U–Pb-dated flowstones restrict South African early hominin record to dry climate phases

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**U–Pb–dated flowstones restrict South African early hominin record to dry climate phases**

Robyn Pickering1,2,a, Andy I. R. Herries3,4, Jon D. Woodhead5, John C. Hellstrom5, Helen E. Green5, Bence Paul5, Terrence Ritzman2,6,7, David S. Strait7, Benjamin J. Schoville2,8 & Phillip J. Hancox9

The Cradle of Humankind (Cradle) in South Africa preserves a rich collection of fossil hominins representing *Australopithecus*, *Paranthropus* and *Homo*. The ages of these fossils are contentious and have compromised the degree to which the South African hominin record can be used to test hypotheses of human evolution. However, uranium–lead (U–Pb) analyses of horizontally bedded layers of calcium carbonate (flowstone) provide a potential opportunity to obtain a robust chronology. Flowstones are ubiquitous cave features and provide a palaeoclimatic context, because they grow only during phases of increased effective precipitation, ideally in closed caves. Here we show that flowstones from eight Cradle caves date to six narrow time intervals between 3.2 and 1.3 million years ago. We use a kernel density estimate to combine 29 U–Pb ages into a single record of flowstone growth intervals. We interpret these as major wet phases, when an increased water supply, more extensive vegetation cover and at least partially closed caves allowed for undisturbed, semi-continuous growth of the flowstones. The intervening times represent substantially drier phases, during which fossils of hominins and other fossils accumulated in open caves. Fossil preservation, restricted to drier intervals, thus biases the view of hominin evolutionary history and behaviour, and places the hominins in a community of comparatively dry-adapted fauna. Although the periods of cave closure leave temporal gaps in the South African fossil record, the flowstones themselves provide valuable insights into both local and pan-African climate variability.

The early hominin fossil record in South Africa is best represented by deposits preserved in a series of dolomite caves 40 km northwest of Johannesburg (Fig. 1). These sites, which are collectively known as the Cradle of Humankind World Heritage Site, have produced hominin fossils attributed to at least five taxa: *Australopithecus africanus*, *Australopithecus sediba*, *Paranthropus robustus*, *Homo naledi* and a poorly understood collection of early Pleistocene fossils that we refer to as ‘early Homo’. Historically, the hominin fossil record in South Africa

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![Map of the localities and analyses of the flowstone ages versus geographic variables.](image)

**Fig. 1** Map of the localities and analyses of the flowstone ages versus geographic variables. **a**, Topographical map showing major hominin localities in East and South Africa. **b**, The Cradle shown in detail with locations of the cave sites (in bold with filled circles, U–Pb ages). **c**, Photograph of Bolt’s Farm deposits shows stacking of fossil-bearing sediments and thick flowstone layers. **d**, U–Pb flowstone ages plotted against site elevation, latitude and longitude reveal no simple relationship, suggesting these factors are not forcing the mode of cave deposition (sediment or flowstone). n = 29; diamonds, individual ages; whisker, 2σ errors.

https://doi.org/10.1038/s41586-018-0711-0
indicated. Data obtained from previous studies 5, 14, 20, 27. Caves are well-known to be dynamic systems, often subject to multiple open-termination, of a flowstone is therefore indicative of the crossing of a considerable threshold in the surface hydroclimate. Caves are more broadly reflects wetter conditions outside the cave. The onset, and therefore, the presence of speleothems, particularly in the form of massive flowstone layers, is indicative of increased cave drip water and sive flowstone layers, is indicative of increased cave drip water and percolate through the bedrock into caves, which if completely, or at least partially, closed to incoming sediment, can lead to the accumulation of horizontally bedded layers of flowstone that are up to several metres thick. The dominant control over speleothem formation is a positive water balance, driven by an increase in regional effective precipitation. Therefore, the presence of speleothems, particularly in the form of massive flowstone layers, is indicative of increased cave drip water and more broadly reflects wetter conditions outside the cave. The onset, and termination, of a flowstone is therefore indicative of the crossing of a considerable threshold in the surface hydroclimate. Caves are well-known to be dynamic systems, often subject to multiple opening and closure events 8, 16. In the Cradle context, increased effective precipitation, coupled with a strong decrease in the flux of externally derived clastic sediment into the caves (that is, completely or partially closed caves) leads to flowstone formation 8. A shift to a drier hydroclimate, with less vegetation, more open environments and increased surface erosion, favours the opening up of caves and deposition of sediment within them 8, 16. The latter also explains the cessation of major flowstone formation during these sedimentation intervals. Given the apparent climatic forcing of these two modes of cave deposition, we argue that they are mutually exclusive, meaning that it is unlikely that sediment and flowstone formation occurs concomitantly. The Cradle is a small area (approximately 10 × 15 km²; Fig. 1), so shifts in local climate conditions should be simultaneous, with flowstone forming in different caves synchronously. Indeed, all Cradle sites preserve alternating stacks of flowstones and sediment (Extended Data Fig. 1), indicating that conditions conducive to the formation of both these deposits occurred repeatedly. Here we argue for a simple, binary, Cradle-wide control on these sedimentary facies, with caves being either open (accumulating sediments) or closed (growing flowstone), driven by changes in the hydroclimate.

The U–Pb method for dating speleothems 17 has progressed in the last decade and now allows routine precise age determination of materials that are a few hundred thousand years to hundreds of millions of years old. Cradle flowstone U–Pb ages (Table 1) have uncertainties of at best 20% (± 20 thousand years on a date of 2.062 million years ago) or at worst 15% (± 390 thousand years on a date of 2.664 Ma), making them comparable to Ar–Ar ages used to date East African

<table>
<thead>
<tr>
<th>Table 1</th>
<th>All U–Pb ages and site information for the Cradle caves</th>
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<td>Site</td>
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<td>Bolt’s Farm</td>
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<td>Cooper’s</td>
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<td>Drimolen</td>
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$^{206}$Pb and $^{208}$Pb, U–Pb ages determined using $^{204}$Pb and $^{208}$Pb, respectively. $\sigma = 29$, errors on individual ages at 2$\sigma$. Ages are given as Ma. FS, flowstone; seds, sediments. ND, not determined. Indicated data obtained from previous studies 5, 14, 15, 30, 27.
hominin sites, which typically have uncertainties}\textsuperscript{18} of 1–2%. Even with this precision, attributing individual flowstones to known records of climate variability is almost impossible, because the age uncertainties are greater than the period of climatic fluctuation. Therefore, we use a kernel density estimate\textsuperscript{19} to sum the Cradle-wide dataset of 29 U–Pb ages and their associated individual errors to produce a single, composite record of flowstone growth intervals (FGIs) (Fig. 2). Our record is one of the most complete chronologies for the Cradle produced by a single method and contextualizes the caves as localities within a single evolving landscape. We can now investigate the duration and frequency of the FGIs, constrain the intervening periods during which caves were open to receive sediments and bones, and correlate the fossil-bearing deposits from different caves (see Supplementary Video 1).

We acknowledge that not all of the Cradle caves were dated in this study; while material older than 3.2 Ma may exist, we have dated the basal flowstones at each site, suggesting that the major time of Cradle flowstone and sediment accumulation occurred between 3.2 and 1.3 Ma (Fig. 2). This range is not compatible with the cosmogenic nuclide burial date estimate of approximately 3.6 Ma for the hominin fossil STW573\textsuperscript{3}, and we favour the reinterpretation of this burial date to around 2.8 Ma\textsuperscript{4}, possibly even more recent, given the reversed paleomagnetic signal of the flowstone\textsuperscript{3}. There are younger U–Th-dated cave deposits in the Cradle, at Gladysvale\textsuperscript{6}, Rising Star\textsuperscript{20} and Plover’s Lake\textsuperscript{21}, but these represent minor deposits and thin flowstones that are only a few centimetres thick, compared to the major flowstones and thick sedimentary layers of the older deposits (Extended Data Fig. 1). This probably reflects an increase in aridity, whereas the thick flowstones of the terminal Pliocene and early Pleistocene indicate an overall wetter climate. We see no simple spatial relationship between the ages of major flowstones and longitude, latitude or elevation (Fig. 1). This indicates that cave location is not the dominant factor in determining the age of the deposits; we argue instead that a changing hydroclimate (repeated wet–dry cycles) provides a better explanation.

We identify six FGIs, which were numbered 1–6 from the earliest (3.19–3.08 Ma) to the most recent (1.41–1.32 Ma) period (Fig. 2), that represent wetter periods and correspond to predominantly closed caves. The amplitude of the kernel density estimate is a function of the number of flowstones that formed during a FGI; the intervals during which the most flowstone was deposited, FGI3 (2.28–2.17 Ma) and FGI4 (1.82–1.63 Ma), consisted of 13 and 7 flowstones forming in five separate caves, respectively (Fig. 2). These extended periods of flowstone formation support our model, which predicts that all of the Cradle caves experienced the same external climatic conditions. Our model predicts that the periods between successive FGIs (3.08–2.83, 2.62–2.29, 2.17–2.12, 2.00–1.82, 1.63–1.41 and less than 1.32 Ma) were drier times during which the fossil-bearing clastic sedimentary
units (Fig. 2) accumulated in open caves. We argue that the entire early Cradle fossil record is restricted to these limited time intervals. Comparing these intervals to previously published ages for the fossils and their surrounding sediments can test this hypothesis; there is good corroboration overall24,22,23 (see Supplementary Information).

Our results have several implications for the interpretation of the South African hominin fossil record. First, the record is discontinuous, with substantial gaps represented by FG1—FG16. These discontinuities suggest that any anagenetic change within hominin lineages across sedimentary periods will appear punctuated. Similarly, gradual trends in faunal extinction or speciation will appear as sudden, correlated changes. This makes it impossible to falsify hypotheses of punctuated equilibrium24 and turnover pulses25. Moreover, our ability to observe pivotal milestones that pertain to the origin of Homo and advances in tool technology are temporarily restricted. Second, the record is biased towards representing drier-adapted plant and animal communities. Although palaeoenvironments may have shifted on average from more mesic to more arid over the time period during which the Cradle sites were accumulating sediments25, the wettest periods are still missing as the caves were closed during speleothem formation. This bias is likely to be manifested in direct measures of hominin behaviour, such as dental microwear, phytoliths that are preserved in dental calculus and isotopes. Moreover, the inability to observe behaviours during wet periods constrains our ability to evaluate hypotheses of hominin adaptation using the Cradle record. Third, Plio-Pleistocene South Africa evidently experienced marked climatic cyclicity over timescales that cannot easily be explained by insolation due to Milankovitch cycles. These wet and dry periods do not obviously correspond to climate cycles in East Africa (Extended Data Fig. 2). Future assessments of hominin adaptations and palaeobiology need to account for this complexity. Moreover, climatic cyclicity has important implications for the biogeography of hominins and other mammals insofar as habitat theory26 predicts that ecological generalists or that they vacated the Cradle landscape during dry periods do not obviously correspond to climate cycles in East Africa (Extended Data Fig. 2). Future assessments of hominin adaptations and palaeobiology need to account for this complexity. Moreover, climatic cyclicity has important implications for the biogeography of hominins and other mammals insofar as habitat theory26 predicts that ecological generalists or that they vacated the Cradle landscape during dry periods do not obviously correspond to climate cycles in East Africa (Extended Data Fig. 2).


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Competing interests The authors declare no competing interests.

Additional information

Extended data is available for this paper at https://doi.org/10.1038/s41586-018-0711-0.

Supplementary information is available for this paper at https://doi.org/10.1038/s41586-018-0711-0.

Correspondence and requests for materials should be addressed to R.P. or J.C.H.

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**METHODS**

Flowstone samples were carefully selected from each field site based on a visual assessment of their level of preservation. The association of flowstones with fossil-bearing sediments was carefully noted and ideally flowstones above and below fossil-rich layers were sampled to provide bracketing ages (Extended Data Fig. 1). The petrography of all major flowstone layers was evaluated using thin sections and standard transmitted light microscopy. All samples were pre-screened for uranium (and in some cases lead) concentrations and distributions using either passive radiation imaging with a FujiFilm BAS-1800 beta-scanner or in situ laser ablation ICP–MS (inductively coupled plasma mass spectrometer). Layers with at least 100 ng g$^{-1}$ of U were selected and up to 15 small 0.5-cm$^3$ blocks were manually cut out using a handheld dentist drill. These blocks were etched in weak HCl to remove surface contamination and all subsequent handling was performed in a Class 350 clean laboratory. Samples were spiked with a mixed $^{235}$U–$^{208}$Pb tracer, and ion chromatography column chemical was used to separate and concentrate U and Pb before measurement by MC-ICP–MS (multi-collector inductively coupled plasma mass spectrometer), following previously published protocols.$^{31}$ $^{234}$U/$^{238}$U was similarly determined from separate sample dissolutions using established protocols.$^{29}$

Instrumental mass bias effects were monitored and corrected using NIST SRM 981 reference material in the case of Pb, and the sample's internal ($^{137}$Rb/$^{238}$U) ratio for U. Instrument data files were processed initially using an in-house-designed importer, operating within the Iolite environment,$^{30}$ which considers all data and reference material analyses obtained throughout a particular analytical session and permits a variety of corrections for instrumental mass bias and drift. The resulting data, now corrected for instrumental effects, were then blank-corrected and isotope-dilution calculations performed using previously described$^{31}$ software.

Age plots were generated using Tera–Wasserburg constructs; the slope of this line and its intercept with an iteratively calculated disequilibrium concordia derived from measured $^{234}$U/$^{238}$U values were used to calculate a final age.$^{17}$ All errors are quoted as ±2σ.

Our 25 U–Pb ages and four ages that have previously been published$^{14}$ were summed together into a simple frequency histogram and a kernel density estimate curve, with a linear transformation, a bandwidth of 0.03 and 45 bins, using a modified importer, operating within the Iolite environment.$^{30}$ Our data and reference material analyses obtained throughout a particular analytical session and permits a variety of corrections for instrumental mass bias and drift. The resulting data, now corrected for instrumental effects, were then blank-corrected and isotope-dilution calculations performed using previously described$^{31}$ software.

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Our 25 U–Pb ages and four ages that have previously been published$^{14}$ were summed together into a simple frequency histogram and a kernel density estimate curve, with a linear transformation, a bandwidth of 0.03 and 45 bins, using a previously published program.$^{13}$ There are five new U–Pb ages from Bolt's Farm, four from Drimolen$^{27}$ and one each from Haasgat, Hoogland and Malapa (Table 1 and Supplementary Table 1). Flowstone U–Pb ages from Sterkfontein, Swartkrans, Cooper's and Malapa have previously been published$^{26,11,29,32,33}$ but here we recalculate the $^{238}$U–$^{204}$Pb ages for Sterkfontein and Cooper's using Tera–Wasserburg concordia plots to avoid using isotope ratios that include $^{206}$Pb and we therefore improve the precision by up to 50%.

We created a video (Supplementary Video 1) as a visualization of the age data on the landscape through time. We used ESRI ArcMap 10.4 (http://desktop.arcgis.com/en/arcmap) and Filmora v.8.6.1 (https://filmora.wondershare.net/video-editor) software. The underlying digital elevation model in the video was generated in ArcMap using the US Geological Survey 1-arcsec (30-m) Shuttle Radar Topography Mission dataset (https://lta.cr.usgs.gov/SRTM1Arc). The underlying digital elevation model in Fig. 1 was generated in ArcMap using the global 30-arcsec digital elevation model (1 km, https://lta.cr.usgs.gov/GTOPO30). The site abbreviations are: BF, Bolt's Farm; CD, Cooper's Cave; DM, Drimolen; GND, Gondolin; GV, Gladysvale; HG, Haasgat; HL, Hoogland; KD, Kromdraai; MP, Malapa; RS, Rising Star; STK, Sterkfontein; SWK, Swartkrans. The animation proceeds in 1,000-year time intervals, starting at 3.2 Ma, using the Time Slider control feature in ArcGIS. When the displayed time interval contains the 2σ age of a sampled speleothem, a blue marker is displayed at that same location. The size of the marker is relative to the magnitude of the error estimate on the sample, such that samples with smaller errors appear as larger circles than samples with larger errors. The colour of the marker is relative to the proximity of the displayed time slice to the mean age of the sample, such that the marker is displayed as the darkest shade of blue when the map is displaying a time slice that contains the mean age of the sample. The marker colour is progressively lighter towards the tail ends of the age distribution before and after the mean age (up to 2σ). The marker-shape file is displayed with 50% transparency to allow multiple samples from the same site to be visible. The time intervals containing wetter PGI–6 and drier sedimentary units (SEDs) 1–6 are also displayed.

**Reporting summary.** Further information on research design is available in the Nature Research Reporting Summary linked to this paper.

**Data availability**

The authors declare that all data supporting the findings of this study are available within the paper and the Supplementary Information (see Supplementary Information and Supplementary Table 1).

Extended Data Fig. 1 | Field photographs showing U–Pb-dated flowstone from the indicated sites, all of which record some variation of an alternating stack of flowstones and fossil-bearing sediments. 

**a.** The basal flowstone from Cooper’s Cave. **b, c.** Flowstones at Haasgat are preserved in the now-deroofed section of the deposits (b) and inside the cave (c). **d.** The flowstone capping the MB1 Lower Bank at Swartkrans.

**e.** Flowstone from Bolt’s Farm Pit 7 at the base (e) and top (f) of the sequence. **g.** Flowstone capping Member 4 at Sterkfontein. **h.** Flowstone underlying fossil bearing sediments at Malapa. **i.** Flowstone sandwiched between fossil-bearing sediments at Drimolen. **j.** Massive flowstone at the base of Member 4 at Sterkfontein is exposed in a borehole. **k.** Flowstone underlying fossil-bearing sediments at Hoogland.
Extended Data Fig. 2 | U–Pb ages plotted against time and by site, additional un-U–Pb dated Cradle sites and non-Cradle hominin cave sites included. a–e, A variation of Fig. 2. U–Pb ages of Cradle sites are shown, with Cradle sites not dated with U–Pb (Gondolin and Kromdraai) included, as well as the non-Cradle hominin cave sites (Makapansgat and Taung) shown for comparison. All U–Pb ages are plotted against time and by site, n = 29, diamonds represent individual ages and 2σ errors are shown as whiskers. Also included here are four records of climate and variability derived from orbital parameters for East African sites (d), specifically arid phases from soil carbonates34, periods of deep rift valley lakes35, phases of extreme climate variability36 and key phases of variability as described previously37. Again, there is no clear relationship between these records and the new South African flowstone record. Indicated data were obtained from previous studies28,34–37.
Reporting Summary

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When statistical analyses are reported, confirm that the following items are present in the relevant location (e.g. figure legend, table legend, main text, or Methods section).

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Our web collection on statistics for biologists may be useful.

Software and code

Policy information about availability of computer code

**Data collection**

U and Pb isotope data were collected using protocols outlines in Woodhead et al (2006) and Pickering et al. (2010). In more detail, isotope ratios were collected using the machine software that comes standard with Nu Instruments MC-ICP-MS, Pb isotopes were corrected using lolite (Paton et al., 2011), spike corrections done using Schmidtz and Schoene (2007).


The 29 U-Pb ages were summed together into a single record using a kernel density estimate - we used the free software by Vermeesch (2012).


Our data visualisation, presented as supplementary video 1, was created using ESRI ArcGIS 10.4 and Filmora v8.6.1

For manuscripts utilizing custom algorithms or software that are central to the research but not yet described in published literature, software must be made available to editors/reviewers upon request. We strongly encourage code deposition in a community repository (e.g. GitHub). See the Nature Research guidelines for submitting code & software for further information.

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All isotope concentration and ratio data needed to calculate U-Pb ages are provided in extended data Table 1. There are no restrictions on data availability.

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Study description
Uranium-lead dating of cave carbonates from hominin fossil bearing caves in South Africa. Individual U-Pb ages (n=29) summed together with a kernel density estimate. One replicate was run, SB1 and STA15 were taken from the same flowstone.

Research sample
Based on my field experience, flowstone rock samples were selected and collected from 8 cave locations in the Cradle of Humankind, South Africa. The sites were chosen based on the importance of the associated fossil record and ease of access/permission to sample. We present 29 U-Pb ages. 13 of these ages are new, 16 previously published but recalculated here. Previous papers include:


Sampling strategy
Not every single cave in the Cradle is represented here, but all major hominin bearing deposits (Sterkfontein, Swartkrans, Drimolen, Coopers, Malapa) and a few non-hominin caves are (Haagast, Hoogland, Bolt’s Farm). This is the largest geochronological collection ever for these sites. This is a geological study, our sample sizes are small, around 2 samples per site is normal.

Data collection
Careful fieldwork included noting the relationship between the flowstones samples for dating and the fossil bearing sediments in a field note book and with photographs. RP did the bulk of the sample collection herself with a geological hammer, with field assistance from AIRH. All U-Pb dating was done at the University of Bern and the University of Melbourne by RP.

Timing and spatial scale
Sample collection in the Cradle began in 2005 as part of RP’s PhD work, continued with yearly field campaigns until 2012. Break in fieldwork since 2012 is mainly due to RP having two babies (2013;2016) and associated time away from work. All U-Pb dating samples were run between 2005 and 2015.

Data exclusions
All collected U-Pb data are included in this paper, one sample taken from Haasag could not provide a final age solution but is included anyway in the spirit of transparency.
Reproducibility

We do not explore the reproducibility of the U-Pb dating in this contribution, but have at length done so in previous publications (see below). The same flowstone sample split between labs and dated by different people using slightly different protocols gave final ages in close agreement.


Randomization

We dated all the flowstones collected, there was no need nor scope for randomization

Blinding

We did not undertake any blinding, samples were collected and analyzed with full knowledge of where they were from etc. This is standard practice in this type of work.

Did the study involve field work?  Yes  No

Field work, collection and transport

Field conditions

Field work was done over a period of 10 years, the exact conditions of collection are not relevant to these geological samples

Location

Cradle of Humankind, South Africa, 25º50’S - 26ºS, 27º70’E - 28º10’E, 1410-1550 mamsl

Access and import/export

The rock samples did not require South African Heritage Agency (SAHRA) permits as they are not fossils, artefacts or meteorites but all sampling was carried out under the umbrella of the SAHRA existing permits held for each site. The relevant permit holders are acknowledged in the paper. A full list of permit numbers and reports is available online from SAHRA.

Disturbance

The study did not cause any disturbance. All samples were collected with a view to minimizing the damage to the cave site.

Reporting for specific materials, systems and methods

Materials & experimental systems

n/a  Involved in the study  

- ☑ Unique biological materials
- ☑ Antibodies
- ☑ Eukaryotic cell lines
- ☑ Palaeontology
- ☑ Animals and other organisms
- ☑ Human research participants

Methods

n/a  Involved in the study  

- ☑ ChIP-seq
- ☑ Flow cytometry
- ☑ MRI-based neuroimaging