



# Combining legacy data with new drone and DGPS mapping to identify the provenance of Plio-Pleistocene fossils from Bolt's Farm, Cradle of Humankind (South Africa)

Tara R. Edwards<sup>1</sup>, Brian J. Armstrong<sup>1</sup>, Jessie Birkett-Rees<sup>2</sup>, Alexander F. Blackwood<sup>1</sup>, Andy I.R. Herries<sup>1,3</sup>, Paul Penzo-Kajewski<sup>1</sup>, Robyn Pickering<sup>4,5</sup> and Justin W. Adams<sup>3,6</sup>

<sup>1</sup>The Australian Archaeomagnetism Laboratory, Department of Archaeology and History, La Trobe University, Melbourne, Victoria, Australia

<sup>2</sup>Centre for Ancient Cultures, Faculty of Arts, Monash University, Clayton, Melbourne, Victoria, Australia

<sup>3</sup>Centre for Anthropological Research, University of Johannesburg, Johannesburg, Gauteng, South Africa

<sup>4</sup>Department of Geological Science, University of Cape Town, Cape Town, Western Cape, South Africa

<sup>5</sup>Human Evolution Research Institute, University of Cape Town, Cape Town, Western Cape, South Africa

<sup>6</sup>Centre for Human Anatomy Education, Department of Anatomy & Developmental Biology, Biomedical Discovery Institute, Faculty of Medicine, Nursing & Health Sciences, Monash University, Clayton, Melbourne, Victoria, Australia

## ABSTRACT

Bolt's Farm is a Plio-Pleistocene fossil site located within the southwestern corner of the UNESCO Hominid Fossil Sites of South Africa World Heritage Site. The site is a complex of active caves and more than 20 palaeokarst deposits or pits, many of which were exposed through the action of lime mining in the early 20th century. The pits represent heavily eroded cave systems, and as such associating the palaeocave sediments within and between the pits is difficult, especially as little geochronological data exists. These pits and the associated lime miner's rubble were first explored by palaeoanthropologists in the late 1930s, but as yet no hominin material has been recovered. The first systematic mapping was undertaken by Frank Peabody as part of the University of California Africa Expedition (UCAE) in 1947–1948. A redrawn version of the map was not published until 1991 by Basil Cooke and this has subsequently been used and modified by recent researchers. Renewed work in the 2000s used Cooke's map to try and relocate the original fossil deposits. However, Peabody's map does not include all the pits and caves, and thus in some cases this was successful, while in others previously sampled pits were inadvertently given new names. This was compounded by the fact that new fossil bearing deposits were discovered in this new phase, causing confusion in associating the 1940s fossils with the deposits from which they originated; as well as associating them with the recently excavated material. To address this, we have used a Geographic Information System (GIS) to compare Peabody's original map with subsequently published maps. This highlighted transcription errors between maps, most notably the location of Pit 23, an important palaeontological deposit given the recovery of well-preserved primate crania (*Parapapio*, *Cercopithecoides*) and partial skeletons of the extinct felid *Dinofelis*. We conducted the first drone and Differential

Submitted 25 October 2018

Accepted 3 December 2018

Published 14 January 2019

Corresponding author

Tara R. Edwards,  
T.Edwards@latrobe.edu.au

Academic editor

William Jungers

Additional Information and  
Declarations can be found on  
page 17

DOI 10.7717/peerj.6202

© Copyright

2019 Edwards et al.

Distributed under

Creative Commons CC-BY 4.0

OPEN ACCESS

Global Positioning System (DGPS) survey of Bolt's Farm. Using legacy data, high-resolution aerial imagery, accurate DGPS survey and GIS, we relocate the original fossil deposits and propose a definitive and transparent naming strategy for Bolt's Farm, based on the original UCAE Pit numbers. We provide datum points and a new comprehensive, georectified map to facilitate spatially accurate fossil collection for all future work. Additionally, we have collated recently published faunal data with historic fossil data to evaluate the biochronological potential of the various deposits. This suggests that the palaeocave deposits in different pits formed at different times with the occurrence of *Equus* in some pits implying ages of <2.3 Ma, whereas more primitive suids (*Metridiochoerus*) hint at a terminal Pliocene age for other deposits. This study highlights that Bolt's Farm contains rare South African terminal Pliocene fossil deposits and creates a framework for future studies of the deposits and previously excavated material.

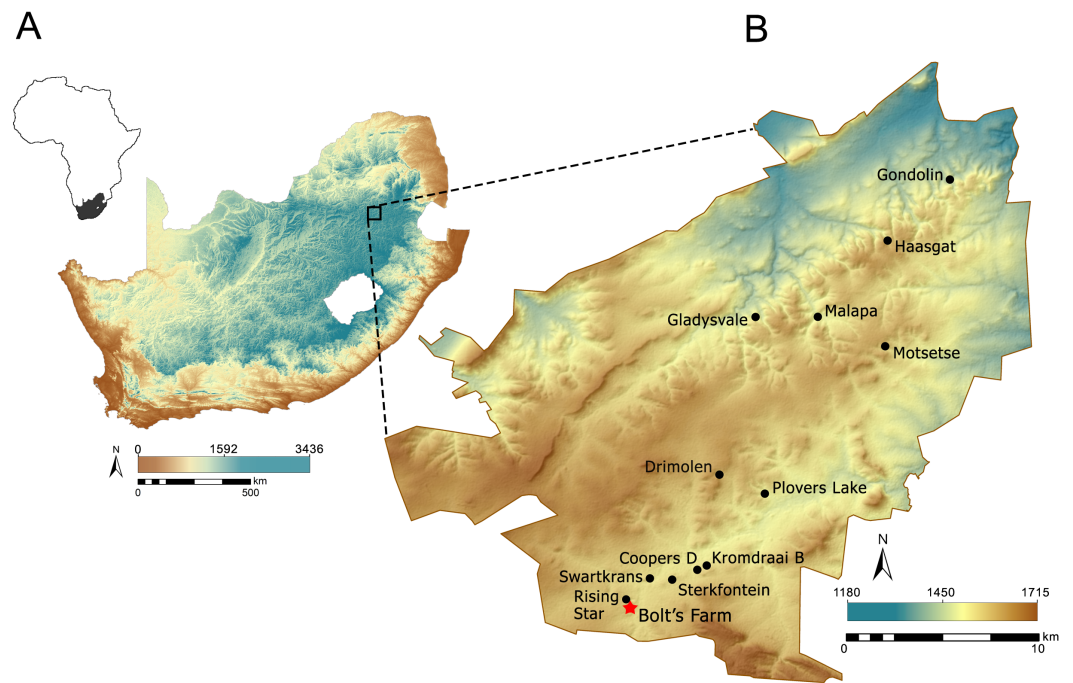
**Subjects** Evolutionary Studies, Paleontology, Spatial and Geographic Information Science

**Keywords** *Equus*, GIS, *Dinofelis*, Legacy data, *Metridiochoerus andrewsi*, Bolt's Farm, Pliocene, Pleistocene, Palaeocave

## INTRODUCTION

Bolt's Farm is the name given to a series of fossil bearing palaeocave remnants located ~1.5–3.0 km to the southwest of the early Pleistocene early hominin (*Paranthropus robustus*, early *Homo* and *Australopithecus africanus*) bearing sites of Swartkrans and Sterkfontein, and ~1 km south of the Rising Star Cave system (*Homo naledi*) (Berger *et al.*, 2015; Dirks *et al.*, 2015) (Fig. 1). Apart from the little explored archaeological and fossil bearing site of Goldsmith's (*Mokokwe*, 2007) 0.5 km to the south, Bolt's Farm is the most southwestern fossil-bearing site in the Gauteng exposures of the Malmani dolomite UNESCO Hominid Sites of South Africa World Heritage Site (colloquially referred to as 'The Cradle'). The pits and caves that are now collectively referred to as Bolt's Farm occur on three properties: the western Klinkerts property, the eastern Greensleeves Property, and the northern Sterkfontein Quarry (Fig. 2). The fossil site is named after Mr Billy Bolt, the owner of the original farm that sat on the eastern Greensleeves property and Sterkfontein Quarry (known as Main Quarry). The western Klinkerts part of the site was owned by the Clyde Trading Company (indicated on the original site map as the Amlors Ors Co.; SOM SF1, SF2).

As with the other caves in the area, Bolt's Farm was heavily mined for speleothem (calcium carbonate from stalagmites, stalactites and flowstones) in the terminal 19th and early 20th centuries. The speleothem was burnt in kilns to make lime for use in the gold extraction process. Evidence for this is preserved as lime miner's cottages and kilns that survive at both the northeast and southeastern end of the Greensleeves Property (Fig. 2). While discrete deposits existed, mining revealed and created a series of pits and dumps from which fossils were collected from the 1936 (Broom, 1937), to the current projects (Pickford & Gommery, 2016).

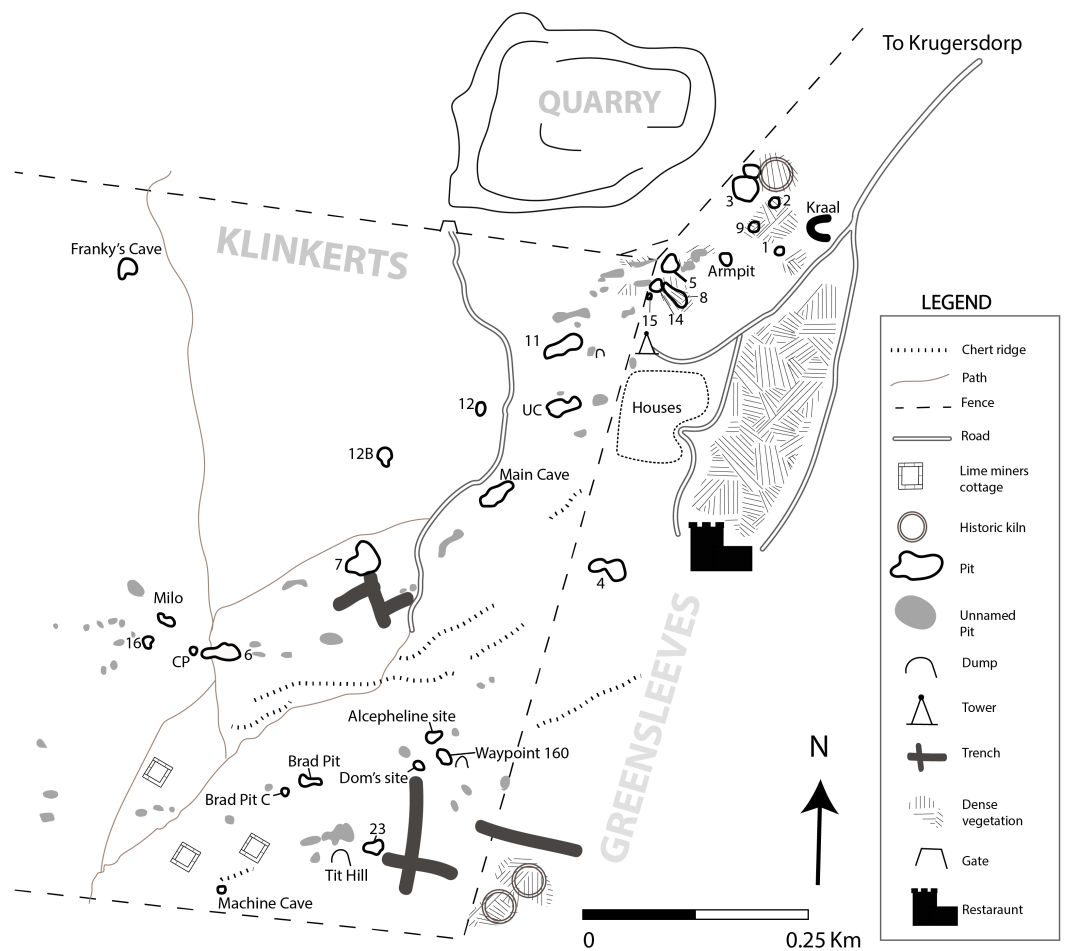


**Figure 1** Location of the Cradle in South Africa (A) and Bolt's Farm within the Cradle (B). Elevation data made available from *Jarvis et al. (2008)*.

Full-size DOI: [10.7717/peerj.6202/fig-1](https://doi.org/10.7717/peerj.6202/fig-1)

The significance of Bolt's Farm lies both within this numerous, extensive network of pits that have yielded a diverse range of faunal material (SOM Text S1) and the suggested Pliocene ages for some of the specimens (*Sénégas & Avery, 1998; Gommery et al., 2008a*). Early mentions described Bolt's Farm as a single deposit (*Cooke, 1963*), while later work recognised the inherent complexity and published faunal data relating to specific pits (e.g., *Delson, 1984; Cooke, 1991; Cooke, 1993*). It is now generally accepted that the site consists of deposits of various ages that formed either as part of the same cave system at different times (*Gommery et al., 2012*), or may represent the infill of several completely unconnected caves. Although several publications have used biochronological correlations to suggest depositional ages for specific pits at Bolt's Farm (e.g., *Delson, 1984; Sénégas & Avery, 1998; Reynolds, 2007; Gommery et al., 2008a*), no comprehensive review of the biochronologically sensitive taxa has been attempted. Recent Cradle-wide dating suggests some cave localities may be younger than previously thought (*Pickering et al., 2018*), which has particular impact on biochronological interpretations of some Bolt's Farm pits forming within the earlier Pliocene (*Sénégas & Avery, 1998; Gommery, Sénégas & Thackeray, 2008b*).

While the use of spatial aids e.g., geographic information system (GIS), remote sensing and photogrammetry for visualising landscapes has a strong history in archaeology (*Gibbons, 1991; Lock & Stancic, 1995; Birkenfeld, Avery & Horwitz, 2015; De l Del la Torre et al., 2015; Fernández-Lozano & Gutiérrez-Alonso, 2016; Jorayev et al., 2016; Dell'Unto et al., 2017*) its application to palaeoanthropology and palaeontology has previously been acknowledged as lagging (*Conroy et al., 2008; Anemone, Conroy & Emerson, 2011*). These



**Figure 2** New georectified map of Bolt's Farm from accurate DGPS survey. Coordinate system WGS1984 UTM35S.

Full-size [DOI: 10.7717/peerj.6202/fig-2](https://doi.org/10.7717/peerj.6202/fig-2)

methods are wide reaching and can be applied on a landscape scale e.g., mapping and identifying fossil bearing outcrops (Oheim, 2007), mapping hominin migration routes (Holmes, 2007) and reconstructing palaeoenvironments (Bailey, Reynolds & King, 2011). GIS is also extremely valuable on an intra-site scale, allowing not only for visualisation (Armstrong et al., 2018) but analysis and reconstruction of bone and stone accumulations (Nigro et al., 2003). While highly valuable, these methods have yet to be applied to Bolt's Farm.

In this contribution, we chronicle the previous work carried out on the Bolt's Farm pits, from the 1930s to the present, with a particular focus on the names and locations of the various deposits (Table 1). To this end, we provide new spatial data and make available accurate survey control points for future use (SOM SF3). The aim of this is to reduce the confusion regarding pit location and naming, which are the result not only of staggered research since the early 20th century but the intrinsically complex nature of the deposits across the surface at Bolt's Farm. We also present an overview of the previously described

**Table 1** Known locations across Bolt's Farm and various names within the literature, sorted by source. Coordinates from DGPS survey given in South African Grid and UTM.

F Peabody (1947, unpublished data)	UCMP Locality	Cooke (1991)	Sénégas et al. (2002)	Thackeray et al. (2008)	Zipfel & Berger (2009)	Gommery et al. (2012)	Monson, Brasil & Hlusko (2015)	Pickford & Gommery (2016)	This publication	SA Harte-beesthoek 94/Lo27	UTM -35
Pit 1 (Kraal Pit)	V67256, V75133	Pit 1 Kraal Pit	Pit 1	Kraal Pit	Kraal Pit (Pit 1)	Pit 1	Pit 1 (Kraal Pit)	Pit 1	Pit 1	-71816.550Y 2880218.092X	7120933.995N 571787.823E
Pit 2 (Kiln Cave)	V67257	Pit 2 Kiln	Pit 2	H Cave	H Cave (Pit 2)	N/A	Pit 2 (Kiln Pit)	H Cave	Pit 2	-71808.454Y 2880137.641X	7121014.414N 571779.731E
Pit 3 (KB Cave)	V67258, V75132	Pit 3 KB Cave	Pit 3	Cobra Cave	KB/Cobra Cave (Pit 3)	Cobra Cave	Pit 3 (Cobra Cave)	Cobra Cave	Pit 3 (Cobra Cave)	-71775.725Y 2880150.923X	7121001.137N 571747.015E
Pit 4 (Garage Ravine)	V67259	Pit 4 Garage Ravine Cave	Pit 4	Garage Ravine Cave	Garage Ravine Cave (Pit 4)	Garage Ravine Cave	Pit 4 (Garage Ravine Cave)	Garage Ravine	Pit 4	-71623.214Y 2880568.009X	7120584.218N 571594.565E
Pit 5 (Smith Cave)	V67260, V75139	Pit 5 Smith Cave	Pit 5	Smith Cave-misidentified	Smith Cave (Pit 5)	Smith Cave	Pit 5 (Smithy Cave)	Aves Cave 4 (listed as Pit 13)	Pit 5	-71692.381Y 2880228.869X	7120923.223N 571663.704E
Pit 6 (Baboon Cave)	V67261	Pit 6 Baboon Cave	Pit 6	Baboon Cave	Baboon Cave (Pit 6)	Baboon Cave	Pit 6 (Baboon Cave)	Baboon Cave	Pit 6	-71196.127Y 2880661.711X	7120490.554N 571167.649E
Pit 7 (Elephant Cave)	V67262	Pit 7 Elephant Cave	Pit 7	Bridge Cave	Elephant/Bridge Cave (Pit 7)	Bridge Cave	Pit 7 (Elephant Cave)	Bridge Cave	Pit 7	-71348.713Y 2880563.021X	7120589.204N 571320.174E
Pit 8	V75269	Pit 8	N/A	Rodent Cave	Rodent Cave (Pit 8)	Rodent Cave	Pit 8 (Rodent Cave)	Aves Cave 2	Pit 8	-71700.181Y 2880266.450X	7120885.656N 571671.501E
Pit 9	N/A	Pit 9	Pit 9	No name	No name (Pit 9)	N/A	N/A	Pit 9	N/A	-71790.951Y 2880193.79X	7120958.288N 571762.235E
Bushman Outcrop	N/A	Breccia outcrop	Breccia Outcrop	Breccia Outcrop	N/A	Milo A	N/A	Milo A	Milo	-71131.98Y 2880625.805X	7120526.445N 571103.527E
Pit 10	V67263	Pit 10 Grey Bird Pit	N/A	Main Quarry	Grey Bird Pit/Main Quarry (Pit 10)	N/A	N/A	N/A	N/A	Destroyed - approx loc. - 71810.363Y 2880123.234X	7121028.815N 571781.639E
Pit 11	N/A	Pit 11	Pit 11	U Cave	N/A (Pit 11)	X Cave	N/A	X Cave	Pit 11	-71569.186Y 2880320.273X	7120831.855N 571540.558E
Pit 12	N/A	Pit 12	Pit 12A	No name	No name (Pit 12A)	Pit 12 (A)	N/A	Pit 12 (A)	Pit 12	-71487.209Y 2880393.871X	7120758.287N 571458.614E
N/A	N/A	N/A	Pit 12B	N/A	No Name (Pit 12B)	Pit 12B	N/A	Pit 12 b	Pit 12B	-71377.978Y 2880444.538X	7120707.640N 571349.426E
Pit 13	N/A	Pit 13	Pit 13-Misidentified (Pit 5 was mapped)	Arm Pit	(Pit 13)	N/A	N/A	Aves Cave 5	N/A	-71684.94606Y 2880222.8518X	7120929.237N 571656.272E

(continued on next page)

Table 1 (continued)

F Peabody (1947, unpublished data)	UCMP Locality	Cooke (1991)	Sénégas et al. (2002)	Thackeray et al. (2008)	Zipfel & Berger (2009)	Gommery et al. (2012)	Monson, Brasil & Hlusko (2015)	Pickford & Gommery (2016)	This publication	SA Harte-beesthoek 94/Lo27	UTM -35
Pit 14 (Benchmark Pit)	V67264	Pit 14 Benchmark Pit	Pit 14	Benchmark Pit	Bench Mark Pit (Pit 14)	Benchmark Pit	Pit 14, Benchmark Pit, Location 10	Aves Cave 1	Pit 14	-71680.196Y 2880248.291X	7120903.808N 571651.524E
Pit 15	V73105	Pit 15	Pit 15- Misidentified	Aves Cave	Aves Cave (Pit 15)	Aves	Pit 15, Aves, Location 11	Aves Cave 6	Pit 15	-71671.637Y 2880262.266X	7120889.838N 571642.968E
Pit 16 (Equine Pit)	V67265	Pit 16 Equine Pit- cut off map	N/A	N/A	N/A	Milo B	N/A	Milo B	Pit 16	-71109.010Y 2880649.901X	7120502.359N 571080.566E
Pits 17-22	N/A	Not mapped	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A
Pit 23	V4888	Pit 23 Tit Hill Pit	Pit 23- Misidentified	Tit Hill Pit - Misidentified	Tit Hill Pit (Pit 23)	Tit Hill Pit - Misidentified	Pit 23, Tit Hill Pit, Location 13	Tit Hill Pit - Misidentified	Pit 23 (Tit Hill Pit)	-71363.419Y 2880879.361X	7120272.991N 571334.874E
Tit Hill	V67270	Old Dumps (Cooke, 1991)	Femur Dump		N/A	Femur Dump	Pit 23, Bolts Farm Dump, Location 13	Femur Dump	Tit Hill	-71326.245Y 2880884.057X	7120268.297N 571297.715E
Pit 24	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	No location data made available	No location data made available
Pit 25 (Gazelle Pit)	V67267	Pit 25 (Gazelle Pit)	N/A	N/A	N/A	N/A	N/A	N/A	N/A	No location data made available	No location data made available
N/A	V67268	N/A	N/A	N/A	N/A	N/A	New Cave	N/A	N/A	No location data made available	No location data made available
N/A	V67269	N/A	N/A	N/A	N/A	N/A	Jackal Cave	N/A	N/A	No location data made available	No location data made available

and undescribed faunal material repositied across US and South African institutions with the aim of providing key biochronological ages for the Bolt's Farm deposits where possible. In doing so we also provide the first basis for associating historic and more recently developed fossil samples excavated from these pits, a critical step in reconciling the faunal record from across this prolific locality and allowing for more justified intra- and intersite faunal, taphonomic and palaeoecological analyses.

## REVIEW OF PREVIOUS EXCAVATIONS, MAPPING AND NOMENCLATURE AT BOLT'S FARM

The first mentions of Bolt's Farm are by *Broom (1937)* but there is confusion as to the definite locality to which he is referring. *Broom (1937)* and *Broom (1939)* used a number of site location names no longer used today: referring interchangeably to 'Sterkfontein Farm', 'Sterkfontein Caves', 'Bolt's Farm' and 'Bolt's Workings at Sterkfontein'. In his initial publications, *Broom (1937)* and *Broom (1939)* described a number of novel carnivores *Leptailurus spelaeus* (Family Felidae, Order Carnivora; figured in *Broom (1939)* but specimen not currently locatable), *Crossarchus transvaalensis* (Family Herpestidae, Order Carnivora; figured in *Broom (1939)* but specimen not currently locatable), and the type specimen of the extinct hedgehog *Atelerix major* (Family Erinaceinae, Order Eulipotyphla; TM 1544; subsequently subsumed into *Erinaceus (Atelerix) broomi* per *Werdelin & Peigne, 2010*). These specimens are described as originating from "Sterkfontein in a cave, about a mile south of that in which *Australopithecus* was found" (*Broom, 1937* pp. 512), which fits the known location of what today is Bolt's Farm. *Broom (1939)* further qualifies the location of these specimens as "found at Bolt's workings on Sterkfontein" (*Broom, 1939* pp. 333) alongside the description of the STS 130-299 specimen *Machairodus transvaalensis* (Family Felidae: Order Carnivora). Broom continued to sample at Bolt's Farm until 1948, describing additional type specimens such as *Felis shawi* (BF 1555; Family Felidae, Order Carnivora; subsequently subsumed into *Panthera leo Linnaeus, 1758*) and *Elephantulus antiquus* (Family Macroscelididae, Order Macroscelididae; figured in *Broom (1948)* but specimen not currently locatable), as well as preserved remains of *Phacochoerus modestus* (BF3-3355; Family Suidae, Order Cetartiodactyla; subsequently subsumed into *Phacochoerus antiquus Broom, 1948; Adams et al., 2015*; see SOM Text S1). There has been considerable confusion over the provenance of these early fossil specimens to what is currently defined as Bolt's Farm, let alone specific pit deposits due to the ambiguity of these early reports that sadly likely cannot be addressed short of direct specimen sampling (e.g., *Trueman et al., 2005*).

Between 1947 and 1948, the southern section of the University of California Africa Expedition (UCAE) visited Bolt's Farm, led by C.L. Camp and F. E. Peabody (*Camp, 1948*). Their aim was to gain further fossil evidence and geological context for the australopithecine specimens described by *Dart (1925)* and *Broom (1936)*. The UCAE undertook systematic sampling of fossiliferous calcified deposits across the Cradle, including from several miners pits and rubble on Bolt's Farm. While members of the UCAE did keep detailed field dairies recording daily activities and discoveries, it is often difficult to reconcile whether

specimens were identified *in situ* or collected from miner's rubble. Further, some localities have several rubble dumps nearby and subsequently it can be difficult to associate a rubble dump with any one pit. Attention was often paid to the matrix adhering to any specimens collected, and attempts made to match this with sediment in a nearby locality. Frank Peabody created the first known map of the site (SOM SF1 SF2; list of pits [Table 1](#)), which was not published in its original form until recently ([Monson, Brasil & Hlusko, 2015](#))—although used by [Cooke \(1991\)](#) to generate his map (see below). The expedition amassed a significant collection of fossils from a range of sites, now housed at the University of California Museum of Paleontology (UCMP) ([Peabody, 1954](#); [Monson, Brasil & Hlusko, 2015](#)), with some specimens repatriated to Evolutionary Studies Institute at the University of the Witwatersrand (Johannesburg) and the Ditsong National Museum of Natural History (Pretoria), South Africa.

Due to his sudden death in 1958, Peabody was unable to prepare a detailed report of his work at Bolt's Farm, as he had done for Taung ([Peabody, 1954](#)). Subsequently, Cooke visited the UCMP in 1957–1958 (as well as in 1975 and 1983) to study the fossils recovered by the expedition ([Cooke, 1991](#)). [Cooke \(1991 p.9\)](#) published a map “redrawn directly” from Peabody's survey map, including pit numbers, associated names and locality numbers from the UCAE (Pits 1–16 and 23–25).

The Palaeontological Expedition to South Africa (PESA) ran from 1996–1999 under the direction of Senut and Pickford ([Sénégas & Avery, 1998](#)). The project undertook further collections from fossil dumps and attempted to relocate all sites from the UCAE using [Cooke's \(1991\)](#) map ([Sénégas et al., 2002](#)). While they were not able to identify all the sites with certainty, the project did discover a new site, Waypoint 160 ([Sénégas & Avery, 1998](#)), and microfauna from the deposits has been used to argue a terminal Miocene or earlier Pliocene age for the deposits (5–4 Ma, [Sénégas & Avery, 1998](#); 5.4–05 Ma, [Gommery et al., 2008a](#)).

The HOPE (Human Origins and Past Environments) project, a collaboration of French and South African researchers based out of the Ditsong National Museum of Natural History, worked at the site from 2001. They attempted to align the UCAE ‘loci’ on [Cooke's \(1991\)](#) map with those observed in the field ([Sénégas et al., 2002](#); [Thackeray et al., 2008](#)). From 2006 HOPE transformed into the HRU (HOPE Research Unit), conducting regular survey and excavations at Bolt's Farm. As a result, several previously undiscovered sites were described ([Gommery et al., 2012](#)). In order to expose the bone rich *in situ* breccias, detailed excavation of several unstudied deposits (Pit 14, Brad Pit A & B, Milo A & B) were undertaken. An updated map was presented in [Thackeray et al. \(2008\)](#), which included the re-identified deposits from [Sénégas et al. \(2002\)](#) and used names rather than the original UCAE Pit numbers: Pit 7 renamed Bridge Cave, Pit 11 renamed X Cave, Pit 14 (incorrectly listed as Pit 15) is renamed Aves Cave and Pit 3 renamed Cobra Cave. Locations for other UCAE Pits, such as Pit 2 (renamed H Cave), Pit 1, Pit 8 (named Rodent Cave) are also suggested. [Thackeray et al. \(2008\)](#) also map a number of ‘new’ sites in addition to Waypoint 160 and Alcelaphine Cave, including Dom's Site, Machine Cave, X Cave and Y Cave.

[Gommery et al. \(2012\)](#) built on this research when describing another series of ‘new’ sites, including a sequence north of Pit 23 called Brad Pit A-C, a series west of Pit 6 called



Milo's Pit A and B, Brigitte Bones A and B, and Carnivore Pit. Further to the northwest another new locality is designated Franky's Cave ([Gommery et al., 2012](#)). [Gommery et al. \(2014\)](#) present a simplified map of the Klinkerts property pits (excluding new localities Brigitte Bones, Dom's and Brad Pit C).

[Monson, Brasil & Hlusko \(2015\)](#) attempted to clarify issues around the naming of pits through a historical summary, along with the accession of taxa from the previously unreported New Cave and Jackal Cave. While the authors included a summary table with alternative names for the original pits recorded in 1947, sites since discovered or with material not accessioned at UCMP (e.g., Waypoint 160) were not included.

The history of staggered research at Bolt's Farm spanning eight decades has created a number of issues regarding the consistency of naming practices across the site, with some pits acquiring two names, or being 'double discovered'. This paper aims to provide clarity and rectify these issues of misidentification. Our intent is to create a transparent scheme, advocating for a return to the original naming practices of the site initiated by Camp and Peabody, while also producing a new georectified map to assist in ongoing research at the site ([Fig. 2](#)).

## METHODS

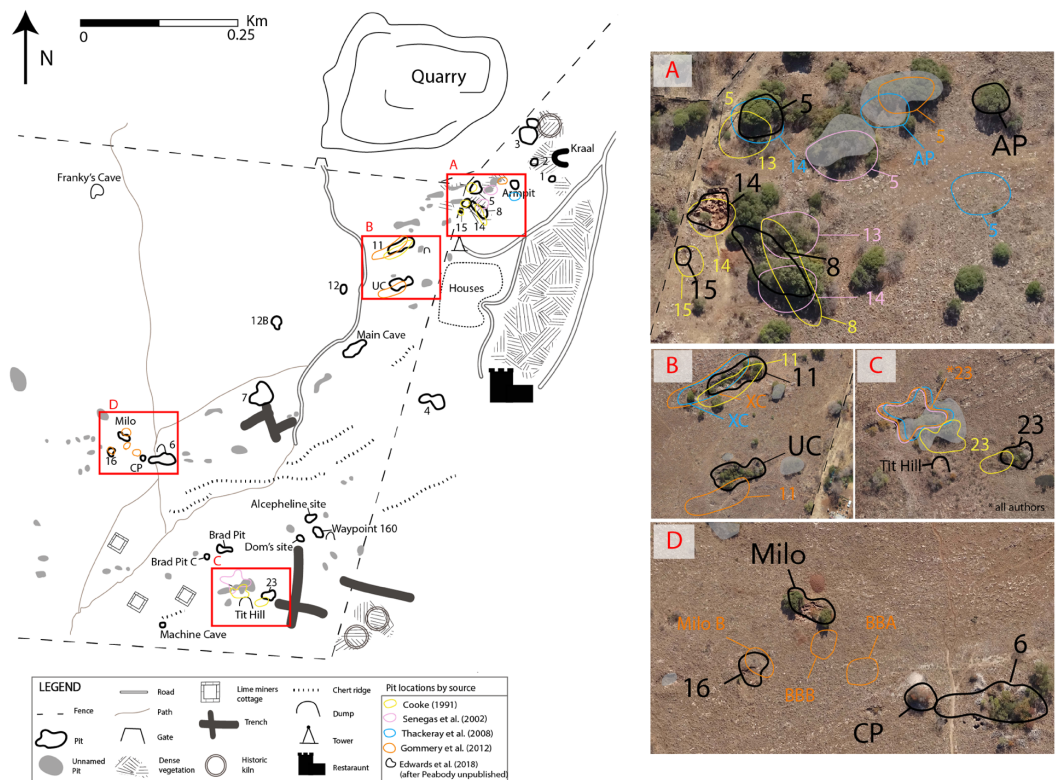
Field work was undertaken as part of South African Heritage Resource Agency Permit ID 866, Ref No. 9/2/233/0032.

### Aerial imagery, site survey and GIS

High-resolution aerial imagery was obtained using an eBee senseFly drone. Imagery was processed using Agisoft PhotoScan Pro 1.16 and Georectified on to the South African Coordinate System (Hartebeesthoek 94/ Lo27, EPSG:2052, SA 2010 GEOID), and later converted to World Geodetic System (WGS) 84 Universal Transverse Mercator (UTM) Zone 35S for convenience. Survey control points were established at twelve locations across the site (SOM F3). These were then exploited for a feature based foot survey of the landscape using a Leica GPS1200+ Differential Global Positioning System (DGPS), which enabled sub-centimetre accuracy of surveying positions. This recorded the location of all pits, caves, trenches, historical structures and geological outcrops. DGPS survey was processed with Leica Geo Office and exported to ascii format. Both the Aerial imagery and survey data were imported into ESRI software, ArcMap and ArcScene 10.4. Historical imagery (Peabody's map and the later maps of ([Cooke, 1991](#); [Sénégas et al., 2002](#); [Thackeray et al., 2008](#); [Gommery et al., 2012](#)) were georectified on to the aerial imagery, allowing for a direct comparison between our new data and the previous maps ([Fig. 3](#)). The raw DGPS data (converted to UTM 35s) has been provided, in addition to drone aerial imagery, and our new georectified site map, made available via figshare.

### Faunal analysis

The Bolt's Farm faunas are curated across three international institutions. The University of California Expedition sample is now curated at the University of California Museum of Paleontology (UCMP) at the University of California, Berkeley ([Cooke, 1991](#); [Cooke,](#)



**Figure 3** New map of Bolt's Farm with areas of pit location error highlighted A–D. Colours represent errors by source. (A) Errors pit locations in the 'Aves Cave Complex' including Pit5, 8, 13, 14, 15, Arm Pit. (B) Errors in location of Pit 11 and U Cave. (C) Misidentification of Pit 23 (D) Misidentification of Pit 16 as new site Milo B and errors in the location of BBA and BBB

Full-size [DOI: 10.7717/peerj.6202/fig-3](https://doi.org/10.7717/peerj.6202/fig-3)

1993; Monson, Brasil & Hlusko, 2015). Decades of intermittent processing and cataloguing has produced a substantial sample across most of the pits across the Bolt's Farm complex. Direct evaluation of specimens to establish primary identification were made in reference to the extensive body of published descriptions of the UCMP and larger South African record, an extensive database of measurements, photographs, and notes on South African fossils and an unpublished summative manuscript on the UCMP collections provided by HBS Cooke (HBS Cooke, pers. comm., 2008). These collections were studied directly by one of us (JWA) during two data collection periods in 2007 and 2012 in collaboration with Dr. Alan Shabel (Department of Integrative Biology, UC Berkeley).

Two South African institutions (Evolutionary Studies Institute, University of the Witwatersrand, Johannesburg; Ditsong National Museum of Natural History, Pretoria) are repositories for some Bolt's Farm specimens and have been regularly studied by JWA over the course of the last 15 years, and were evaluated specifically for this study during field seasons in 2015–2017. Fossils described from recent excavations at Bolt's Farm (e.g., those conducted since the UCAE) were not available for direct study, and any reference to these fossils in our review of the biochronologically relevant taxa comes from published

**Table 2** Summary of localities discovered subsequent to UCAE mapping. GPS coordinates as first published and where possible, new accurate DGPS data.

New Locality 1996–2016	WGS 84 position and reference	SA Hartebeesthoek 94/ Lo27 (This publication)	UTM -35 Location (This publication)
Waypoint 160	S26°02'02.0"E27°42'50.0" ( <i>Sénégas et al., 2002</i> )	−71441.694Y 2880778.398X	7120373.913N 571413.117E
Brad Pit A and B	S26°02'02.8"E27°42'44.2" and S26°02'02.6"E27°42'43.8" ( <i>Gommery et al., 2012</i> )	−71285.624Y 2880805.139X	7120347.183N 571257.110E
U Cave	S26°1'49.20"E27°42'54.25" ( <i>Thackeray et al., 2008</i> )	−71570.450Y 2880386.746X	7120765.408N 571541.822E
Brigitte Bones A	S26°01'57.4"E27°42'38.6" ( <i>Gommery et al., 2012</i> )	Not located from provided coordinates	Not located from provided coordinates
Brigitte Bones B	S26°01'57.6"E27°42'38.2" ( <i>Gommery et al., 2012</i> )	Not located from provided coordinates	Not located from provided coordinates
Alcephaline Site	S26°02'00.8"E27°42'49.0" ( <i>Sénégas et al., 2002</i> )	−71428.251 2880756.014	7120393.54N 571398.117E
Franky's Cave	S26°01'44.6"E27°42'36.6" ( <i>Gommery et al., 2012</i> )	−71087.901 2880229.732	7120922.934N 571057.728E
Carnivore Pit	S26°01'57.8"E27°42'39.1" ( <i>Gommery et al., 2012</i> )	−71167.72 2880654.998	7120497.072N 571140.817E
Dom's Site	S26°02'02.0 E27°42'48.8" ( <i>Thackeray et al., 2008</i> )	−71413.037 2880786.441	7120366.659N 571385.409E
Machine Cave	S26°02'06.6"E27°42'40.4" ( <i>Thackeray et al., 2008</i> )	−71191.354 2880923.537	7120228.221N 571161.893E

literature—with the exception of the Milo's A suids which were examined earlier (*Gommery et al., 2012*).

## RESULTS

### Combining legacy maps and accurate spatial data

**Table 1** shows the Peabody map localities and associated modern pit names and new DGPS coordinates for known locations. Note that some pits from 1947 have now been re-identified but were listed as 'new discoveries' by subsequent publications (*Sénégas et al., 2002*; *Thackeray et al., 2008*; *Gommery et al., 2012*). **Table 2** presents a list of new locales, from work conducted between 1996–2016 which have published fauna associated with the deposits (*Sénégas & Avery, 1998*; *Sénégas, 2000*; *Sénégas et al., 2002*; *Thackeray et al., 2008*; *Gommery et al., 2012*; *Gommery et al., 2014*; *Gommery et al., 2016*; *Pickford & Gommery, 2016*).

Accurate locations of all pits across the Klinkerts and Greensleaves properties are presented in **Fig. 2**. These data have been overlain with a georectified version of Peabody's original map, *Cooke (1991)*'s interpretation of this map, and subsequent publications which relocated pits and announced new localities; *Sénégas et al. (2002)*, *Thackeray et al. (2008)* and *Gommery et al. (2012)* with discrepancies and clarification of complicated areas shown in **Fig. 3**.

Importing and georectifying Peabody's original map with our DGPS data and published maps from 1991–2012 identifies discrepancies in four areas (**Table 1**; **Figs. 3A–3D**). Three

of these relate to ambiguity in the first published map (Cooke, 1991), from which all subsequent maps until now were produced. Firstly, the precise locations of Pits 5 and 13–15 are not easily discernible (Fig. 3A). The location of Pit 11 is correctly identified by Cooke (1991) (Fig. 3B). The designation of Pit 23 is placed between two localities whereas Peabody labels Pit 23 as the more easterly of the two pits (Fig. 3C). Through georectification of the original map and archival research (SOM SF2, SF3) we have determined Pit 23 to be the more easterly of the two pits, however it has been continually misidentified in the literature. The location of Pit 16 is cut off the map, allowing for this to be re-discovered as a new site more than twenty years later (Fig. 3D). Without direct comparison with the original Peabody map it is impossible to interpret these complex areas on Cooke's map.

Sénégas *et al.* (2002) published a map following the Cooke (1991) version along with GPS coordinates for Pits 3–7, 9, 11–15 and 23 (Table 1). This new map features 'Breccia outcrop' from Cooke's (1991) map and 'new' locations Waypoint 160, Alcelaphine Site and the Femur Dump (Sénégas *et al.*, 2002; Gommery, Sénégas & Thackeray, 2008b). While the latter is present as 'Tit Hill' on Peabody's map, it was not copied over by Cooke (1991) and ambiguity in this region led to misidentification of Pit 23 (Fig. 3B). Most of the locations reported in Sénégas *et al.* (2002) plot close to identifiable pits on new aerial imagery, with a few exceptions. Firstly, 'Breccia outcrop' plots directly adjacent to Pit 6, making it possible that a breccia dump was mistakenly logged as an outcrop. Digital comparison of both maps (Cooke, 1991; Sénégas *et al.*, 2002) show that the 'Breccia outcrop' locations do not correlate spatially. There was uncertainty regarding which deposit represented Pit 12, resulting in the creation of Pit 12A and 12B. Moreover, the location for Pits 5 and 13, while being associated with a pit on aerial imagery is not where the original Pits 5, 13 and 14 are located (Fig. 3A). Archival research of original field notebooks at the UCMP showed Pit 13 to be a dump associated with Pits 5 and 14 (SOM SF5), which is not clear from looking at either the Peabody or Cooke (1991) map.

Thackeray *et al.* (2008) present an overview of research at Bolt's Farm and include an updated map with several new localities along with GPS coordinates. Plotting these coordinates on georectified aerial image shows several inconsistencies with the original mapped pits (Fig. 3). While Pit 14 was correctly identified as Benchmark Pit, coordinates given match those at Pit 8 (Fig. 3A). Pit 5 was placed more than 20m away from the original mapped pit. They map in a pit which is identified as Pit 13 and given the name Arm Pit; however, as stated above, archival research reveals Pit 13 was a dump. Ultimately, Arm Pit does correspond to a real world location and moving forward should continue with this name without the designation of Pit 13 (Fig. 3A). GPS coordinates show that Pit 11 is incorrectly identified as a new site, X Cave while U Cave located to the south is labelled Pit 11 (Fig. 3B). Following Cooke (1991)'s map and Sénégas *et al.* (2002) Pit 23 is incorrectly identified (Fig. 3C).

Gommery *et al.* (2012) present nine newly discovered localities with GPS coordinates. While many of the discoveries are legitimate with coordinates that plot close to identifiable pits (Brad Pit A–C, Alcelaphine Site, Dom's Cave) others are misidentifications of old sites or there are issues with the coordinates. Several misidentifications continue through the literature including Pit 11, Pit 23, Pit 14 and Pit 5 (Fig. 3). The new sites Milo A and Milo

**Table 3** List of Pits with maximum and minimum depositional ages as indicated by biochronologically informative species.

Pit Number	Max Age	Min Age
Pit 1	<2.33 Ma	0.78
Pit 2	NA	NA
Pit 3	<2.33 Ma/1.89 Ma	0.78
Pit 4	<2.33 Ma	NA
Pit 5	<2.33 Ma	NA
Pit 6	<2.33 Ma	0.78
Pit 7	4.4 Ma	2.5 Ma (2.0 Ma)
Pit 8	NA	NA
Pit 10	<3.7 Ma	NA
Milo A	3.03–2.58	>1.95
Pit 11	<2 Ma	NA
Pit 14	3.03–2.58	>1.95
Pit 15	NA	NA
Pit 16	<2.33 Ma	0.99 Ma
Pit 23	3.03–2.58	>1.95
Pit 25	<2.33 Ma	0.78
Jackal Cave	NA	NA
New Cave	<2.33 Ma	NA
Waypoint 160	<5.0	NA
Brad Pit	N/A	N/A

B correspond to localities mapped by the UCAE in 1947: ‘Bushman outcrop’ and Pit 16 respectively (Fig. 3D). Using both supplied coordinates and overlaying our georectified map, we were unable to align Brigitte Bones A or B with any identifiable pits (Fig. 3D).

Some of the issues raised here were addressed by *Pickford & Gommery (2016)* who used, but did not publish in full, Peabody’s original map. Access to this allowed them to identify and correct many errors made especially in the area they have called the ‘Aves Cave Complex’. However, while Pits 8, 14 and 15 are correctly identified Pit 5 is incorrectly labelled Pit 13. Direct comparison with the map published in *Pickford & Gommery (2016)* was not possible due to small size of their map, which limited accurate georectification.

### Biochronologically Significant Bolt’s Farm Fauna

A full description of the biochronologically-informative faunas from the Bolt’s Farm localities described to date is provided in full in our SOM (Text S1) and the summed results of our evaluation are presented in Table 3. We wish to emphasise that the faunal data and descriptions provided here and within supplementary online material, while reflecting a substantial advance over prior taxon-focused or summative publications on the Bolt’s Farm fossil faunas, is only inclusive of specimens broadly relevant for establishing biochronological interpretations of the pit deposits. The descriptions and discussion should not be taken as a comprehensive description or listing of taxa from these deposits across these institutions.

There is insufficient faunal data from Pits 2, 8, 15, 17, Jackal Cave and Brad Pit A and B to establish a biochronological age bracket for these deposits. The majority of the described Bolt's Farm localities were deposited after 2.33 Ma given the regular recovery of *Equus* specimens that must postdate the entry of the genus into Africa (Table 3; Geraads, Raynal & Eisenmann, 2004). A probable minimum depositional age boundary of 0.78 Ma can be established for Pits 1, 3, and 25 by the occurrence of the extinct bovid *Antidorcas recki*, which disappears from South African deposits after the formation of Elandsfontein (Klein et al., 2007; Braun et al., 2013). Pit 16 contains extinct three-toed horse (*Eurygnathohippus*) and was likely deposited prior to 0.99 Ma (SOM Text S1). Pits 4, 5, and New Cave lack fauna that can restrict the minimum depositional age.

Only the Pits 7, 10, 14, 23, Waypoint 160 and Milo's A deposits contain fauna that may have been deposited prior to 2.33 Ma. The recovery of an extinct elephant (*Elephas*) from Pit 7 suggests a maximal depositional age of 4.4–2.5 Ma (potentially extending to 2.0 Ma; SOM Text S1); however, as noted above the provenance of the specimen within the deposits is unknown and a recent U-Pb age indicates some flowstones in the cave formed <~1.8 Ma (Pickering et al., 2018). As such, an in depth study of the Pit 7 stratigraphy and potential associations of the specimen will be necessary to establish a robust chronology for this location. The Pit 10 deposits contain the type specimen of the herpestid *Ictonyx bolti* (subsequently subsumed into *Prepoecilogale bolti* Cooke, 1985) known only to occur in the late Pliocene (~3.7–2.5 Ma) from northern and eastern African deposits (SOM Text S1). The Pit 14, 23 and Milo's A deposits all contain Stage I *Metridiochoerus andrewsi* craniodental remains that are morphologically analogous to those recovered from the Makapansgat Member 3 deposits (3.03–2.58 Ma) (Partridge, 1973; Herries, Curnoe & Adams, 2009; Herries et al., 2013). This may reflect a similar maximal depositional age; however, the limits of the South African suid record mean that at present we can only infer deposition of these specimens prior to 1.95 Ma (SOM Text S1). Finally, although Waypoint 160 has been previously suggested to date to after the Langebaanweg E Quarry deposits (~5.2 Ma; Roberts et al., 2011) and prior to the Makapansgat Member 3 deposits (3.03–2.58 Ma), as noted above and in SOM Text S1, without an established FAD or LAD for *Eurytomys bolti* and the recent identification of *Panthera* cf. *leo*, such a Pliocene age is not clearly supported by the fauna. Equally, recent U-Pb ages suggest flowstones in the cave formed at <~2.3 Ma, supporting the notion that at least some of this deposit is Early Pleistocene (Pickering et al., 2018).

## DISCUSSION

The extensive history of research at Bolt's Farm has yielded a substantial and diverse faunal sample from the known localities. The palaeontological significance of Bolt's Farm has lagged behind that of other South African deposits due to the divided curation of materials from across the deposits, the sporadic history of excavation, and confusion over location and nomenclature of specific pits.

The combination of several different teams working at Bolt's Farm through the decades, often with significant time between excavations and collections, and the disturbance of

many of the deposits by lime mining has cumulatively lead to the present situation of multiple names for individual deposits and ambiguity as to the exact location of a number of the pits. While attempts have been made to reconcile disparity between the naming of deposits and faunal assemblages (*Monson, Brasil & Hlusko, 2015*) and to build new naming strategies for the pits (*Pickford & Gommery, 2016*), the lack of an overarching approach focused on the accurate spatial identification of original and recently discovered pits has only added to the confusion.

By digitally overlaying Peabody's original map (*Monson, Brasil & Hlusko, 2015*) and subsequently published maps (*Cooke, 1991; Sénégas et al., 2002; Gommery et al., 2012*) with new aerial imagery and survey data, we are able to recognise pit misidentifications and errors with naming (*Fig. 3*). Spatially accurate mapping of palaeontological sites is crucial for ongoing work, especially palaeomagnetic and Uranium-Lead (U-Pb) dating, which both require secure stratigraphic contexts. In addition, the provision of 3D surveying benchmarks across the site means that all future fossil and geological samples can be recorded *in situ* and to a high degree of spatial accuracy, thereby resolving the issue of contextual and provenance problems. The work presented here is the first of its kind conducted on the site since 1947–1948, reinforcing the need for these types of surveys to be conducted, both in the context of ongoing excavation and with the analysis of historical collections.

Given our comparison of Peabody's original map with published material and the errors in naming identified (*Fig. 3*), we strongly recommend that all pits be referenced by their number or original title where possible (*Table 1; Fig. 2*). For the majority of pits across the site this is the numerical designator assigned during the UCAE (e.g., Pits 1–23). However, for all truly new sites subsequently discovered (e.g., Waypoint 160), their first published name should be used to prevent any further confusion. Since no material was recovered from “Bushman outcrop” it should henceforth be known by the first name associated with published faunal material “Milo”. Additionally, due to the questionable name attributed Pit 3 by the UCAE, the numerical designator (3) or new HRU name (Cobra Cave) is favoured (*Table 1*).

Biochronological assessment of the faunal specimens from the Pits suggests that parts of the Bolt's Farm complex may be the oldest in the Blaubank Stream Valley, possibly forming as early as the mid- (e.g., Pits 7 and 10) or late (e.g., Pits 14, 23 and Milo's A) Pliocene, and therefore prior or contemporaneous with the formation of the Makapansgat Member 3 deposits (3.03–2.58 Ma; *Herries et al., 2013*). Recent U-Pb ages for flowstones at some of these deposits (Pit 7, Pit 14, Waypoint 160; *Pickering et al., 2018*) may help to further refine or constrain these ages when combined with in depth stratigraphic interpretation and other chronological methods. These ages appear to suggest that deposits within the Cradle are all younger than ~3.2 Ma. With a combined record that may span over 2 Ma of deposition, Bolt's Farm represents—alongside Sterkfontein—one of few site complexes to cover such a long span of time in the Cradle region, providing a rare opportunity for more detailed comparisons of the fauna from these different localities through time (*Pickering et al., 2018; Herries et al., 2018*).

Additionally, within the Cradle it is unusual to have an extensive site complex like Bolt's Farm that is devoid of hominin specimens, and a small non-hominin primate sample, in such close proximity to well-known hominin- and primate-bearing sites (e.g., Sterkfontein, Swartkrans, Rising Star). There are many potential reasons why hominins or primates may not occur within the Bolt's Farm deposits which warrant mention. There are numerous references within the original field notes of Camp to australopithecine and "ape man" remains from Pit 3 (SOM SF6, SF7, SF8); however, these specimens are not known to have been subsequently catalogued within any current collections. It is possible that these specimens were incorrectly identified in the field (e.g., reclassified as non-hominin primate or other mammal remains), or that they were accidentally integrated into other fossil samples during the removal of Bolt's Farm materials which saw them organised and packed at the Ditsong National Museum of Natural History prior to export. We can establish that some specimens were simply never accessioned. For example, while Pit 3 is the only location from which a single stone tool is known to have been recovered; however, Camp's notes provide insight citing that he "scraped out 10–15 blades and gave them to the (Bolt) sisters" (SOM SF9). He goes on to list artefacts "thin blades, quartz chips. One core of chert and some slate artefacts"; none of these artefacts are known today. Equally, variable taphonomic processes exert a strong mediating role in faunal assemblage composition ([Brain, 1981](#); [Pickering, 1999](#); [Adams, 2006](#); [Pickering et al., 2004](#); [Val & Stratford, 2015](#)) and the taphonomic histories of these Pits have not yet been addressed (excepting Pit 23; see [Brain, 1981](#)). Ultimately, it is important to highlight that a bias towards excavating and analysing the well-known hominin fossil sites located nearby may be distorting our perception of how regularly hominins, primates and archaeological materials were integrated into the Cradle localities. In this respect, the Bolt's Farm Pits may be typical of penecontemporaneous deposition across the region in representation of fauna.

## CONCLUSIONS AND FUTURE RESEARCH

In the more than 80 years since Broom first prospected at Bolt's Farm, continued research has proven the value of the site to yield important palaeontological remains, the summed sample of which indicates an extensive depositional history that has been suggested to date back into the Pliocene.

Bolt's Farm differs significantly from other sites in the Cradle in two ways. Firstly, while palaeokarst features are commonplace throughout the Cradle, most fossil bearing sites are either caves (e.g., Sterkfontein) or single palaeokarst deposits (e.g., Malapa). It is unprecedented to have such a high density of fossil bearing palaeokarst deposits and active caves in a small area, as is the case at Bolt's Farm. Additionally, biochronology suggests there is significant temporal variation within, and between, the more than twenty known localities across the site. The unique conditions which have led to the preservation of so many palaeokarst remnants and caves is inherently linked to the geology observed at the site, requiring further research to fully disentangle.

It is critical to the next stage of research at Bolt's Farm that all areas be accurately mapped and a uniform naming scheme be settled on. As a result, the detailed survey



provided here seeks to clarify the naming issues and we present the first new map of the site in more than 70 years. Our study highlights the importance of field survey paired with high-resolution spatial mapping and drone survey, as our new map and site surveying control points allow the historical fossil collection to be accurately placed within its original context. The continued use of 3D data collection methodologies at the site will rectify some of the problems researchers have encountered. Although the site has been disturbed by mining activities and some contexts destroyed, the importance of this information is only being realised as new methods enable these distinct areas to be dated. While additional biochronological dating (after full description of more recently excavated faunas) and absolute dating methods will provide clarification of the age of deposits, spatial aids provided here should be adopted by researchers continuing to excavate at Bolt's Farm, to ensure an accurate spatial and contextual record of all finds from this key palaeontological site in the Cradle.

## ACKNOWLEDGEMENTS

The authors wish to thank Dr. Robert Anemone and one anonymous reviewer for helpful suggestions which improved this manuscript. The authors wish to thank Stepheny Potze and Lazarus Kgasi for access to the site and assistance with fieldwork, Stephany Potze was the SAHRA permit holder during initial stages of field work Dominique Gommery and Lazarus Kgasi SAHRA permit holders during surface survey; Ditsong National Museum of Natural History; Pat Holroyd for access to original notes and collections of UCAE, UCMP; Tara R. Edwards thanks Tesla Monson for assistance, support and helpful discussion, Justin W. Adams thanks Alan Shabel for assistance, support and expertise at UCMP; J Gaylord, landowner of Greensleeves. We thank Norbert Plate of iQlaser (<http://www.iqlaser.co.za>) for his time, equipment and provision of aerial imagery. Elevation data available from USGS.

## ADDITIONAL INFORMATION AND DECLARATIONS

### Funding

Funding received from Australia Research Council (grant FT120100399 to Andy I.R. Herries and DP170100056 to Andy I.R. Herries and J.W. Adams), the La Trobe University Humanities and Social Science Internal Research Grant Scheme (#2015-1-HDR-1 to Brian J. Armstrong and #2017-1-HDR-0009 to Tara R. Edwards) and National Research Foundation African Origins Platform (grant AOP150924142990 to Robyn Pickering). 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:

Australia Research Council: FT120100399, DP170100056.

The La Trobe University Humanities and Social Science Internal Research Grant Scheme: #2015-1-HDR-1 to BJA, #2017-1-HDR-0009.

National Research Foundation African Origins Platform: AOP150924142990.

## Competing Interests

The authors declare we have no competing interests.

## Author Contributions

- Tara R. Edwards conceived and designed the experiments, performed the experiments, analyzed the data, contributed reagents/materials/analysis tools, prepared figures and/or tables, authored or reviewed drafts of the paper, approved the final draft.
- Brian J. Armstrong conceived and designed the experiments, performed the experiments, analyzed the data, contributed reagents/materials/analysis tools, prepared figures and/or tables, approved the final draft.
- Jessie Birkett-Rees, Alexander F. Blackwood performed the experiments, analyzed the data, contributed reagents/materials/analysis tools, prepared figures and/or tables, approved the final draft.
- Andy I.R. Herries conceived and designed the experiments, authored or reviewed drafts of the paper, approved the final draft.
- Paul Penzo-Kajewski performed the experiments, analyzed the data, contributed reagents/materials/analysis tools, approved the final draft.
- Robyn Pickering authored or reviewed drafts of the paper, approved the final draft.
- Justin W. Adams conceived and designed the experiments, performed the experiments, authored or reviewed drafts of the paper, approved the final draft.

## Field Study Permissions

The following information was supplied relating to field study approvals (i.e., approving body and any reference numbers):

South African Heritage Resource Agency approved the study (Permit ID 866, Ref No. 9/2/233/0032).

## Data Availability

The following information was supplied regarding data availability:

Edwards, Tara (2018): Edwardsetal\_BFSOM. figshare. Fileset. <https://doi.org/10.26181/5bce7a0611c4b>.

## REFERENCES

- Adams JW. 2006.** Taphonomy and palaeoecology of the Gondolin Plio-Pleistocene cave site, South Africa. Unpublished Ph.D. Thesis, Washington University, St. Louis.
- Adams JW, Olah AH, McCurry MR, Potze S. 2015.** Surface model and tomographic archive of fossil primate and other mammal holotype and paratype specimens of the Ditsong National Museum of Natural History, Pretoria, South Africa. *PLOS ONE* **10(14)**:e0139800 DOI [10.1371/journal.pone.0139800](https://doi.org/10.1371/journal.pone.0139800).
- Anemone RL, Conroy GC, Emerson CW. 2011.** GIS and paleoanthropology: incorporating new approaches from the spatial sciences in the analysis of primate and human evolution. *Yearbook of Physical Anthropology* **54**:19–46.

- Armstrong BJ, Blackwood AF, Penzo-Kajewski P, Mentor CG, Herries AIR. 2018.** Terrestrial laser scanning and photogrammetry techniques for documenting fossil-bearing palaeokarst with an example from the Drimolen Palaeocave System, South Africa. *Archaeological Prospection* **25**(1):45–158 DOI [10.1002/arp.1580](https://doi.org/10.1002/arp.1580).
- 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](https://doi.org/10.1016/j.jhevol.2010.01.004).
- Berger LR, Hawks J, De Ruiter DJ, Churchill SE, Schmid P, Deleuzene LK, Kivell TL, Garvin HM, Williams SA, Desilva JM, Skinner MM, Musiba CM, Cameron N, Holliday TW, Harcourt-Smith M, Ackermann RR, Bastir M, Bogin B, Bolter D, Brophy , Cofran ZD, Congdon KA, Deane AS, Dembo M, Drapeau M, Elliot MC, Feurriegel EM, Garcia-Martinez D, Green DJ, Gurtov A, Irish JD, Kruger A, Lairs MF, Marchi D, Meyer MR, Nalla S, Negash EW, Orr CM, Radovic D, Schroeder L, Scott JE, Throckmorton Z, Tocheri MW, Vansickle C, Walker CS, Wei P, Zipfel B. 2015.** *Homo naledi* a new species of the genus *Homo* from the Dinaledi Chamber, South Africa. *eLife* **4**:e09560 DOI [10.7554/eLife.09560](https://doi.org/10.7554/eLife.09560).
- Birkenfeld M, Avery MD, Horwitz LK. 2015.** GIS virtual reconstructions of the temporal and spatial relations of fossil deposits at wonderwerk cave (South Africa). *African Archaeological Review* **32**(4):857–876 DOI [10.1007/s10437-015-9209-4](https://doi.org/10.1007/s10437-015-9209-4).
- Brain C. 1981.** *The hunters or the hunted? An introduction to African cave taphonomy*. Chicago: University of Chicago Press.
- Braun DR, Levin NE, Stynder D, Herries AIR, Archer W, Forrest F, Roberts DL, Bishop LC, Matthews T, Lehmann SB, Pickering R, Fitzsimmons KE. 2013.** Mid Pleistocene hominin occupation at Elandsfontein, Western Cape, South Africa. *Quaternary Science Reviews* **82**:145–166 DOI [10.1016/j.quasci.2013.09.027](https://doi.org/10.1016/j.quasci.2013.09.027).
- Broom R. 1936.** A new fossil Anthropoid skull from South Africa. *Nature* **138**:486–488.
- Broom R. 1937.** Notices of a few more new fossil mammals from the caves of the Transvaal. *Annals and Magazine of Natural History* **20**:509–514 DOI [10.1080/00222933708655373](https://doi.org/10.1080/00222933708655373).
- Broom R. 1939.** A preliminary account of the Pleistocene carnivores of the Transvaal caves. *Annals of the Transvaal Museum* **19**:331–338.
- Broom R. 1948.** Some south African Pliocene and Pleistocene mammals. *Annals of the Transvaal Museum* **21**:1–38.
- Camp CL. 1948.** University of California African expedition—southern section. *Science* **108**:550–552 DOI [10.1126/science.108.2812.550](https://doi.org/10.1126/science.108.2812.550).
- Conroy G, Anemone R, Van Regenmorter J, Addison A. 2008.** Google earth, GIS, and the great divide: a new and simple method for sharing palaeontological data. *Journal of Human Evolution* **55**:751–755 DOI [10.1016/j.jhevol.2008.03.001](https://doi.org/10.1016/j.jhevol.2008.03.001).
- Cooke HBS. 1963.** Pleistocene mammal faunas of Africa, with particular reference to southern Africa. In: Howell FC, Bourlière F, eds. *African ecology and human evolution*. Chicago: Aldine press, 65–116.
- Cooke HBS. 1985.** *Ictonyx bolti*, a new mustelid from cave breccias at bolt's farm, Sterkfontein area. *South African Journal of Science* **81**:618–619.

- Cooke HBS. 1991.** *Dinofelis barlowi* (Mammalia, Carnivora, Felidae) cranial material from Bolt's Farm, collected by the University of California African expedition. *Palaeontologica Africana* **28**:9–21.
- Cooke HBS. 1993.** Undescribed suid remains from Bolt's Farm and other Transvaal cave deposits. *Palaeontologica Africana* **30**:7–23.
- Dart RA. 1925.** *Australopithecus africanus*: the Man-Ape of South Africa. *Nature* **115**:195–199 DOI [10.1038/115195a0](https://doi.org/10.1038/115195a0).
- Dell'Unto N, Landeschi G, Apel J, Poggi G. 2017.** 4D recording at the trowel's edge: using three-dimensional simulation platforms to support field interpretation. *Journal of Archaeological Science: Reports* **12**:632–645 DOI [10.1016/j.jasrep.2017.03.011](https://doi.org/10.1016/j.jasrep.2017.03.011).
- Delson E. 1984.** Cercopithecoid biochronology of the African Plio-Pleistocene: correlation among eastern and southern hominid-bearing localities. *Courier Forschungsinstitut Senckenberg* **69**:199–218.
- Del la Torre I, Arroyo A, Proffitt T, Martín Ramos C, Theodoropoulou A. 2015.** Archaeological fieldwork techniques in stone age sites. *Treballs d'arqueologia* **20**:0021–0040 DOI [10.5565/rev/tda.51](https://doi.org/10.5565/rev/tda.51).
- Dirks PHGM, Berger LR, Roberts EM, Kramers JD, Hawks J, Randolph-Quinney PS, Elliott M, Musiba CM, Churchoff SE, De Ruiter DJ, Schmid P, Backwell LR, Belyanin GA, Boshoff P, Hunter KL, Feurriegel EM, Gurtov A, Harrison JDG, Hunter R, Kruger A, Morris H, Makhubela TV, Peixotto B, Tucker S. 2015.** Geological and taphonomic context for the new hominin species *Homo naledi* from the Dinaledi chamber, South Africa. *eLife* **4**:e09561 DOI [10.7554/eLife.09561](https://doi.org/10.7554/eLife.09561).
- Fernández-Lozano J, Gutiérrez-Alonso G. 2016.** Improving archaeological prospection using localized UAVs assisted photogrammetry: an example from the Roman Gold District of the Eria River Valley (NW Spain). *Journal of Archaeological Science: Reports* **5**:509–520 DOI [10.1016/j.jasrep.2016.01.007](https://doi.org/10.1016/j.jasrep.2016.01.007).
- Geraads D, Raynal J, Eisenmann V. 2004.** The earliest human occupation of North Africa: a reply to Sahnouni, et al. (2002). *Journal of Human Evolution* **46**:751–761 DOI [10.1016/j.jhevol.2004.01.008](https://doi.org/10.1016/j.jhevol.2004.01.008).
- Gibbons A. 1991.** A new look for archaeology. *Science* **252**:918–920 DOI [10.1126/science.252.5008.918](https://doi.org/10.1126/science.252.5008.918).
- Gommery D, Badenhorst S, Potze S, Senegas F, Kgasi L, Thackeray JF. 2012.** Preliminary results concerning the discovery of new fossiliferous sites at Bolt's Farm (Cradle of Humankind, South Africa). *Annals of the Ditsong National Museum of Natural History* **2**:33–45.
- Gommery D, SÉNÉGAS F, Kgazsi L, Vilakazi N, Kuhn B, Pickford M, Herries AIR, Hancox J, Saos T, Segalen L, Aufort J, Thackeray JF. 2016.** Bolt's Farm cave system dans le cradle of humankind (Afrique du Sud): un exemple d'approche multidisciplinaire dans l'étude des sites à primates fossiles. *Revue de primatologie* Epub ahead of print Jan 31 2017.
- Gommery D, SÉNÉGAS F, Potze S, Kgasi L, Thackeray JF. 2014.** Cercopithecoidea material from the Middle Pliocene Site, Waypoint 160, Bolt's Farm, South Africa. *Annals of the Ditsong Museum of Natural History* **4**:1–8.

- Gommery D, Sénégas F, Thackeray JF. 2008b.** Plio-Pleistocene fossils from femur dump, Bolt's farm, cradle of humankind world heritage site. *Annals of the Transvaal Museum* **45**:67–76.
- Gommery D, Thackeray JF, Sénégas F, Potze S, Kgasi L. 2008a.** The earliest primate (Parapapio sp.) From the Cradle of Humankind World Heritage Site (Waypoint 160, Bolt's Farm, South Africa). *South African Journal of Science* **104**:405–408.
- Herries AIR, Curnoe D, Adams JW. 2009.** A multi-disciplinary seriation of early Homo and Paranthropus bearing palaeocaves in southern Africa. *Quaternary International* **202**(1–2):14–28 DOI [10.1016/j.quaint.2008.05.017](https://doi.org/10.1016/j.quaint.2008.05.017).
- Herries AIR, Murszewski A, Pickering R, Mallett T, Johannes-Boyau R, Armstrong B, Adams JW, Baker S, Blackwood AF, Penzo-Kajewski P, Kappen P, Leece AB, Martin J, Rovinsky D, Boschiani G. 2018.** Geoarchaeological and 3D visualisation approaches for contextualising in-situ fossil bearing palaeokarst in South Africa: a case study from the ~2.61 Ma Drimolen Makondo. *Quaternary International* **483**:90–110 DOI [10.1016/j.quaint.2018.01.001](https://doi.org/10.1016/j.quaint.2018.01.001).
- Herries AIR, Pickering R, Adams JW, Curnow D, Warr G, Latham AG, Shaw J. 2013.** A multi-disciplinary perspective on the age of Australopithecus in Southern Africa. In: Reed K, Fleagle J, Leakey R, eds. *The paleobiology of Australopithecus. Vertebrate paleobiology and paleoanthropology*. Dordrecht: Springer DOI [10.1007/978-94-007-5919-0\\_3](https://doi.org/10.1007/978-94-007-5919-0_3).
- Holmes K. 2007.** *GIS simulation of the earliest hominid colonisation of Eurasia*. Oxford: Archaeo press, 154.
- Jarvis A, Reuter HI, Nelson A, Guevera E. 2008.** Hole-filled SRTM for the globe. Version 4. Available at <http://srtm.csi.cgiar.org>.
- Jorayev G, Wehr K, Benito-Calvo A, Njau J, De la Torre I. 2016.** Imaging and photogrammetry models of Olduvai Gorge (Tanzania) by unmanned aerial vehicles: a high-resolution digital database for research and conservation of early stone age sites. *Journal of Archaeological Science* **75**:40–56 DOI [10.1016/j.jas.2016.08.002](https://doi.org/10.1016/j.jas.2016.08.002).
- Klein RG, Avery G, Cruz-Uribe K, Steele TE. 2007.** The mammalian fauna associated with an archaic hominin skullcap and later Acheulean artifacts at Elandsfontein, Western Cape Province, South Africa. *Journal of Human Evolution* **52**:164–186 DOI [10.1016/j.jhevol.2006.08.006](https://doi.org/10.1016/j.jhevol.2006.08.006).
- Linnaeus C. 1758.** *Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis*. In: *Editio decima, reformata*. Holmiae, Stockholm: Laurentii Salvii.
- Lock G, Stancic Z (eds.) 1995.** *GIS in archaeology: a European perspective*. London: Taylor & Francis.
- Mokokwe WD. 2007.** Goldsmiths: preliminary study of a newly discovered Pleistocene site near Sterkfontein. Unpublished MSc Thesis, University of the Witwatersrand, Johannesburg.
- Monson TA, Brasil MF, Hlusko LJ. 2015.** Materials collected by the southern branch of the UC Africa Expedition with a report on previously unpublished Plio-Pleistocene fossil localities. *Paleobios* **32**:1–17.

- Nigro JD, Ungar PS, De Ruiter DJ, Berger LR. 2003.** Developing a geographic information system (GIS) for mapping and analysing fossil deposits at Swartkrans, Gauteng Province, South Africa. *Journal of Archaeological Science* **30**:317–324 DOI [10.1006/jasc.2002.0839](https://doi.org/10.1006/jasc.2002.0839).
- Oheim KB. 2007.** Fossil site prediction using geographic information systems (GIS) and suitability analysis: the two medicine formation, a test case. *Palaeogeography, Palaeoclimatology, Palaeoecology* **251**(3–4):354–365 DOI [10.1016/j.palaeo.2007.04.005](https://doi.org/10.1016/j.palaeo.2007.04.005).
- Partridge TC. 1973.** Geomorphological dating of cave openings at Makapansgat, Sterkfontein, Swartkrans and Taung. *Nature* **246**:75–79 DOI [10.1038/246075a0](https://doi.org/10.1038/246075a0).
- Peabody FE. 1954.** Travertines and cave deposits of the Kaap escarpment of South Africa, and the type locality of *Australopithecus africanus* Dart. *Geological Society of America Bulletin* **65**:671–706 DOI [10.1130/0016-7606\(1954\)65\[671:TACDOT\]2.0.CO;2](https://doi.org/10.1130/0016-7606(1954)65[671:TACDOT]2.0.CO;2).
- Pickering TR. 1999.** Taphonomic interpretations of the sterckfontein early hominid site (Gauteng, South Africa) reconsidered in light of recent evidence. Unpublished PhD Thesis, University of Wisconsin, Madison.
- Pickering TR, Dominguez-Rodreigo M, Egeland CP, Brain CK. 2004.** Beyond leopards: tooth marks and the contribution of multiple carnivore taxa to the accumulation of the Swartkrans Member 3 fossil assemblage. *Journal of Human Evolution* **46**(5):595–604 DOI [10.1016/j.jhevol.2004.03.002](https://doi.org/10.1016/j.jhevol.2004.03.002).
- Pickering R, Herries AIR, Woodhead JD, Hellstrom JC, Green HE, Paul B, Ritzman T, Strait D, Schoville BJ, Hancox H. 2018.** U-Pb dated flowstones restrict South African early hominin record to dry climate phases. *Nature* Epub ahead of print Nov 21 2018 DOI [10.1038/s41586-018-0711-0](https://doi.org/10.1038/s41586-018-0711-0).
- Pickford M, Gommery D. 2016.** Fossil suidae (Artiodactyla, Mammalia) from Aves Cave and nearby sites in Bolt's Farm palaeokarst system, South Africa. *Estudios Geológicos* **72**:e059 DOI [10.3989/egeol.42389.404](https://doi.org/10.3989/egeol.42389.404).
- Reynolds SC. 2007.** Temporal variation in Plop-Pleistocene *Antidorcas* (Mammalia, Bovidae) horncores: the case from Bolt's farm and why size matters. *South African Journal of Science* **103**:47–50.
- Roberts DL, Matthews T, Herries AIR, Boulter C, Scott L, Dondo C, Mtembi P, Browning C, Smith RMH, Haarhoff P, Bateman MD. 2011.** Regional and global context of Late Cenozoic Langebaanweg (LBW) palaeontological site: West Coast of South Africa. *Earth Science Reviews* **106**(3–4):191–214 DOI [10.1016/j.earscirev.2011.02.002](https://doi.org/10.1016/j.earscirev.2011.02.002).
- Sénégas F. 2000.** Les faunes de rongeurs (Mammalia) Plio-Pléistocènes de la province de Gauteng(Afrique du Sud): mises au point et apports systématiques, biochronologiques et précisions paléoenvironnementales. Non publiée thèse doctorat, Universitémontpellier ii et ephe, Montpellier.
- Sénégas F, Avery DM. 1998.** New evidence for the murine origins of the otomyinae (Mammalia, Rodentia) and the age of Bolt's Farm (South Africa). *South African Journal of Science* **94**:503–507.
- Sénégas F, Thackeray JF, Gommery D, Braga J. 2002.** Scientific notes palaeontological sites on 'Bolt's Farm', Sterkfontein valley, South Africa. *Annals of the Transvaal Museum* **39**:65–67 DOI [10.4000/primatologie.2715](https://doi.org/10.4000/primatologie.2715).

- Thackeray JF, Gommery D, Sénégas F, Potze S, Kgasi L, Mcgrae C, Prat S. 2008.** A survey of past and present work on Plio-Pleistocene deposits on Bolt's Farm, Cradle of Humankind, South Africa. *Annals of the Transvaal Museum* **45**:83–89.
- Trueman CNG, Field JH, Dortch J, Charles B, Wroe S. 2005.** Prolonged coexistence of humans and megafauna in Pleistocene Australia. *Proceedings of the National Academy of Sciences of the United States of America* **102**:8381–8385  
[DOI 10.1073/pnas.0408975102](https://doi.org/10.1073/pnas.0408975102).
- Val A, Stratford DJ. 2015.** The macrovertebrate fossil assemblage from the Name Chamber, Sterkfontein: taxonomy, taphonomy and implications for site formation processes. *Palaeontologica Africana* **50**:1–17.
- Werdelin L, Peigne S. 2010.** Carnivora. In: Werdelin L, Sanders W, eds. *Cenozoic mammals of Africa*. Berkeley: University of California Press, 603–658.
- Zipfel B, Berger LR. 2009.** New Cenozoic fossil-bearing site abbreviations for collections of the University of the Witwatersrand. *Palaeontologia Africana* **44**:77–81.