM Section 4, SOM Table S6). Branch labels show consensus support (%) for the particular node. The tree was rooted using *Equus asinus*. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

fragments (SOM Table S5), displaying post-mortem deaminations to verify the haplogroup calls (Skoglund et al., 2014), which yielded comparable results as the unfiltered data (SOM Table S2). Two of the individuals, plo001 and plo002, could be ascribed to mitochondrial haplogroup L3d1a1a1 (Table 2; SOM Section 3, SOM Table S3). The third, plo005, could not be called unambiguously (Table 2; SOM Section 3, SOM Table S4), but L3d1a1a1 is one of two possible haplogroups for this individual. Given the similar radiocarbon dates of plo001 and plo002 (Table 1), and the inferred same mitochondrial haplogroup for them, it is possible that these remains belonged to the same individual.

Haplogroup L3 is common in present-day populations from East and West Africa, whereas L0d and L0k haplogroups are common among San hunter-gathers of southern Africa (Behar et al., 2012; Schlebusch et al., 2013; Barbieri et al., 2014). L3d is frequent among central, south-eastern and south-western Bantu-speaking populations reaching the highest frequency (60%) in the Herrero from Namibia (Schlebusch et al., 2013), and the time depth of the haplogroup is estimated at ~30–20 ka (Behar et al., 2012). The L3d and the L3d1a1 sub-lineage were likely brought to southern Africa with the expansion of Bantu-speaking farmer populations during the last few millennia (Soares et al., 2011), and these haplogroups are today also present in low frequency among Khoe and San populations due to recent admixture (Schlebusch et al., 2013, 2017). No L3d lineages have been found yet from archaeological remains, although we found L3e-variants in three Iron Age farmers from KwaZulu-Natal, South Africa, dated to ~500–300 bp, whose

genome-wide DNA grouped them with southern African Bantu-speaking groups (Schlebusch et al., 2017; Steyn et al., 2019). Hence, the investigated human remains from Plovers Lake are likely related to Iron Age farmers, probably speaking Bantu languages.

The stable carbon and nitrogen values obtained from two of the human remains from Plovers Lake (Table 2) are also on par with values found among Iron Age farmers from nearby regions (Lee-Thorp et al., 1993). This line of evidence, together with the mtDNA profile of cattle found at the site, contradicts a Late Pleistocene origin for the Plovers Lake human remains. Instead, it fits well with current interpretations of population distribution and genetic variation among Iron Age farmers in southern Africa (Mitchell and Lane, 2013; Schlebusch et al., 2013, 2017).

5. Implications of our study for Plovers Lake as a Middle Stone Age hominin-bearing site

Our work provides at least four strands of independent evidence revealing that the Plovers Lake deposits reported by de Ruiter et al. (2008) cannot be considered exclusive to the Late Pleistocene MSA:

1. Direct C14 dates of only a few hundred years old.
2. Bovid mtDNA profiles consistent with domestic cattle (most likely Nguni), instead of buffalo.
3. Human mtDNA profiles strongly associated with current-day Bantu-speakers, instead of hunter-gatherers from southern Africa.

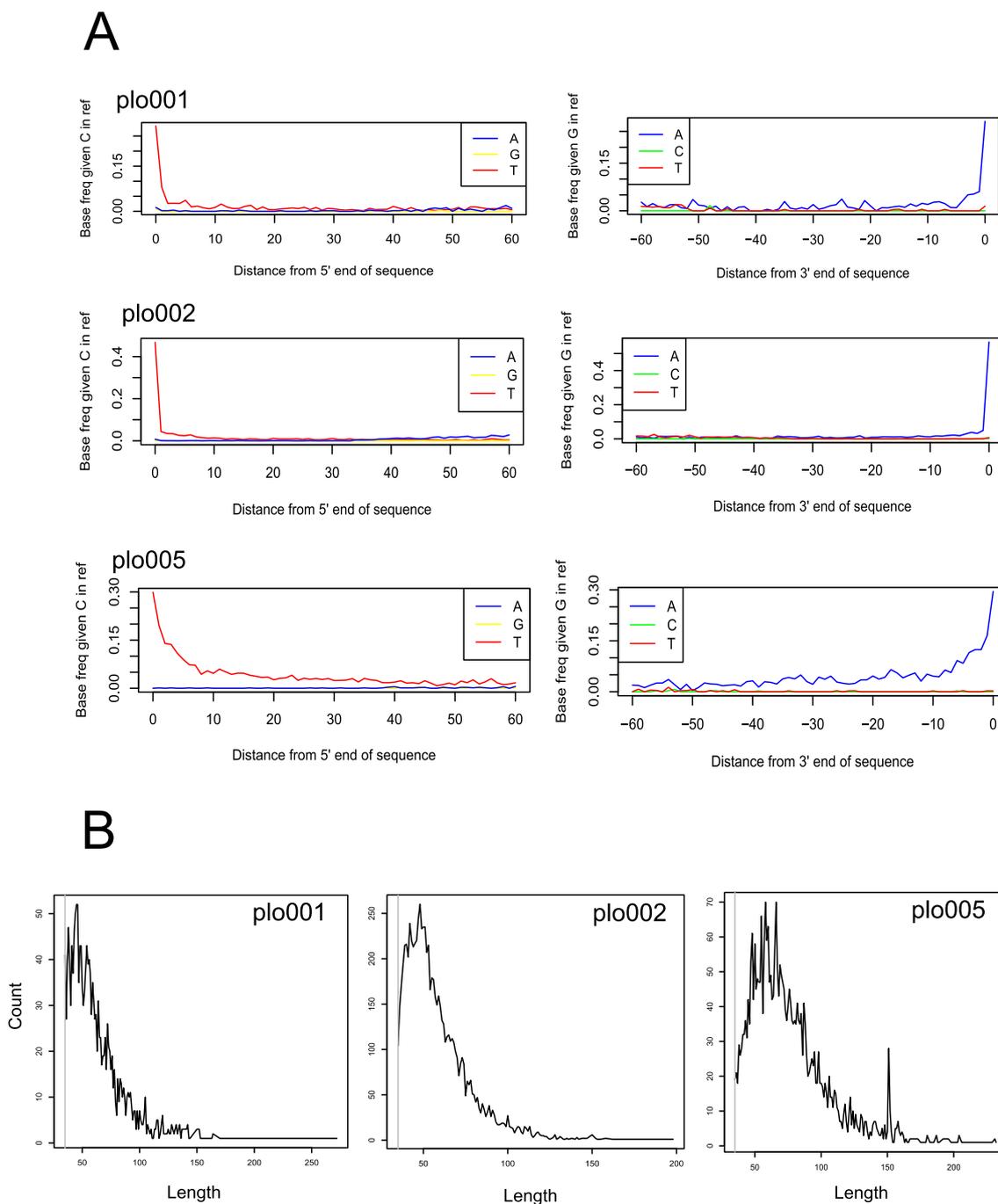


Figure 3. Results showing: A) damage patterns at the ends of the sequence reads, and B) average read length in merged mitochondrial data from three human remains from Plovers Lake.

4. Isotope values consistent with a farming way of life.

Thus, the faunal material, including the human remains, published in 2008 is either mixed, or only a few hundred years old. Cave deposits, geomorphological processes and their dating in the Cradle of Humankind are notoriously complex, with false and collapsing flowstone floors and the mixing of sediments a reality (for recent examples see [Dirks et al., 2017](#); [Kramer and Dirks, 2017](#)).

If we accept that the U-series age estimates for the two flowstone layers of 62.9 ka and 88.7 ka at Plovers Lake are accurate, the only explanation for our results is that the original sediment underlying the upper flowstone layer was eroded or partially eroded

in the past, and that it was subsequently filled with more recent deposits. If the previous ESR age of ~75 ka for a bovid tooth is correct, it could represent the original deposit. In light of our findings, we suggest that further dating work is required to assess the notion that some of the deposit at Plovers Lake dates to the Late Pleistocene MSA. Also, additional studies on the human remains not sampled by us for DNA and dating may yet reveal their Pleistocene age.

The outcome of our study does not only impact on the notion that Plovers Lake represents a hominin-bearing MSA site, but it could also have implications for the palaeo-faunal record. For example, the only extinct species identified by [de Ruiter et al.](#)

(2008) for the assumed in situ MSA material is *Antidorcas bondi*, a springbok species that became extinct at ~7 ka (e.g., Brink and Lee-Thorp, 1992). From ten bone pieces, four individuals were identified for this species belonging to the FBU1 context. We do not know the exact criteria used for the identification, but since Plug and Peters (1991), the key reference for distinguishing between springbok species was not cited, these pieces deserve further consideration. If the presence of *A. bondi* for the Plovers Lake FBU1 context is confirmed, it could support the notion that some of the material dates to the Stone Age. Alternatively, new direct C14 dates for this species may alter its last known appearance on the Highveld. Previously Plug (1993, Plug and Badenhorst, 2001) reported on *A. bondi* found in the Northern Cape from a context dated to ~500 bp, but the material was considered to be intrusive.

Our results also impact on the debate regarding the 'first fossil' Congo peafowl (*Afropavo congensis*) (Stidham, 2008; Manegoldand and Louchart, 2009). This is a species considered endemic to the Democratic Republic of Congo, central Africa. Initially, it was suggested that its accepted Late-Pleistocene presence at Plovers Lake greatly extended the known geographic range of this taxon (Stidham, 2008). Its correct identification was, however, drawn into question by Manegoldand and Louchart (2009), alternatively its age may be wrong unless directly dated.

This is the first (but almost certainly not the last) example from southern Africa of how cross-disciplinary investigation and current methods in DNA research from archaeological contexts (and their unexpected outcomes) may be used to refine and assess our interpretations of the known palaeo-record.

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Supplementary Online Material

Supplementary online material to this article can be found online at <https://doi.org/10.1016/j.jhevol.2019.03.014>.

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