# Sterkfontein at 75: review of palaeoenvironments, fauna and archaeology from the hominin site of Sterkfontein (Gauteng Province, South Africa)

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Seventy-five years after Robert Broom's discovery of the first adult *Australopithecus* in 1936, the Sterkfontein Caves (Gauteng Province, South Africa) remains one of the richest and most informative fossil hominin sites in the world. The deposits record hominin and African mammal evolution from roughly 2.6 million years (Ma) until the Upper Pleistocene. Earlier excavation efforts focused on the Member 4 australopithecine-bearing breccia and the Member 5 stone tool-bearing breccias of Oldowan and Early Acheulean age. Ronald J. Clarke's 1997 programme of understanding the cave deposits as a whole led to the discovery of the near-complete StW 573 *Australopithecus* skeleton in the Member 2 deposit of the Silberberg Grotto, and the exploration of lesser known deposits such as the Jacovec Cavern, Name Chamber and the Lincoln Cave. Our aim is to produce a cogent synthesis of the environments, palaeodietary information, fauna and stone artefacts as recorded in the Sterkfontein sequence. We begin with an overview of the site and early accounts of the interpretations of the site-formation processes, after which we discuss each Member in turn and summarize the various types of evidence published so far. Finally, we review the most pertinent debates about the site, including the ages of Sterkfontein Member 2 and 4, and the types of habitats represented at the site through time.

**Keywords**: Sterkfontein, *Australopithecus, Paranthropus, Homo,* mammals, hominins, stable isotopes, climatic change, cave formation.

## INTRODUCTION

The Sterkfontein site lies in the Cradle of Humankind World Heritage Site (Gauteng Province, South Africa). Formed within the pre-Cambrian Malmani dolomite, the caves contain sedimentary infills that record palaeoenvironmental information relating to hominin evolution from roughly 2.6 million years until the Upper Pleistocene. Sterkfontein remains one of the most important fossil hominin and Earlier Stone Age (ESA) sites within Africa, and the world (Fig. 1). While numerous other rich fossil sites are known from this region, such as Swartkrans, Kromdraai, Drimolen and the new fossil locality Malapa (Berger *et al.* 2010), Sterkfontein inarguably contains the richest deposits of vertebrate remains spanning the Plio-Pleistocene. This site (26°00′56.44′S, 27°44′03.48′E) lies on a hill overlooking the Blaaubank (also spelled 'Bloubank') River.

### Dating and climatic context for Sterkfontein Members

Climate change studies on both larger and regional scales (deMenocal 1995, 2004; Hopley *et al.* 2007) provide a vital framework for how faunal changes can be interpreted, both in terms of individual species' morphology, but also large-scale changes in faunal communities (e.g. Vrba 1974, 1975). The earlier deposits at Sterkfontein appear to sample warmer climates, while later deposits reflect the cooling drying trends associated with the Pleistocene. This fits well with broader reconstructions of climate change in Africa (e.g. deMenocal 2004: 3), which suggest step-wise drying trends resulting in 'more varied and open habitats at 2.9–2.4 Ma and after 1.8 Ma' in east-ern Africa. In southern Africa, aridification in Namibia suggests that this region became drier after about 2.1 Ma (Weigelt *et al.* 2008).

However, there is a lack of clear agreement between large and regional scale signals (e.g. Hopley *et al.* 2007), and this is complicated by the cyclical nature of climate shifts and the deposition times of karst deposits (Hopley & Maslin 2010).

The year 2011 marks the 75th anniversary of Robert Broom's discovery of the first adult *Australopithecus africanus* Dart 1925 (Broom 1936). Initial excavation efforts, under the auspices of the Transvaal Museum by Robert Broom and John T. Robinson focused on the Member 4 australopithecine-bearing deposits. Later work by Robinson focused on the so-called Extension Site of Member 5 stone tool-bearing breccias (Robinson 1962; Kuman & Clarke 2000).

When Phillip V. Tobas and Alun R. Hughes began their excavation programme under the auspices of the University of the Witwatersrand in 1966, one of their aims was to establish the relationship between Member 4 and the Member 5 deposits (Clarke, in press). The ongoing research by Ronald Clarke and Kathleen Kuman concentrated on understanding the cave deposits as a whole. Specifically, the excavation and analyses of the infills of Member 5 has shown that three separate infills are present, differentiated by presence or absence of Earlier Stone Age artefacts (Kuman 1994a,b; Clarke 1994; Kuman & Clarke 2000).

The discovery of the near-complete StW 573 *Australopithecus* skeleton by Clarke in 1997 in the Member 2 deposit of the Silberberg Grotto has led to numerous studies on this deposit (Clarke 1998, 1999, 2002a,b; Berger

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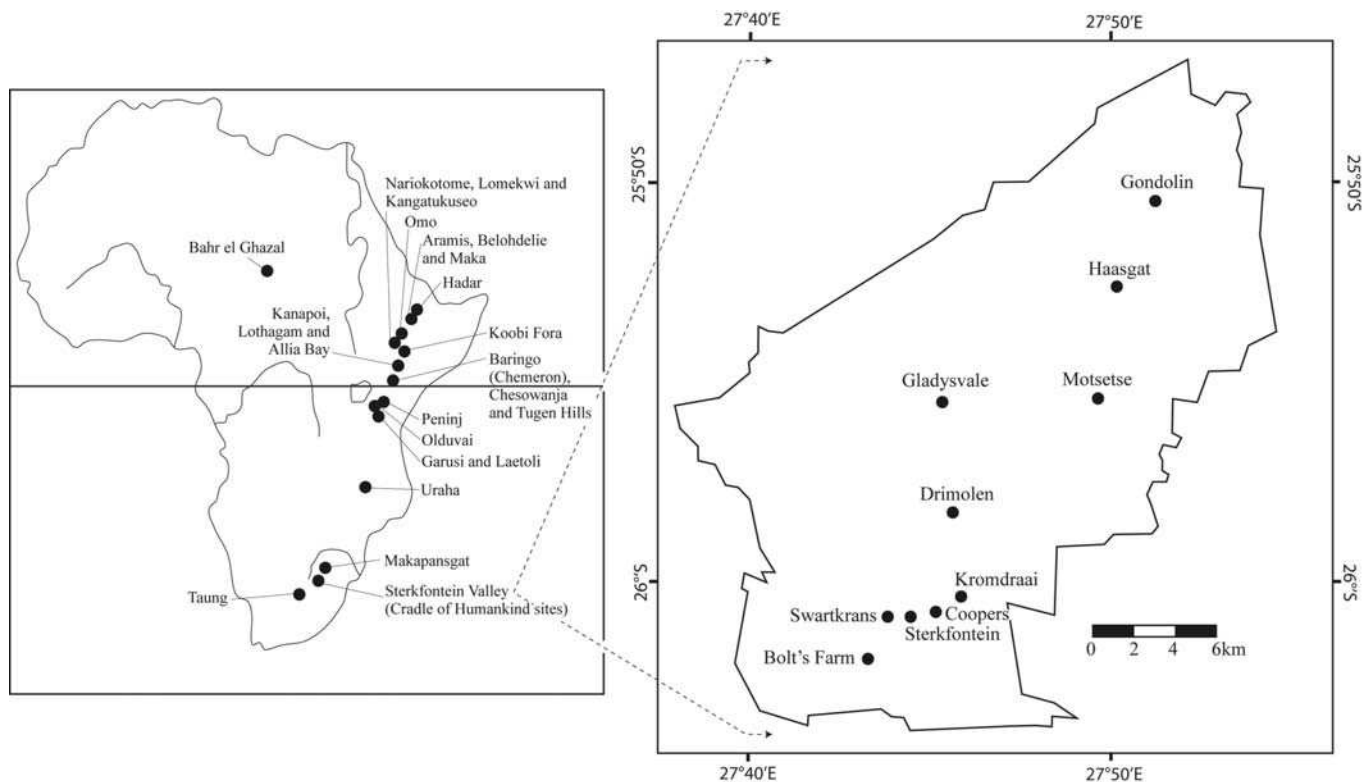 E-mail: reynolds@ipgp.fr

**Figure 1**. Major African hominin sites shown on the left (after Tobias 2000), compared with the sites of the Cradle of Humankind on the right.

*et al.* 2002; Partridge *et al.* 2003; Pickering *et al.* 2004a; Pickering & Kramers 2010; Herries & Shaw 2011). Several other deposits have also recently been systematically excavated and analysed, specifically the Jacovec Cavern (also spelled 'Jakovec'; Wilkinson 1973, 1983, 1985; Partridge *et al.* 2003; Kibii 2000, 2004, 2007), the Name Chamber (Partridge & Watt 1991; Clarke 2006; Stratford 2008; Avery *et al.* 2010) and the Lincoln Cave deposits (Boshoff *et al.* 1990; Reynolds *et al.* 2003, 2007). These deposits and their approximate spatial relation to each other are indicated in Fig. 2.

These studies of the Sterkfontein fauna and palaeo-environments offer unparalleled insights into various aspects of southern African hominin morphology and habitats through time. Over 600 hominin specimens, possibly representing as many as five species, seven primates species, 52 species of macromammals, 28 micromammal species, several reptile and bird species and at least two plant species have been identified in the Sterkfontein deposits and other cave deposits within the same site region, such as the Lincoln Cave (Pickering 1999; Bamford 1999; Kuman & Clarke 2000; Avery 2001; Kibii 2004; Reynolds *et al.* 2003, 2007; Avery *et al.* 2010).

Our aim is to present and review the faunal, taphonomic and archaeological evidence from the Sterkfontein site, as pertains to hominin habitats and environments over the time periods represented. The hominin material itself has been described in detail in an extensive number of studies, (e.g. Broom 1936; Broom *et al.* 1950; Hughes & Tobias 1977; Kimbel & White 1988; Spoor *et al.* 1994; Tobias & Clarke 1996; Berger & Tobias 1996; Thackeray 1997; Spoor 1997; Lockwood 1997; Ripamonti *et al.* 1997; Schwartz *et al.* 1998; Berge & Gommery 1999; Lockwood & Tobias 1999; Tobias 2000, 2002; Häusler &

Berger 2001; de Ruiter 2004; Dobson 2005; Prat 2005; Moggi-Cecchi *et al.* 2006; Curnoe & Tobias 2006; Clarke 2008; Curnoe 2010, Fornai 2010; Kibii *et al.* 2011 and many others). However, much more material awaits cleaning and reconstruction before it can be described (Clarke, pers. comm.).

We begin with a brief overview of the climate records of the African Pliocene and Pleistocene, before outlining the site stratigraphy and early accounts of the interpretations of the site-formation processes, after which we discuss each Member in turn and summarize the various types of evidence published so far.

One of the reasons why Sterkfontein is such an important site is that it samples the Pliocene to Pleistocene transition, at 2.58 Ma (Cohen & Gibbard 2011). Climatically, this transition is characterized by a series of transitions towards cooler, drier, more seasonal conditions (deMenocal 2004; Weigelt *et al.* 2008), with corresponding effects on faunal communities and morphologies (Vrba 1974; 1975; Reynolds 2007, 2010). One of the most important changes is the increase in the proportions of $C_4$ grasses within the vegetation present at the hominin sites. Carbon isotope data from flowstones from the Makapansgat Valley (Limpopo Province, South Africa) caves indicate that there was an increase in the proportion of $C_4$ grasses from the period represented by Member 1 speleothem deposits of the Collapsed Cone (4–5 Ma) to the later Buffalo Cave, for which the basal flowstone has been dated to 1.95 and 0.78 Ma, with the fossils being in the 1.07 to 0.78 Ma time range (Hopley *et al.* 2007).

Specifically the data indicate an expansion of the $C_4$ (grass) plants at approximately 1.7 Ma, which Hopley *et al.* (2007) have related to the onset of the Walker Circulation. Additionally, Weigelt and colleagues (2008) have identi-
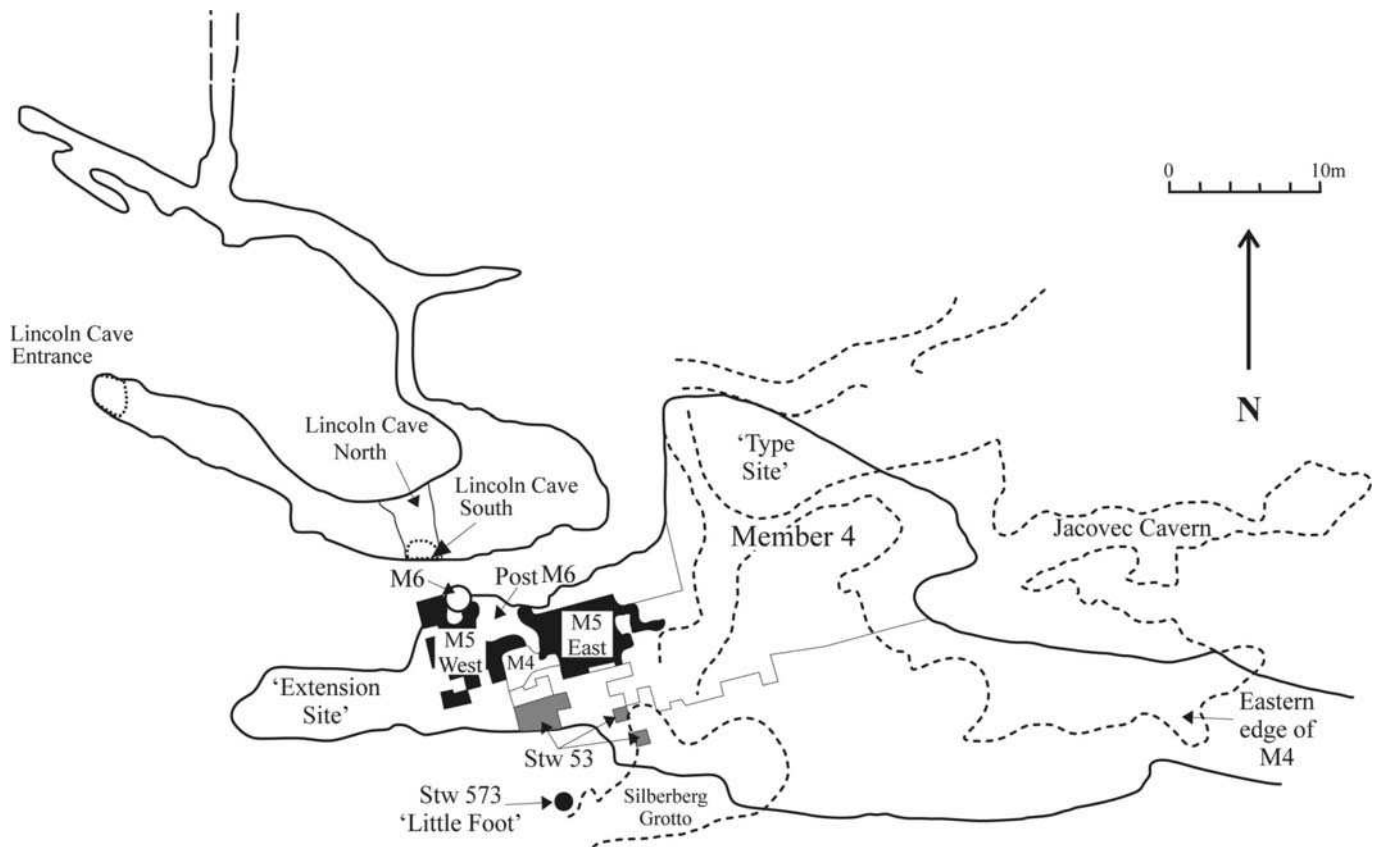
**Figure 2**. Composite plan view of Sterkfontein deposits, showing the exposed deposits of the Sterkfontein excavation (Member 4, and Member 5), the underground deposits (Silberg Grotto and Jacovec Cavern) and the approximate spatial relationship of the Lincoln Cave to the main Sterkfontein Cave system. Based on Kuman & Clarke (2000), Partridge *et al.* (2003) and Reynolds *et al.* (2007). Please note: the two cave systems are not shown to exactly the same scales. The Name Chamber lies directly under Member 5 (Clarke 1994).

fied increasing aridity in southern Africa after 2.1 Ma, which would also have favoured the development of grasslands. The climate data from the Makapansgat Valley (Fig. 1) suggests that the region including Sterkfontein would have experienced similar aridification and increase in $C_4$ grasses over the period represented. While the Collapsed Cone predates the earliest Sterkfontein deposits, it appears likely that similar climatic trends would have been experienced by the *Australopithecus* in Member 2 through to the younger Member 4 deposits and finally to the *Paranthropus* and early *Homo*-bearing Member 5 infills (Kuman & Clarke 2000; Hopley *et al.* 2007).

**Overview of the excavation of the Sterkfontein deposits**

Early work on Sterkfontein sediments considered that the deposits followed a layer-cake model of deposition (Partridge's 1978 classification of Members 1–6), with the older deposits likely to be at lower levels and younger sediments at higher levels (e.g. Robinson 1952, 1962). Later excavations and analyses of Member 5 breccia have demonstrated that several different infills can exist within a single Member (Kuman & Clarke 2000) and that reworking of older artefacts and fauna into younger deposits occurs as a common process within karstic caves (e.g. for the Lincoln Cave, see Reynolds *et al.* 2007). Therefore, the site formation processes and contents of the deposits must be interpreted together as part of a larger picture of site formation (considering also cycles of collapse, erosion and reworking). The absolute dates of the deposits

may differ according to which method is employed (e.g. Herries & Shaw 2011), making this interpretive framework critical in assessing the validity of dating results.

**Exposed deposits**

The Sterkfontein deposits were first characterized as a single conformable breccia (e.g. Brain 1958); then later as several distinct breccia bodies, specifically the 'Type Site' where the first specimens of *Australopithecus africanus* were found, and the 'Extension Site' where Robinson discovered stone tools during excavations conducted between 1957 and 1958 (Robinson & Mason 1957; Robinson 1962; Mason 1962a,b).

Robinson identified at least three disparate deposits: the pink 'Lower Breccia', which yielded the *Australopithecus* fossils and which lies within the Type Site; the red-brown 'Middle Breccia', in which the stone tools were found and which lies in the Extension Site (Fig. 2), and the youngest of the three breccias, which he termed the 'Upper Breccia': a dark brown breccia, known only from a small part of the Extension Site (Robinson 1962).

Still later, Partridge (1978, also 2000) identified six major units, and this scheme was later refined by borehole studies (Fig. 3; Partridge & Watt 1991). This study associated the deposits exposed at the surface with the underground deposits of the Silberg Grotto, and defined the spatial relationship between these deposits and the other fossiliferous deposits in Jacovec Cavern and Name
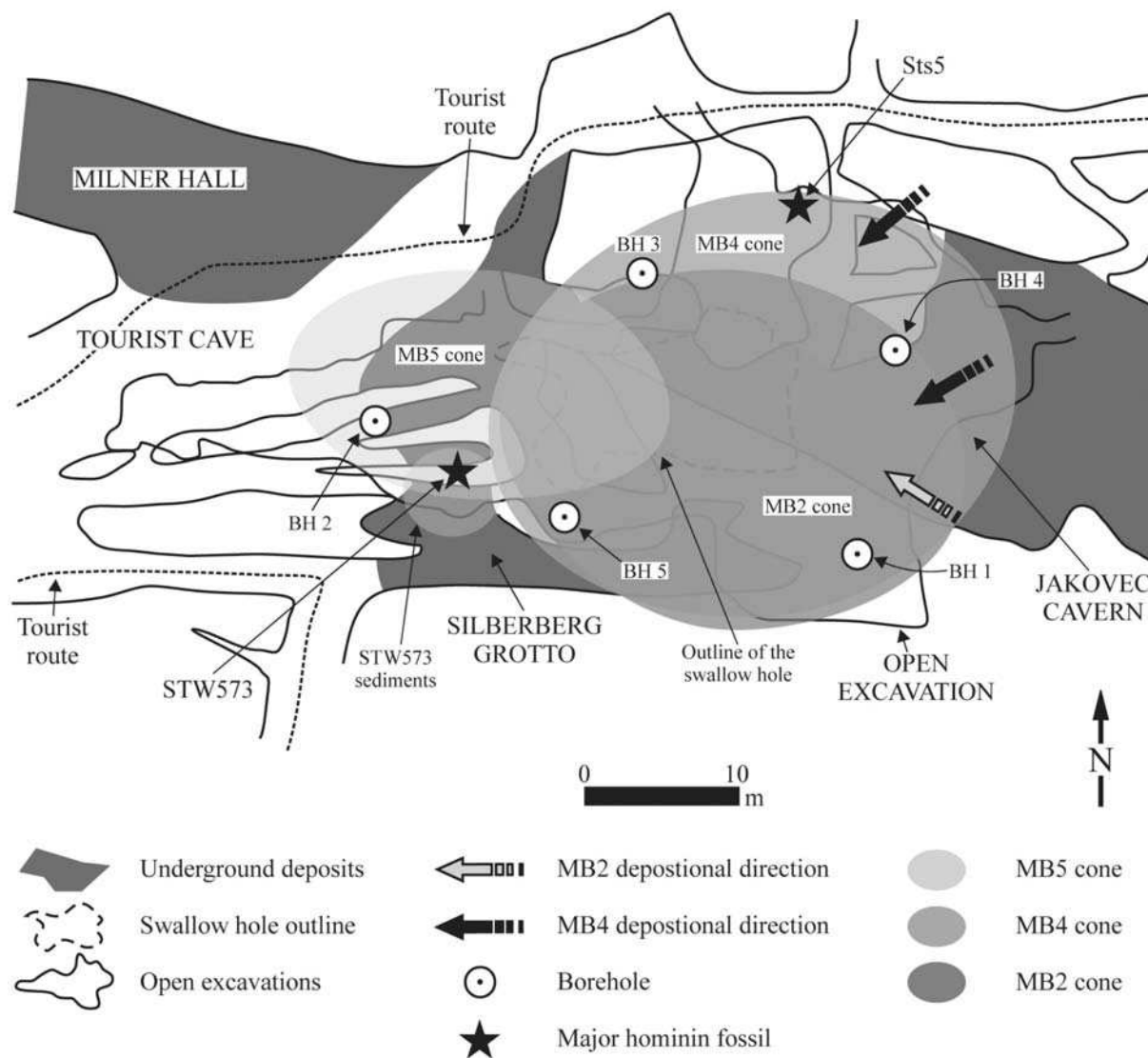
**Figure 3**. Recent re-examination of Sterkfontein boreholes by Pickering & Kramers (2010), based on original boreholes (labeled as BH) drilled by Partridge & Watt (1991). The conclusion of the Pickering & Kramers (2010) study was that Member 3 (exposed in the Silberberg Grotto) is likely to be part of Member 4 sediment cone. The darker arrows indicate possible entrances for the sediments during Member 4 accumulation, and the lighter grey arrow indicates the possible location of the Member 2 material (redrawn after Pickering & Kramers 2010).

Chamber. The stratigraphy was viewed as a relatively simple 'layer cake' formation, with the oldest Member 1 at the bottom of the sequence and the younger deposits exposed at the surface.

Recent studies have re-evaluated this layer-cake model, and emphasize the complexity of karst infills (e.g. Pickering *et al.* 2010). This complexity is well-illustrated by the example of Member 5, which is discussed below. A more appropriate model of successive layers of talus cone infills (Fig. 3), or even the infilling of disconnected, but contemporaneous caverns has been proposed (e.g. Partridge 2000; Herries *et al.* 2009; Pickering & Kramers 2010). The historical perspective of the changes in the understanding of the stratigraphy of Sterkfontein is reviewed by Clarke (2006).

In early studies, Member 5 appeared to be a geologically uniform deposit (Partridge 1978; Partridge & Watt 1991), but three separate infills have been identified on the basis of fauna and artefacts, namely the StW 53; the Member 5 East and Member 5 West infills (also referred to as the M5A–C by Partridge; Table 1; Kuman & Clarke 2000,

Fig. 2). StW 53 is a small Member without stone tools where the StW 53 cranium was discovered (Hughes & Tobias 1977) and that is separated from the stone-tool-bearing Member 5 East and Member 5 West deposits by a thick flowstone (Clarke, pers. comm.). The Member 5 East deposit contains one of the earliest stone tool industries in South Africa, assigned to the Oldowan Industry while the Member 5 West infill contains tools of the Early Acheulean industry (Kuman & Clarke 2000) (Table 1).

The total number of Members has now been increased to seven, with the recent identification of the Sterkfontein 'Post Member 6 infill', which Kuman and Clarke (2000) suggest dates to approximately the mid- to late Pleistocene. The deposits exposed at the surface comprise the Member 4 breccia, all three Member 5 infills and Member 6 (an unexcavated small hanging remnant) (Fig. 2). The youngest deposits are the Post-Member 6 solution pocket into Member 5 West (known as the 'L/63' infill), part of which appears to be connected to the adjoining Lincoln-Fault cave system. Within this cave system, the Lincoln Cave North and South deposits have been dated to the

**Table 1**. Excavated Sterkfontein deposits.

| Deposit | Published dates for deposits | Species | Number of artefacts and industries |
|---|---|---|---|
| Jacovec Cavern | **4.0 Ma,** Cosmogenic nuclides (Partridge *et al.* 2003) <br> **>2.36,** fauna, in particular, *Equus* sp. (Kibii 2004) | *Australopithecus africanus* | 0 |
| Member 2 | **4.0 Ma,** Cosmogenic nuclides (Partridge *et al.* 2003) <br> **3.30–3.33 Ma,** Palaeomagnetism (Partridge *et al.* 1999) <br> **2.2 Ma,** Uranium-Lead isotopes (Walker *et al.* 2006) <br> **2.6–2.8 Ma,** Uranium-lead and Uranium-Thorium isotopes (Pickering & Kramers 2010) <br> **2.6–1.8 Ma** ESR, isotopes and palaeomagnetism (Herries & Shaw 2011) | *Australopithecus* sp. | 0 |
| Member 4 | **2.8–2.4 Ma,** Bovid biochronology (Vrba 1976, 1980) <br> **~ 2.5 Ma,** Primate biochronology (Delson 1984, 1988). <br> **2.8–2.6 Ma,** Faunal seriation (McKee 1993) <br> **~ 2.1 Ma,** Electron Spin Resonance (Schwarcz *et al.* 1994) <br> **2.15–2.14 Ma** Palaeomagnetism (Partridge 2005). <br> **2.65–2.01,** Uranium-lead and Uranium-Thorium isotopes (Pickering & Kramers 2010) <br> **2.8 ~2.0 Ma,** ESR, isotopes and palaeomagnetism (Herries & Shaw 2011) | *Australopithecus africanus* and a possible 'Second species' (discussed in e.g. Clarke 1988) | 0 |
| Member 5: *StW 53 Infill* | **2.6–2.0 Ma,** Fauna (Kuman & Clarke 2000) <br> **1.8–1.4 Ma** dating seriation (Herries *et al.* 2009). <br> **1.8–1.5 Ma** ESR, isotopes and palaeomagnetism (Herries & Shaw 2011) | *Homo habilis* /or Late *Australopithecus?* | 0 |
| Member 5: East Infill | **2.0–1.7 Ma**; Biochronology and archaeology (Kuman and Clarke 2000). <br> **1.4–1.1 Ma** dating seriation (Herries *et al.* 2009). <br> **1.4–1.2 Ma** ESR, isotopes and palaeomagnetism (Herries & Shaw 2011) | *Paranthropus robustus* | 3245 <br> Oldowan Industry |
| Member 5: West Infill | **1.7–1.4 Ma,** Biochronology and archaeology (Kuman & Clarke 2000). <br> **1.3–0.8 Ma** dating seriation (Herries *et al.* 2009). <br> **1.3–1.1** (Herries & Shaw 2011) | *Homo ergaster* | 701 <br> Early Acheulean industry |
| Post Member 6: L/63 Infill | **Mid- late Pleistocene** age, faunal correlations and archaeology; (Reynolds *et al.* 2007) <br> **0.5–0.3 Ma** (Herries & Shaw 2011) | *Homo* sp. | 50 <br> Middle Stone Age, debitage |
| Lincoln Cave North | **0.253–0.115 Ma** Uranium series (Reynolds *et al.* 2003, 2007) | 0 | 5 <br> Early Acheulean |
| Lincoln Cave South | **Mid- late Pleistocene** age, archaeology, **(**Reynolds *et al.* 2007) | *cf. Homo ergaster* | 69 <br> Middle Stone Age, and Early Acheulean mix |

mid- to late Pleistocene, a time period that was, until recently poorly represented at Sterkfontein (Boshoff *et al.* 1990; Reynolds *et al.* 2003, 2007). These two deposits are roughly equivalent to Post-Member 6 in the main excavation, and extend the hominin and human occupation of the site until less than 115 ka years ago (Reynolds *et al.* 2003, 2007). The Lincoln Cave deposits appear to be connected to the main excavation via the solution cavity in the L/63 area (Fig. 2).

**Lower Cave deposits**

The balance of the Sterkfontein Members lies within the extensive underground network of the Sterkfontein Cave System (Wilkinson 1973, 1983, 1985; Kuman & Clarke 2000; Clarke 2006). The underground deposits are: Member 1 (largely sterile), the Member 2 StW 573 'Little Foot' deposit, and the fossiliferous Member 3 (unexcavated), all exposed within the Silberberg Grotto. A recent

re-examination of the stratigraphy and sedimentology of Sterkfontein has indicated that Member 3 should be reassigned to Member 4 (Fig. 3; Pickering & Kramers 2010).

Other underground deposits include the Jacovec Cavern and the Name Chamber. The former appears to be unconnected to the Sterkfontein Formation but contains *Australopithecus* sp. fossils and is inferred to be contemporaneous with Member 2, based on similar dating cosmogenic nuclide results (Partridge *et al.* 2003; Table 1; Fig. 4).

The Name Chamber contains a very large collapsed talus cone and lies directly beneath Member 5 (Clarke 1994). The Name Chamber contains two talus deposits, known as the Eastern and Western Talus cones (Avery *et al.* 2010). This material derived from a shaft in the vicinity of grid square R57 of the main excavation at the surface, and shows several episodes of collapse from the
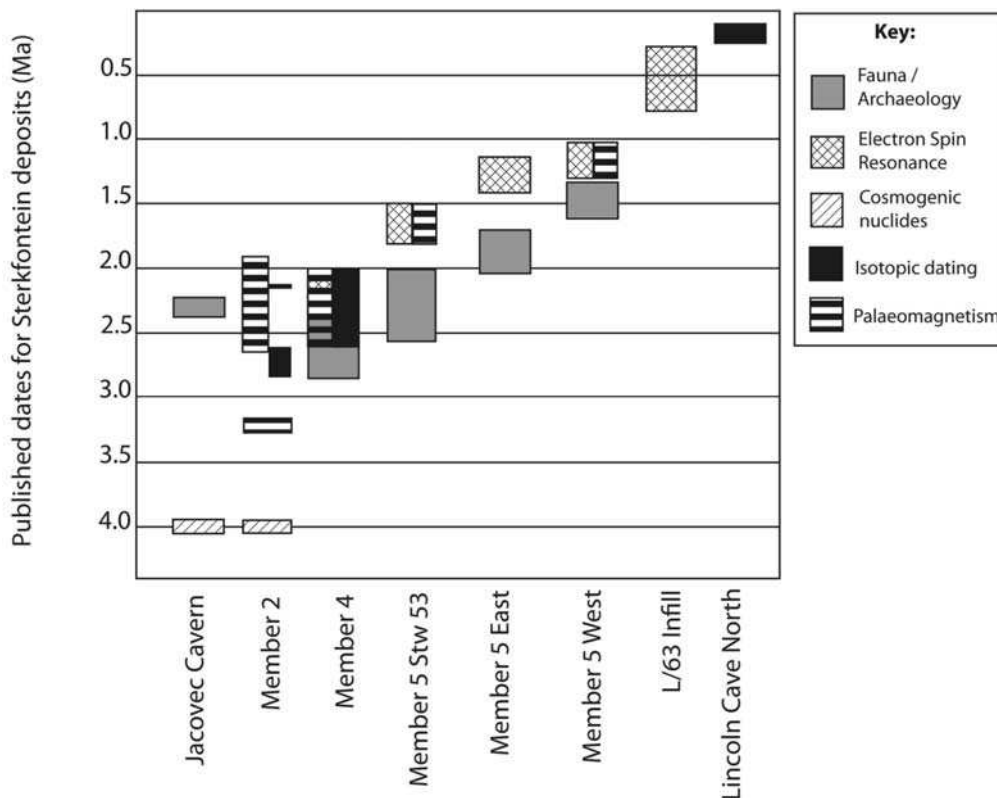
**Figure 4**. Dates for all Sterkfontein deposits. The dates shown here are given in Table 1, along with the references. Note: For Jacovec Cavern, the cosmogenic date comes from Partridge *et al.* (2003), while the faunal estimation is based on the presence of *Equus* sp. in this deposit, according to Kibii (2004). For Member 2, Herries & Shaw (2011) consider the previous palaeomagnetism date of Partridge *et al.* (1999; indicated) to be invalidated in favour of their date of 2.6–1.8 Ma. Uranium-lead isotope date of 2.2 Ma is from Walker *et al.* (2006), while the 2.6–2.8 Ma is from Pickering and Kramers (2010). For Member 4, there is some overlap between the faunal estimates (Kuman & Clarke 2000) and ESR and palaeomagnetism results, as well as Uranium-thorium dating (Schwarcz *et al.* 1994; Partridge 2005; Pickering & Kramers 2010, and Herries & Shaw 2011). The younger StW 53 date of 1.8–1.5 Ma is derived from the assessment of a combination of methods, in particular ESR and palaeomagnetism (Herries & Shaw 2011). Member 5 East ESR date is from Herries and Shaw (2011). Member 5 West dates are the combined palaeomagnetic and ESR dates are taken from Herries and Shaw (2011), in addition to the faunal and archaeological dates from Kuman & Clarke (2000). The Lincoln Cave North dates are from Reynolds *et al.* (2003, 2007) while the dates for the L/36 area are from Reynolds *et al.* (2007). The older dates for 'Member 6' (L/63) are ESR dates from Herries & Shaw (2011).

surface. The presence of an extinct micromammal genus, *Proodontomys,* suggests that some material in the Name Chamber derives from Members 4 and 5, while the presence of three genera found in the younger Post-Member 6 deposits suggest that younger material is also included in the Name Chamber material (Avery *et al.* 2010).

Each of these Members presents a sampling of palaeo-environmental conditions spanning close from 2.6 Ma to less than 115 ka (Fig. 4), which can be interpreted as a series. The following presents a summary of dating and paleoenvironmental reconstructions of data for each of the Sterkfontein Members.

## STERKFONTEIN MEMBERS

### Member 1

*Stratigraphy*: Member 1 is largely sterile deposit that formed when the first cave openings were absent or too small to admit surface-derived bone (Partridge 2000). This Member, which is up to 12 m thick in places, is exposed on the floor of the Silberg Grotto, where it lies under Member 2 and on top of a dolomite floor. This Member is also exposed as a hanging remnant in younger chambers, such as the Name Chamber (Partridge 2000).

### Jacovec Cavern

*Stratigraphy*: The Jacovec Cavern contains the deepest fossil-bearing deposits of the Sterkfontein Cave System, approximately 30 m from the ground surface (Wilkinson 1973, 1983, 1985). The cavern comprises two breccias of different ages; the Orange and the Brown breccias (Fig. 4; Partridge *et al.* 2003). Firstly, the older Orange breccia was deposited and subsequently a portion of it collapsed onto the floor of the cavern. Part of the Orange breccia remains *in situ* as a hanging remnant in the cavern, and this is where parts of the first *Australopithecus* cranium (StW 578) were discovered in August 1995 by Ronald J. Clarke (Clarke, in Partridge *et al.* 2003). All hominin specimens recovered from Jacovec Cavern derive from this Orange breccia (Partridge *et al.* 2003; Kibii 2004). The younger Brown breccia was deposited in a talus cone into the Jacovec Cavern some time after the collapse and erosion of the older Orange breccia. Later, a partial slump or collapse of the Brown breccia resulted in some mixing of the two breccias on the floor of the cavern, but leaving a portion of the Brown breccia *in situ* (Fig. 5). The excavation of the Brown breccia has not produced any hominins.

Sedimentological analysis of breccia blocks that were excavated from the collapsed and mixed section of the cavern indicates that as many as nine different rock types

**Table 2**. Sediment and rock types from the Jacovec Cavern breccia (Kibii 2000).

| Sample | Rock type | Description |
|---|---|---|
| A | Clear grey to white 5.0 mm long crystals of calcite ($CaCO_3$) | Crystallized in situ either from groundwater saturated with Ca and $CO_2$, or precipitation from limestone. |
| B | Greyish white brown calcrete ($CaCO_3$) | Formed as part of regolith (weathered rock) or soil horizon by the concentration of $CaCO_3$ and removal of other elements. |
| C | Reddish brown, brecciated regolith consisting of angular clasts (fragments) of 5.0–10 mm thick, finely bedded (0.5–1.0 mm) limestone, and small (0.5 mm) discrete crystals of clear grey calcite. | Slump deposits formed from collapsed limestone and other superficial material cemented together and weathered to form regolith, with calcite being formed by circulating groundwater. Angularity of clasts indicates that they have not been transported far from the origin. |
| D | Dark reddish brown to brown regolith with angular, 10–20 mm thick, isolated clasts of fine-grained bedded, white grey limestone, as well as discrete 0.2–0.5 mm calcite crystals. | The weathering of a breccia forms this form of brecciated regolith with some precipitation from groundwater. |
| E | Dark reddish brown with thin lenses (3.0–4.0 mm thick) of greyish white calcrete throughout. | This is regolith that is further weathered with calcrete resulting from the soil forming process. |
| F | Very dark brown regolith with small 0.5 mm dark brown rounded clasts (concretions) and angular clasts of greyish white, finely bedded, limestone (8.0–10 mm). | This is formed from the weathering of a limestone breccia, with concentrations possibly forming by the concentration of iron (Fe), or derived from another soil horizon. |
| G | Dark brown regolith with numerous clear grey, 2–10 mm thick, calcite veins throughout. | These form from weathered rock that was infiltrated by circulating groundwater, with precipitation out of $CaCo_3$ in joints and fractures within the host rock. |
| H | Dark reddish brown to red regolith with fine (2.0–3.0 mm) rounded hematite clasts throughout, with angular (10–15 mm) clasts of greyish white, finely bedded limestone, and rare fine (0.5–1.0 mm) clear grey calcite crystals. | This is formed from weathered limestone breccia where removal of other elements result in the concentration of Fe into nodules, and circulating groundwater precipitated out calcite. |
| I | Has two components, the first consisting of reddish brown regolith similar to Rock H, and a brown limestone regolith similar to Rock C. | This was probably formed elsewhere and cemented together in another slump deposit. |

are present, some of which were formed as a result of speleothem precipitation within the cave while others were calcified sediments that were fluvially transported from the grounds above and within the cave's vicinity (Table 2; Kibii 2000). Thus far, the Jacovec Cavern appears devoid of artefacts.

*Dating*: The two breccias within the Jacovec cavern have been dated through cosmogenic nuclides ($^{26}$Al and $^{10}$Be). The Orange breccia has been dated to *c.* 4.02 ± 0.27 (0.41) Ma, and the Brown breccia to *c.* 3.76 ± 0.26 (0.41) Ma (Table 1; Partridge *et al.* 2003). However, the presence of an equid in this deposit (Kibii 2000, 2004) suggests an age of less than 2.36 Ma for some of the material and that older and younger material are mixed together in this deposit (Fig. 4).

*Taxonomy*

*Primates*: Within the Jacovec Cavern, a single hominin taxon (assigned only to the genus *Australopithecus*) is identified (Table 3). Jacovec Cavern has yielded a hominin sample of 12 cranial, postcranial and dental specimens. Taken together, these specimens represent three old individuals and three juvenile individuals, all assigned to *Australopithecus* sp. (Partridge *et al.* 2003). Most complete is the partial cranium of a single old individual (StW 578). This cranial specimen also preserves portions of the occipital, parietals, the left sphenoid, right temporal, frontal,

the left naso-orbital margins, nasal bones and a right maxilla containing three heavily worn molars (Partridge *et al.* 2003). Two additional elderly *Australopithecus* individuals are represented by two worn upper right premolars (StW 590), and a single heavily worn lower left fourth premolar (StW 603). Wear slope differences between these teeth confirm the presence of three elderly individuals (Partridge *et al.* 2003). Juvenile *Australopithecus* individuals are represented by a left deciduous upper canine (StW 599); a moderately worn lower first molar (StW 601), and finally, an unworn lower right second molar (StW 604; Partridge *et al.* 2003). The Jacovec femur (StW 598) has a 'small head relative to a long neck' a feature more closely resembling *Paranthropus* femora from Swartkrans, as well as the femur (StW 99) from Member 4 (Partridge *et al.* 2003: 611). Also from Jacovec Cavern, there is a well-preserved lateral portion of a left clavicle (StW 606), which preserves evidence of carnivore gnaw-marks (Partridge *et al.* 2003). It exhibits 'a unique and ape-like morphology' more similar to that of chimpanzees, relative to humans or to other *Australopithecus* clavicles (Partridge *et al.* 2003: 612).

Additionally, the species *Parapapio jonesi, Parapapio broomi,* colobine, *Papio izodi* and taxonomically indeterminate cercopithecoid have been identified from this breccia (Table 3; Kibii 2000, 2004, 2007; Partridge *et al.* 2003).

*Carnivores*: Five families of the order Carnivora are

**Table 3**. Hominin and non-hominin primate species from the Sterkfontein Members. Key to deposits: J C: the Jacovec Cavern; M 2: Member 2 exposed in Silberberg Grotto; M 4: Member 4, the 'Type Site' where *Australopithecus africanus* was first recovered. Stw 53: is the small infill where the StW 53 cranium was recovered; M 5 E/ W: Member 5 East / West (stone-tool-bearing breccias). L/63: named for its excavation provenance, is located within Member 5 West. L C: is Lincoln Cave, lying within a separate cave system.

| Macromammalian species | Common name | J C | M 2 | M 4 | Stw 53 | M 5 E | M 5 W | L/63 | L C |
|---|---|---|---|---|---|---|---|---|---|
| **Family Hominidae** | | | | | | | | | |
| Hominidae indet. | Early *Homo* or *Australopithecus* | | | | x | | | | |
| *Homo* sp. | Modern human | | | | | | | x | |
| *Australopithecus* sp. | Extinct hominin | x | x | x | | | | | |
| *Australopithecus africanus* | Extinct hominin | | | x | | | | | |
| *Homo ergaster* | Extinct hominin | | | | | | x | | x |
| *Paranthropus robustus* | Extinct hominin | | | | | x | | | |
| **Family Cercopithecidae** | | | | | | | | | |
| Cercopithecoides indet. | Cercopithecine monkey | x | | x | x | x | x | | |
| *Theropithecus oswaldi* | Extinct gelada baboon | | | | x | x | | | |
| *cf. Cercopithecoides williamsi* | Extinct colobine monkey | | x | x | x | | | | |
| *cf.* Colobine | Colobine | x | | | | | | | |
| *Parapapio jonesi* | Extinct parapapio | x | x | x | | | | | |
| *Parapapio whitei* | Extinct parapapio | | | x | | | | | |
| *Parapapio broomi* | Extinct parapapio | x | x | x | | | | | |
| *Parapapio* sp. | Extinct parapapio | | | x | | | | | |
| *Papio izodi* | Extinct baboon | x | x | x | | | | | |
| *Papio cynocephalus* | Chacma baboon | | | | | | | x | x |

represented within the Jacovec Cavern fossil fauna (Table 4). These include: Viverridae, represented by *Genetta genetta*; Herpestidae, represented by *Cynictis penicillata* and a taxonomically indeterminate Herpestes; Canidae, represented by *Canis mesomelas, Vulpes chama,* and a taxonomically indeterminate canid; Felidae, represented by *Homotherium latidens, Felis caracal, Panthera leo, Panthera pardus* and taxonomically indeterminate felid; and Hyaenidae, represented by *Chasmaporthetes nitidula, Chasmaporthetes silberbergi, Chasmaporthetes* sp., and a taxonomically indeterminate hyaenid (Kibii 2000, 2004).

*Bovids*: Three subfamilies of the family Bovidae, are represented in the Jacovec Cavern fossil assemblage (Table 5). These are: Hippotraginae; Bovinae and Alcelaphinae. The tribes represented within the three subfamilies include: Hippotragini, Reduncini, Cephalophini, Tragelaphini, Bovini, and Alcelaphini (Kibii 2000, 2004). Indeterminate individuals were recovered for each of the tribes, except the Alcelaphini, which is represented by the wildebeest (*Connochaetes taurinus*) (Kibii 2000; 2004).

*Other fauna*: Other fauna represented in this infill include a single tortoise individual, an equid, the springhare (*Pedetes capensis*), the bushpig (*Potamochoerus porcus*), the Cape hare (*Lepus capensis*), and hyraxes (Table 6; Kibii 2000, 2004).

### Taphonomy

Taphonomic assessment indicates that several processes were involved in accumulation of different taxa within the Jacovec Cavern. Carnivores and fluvial transport have been identified as having played a major role in the accumulation of the fossils (Kibii 2004). Skeletal element representation, in part, suggests that some primate individuals were victims of carnivores (Kibii 2004, 2007). The remains of primate individuals were, however, not deposited into the cave by the predators; rather the skeletal elements were accumulated within the catchment area around the cave, and subsequently water activity incorporated the remains into the cavern (Kibii 2004, 2007). Larger carnivores appear to have been responsible for accumulating the remains of smaller carnivores on the grounds above the cave (Kibii 2004, 2007). Current evidence points to natural death of the larger carnivores within the catchment area of the cave. The skeletal remains of both groups of carnivores were eventually washed into the cave through fluvial action (Kibii 2004). Paucity of biotically derived bone modification, in addition to skeletal element representation suggest that the fossil bovid assemblage from Jacovec Cavern was not accumulated by carnivores, but instead selectively washed in from the grounds above and within the vicinity of the cave (Kibii 2004).

### Palaeoenvironments

The faunal composition of the Jacovec Cavern deposits suggest that a mosaic of open and closed habitats, which comprised a riverine gallery forest, with bushland and open country was present at the site (Kibii 2004). The presence of non-hominin primates, especially the colobine monkeys, suggests the presence of substantial tree cover within the vicinity of the cave. Modern colobines 'rarely leave the trees and no contemporary species occur beyond the main outliers of Africa's tropical and montane forest belt' (Kingdon 1997: 18). Thus the presence of colobine species within the Jacovec Cavern is highly indicative of the presence of a forest probably equivalent

Table 4. Carnivoran species. Key to deposits: J C: the Jacovec Cavern; M 2: Member 2; M 4: Member 4, Stw 53: is the StW 53 cranium infill; M 5 E/W: Member 5 East/West (stone-tool-bearing breccias). L/63: is an infill within Member 5 West. L C: is Lincoln Cave, lying within a separate cave system.

| Macromammalian species | Common name | J C | M 2 | M 4 | Stw 53 | M 5 E | M 5 W | L/63 | L C |
|---|---|---|---|---|---|---|---|---|---|
| **Family Machairodontinae** | | | | | | | | | |
| *Dinofelis barlowi* | Extinct false sabretooth cat | | x | x | | | x | | |
| *Megantereon cultridens* | Extinct sabretooth cat | | x | x | | | | | |
| *Homotherium latidens* | Extinct sabretooth cat | x | | x | | | | | |
| **Family Felidae** | | | | | | | | | |
| *Panthera* sp. | Pantherine cat | | | | x | | | | |
| *Panthera leo* | Lion | x | x | x | | x | x | | |
| *Panthera pardus* | Leopard | x | x | x | | | | | |
| *Acinonyx jubatus* | Cheetah | | x | | | | | | |
| *Felis* indet. | Indeterminate felid | x | | x | | x | | x | x |
| *Felis caracal* | Caracal | x | x | | | | | | |
| **Family Canidae** | | | | | | | | | |
| *Canis* sp. | Jackal | | | x | | x | | | x |
| *Canis mesomelas* | Black-backed jackal | x | | x | x | | x | x | x |
| *Canis brevirostris* | Short-faced jackal | | | x | | | | | |
| *Canis antiquus* | Extinct jackal | | | x | | | | | |
| *Vulpes chama* | Cape fox | x | | | | | | | x |
| *Otocyon megalotis* | Bat-eared fox | | | | | | | | x |
| *Nyctereutes terblanchei* | Extinct raccoon dog | | | | | | x | | |
| **Family Viverridae** | | | | | | | | | |
| *cf. Mungos* sp. | Mongoose | | | | | x | x | | |
| *Suricata* sp. | Suricate | | | | x | x | x | x | x |
| *Herpestes ichneumon* | Grey mongoose | | | | | | | x | |
| *Herpestes* indet. | Mongoose | | | | | x | | | |
| *Genetta genetta* | Common genet | x | | | | | | | |
| *Cynictis penicillata* | Yellow mongoose | x | | | | | | | |
| **Family Hyaenidae** | | | | | | | | | |
| Hyaenidae indet. | Hyaena | x | x | x | | x | x | | x |
| *Chasmaporthetes* sp. | Extinct hunting hyaena | x | | x | x | | | | |
| *Chasmaporthetes nitidula* | Extinct hunting hyaena | x | x | x | | | | | |
| *Chasmaporthetes silberbergi* | Extinct hunting hyaena | x | x | x | | | | | |
| *Pachycrocuta brevirostris* | Extinct short-faced hyaena | | | x | | x | | | |
| *Crocuta crocuta* | Spotted hyaena | | | x | | | x | | |
| *Parahyaena brunnea* | Brown hyaena | | | x | | | x | | |
| *Proteles* sp. | Aardwolf | | | | | | x | | |

to Africa's tropical and montane forests.

Several tentative inferences can be made about the types of habitats indicated by the Jacovec fauna. Presently, leopards (*Panthera pardus*) have a wide range of habitats from dense forests to open grassland plains, while lions (*Panthera leo*) are also common in most habitats, except for very dry deserts and dense forests. The Cape fox (*Vulpes chama*) is found in open grassy countryside, while the black-backed jackal (*Canis mesomelas*) occupies most habitats ranging from bush, woodland and savannahs to coastal desert (Haltenorth & Diller 1980; Kingdon 1997). The modern habitat of the caracal (*Felis caracal*) is plains and rocky countryside, with little grass cover. Extinct species, such as the long-legged hunting hyaenas (*Chasmaporthetes silberbergi* and *C. nitidula*), and extinct sabretooth cat, the *Homotherium latidens,* are thought to

have occupied open habitats (e.g. Lewis 1997). The overall scarcity of *H. latidens* in the fossil record of the Cradle of Humankind led Reynolds (2010) to propose that this species may not have been continuously resident in the but instead a transient species, perhaps to reduce competition with other large carnivore species. The morphology and inferred behaviour of the genus *Chasmaporthetes* suggests that its members 'may have preferred relatively open country and/or broken woodland, in which its cursorial adaptations could be used to best advantage' (Pickering *et al.* 2004b: 292).

The species of bovids present indicate a wide range of habitat types, from more closed deposits, (e.g. the small duikers and the tragelaphines), to those tribes indicating mixed habitats of grassland and savannah woodland ( e.g. the bovines) and finally, those bovid tribes which may

Table 5. Bovid species.

| Macromammalian species | Common name | J C | M 2 | M 4 | Stw 53 | M 5 E | M 5 W | L/63 | L C |
|---|---|---|---|---|---|---|---|---|---|
| **Family Bovidae** **Tribe Alcelaphini** | | | | | | | | | |
| *cf. Megalotragus* sp. | Extinct alcelaphine | | | x | | | | | x |
| Alcelaphini indet. | Wildebeest-sized bovid | x | x | | x | x | x | x | x |
| *Connochaetes* sp. | Indet. wildebeest | | | x | | | | | |
| *Connochaetes taurinus* | Wildebeest | x | | | | | | | |
| *Damaliscus parmularius* | | | | x | | | | | |
| *Damaliscus* sp. | Blesbok | | | | | x | x | x | |
| **Tribe Hippotragini** | | | | | | | | | |
| *Hippotragus* sp. | Roan /sable | x | | x | | | | | x |
| *Hippotragus equinus* | Roan antelope | | | x | | | | | |
| *Hippotragus cookei* | Extinct Cooke's antelope | | | x | | | | | |
| **Tribe Bovini** | | | | | | | | | |
| *Syncerus* sp. | Buffalo | x | | x | | | | | |
| **Tribe Ovibovini** | | | | | | | | | |
| *Makapania* sp. | Extinct Indet. *Makapania* | | | x | | | | | |
| *Makapania broomi* | Extinct musk-ox like bovid | | x | x | x | | | | |
| **Tribe Aepycerotini** | | | | | | | | | |
| *Aepyceros* sp. | Indet. impala | | | x | | | x | | |
| *Aepyceros melampus* | Impala | | | x | | | | | |
| **Tribe Tragelaphini** | | | | | | | | | |
| Tragelaphini indet. | Probable eland | x | | | | | x | | |
| *cf. Taurotragus oryx* | Eland | | | | | x | | | |
| *Tragelaphus scriptus* | Bushbuck | | | | | | | | x |
| *Tragelaphus strepsiceros* | Kudu | | | x | | | | | |
| *Tragelaphus angasi* | Nyala | | | x | | | | | |
| **Tribe Reduncini** | | | | | | | | | |
| *Redunca* sp. | Indet. reedbuck | x | | | | | | x | |
| *Raphicerus campestris* | Steenbok | | | | | | | | |
| *Raphicerus* sp. | Steenbok | | | | | x | x | | x |
| *Redunca darti* | Extinct Dart's steenbok | | | x | | | | | |
| *Redunca* cf. *arundinum* | Reedbuck | | | x | | | | | |
| **Tribe Antelopini** | | | | | | | | | |
| *Gazella* sp. | Gazelle | | | x | | | | | |
| *Gazella* cf. *gracilior* | Extinct small gazelle | | | | x | | | | |
| *Antidorcas* sp. | Springbok | | | | | x | x | x | x |
| *Antidorcas bondi* | Extinct springbok | | | x | | | | | |
| *Antidorcas recki* | Extinct springbok | | | x | | | | | |
| Antilopini sp. | Indet. antilopine | | | x | | | | | |
| **Tribe Neotragini** | | | | | | | | | |
| *Sylvicapra grimmia* | Grey duiker | | | | | | | x | |
| Cephalophini indet. | Indet. duiker | x | | | | | | | x |
| *Oreotragus oreotragus* | Klipspringer | | | | | x | | | |
| **Tribe Peleini** | | | | | | | | | |
| *Pelea capreolus* | Grey rhebok | | | x | | | | x | x |
| **Tribe Boselaphini** | | | | | | | | | |
| Boselaphini sp. | Extinct antelope | | | x | x | | | | |

**Table 6**. Other fauna from Sterkfontein.

| Macromammalian species | Common name | J C | M 2 | M 4 | Stw 53 | M 5 E | M 5 W | L/63 | L C |
|---|---|---|---|---|---|---|---|---|---|
| **Family Equidae** | | | | | | | | | |
| *Hipparion lybicum* | Extinct three-toed horse | | | x | | | | | |
| *Equus* sp. | Indet. zebra | x | | x | x | x | x | | |
| *Equus burchellii/quagga* | Plains zebra | | | | | | | x | x |
| **Family Elephantidae** | | | | | | | | | |
| *Elephas recki* | Extinct elephant | | | x | | | | | |
| **Family Hippopotamidae** | | | | | | | | | |
| *Hippopotamus amphibius* | Hippopotamus | | | | | | | | x |
| **Family Suidae** | | | | | | | | | |
| Suidae indet | Indet. pig | | | x | | | | | |
| *Phacochoerus africanus* | Warthog | | | | | | x | | x |
| *Potamochoerus porcus* | Bushpig | x | | | | | | | |
| *Metridiochoerus modestus* | Extinct pig | | | | | x | | | |
| *Metridiochoerus* sp. | Extinct pig | | | x | | | | | |
| **Family Hyracoidae** | | | | | | | | | |
| *Procavia antiqua* | Small extinct hyrax | | | x | x | x | x | | |
| *Procavia transvaalensis* | Large extinct hyrax | | | x | x | x | | | |
| *Procavia capensis* | Modern hyrax | | | | | | | x | x |
| **Family Hystricidae** | | | | | | | | | |
| *Hystrix africaeastralis* | Porcupine | | | x | | | x | x | x |
| **Family Pedetidae** | | | | | | | | | |
| *Pedetes capensis* | Springhare | x | | | | x | | x | x |
| **Family Lagomorpha** | | | | | | | | | |
| *Lepus capensis* | Cape hare | x | | | | | | x | x |
| **Family Aves** | | | | | | | | | |
| *Struthio camelus* | Ostrich | | | | | x | | | |
| Aves indet. | Indet. bird | x | | | | | | | |
| **Family Chelonia** | | | | | | | | | |
| Chelonian indet. | Tortoise | x | | | | | | | |

indicate more open, grassland habitats (e.g. alcelaphines, hippotragines and reduncines).

The palaeoenvironmental reconstruction is similar to that which has been suggested for Member 2, Sterkfontein (Partridge *et al.* 2003; Pickering *et al.* 2004a). However, due to the possible mix of assemblages in Jacovec due to the collapse of the Orange and Brown breccias, there is a need for further studies aimed at analysing samples from the Orange and Brown breccias separately. This might be achieved by isotope analyses of tooth elements deriving from secure horizons or that have embedded matrix that can be associated with a particular breccia.

## Member 2

### Stratigraphy

Member 2 is exposed in the underground cavern known as the Silberberg Grotto (formerly also known as 'Daylight Cave') and consists of 0.5–5.0 m of reddish brown sandy silt that rests unconformably on Member 1. In some places, Member 1 and 2 are separated by a flowstone layer and prior to lime-mining activities, this cavern would have contained an enormous stalagmite, which was removed during mining (Partridge 2000). The infill is calcified, devoid of artefacts and with high fossil concentration (carnivores and primate fossils are visible) in its lower levels (Partridge 1978; Brain 1981). The deposit is a talus cone, which lenses out from NE to SW (Fig. 6; Clarke 2006; Pickering & Kramers 2010).

### Dating

A fossil hunting hyaena of the genus *Chasmaporthetes* provided an initial age estimate of 3.0 to 3.5 Ma, based on similar morphology noted for a fossil from the lower Pliocene site of Langebaanweg, Western Cape (Turner 1997; Clarke 1998). Subsequent palaeomagnetic dating placed Member 2 between the Mammoth-Gauss and Gilbert-Gauss magnetic polarities, as *c.* 3.22 to 3.58 Ma (Partridge *et al.* 1999). Cosmogenic nuclides ($^{26}$Al and $^{10}$Be) burial dates pushed back the age of this Member to *c.* 4.17 Ma (Partridge *et al.* 2003).

This finding sparked debate, and some authors have pointed out that: 'the Member 2 'Little Foot' skeleton is not older than 3.04 Ma, and may be as young as 1.07–1.95 Ma
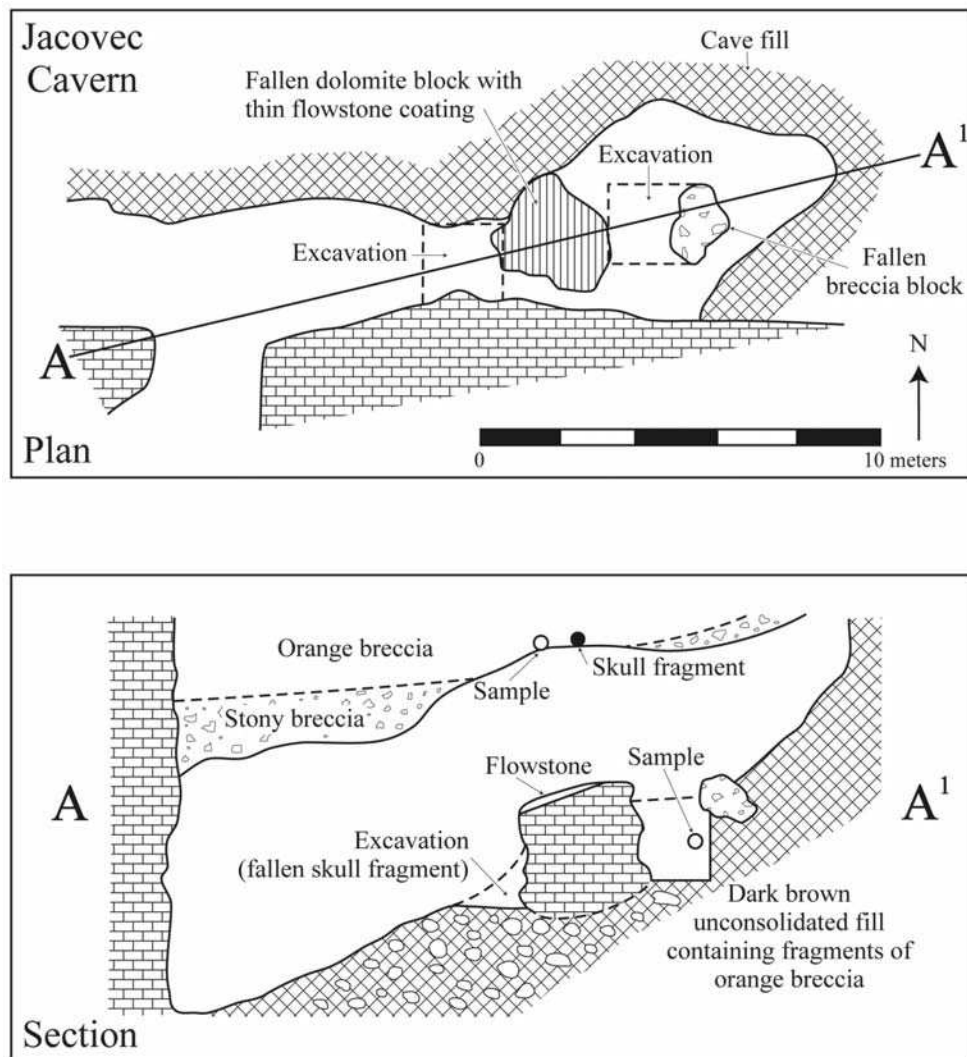
**Figure 5**. Jacovec Cavern profiles, showing the location of the *Australopithecus* sp. specimens, as well as the location of the collapse and mixing of the Brown and Orange breccias (redrawn from Partridge *et al.* 2003).

(Berger *et al.* 2002: 195). This claim was countered by Clarke (2002b). Recently, Walker and colleagues (2006), proposed an age of close to 2.2 Ma based on uranium–lead (U-Pb) isotopic dating while Pickering & Kramers (2010) obtained the same age within error of 2.01 ± 0.06 for the capping flowstone associated with StW 573, confirming the reproducibility of these ages. Dates ranging from 2.8 ± 0.82 to 2.6 ± 0.30 Ma using the same isotopic method (Table 1) were obtained for Member 2 (Pickering & Kramers 2010), while Herries & Shaw (2011) suggested an age range of 2.6–1.8 Ma based on palaeomagnetic analysis. The age discrepancies for Member 2 may be explained by the reworking of certain sediments (specifically, the quartz grains sampled for the cosmogenic nuclide analysis) in the cave, thus giving rise to different ages for this deposit (Pickering & Kramers 2010). A summary of these dates is presented in Fig. 4.

*Taxonomy*

Pickering and colleagues (2004a: 282) separate the species recovered from the *in situ* excavations from the fossil species published in several previous publications on the Silberberg Grotto by Broom (1945a,b), Broom & Schepers (1946), McKee (1996) and Turner (1997). Here we

have presented the combined species lists from the Member 2 excavations and older Silberberg Grotto publications.

*Primates*: Member 2 has yielded one of the oldest and arguably the most complete hominin fossil recovered in southern Africa: the 'Little Foot' skeleton, StW 573, which has been referred to the *Australopithecus* genus (Clarke & Tobias 1995; Tobias & Clarke 1996; Clarke 1998, 1999; Partridge *et al.* 1999, 2003). In addition, four other extinct primate species; the colobus-type monkey (*Cercopithecoides williamsi*), and three species of fossil baboons (*Parapapio broomi, Parapapio jonesi* and *Papio izodi*) are also represented (Pickering *et al.* 2004a) (Table 3).

*Carnivores*: At least two families of the order Carnivora are presented in the Member 2 fossil fauna assemblage (Table 4). The family Hyaenidae is represented by both species of extinct long-legged hunting hyaena (*Chasmaporthetes silberbergi, C. nitidula*) as well as an indeterminate hyaena. The family Felidae is represented by extinct machairondonts (*Dinofelis barlowi, Megantereon cultridens*), as well as four extant felid species, namely the lion, leopard, cheetah and caracal (*cf. Panthera leo, Panthera pardus, Acinonyx jubatus* and *Felis caracal*, respectively; Pickering *et al.* 2004a). The cheetah is another scarce carni-
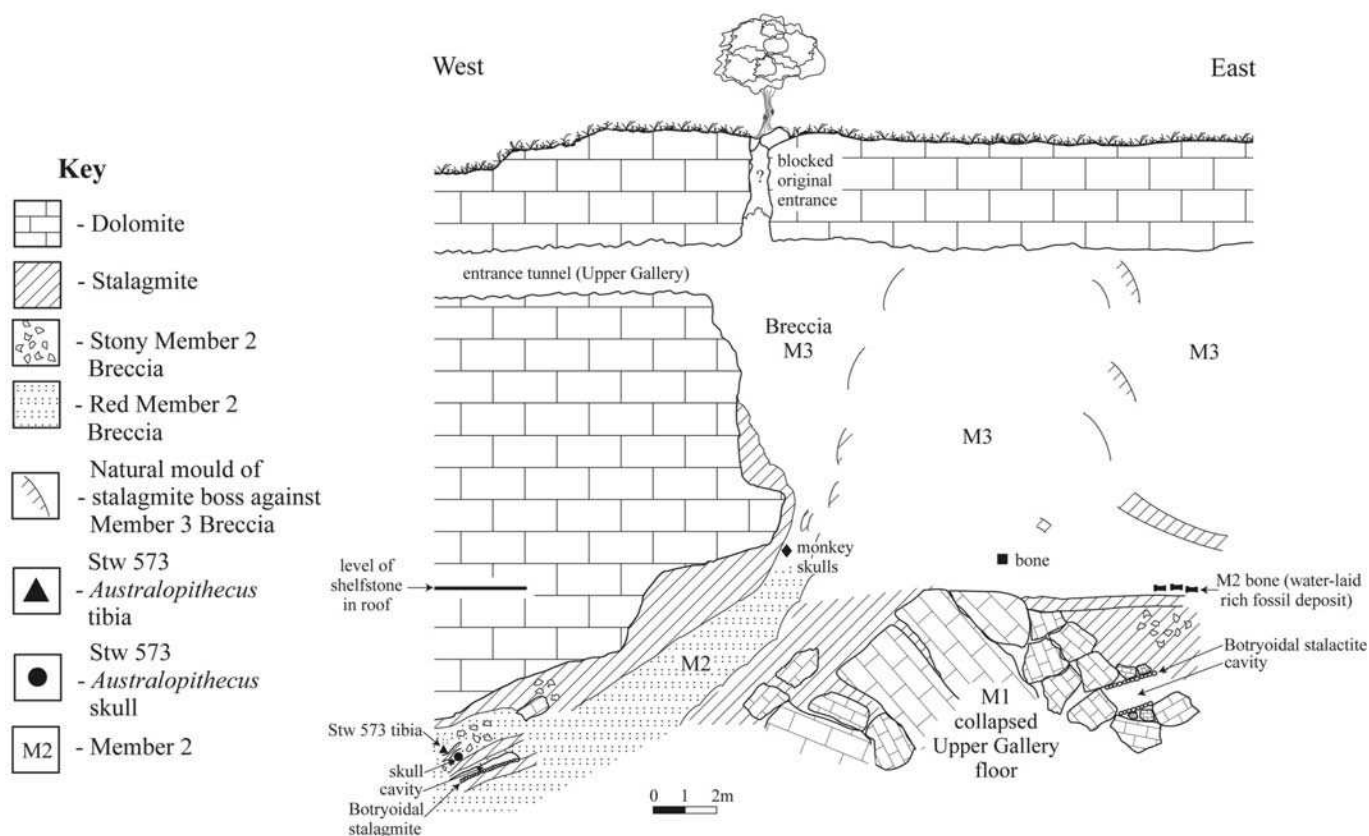
**Figure 6**. Profile of the Silberberg Grotto, showing the location of the *Australopithecus* sp. skeleton (StW 573). The position of exposed Members 1–3 within the cavern are also indicated (redrawn after Clarke 2006).

vore in the Cradle of Humankind, and spatial distributions show that this species is found only at the southern end of the Cradle, at Sterkfontein and Swartkrans (Reynolds 2010).

*Bovids*: The family Bovidae is represented by the extinct ovibovine, *Makapania broomi,* and an indeterminate Alcelaphini, and a non-Alcelaphini Size Class 2 bovid (Table 5; Pickering *et al.* 2004a).

*Palaeoenvironment and taphonomy*

The presence of extinct primates, specific carnivore taxa associated with open grassland, the extinct hunting hyaena (*Chasmaporthetes*) and the extinct ovibovine (*Makapania broomi*) all suggest the presence of open grassland with rocky outcrops during the deposition of Member 2. Obligate drinkers, specifically members of the Alcelaphini tribe (including hartebeests, wildebeests and blesbok), suggests a permanent water supply reasonably close to the Sterkfontein site (such as the Blaaubank river), which would in turn have supported a riverine gallery forest ideal for leopards and monkeys (Pickering *et al.* 2004a). Unpublished micromammal specimens have been provisionally identified as elephant shrew (genus *Elephantulus*), which may indicates the presence of wetter habitats (Clarke, pers. comm.). The recovery of articulating bone specimens and antimeric (i.e. both left and right elements) specimens, in addition to paucity of bone surface modification signals that a death trap within the cavern was probably responsible for the accumulation of the fauna (Pickering *et al.* 2004a).

**Member 4**

*Stratigraphy*

Partridge (1978) subdivided this Member into four stratigraphic layers, referred to as Beds A–D. Bed A is exposed in the Type Site and in the Lower Cave and consists of 2–3 m of brownish red calcified sandy silt. The bed contains occasional bone fragments and shows evidence of a series of successive major roof collapses that resulted in the enlargement of cave shaft connecting to the outside. Bed B is exposed in the Type Site, Lower Cave and lower levels of the 'Extension Site' (i.e. to the west of the Type Site) and consists of reddish brown sandy loam. Bed C rests on eroded surface of Bed B, and is exposed in the Type Site and the Lower Cave. It consists of 0.5–2.0 m of well-calcified dark reddish brown silty sand. Bed B and Bed C are the *Australopithecus*-bearing beds, including the famous 'Mrs Ples' Sts 5 specimen from Bed C (Partridge 1978). Bed D is exposed in the Type Site and lower Cave and consists of discontinuous brownish red heavily calcified silty sand. A marked erosional unconformity separates this bed from Bed C, and Bed D represents a temporal period of greater water abundance in the cave, but also episodes of roof instability and collapse (Partridge 1978).

Members 2 and 4 are important *Australopithecus*-bearing deposits, while Member 3 (exposed in the Silberberg Grotto) is as yet unexcavated. Recently, Pickering & Kramers (2010) suggested that material assigned to Member 3 may possibly be distal deposits of Member 4

(shown in Fig. 3). If this hypothesis can be confirmed through excavation and analysis, then the volume of Member 4 would be far greater than previously appreciated, which may in turn explain some of the high levels of palaeoenvironmental variation and biodiversity observed in Member 4 as being due to the temporal period covered by this deposition.

*Dating*

Early faunal dating relied on correlations with fossiliferous volcanic deposits in eastern Africa which could be dated absolutely (Table 1). Age estimates of *c.* 2.5 Ma based on fossil cercopithecoids (Delson 1984, 1988) and *c.* 2.8–2.4 Ma (Vrba 1975, 1976, 1980, 1985; Kuman & Clarke 2000), based on fossil Bovidae were proposed. McKee used detailed faunal seriation methods to derive a date of between 2.6 and 2.8 Ma (McKee 1993). Electron spin resonance (ESR) studies on bovid teeth yielded a date of 2.1 ± 0.5 million years old (Schwarcz *et al.* 1994). The presence of *Equus* in the deposit suggests an upper age limit of less than 2.36 Ma (Herries & Shaw 2011).

Recent reanalysis of palaeomagnetic dates has positioned Member 4 within the younger Réunion event at 2.15–2.14 Ma (Partridge 2005; Herries & Shaw 2011). Palaeomagnetic analysis suggests Member 4 formed between 2.58 and 2.05 Ma, with the Sts 5 fossil dating to between 2.16 and 2.05 Ma (Fig. 3). Pickering and Kramers (2010) propose that Member 4 is dated to between 2.65 ± 0.30 and 2.01 ± 0.06 Ma, based on isotopic (U-Pb) dating methods. Some of the Member 4 sediment may be younger than 2.36 Ma, based on the presence of fossils of *Equus.* More recently, Herries & Shaw (2011) revised the dates for the stratigraphic layers within Member 4 as: Member 4A at 2.8–2.2 Ma, Member 4B at 2.6–2.2 Ma and Member 4C at 2.2–2.0 Ma.

*Taxonomy*

This important Member is where the first adult cranium of australopithecine was discovered by Robert Broom in 1936. Initially assigned to a new species, *Plesianthropus transvaalensis,* some of the hominin specimens from this Member are assigned to *Australopithecus africanus* Dart, 1925, while Clarke (1988) has argued for a second species (Fornai 2010).

*Primates*: One hominin species, *Australopithecus africanus,* (and a proposed second *Australopithecus* species) and five primate species are identified from Member 4, including extinct primate species (*Parapapio broomi, Parapapio jonesi, Papio izodi, Parapapio whitei,* and *Cercopithecoides williamsi*). Additionally, several indeterminate hominins, parapapionins and cercopithecoid monkey specimens have been identified (Kibii 2004; Table 3). The australopithecine fossil sample from Member 4 is world-famous. Here we outline the most remarkable fossil finds, but discuss the interpretations of these fossils later in the text.

Member 4 has yielded numerous hominin specimens assigned to *Australopithecus africanus,* including the Sts 5 'Mrs Ples' cranium (Broom *et al.* 1950). Recent researches through the Transvaal Museum, Pretoria, fossil collections by de Ruiter (2004) have recovered 10 previously undes-cribed craniodental *Australopithecus africanus* specimens from Sterkfontein Member 4 (including a natural endocast, Sts 1960b) and a further hominin maxillary molar fragment from Sterkfontein Member 5 (de Ruiter 2004). The Member 4 hominin postcranial specimen (Sts 14) possesses a sacral specimen (Sts 14Q) appears to derive from a 'post-pubertal individual which had not finished its growth concerning the sacral breadth, and probably the pelvic breadth' (Berge & Gommery 1999: 227). Even more recently, one of us (JMK) identified a hominin scaphoid from the Member 4 faunal remains excavated by Alun Hughes and his team in 1990. This scaphoid sheds light on the wrist morphology and grip capabilities of the Sterkfontein hominins (Kibii *et al.* 2011).

The possibility of another species of *Australopithecus* being present in Member 4, the so-called 'second species' has been studied by various researchers since the original suggestion was made by Clarke (1988, 1994; Kimbel & White 1988; Kimbel & Rak 1993; Lockwood 1997; Moggi-Cecchi *et al.* 1998). Clarke (1988, 1994), in particular, has suggested that, among the better preserved crania, Sts 71, StW 252 and StW 505 can be distinguished from Sts 5, Sts 17 and Sts 52. While it does indeed appear that there are two morphological extremes (represented by specimens such as Sts 5 and Sts 71), several crania, including the male australopithecine StW 505, represent various intermediate morphologies (Lockwood & Tobias 1999, but see Clarke 2008). Another morphologically unusual specimen is Sts 19, the taxonomic attribution of which has been debated. Certain researchers maintain that this cranium 'has more affinity with *A. africanus* (especially Sts 5) than with *Homo habilis*' (Prat 2005: 221).

There are also signs of pathologies on some of the specimens from Member 4. Sts 24a is a juvenile *Australopithecus africanus* showing clear signs of pre-pubertal periodontitis (Ripamonti *et al.* 1997). A recent re-examination by D'Anastasio and colleagues (2009) of the partial skeleton, Stw 431, (representing and adult male individual of *A. africanus*) is composed of 18 bones from the axial skeleton, pelvic girdle and shoulder girdle as well as elements of the upper limb. This skeleton has pathological lesions on two of the lumbar vertebrae which are reminiscent of early brucellosis, which is an infectious disease caused by the consumption of infected animal proteins (D'Anastasio *et al.* 2009). While the authors do state that alternative cause of the lesions cannot be definitively excluded, they posit that the possible presence of this disease in a hominin from Member 4 raises the possibility that some meat was included in the diets of *Australopithecus africanus* (D'Anastasio *et al.* 2009).

StW 151 is a partial cranium of a juvenile hominin from Member 4, which is remarkable due to the preservation of a stapes (one of the three bones of the middle ear), showing similarities between the early hominins and living great apes in stapedial morphology (Moggi-Cecchi & Collard 2002).[1]

There is much scientific interest in dating and con-

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[1]Stapedial morphology suggests that *Australopithecus africanus* may have possessed more sensitivity to high frequency sounds than modern humans do (Moggi-Cecchi & Collard 2002).

texualizing the abundant and well-preserved hominin material of Member 4, and clarifying the relationship between the australopithecine-bearing Member 4 deposit exposed at the surface, with the underground australopithecine-bearing Member 2 and Jacovec Cavern deposits (e.g. Berger *et al.* 2002; O'Regan & Reynolds 2009; Hopley & Maslin 2010; Pickering & Kramers 2010). These are discussed in a later section of this paper.

*Carnivores*: The carnivore species total 14 taxa, including extant large carnivores, such as the lion, leopard, spotted and brown hyaenas (*Panthera leo, Panthera pardus, Crocuta crocuta, Parahyaena brunnea,* respectively), as well as the extinct machairodonts (*Megantereon cultridens, Homotherium latidens* and *Dinofelis barlowi*). Long-legged hunting hyaenas (*Chasmaporthetes silberbergi, Chasmaporthetes nitidula*) combined with the extinct giant hyaena (*Pachycrocuta brevirostris*) make for a densely populated carnivore guild, with a predominance of medium-sized carnivores (Turner & Antón 1996). Indeterminate Felidae, Canidae and Hyaenidae round out the balance of the Member 4 carnivores (Table 4). Alternative explanations for the high numbers of carnivore species include possible time averaging (O'Regan & Reynolds 2009) and also the possibility that scarce taxa were only rarely present in the Cradle of Humankind area (Reynolds 2010). In addition to these species, the common black-backed jackal (*Canis mesomelas*), and taxonomically poorly understood extinct canid species of *Canis brevirostris* and *Canis antiquus* (Ewer 1956; Brain 1981) are represented. The latter two species may instead be morphologically variable specimens of black-backed jackal (*Canis mesomelas*) or side-striped jackal (*Canis adustus*), as has been suggested elsewhere (Reynolds 2012).

*Bovids*: Bovids are extremely well-represented in the Member 4 assemblage. Five subfamilies of the family Bovidae have been identified: Caprinae, Alcelaphinae, Antilopinae, Hippotraginae and Bovinae (Table 5). Of the Caprinae, the tribe Ovibovini is represented by the extinct musk-ox like *Makapania broomi* and *Makapania* sp. The subfamily Alcelaphinae (tribe Alcelaphini) is represented by a mix of extinct and extant genera, including the extinct blesbok (*Damaliscus parmularis*), the wildebeest (*cf. Connochaetes* sp.) the giant hartebeest, (*cf. Megalotragus* sp.) and a wildebeest-sized indeterminate Alcelaphini individual (Table 5; Kibii 2004). The tribe Antilopini is represented by two extinct springbok species and an extinct gazelle (*Antidorcas recki, Antidorcas* cf. *bondi, Gazella* sp., respectively) as well as an indeterminate Antilopini individual. The tribe of the horse antelopes, the Hippotragini, is represented by the roan antelope (*Hippotragus equinus*), the extinct Cooke's antelope (*Hippotragus cookei*) and an indeterminate Hippotragini. The Reduncini include the extinct Dart's reedbuck (*Redunca darti*), and the extant reedbuck (*Redunca* cf. *arundinum*), with an indeterminate Reduncini also present. The impala tribe (Aepycerotini), are represented by fossils assigned to the extant impala (*Aepyceros melampus*) and by an indeterminate *Aepyceros* species. The tribe Peleini is represented by the extant grey rhebok (*Pelea capreolus*); Boselaphini by just a Boselaphini sp. specimen; the tribe Tragelaphini by the extant kudu

(*Tragelaphus strepsiceros*), a possible nyala specimen (*Tragelaphus* sp. aff. *angasi*) and an indeterminate tragelaphine (*Tragelaphus* sp). Finally, the tribe Bovini is represented by an indeterminate species of African buffalo (*Syncerus* sp.) (Table 5; Kibii 2004).

*Other fauna*: This group includes a tortoise, a suid; an indeterminate reptile; the Cape Hare (*Lepus capensis*); an indeterminate *Equus; Hystrix africaeaustralis*; a fossil suid (*cf. Metridiochoerus* sp)., the extinct elephant (*Elephas recki*) and two extinct species of hyrax (*Procavia antiqua* and *Procavia transvaalensis*) (Table 6; Kibii 2004).

*Taphonomy*

The fossil bovid and carnivore remains were accumulated by several agents including: 1) carnivores, 2) death trap, and 3) slope wash (Brain 1981; Kibii 2004). These processes may have taken place at different times, or alternatively there may have existed different entrances. The majority of all modification on fossil bovid modified bones is carnivore-induced (84%); however, the recovery of low structural density skeletal elements, such as ribs and vertebrae (including juveniles) but without signs of carnivore modification indicate that some of the carcasses, and/or carcass parts were brought in naturally (by slope-wash, or death-trap). Large carnivores are also implicated in the accumulation of smaller carnivores and other fossil fauna in the Member 4 assemblage (Kibii 2004). It is likely that during initial stages of cave formation, when the aven was concealed, some of the carnivore and bovid individuals fell into the cave below. Slopewash of carcasses from the catchment area into the cave cannot be ruled out, as some bovid specimens show signs of abrasion (Kibii 2004). The accumulation of numerous large carnivore cranial elements may have resulted from individuals dying within the cave, possibly while using the cave for denning or voiding (Kibii 2004).

The hominin accumulation follows a somewhat different pattern than the bovid and carnivore fossil assemblages. The *A. africanus* sample appears to show a bias toward females and small or immature males, suggesting the deliberate selection of smaller individuals by predators during the formation of this deposit (Lockwood & Tobias 2002). Skeletal element representation, in addition to bone modification, suggests that carnivores contributed significantly to the hominin assemblage (Pickering *et al.* 2004b). For the other primates, numerous cranial and postcranial elements with minimal or no biotic modification (i.e. tooth marks, evidence of digestion) indicate that some primates were naturally accumulated, perhaps while utilizing the cave as a sleeping den, or that they may have fallen to their death into the cave. Nevertheless a small number of primate elements display carnivore-related bone modification, suggesting some predator involvement (Brain 1981; Kibii 2004).

*Palaeoenvironments*

Member 4 palaeoenvironments were first reconstructed using fossil fauna and later, fossil wood, which is uniquely and abundantly preserved in this Member. Several earlier studies stressed the closed, forested nature of the Member 4

**Table 7**. Plants species identified (from Bamford 1999).

| Plant species | Common name | M 4 | M 5 E | M 5 W | Post M 6 |
|---|---|---|---|---|---|
| **Family Dichapetalaceae** | | | | | |
| *Dichapetalum mombuttense* | Liana | x | | | |
| **Family Scrohulariaceae** | | | | | |
| *Anastrabe integerrima* | Pambati tree | x | | | |

environments (Vrba 1975). Over time, more studies have identified indications of mosaic habitats during Member 4 accumulation. Vrba (1974, 1975, 1976, 1980) suggested a wooded environment with close proximity to open grassland based on the types of bovid species present. Specifically, the presence of ovibovines (*Makapania broomi*) and hippotragines were interpreted as suggesting wooded environments, along with open grassland indicator species such as members of the Alcelaphini and Antelopini. Vrba's conclusions were later corroborated by Reed (1997), who suggested that open woodland with bushland and thicket had been present, based on the presence of a high percentage of terrestrial animals (23.33%), a significant proportion of frugivorous mammals (16.67%) and only a few arboreal animals (3.3%). These reconstructions were corroborated by the discovery and analysis of over 300 fossil wood fragments from this infill (Bamford 1999). The presence of liana vines (most similar to the extant species *Dichapetalum mombuttense*) and the Pambati tree (*Anastrabe integerrima*) in the fossil wood sample suggested a forest fringe environment equivalent to the present day tropical forest of the Democratic Republic of Congo and Cameroon (Table 7; Bamford 1999), corroborated by the presence of the extinct colobus monkey (*Cercopithecoides williamsi*) (Kuman & Clarke 2000).

Studies of cercopithecoid postcranial morphology indicate the presence of several distinct habitat types: forest, open woodland/bushland and grassland (Elton 2001). Individuals falling into the 'open terrestrial' habitat category dominate the cercopithecoid sample, signalling a significant open component during Member 4 times. In contrast, australopithecine locomotor behaviour has been interpreted as having a strong arboreal component (Wood & Richmond 2000).

However, additional work on the micromammal species by Avery (2001) has given a different perspective to the debate regarding the Member 4 palaeoenvironments (Table 8). Member 4 contains a total of 11 identified species, and every one of those is represented in other Sterkfontein assemblages analysed by Avery (2001). This suggests that environments in Member 4 times were not dissimilar to those of subsequent Member 5 infills and Post Member 6. A single extinct species of unknown habitat preference (*Proodontomys cookei*) is represented, which also occurs in Member 5 East, Member 5 West, and at Swartkrans (Members 1–3; Avery 2001). However, the short-snouted elephant shrew (*Elephantulus fuscus*) is found only in Member 4 and Member 5 East and this species is known to prefer moist, woodland environments. Taken together, Avery's interpretation of the environmental reconstruction was that 'grass with trees along the river, bush with grass on the hillsides and grass with

some trees and bushes on the plains' prevailed during Member 4 times (Avery 2001: 127).

Stable carbon isotope work by Luyt and colleagues (Luyt 2001; Luyt & Lee-Thorp 2003) has identified the full spectrum of browsers, grazers and mixed feeders within Member 4. The results revealed that the extent of woodland would have been heavier than originally proposed by Vrba (Luyt 2001). The extinct $C_3$ feeders (consuming trees, shrubs and herbs, or their consumers) include *Antidorcas recki*, *Hippotragus* sp. and the carnivore *Homotherium latidens*. The extinct $C_4$ consumers (grazers) include *Antidorcas bondi*, while the mixed feeders include *Makapania broomi*, and *Tragelaphus* sp. aff. *angasi* for bovids, and the extinct hyaena *Chasmaporthetes nitidula* (Luyt 2001).

Isotopic evidence for diets of Member 4 *Australopithecus africanus* have confirmed that these hominins were consuming significant proportions of $C_4$ foods, and that their diets were highly variable (van der Merwe *et al.* 2003, Sponheimer *et al.* 2005a, data reproduced in Table 9). These variable dietary signals have also been confirmed for *Australopithecus* at Makapansgat (Sponheimer & Lee-Thorp 1999). Analyses using ratios of strontium and calcium (Sr/Ca) in hominin enamel indicate that the *Australopithecus* diets from Sterkfontein Member 4 show higher Sr/Ca ratios relative to *Paranthropus robustus* from Swartkrans Member 1 (Sponheimer *et al.* 2005b; data reproduced in Table 10). The authors suggest that these results may suggest either high levels of grazing, or insectivory in the diets of *Australopithecus* from Sterkfontein (Sponheimer *et al.* 2005b). Both studies indicate that *Australopithecus* exploited grassland and woodland food sources regularly, or ate animals (termites, other fauna) that had eaten significant quantities of $C_4$ foods. Recent results of a study of strontium isotope analysis indicate that smaller *Australopithecus* and *Paranthropus* individuals (based on tooth size) appear to have ranged further afield than larger individuals (Copeland *et al.* 2011). The authors interpret these results as indicating that female hominins dispersed from their natal troops, while males utilized smaller home ranges on the dolomites (Copeland *et al.* 2011). Alternatively, these data may suggest a convergence of hominins to the sites of Sterkfontein and the surrounding valley from areas further afield. This may be due to the attractive combination of habitats and landscape features available at the Sterkfontein and Swartkrans (Reynolds *et al.* 2011).

Based on these data and the other palaeoenvironmental proxies discussed above, the Member 4 environments appear to have sampled a continuum of forested, open woodland, and grassland habitats, leading to debate about the possible effects of time- and climate averaging

**Table 8**. Micromammalian genera from Sterkfontein (species from Avery 2001, and Avery *et al.* 2010). Key to deposits: J C: the Jacovec Cavern; M 2: Member 2 M 4: Member 4, M 5 E/ W: Member 5 East / West (stone-tool-bearing breccias). N C is the Name Chamber and Post M6 is the deposit from L/ 63 and Lincoln Cave, lying within a separate cave system.

| Micromammalian genera | Common name | M 4 | M 5 E | M 5 W | N C | Post M 6 |
|---|---|---|---|---|---|---|
| **Family Chrysochloridae** | | | | | | |
| *Cholorotalpa* | Golden mole | | x | | | |
| *Chrysospalax* | Rough-haired golden mole | | | x | x | x |
| *Neamblysomus* | Golden mole | | x | x | x | x |
| **Family Macroscelididae** | | | | | | |
| *Elephantulus* | Elephant shrew | x | x | x | x | x |
| *Macroscelides* | Elephant shrew | | | | | x |
| **Family Soricidae** | | | | | | |
| *Crocidura* | Musk shrew | | | | x | x |
| *Mysosorex* | Forest shrew | x | x | x | x | x |
| *Suncus* | Dwarf shrew | x | x | x | x | x |
| **Family Rhinolophidae** | | | | | | |
| *Rhinolophus* | Horseshoe bat | | x | x | x | x |
| **Family Vespertilionidae** | | | | | | |
| *Tadarida* | Tomb bat | | | | x | |
| *Myotis* | Hairy bat | | x | x | x | x |
| *Neoromicia* | Serotine bat | | | | x | |
| **Family Gliridae** | | | | | | |
| *Graphiurus* | Dormouse | | x | x | x | x |
| **Family Nesomyidae** | | | | | | |
| *Saccostomus* | Pouched mouse | | | | x | x |
| *Dendromus* | Climbing mouse | x | x | x | x | x |
| *Malacothrix* | Gerbil mouse | | x | | x | x |
| *Steatomys* | Fat mouse | | x | x | x | x |
| *Mystromys* | White-tailed mouse | x | x | x | x | x |
| *Proodontomys* (extinct) | Extinct mouse species | x | x | x | x | |
| **Family Muridae** | | | | | | |
| *Acomys* | Spiny mouse | | x | | x | |
| *Gerbilliscus* | Gerbil | x | x | x | x | x |
| *Aethomys* | Veld rat | | x | x | x | x |
| *Dasymys* | Marsh rat | x | x | x | x | x |
| *Mastomys* | Multimammate mouse | | x | x | x | x |
| *Mus* | Mouse | | x | x | x | x |
| *Rhabdomys* | Grass mouse | x | x | x | x | x |
| *Thallomys* | Tree rat | | | | x | x |
| *Zelotomys* | Desert mouse | x | x | x | x | x |
| *Otomys* | Vlei rat | x | x | x | x | x |
| **Family Bathyergidae** | | | | | | |
| *Cryptomys* | Molerat | | x | x | x | x |
| *Georychus* | Molerat | | x | | | x |

on this important deposit (O'Regan & Reynolds 2009; Hopley & Maslin 2010). Recent studies have examined the role of the landscape in creating and sustaining such mosaic habitats (Bailey *et al.* 2011; Reynolds *et al.* 2011).

**Member 5 deposits**

Member 5 is exposed from the Extension Site to the western end of the Type Site (Robinson 1962; Partridge 1978; Fig. 2). Study of the artefacts and fauna of the Member 5 deposit revealed that it is composed of three separate units, which together appeared geologically uniform; namely the StW 53; the Member 5 East and Member 5 West deposits. These infills contain one of the earliest records of stone tool use from a southern African site, the Oldowan industry and the later Early Acheulean artefact industry from Member 5 West. The StW 53 infill,

**Table 9**. Stable carbon isotope values for Member 4 *Australopithecus africanus* (data taken from van der Merwe *et al.* 2003, and Sponheimer *et al.* 2005a).

| Specimen number | Species attribution | Diet | δ¹³C values |
|---|---|---|---|
| STS 72 | *Australopithecus africanus* | | –9.7 |
| StW 73 | *Australopithecus africanus* | | –8.8 |
| StW 276 * | *Australopithecus* 'second species' | | –8.0 |
| STS 32 | *Australopithecus africanus* | | –7.8 |
| StW 252 * | *Australopithecus* 'second species' | Grazing | –7.7 |
| StW 211 | *Australopithecus africanus* | ↑ | –7.5 |
| StW 304 | *Australopithecus africanus* | | –7.4 |
| STS 31 | *Australopithecus africanus* | | –6.8 |
| StW 14 * | *Australopithecus* 'second species' | | –6.7 |
| StW 315 | *Australopithecus africanus* | | –6.4 |
| StW 309b * | *Australopithecus* 'second species' | | –6.1 |
| STS 2218 | *Australopithecus africanus* | | –5.9 |
| StW 229 | *Australopithecus africanus* | ↓ | –5.8 |
| StW 303 * | *Australopithecus* 'second species' | | –4.4 |
| STS 45 | *Australopithecus africanus* | Browsing | –4.0 |
| StW 236 | *Australopithecus* ? | | –3.7 |
| StW 207 | *Australopithecus* ? | | –2.0 |
| StW 213i | *Australopithecus* ? | | –1.8 |

**Table 10**. Strontium calcium ratios for Member 4 *Australopithecus africanus* (data taken from Sponheimer *et al.* 2005b).

| Specimen number | Species attribution | Sr/Ca values |
|---|---|---|
| STS 72 | *Australopithecus* | 1.62 |
| STS 32 | *Australopithecus* | 1.49 |
| TM 1532 | *Australopithecus* | 1.39 |
| STS 61 | *Australopithecus* | 0.98 |
| STS 2218 | *Australopithecus* | 0.90 |
| STS 31 | *Australopithecus* | 0.69 |
| STS 45 | *Australopithecus* | 0.60 |
| Mean ± SD | | 1.09 ± 0.41 |

however, is separated from the remaining Member 5 deposits by a thick flowstone layer, and does not contain stone tools, leading Kuman and Clarke (2000) to argue that it is a hanging remnant of Member 4, or alternatively, a temporally intermediate deposit between Member 4 and Member 5 East (Kuman & Clarke 2000). Herries and Shaw (2011) also suggest it is distinct from Member 5, but is intermediate in age between Members 4 and 5.

**The StW 53 Infill**

*Stratigraphy*

A small infill within the Member 5 area is where the StW 53 cranium was discovered in August 1976. The hominin cranium was recovered partially *in situ* in the calcified breccia and partially from a decalcified portion of the deposit, in a mokondo, or sinkhole (Hughes & Tobias 1977; Curnoe & Tobias 2006). Discovered by Alun Hughes and described initially by Hughes and Tobias as *Homo,* aff *Homo habilis* (Hughes & Tobias 1977), this specimen has continued to spark debate and controversy. The specimen was assigned to *Homo habilis,* in part due to its presumed association with stone tools (Hughes & Tobias 1977). Later stratigraphic studies done by Kuman and Clarke (2000) concluded that the StW 53 infill does not contain stone tools, thereby differentiating it from the contiguous Member 5 West infill (Clarke 1994; Kuman & Clarke 2000). Although the infill contains some fauna

not present in Member 4 (e.g. *Theropithecus oswaldi,* Table 3), it does resemble Member 4 in that it contains no *in situ* stone tools. The presence of stone tools around the time of death of the StW 53 individual is confirmed by three sets of short striations on the cranium, suggesting deliberate disarticulation (Pickering *et al.* 2000). Fossil macromammalian species identified from this infill are listed in Tables 3–6.

*Dating*

Based on the species of fauna present, Kuman & Clarke (2000) suggested that StW 53 infill is younger than Member 4 but older that Member 5 Oldowan infill (Table 1; Fig. 4). *Theropithecus oswaldi* is present in StW 53 and Oldowan Infills, but is absent in Member 4, suggesting that Member 4 and Member 5 deposits sample slightly different environmental conditions and so are of different ages (Kuman & Clarke 2000). Closely associated with grassland environments, *T. oswaldi* is argued to have appeared within the Sterkfontein region after a shift in the environment towards drier conditions at 2.1 Ma (Weigelt *et al.* 2008). The earliest record of this genus is dated to around 3.7–3.5 Ma, is from the Kalochoro Member at Lothagam, in Kenya (Leakey *et al.* 1996). The last appearance of the species *Theropithecus oswaldi* in Africa is at Hopefield (Western Cape Province, South Africa) which dates to about 0.4 Ma (Pickford 1993).

The absence of stone tools may also indicate that the StW 53 infill predates the Oldowan infill (Kuman & Clarke 2000). From these two points, Kuman and Clarke (2000: 834) suggest that the StW 53 infill 'is likely to be less than 2.6 and more than 2 Ma'. However, Herries and colleagues (2009) have recently proposed a younger date of 1.8–1.4 Ma using palaeomagnetism and ESR. Herries & Shaw (2011) have further revised this date to 1.8–1.5 Ma for this infill (Fig. 4).

*Taxonomy*

*Primates*: At least four primate species have been identified from the StW 53 infill. These include a hominin (early

*Homo* or *Australopithecus*; Kuman and Clarke 2000), a species indeterminate cercopithecine monkey, *cf. Cercopithecoides williamsi* and the first recorded occurrence of *Theropithecus oswaldi* (Pickering 1999) within the site (Table 3). There are a minimum of two hominin individuals identified from the StW 53 infill; the adult cranial specimen (StW 53) and a juvenile represented by upper left maxilla with incisors, canine and third premolar present (StW75a–d). Additionally, there may be a third hominin specimen from StW53: an adult ulna (StW 571) was found a considerable distance from the StW 53 cranium and so the relationship between the adult cranium and the ulna is unclear (Pickering 1999).

The taxonomic position of the cranium StW 53 has been much debated. First assigned to *Homo* by Hughes and Tobias (1977), subsequent arguments were made that this specimen represents a late *Australopithecus* (Clarke 1985, 1998, 2008; Wolpoff 1996; Braga 1998; Thackeray *et al.* 2000; Kuman & Clarke 2000). Recent studies and reconstructions continue to highlight specific traits indicating the similarity of StW 53 to *Homo habilis* (Prat 2005; Curnoe & Tobias 2006), while other studies assert that this specimen represents a male *Australopithecus africanus* (Clarke 2008). Recently a new species has been named, *Homo gautengensis,* with StW 53 as the type specimen (Curnoe 2010). Spoor and colleagues (1994) report that the morphology of the bony labyrinth of the ear preserved in StW 53 is: 'unlike those seen in any of the hominids, or great apes' (Spoor *et al.* 1994: 645), and instead more closely resembles those of the large cercopithecoids. The authors state that this different morphology may have bearing on the locomotor repertoire of StW 53, which may have been a combination of climbing and bipedal locomotion (Spoor *et al.* 1994). Interestingly, another early *Homo* bony labyrinth specimen from Swartkrans (SK 847) shows a very modern human-like appearance (Spoor *et al.* 1994).

*Carnivores*: At least four families of the order Carnivora are represented, and apart from the extinct hunting hyaena, all carnivores represent extant forms (Table 4). The family Canidae is represented by *Canis* cf. *mesomelas*; Viverridae by *Suricata* sp.; Hyaenidae by the extinct *Chasmaporthetes* sp. and Felidae by a leopard-sized cat (Pickering 1999).

*Bovids*: Four subfamilies of the family Bovidae have been identified: the subfamily Bovinae is represented by *cf.* Boselaphini; Antilopinae by an extinct gazelle species also known from Makapansgat (*Gazella* cf. *gracilior*); Caprinae by the extinct musk-ox like *Makapania broomi* and Alcelaphinae by typically savannah dwelling blesbok genus (*Damaliscus* sp.) and a wildebeest-sized Alcelaphini (Table 5; Pickering 1999).

*Other fauna*: Although the faunal sample is small, three additional mammal species have been identified by Pickering (1999), including two extinct hyrax species (*Procavia antiqua, Procavia transvaalensis*), and an indeterminate equid (Table 6).

*Taphonomy*

The StW 53 infill has quite a small bone sample with relatively low numbers of biotically-modified bones. A total of 28 bone specimens show signs of mammalian feeding that is most likely carnivore in origin and just five digested bone specimens are present. While the precise identification of the carnivore species responsible is not possible, Pickering (1999) suggests that leopards (*Panthera pardus*) may have played a role in the bone damage.

The StW 53 bears cut-marks on the zygomatic arch, even though no stone tools are preserved in the StW 53 deposit (Pickering *et al.* 2000; Kuman & Clarke 2000). It appears from the type and location of these cutmarks, that the intention was to deliberately disarticulate the mandible from the StW 53 cranium. The reasons for this activity are unclear, but may be related to cannibalism, or funerary practices (Pickering 1999; Pickering *et al.* 2000).

*Palaeoenvironments*

The small faunal sample does not shed very much light on the palaeoenvironments, but open, drier, grassland conditions are suggested by the presence of the gelada, *Theropithecus oswaldi,* and an equid in the StW 53 infill. This is suggested by Kuman & Clarke (2000) to mark a shift from largely closed, wetter conditions present in Member 4 to drier, more grassland conditions in Member 5.

**Member 5 East Oldowan**

*Stratigraphy*

The Oldowan infill is limited to the eastern portion of Member 5 (Fig. 2). This infill contains one of the oldest artefact assemblages recovered in southern Africa (Clarke 1994; Kuman 1994a,b; Field 1999). The Sterkfontein Oldowan deposit is unique because it contains a near-complete accumulation profile, and the large number of artefacts (3245 artefacts) suggests that Oldowan toolmakers returned repeatedly to the site. In addition to these stone tools, a few *Paranthropus robustus* specimens have been recovered (Kuman & Clarke 2000).

*Dating*

The Oldowan infill has been biochronologically estimated to be *c.* 2.0–1.7 Ma on the basis of the presence of *Phacochoerus modestus* and a giant ostrich, *Struthio* and *Equus* (Kuman & Clarke 2000). The occurrence of *Phacochoerus modestus* is morphologically similar to the same species from Olduvai Bed I and lower Bed II. Also present is the giant ostrich (known from Olduvai Bed I) and three teeth of *Paranthropus robustus,* which are similar to teeth recovered from Kromdraai (Table 2; Clarke 1994; Kuman 1994a,b). Herries and colleagues (2009) and Herries & Shaw (2011) recently proposed a refined date of 1.4–1.2 Ma for the age of this infill based on ESR and palaeomagnetism (Fig. 4).

*Taxonomy*

*Primates*: At least three primate species have been recovered from the Oldowan infill and all are extinct: the robust hominin species *Paranthropus robustus,* the fossil gelada *Theropithecus oswaldi* and a taxonomically indeterminate cercopithecine (Table 3; Pickering 1999). In total, 10 primate individuals have been identified: two *Paranthropus*

*robustus,* a *Theropithecus oswaldi* and seven indeterminate cercopithecines (Pickering 1999).

*Carnivores*: Four families of the order Carnivora are represented in this infill: Canidae, represented by an interminate jackal (*Canis* sp.); Viverridae, represented by a mongoose (*Mungos* sp.), individuals assigned to the meercat, or suricate (*Suricata* sp.), and the grey mongoose genus (*Herpestes* sp.); as well as the Hyaenidae represented by an indeterminate hyaena; and Felidae, represented by the lion (*Panthera leo*) and an indeterminate felid (Table 4; Pickering 1999).

*Bovids*: At least three subfamilies of the family Bovidae are represented in the Oldowan infill. These include: Bovinae, represented by a possible eland (*cf. Taurotragus*); the Antilopinae, represented by the small klipspringer, the steenbuck and the springbok (*Oreotragus, Raphicerus* and *Antidorcas,* respectively); and Alcelaphinae, represented by the blesbok genus (*Damaliscus*), and two indeterminate Alcelaphini species, one of which is wildebeest-sized and the other *Megalotragus*-sized (Table 5; Pickering 1999).

*Other fauna*: Other fauna represented in the Oldowan infill include the extinct suid, *Metridiochoerus modestus,* and indeterminate *Equus* sp., and two extinct species of hyrax (*Procavia transvaalensis, Procavia antiqua*; Table 6; Cooke 1994; Pickering 1999). A diverse micromammal assemblage has been identified from the entire Member 5 East infill, and these species are all generally recovered across the Sterkfontein deposits (Table 8; Avery 2001; Avery *et al.* 2010).

*Taphonomy*

The skeletal part representations observed in the Oldowan led Pickering (1999) to suggest that the fauna represents a death-trap accumulation. While one certain cut-marked bone indicates hominin butchering activities within the catchment area, the low numbers of hominin- and carnivore-modified bone (0.615% of the assemblage, Pickering 1999) indicate that the remainder of the fauna was accumulated through slope-wash action via a narrow chimney or aven in the location of rows Q and R of the main Sterkfontein excavation. This supports Kuman's (1994a,b) conclusion that the Oldowan stone tools were 'washed in from surface deposits through a small diametre, vertical opening or avens' (Pickering 1999: 132). This in turn suggests that the entrance to the cave during this time was not accessible even to the most agile of climbers such as carnivores and primates (Pickering 1999).

*Palaeoenvironments*

Faunal composition from the Oldowan infill, including the equids, springhare, ostrich and lion as well as the various species of antelopine and alcelaphine, have been interpreted as indicating a drier and more open environment (Pickering 1999). The tibia of the giant ostrich (*Struthio* sp.), from this infill is similar to specimens from Olduvai (Clarke 1994). Likewise, Cooke (1994) suggests a similarity between extinct giant warthog (*Metridiochoerus/ Phacochoerus modestus*) specimens with those identified from Olduvai Bed I. However, a taxon-free analysis of the bovids from this infill indicates that a significant amount of tree cover was available in the vicinity (Bishop *et al.* 1999).

**Member 5 Early Acheulean**

*Stratigraphy*

The early Acheulean deposits are more widely distributed than the Oldowan infill, and are spread across the eastern and western areas of Member 5 (Fig. 2). However, the early Acheulean infill in the best context is Member 5 West. Natural concentrations of hematite are also common in these deposits, but are absent in the preceding Oldowan infill. This may be related to drier conditions during the time of Member 5 West formation (Kuman & Clarke 2000). Robinson (1962) mentions a block of Member 4 ('Lower Breccia') found in the Member 5 excavation, suggesting that such material must be present, although it is not yet identified. The faunal sample studied by Pickering (1999) does not apparently contain any reworked material from older deposits. Clarke's schematic representation of the relationship between surface and underground Members is given in Fig. 7 (Clarke 2006).

*Dating*

The Acheulean infill has been estimated at *c.* 1.7–1.4 Ma based on the stone tool typology and the associated *Homo* cf. *ergaster* fossils (Table 1; Kuman & Clarke 2000). In contrast, Herries and colleagues suggest a significantly younger date of 1.3–0.8 Ma for the age of Member 5 West (Herries *et al.* 2009). Herries and Shaw (2011) suggest a more refined age of 1.3–1.1 Ma based on ESR and palaeomagnetism (Fig. 4).

*Taxonomy*

*Primates*: At least two primate species, both extinct, have been recovered from the Acheulean infill; these are the hominin species *Homo* cf. *ergaster* and an indeterminate cercopithecoid (Table 3; Pickering 1999). The hominins from Member 5 West have been studied by Pickering in collaboration with Clarke and Moggi-Cecchi (in Pickering 1999). The minimum number of individuals represented in the Member 5 West deposit is four, based on cranial specimens and teeth (Pickering 1999). Two of these individuals are juveniles in different developmental stages (represented by right maxilla SE 255 and hemimandible StW 84). The other two individuals are adults (represented by left canine SE 1937 and mandible fragment StW 80). In addition, three isolated adult specimens were recovered, namely a right upper second molar (SE 1508), a left upper second molar (SE 1579) and a right upper fourth premolar (SE 2396), which may derive from either SE 1937 or STW 80 (Pickering 1999).

Kuman & Clarke (2000) state that StW 80 mandible bears similarities to Swartkrans specimen SK 15, which has been classified as *Homo ergaster*. The second specimen, StW 84, was recovered from the post-Member 6 area (from Square M/61, whereas in this study only L/63 and M/63 are studied as the L/63 sample). While it was found in decalcified sediments, breccia adhering to the StW 84
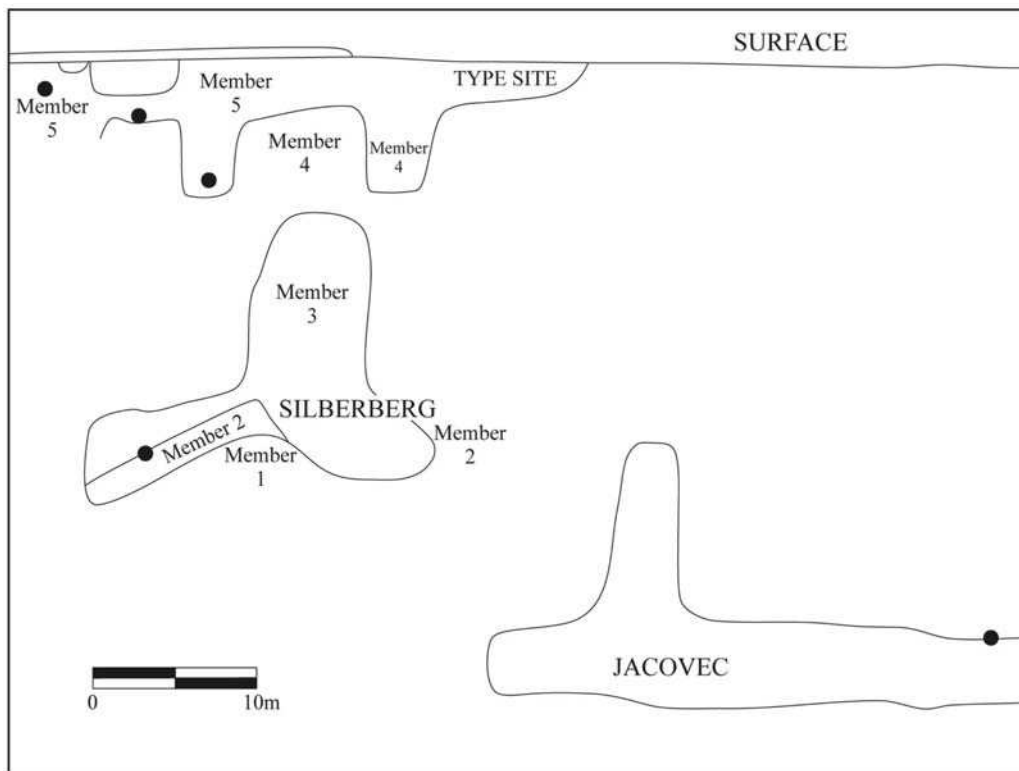
**Figure 7**. Schematic profile showing spatial relationships between the deposits exposed at the surface (Member 4 and 5), and the locations of the underground Silberberg Grotto and Jacovec Caverns. Black dots indicate the locations of hominin finds (redrawn after Clarke 2006).

specimen, combined with an archaic *Homo*-like morphology, led Kuman & Clarke (2000) to conclude that it derived originally from the Member 5 West deposit, but was eroded and reincorporated into the younger decalcified material. The StW 84 specimen demonstrates two points: that decalcification of the Member 5 West material occurred, and that this material was subsequently redeposited into younger deposits. Thus the process of reworking into later infills is convincing, at least within the main Sterkfontein excavation, and for the Lincoln Cave, where sediments appear to have made their way into a neighbouring cave system (Reynolds *et al.* 2003, 2007).

*Carnivores*: The order Carnivora is represented by at least four families, and only one extinct species. The Canidae, represented by the black-backed jackal (*Canis* cf. *mesomelas*); Viverridae, represented by mongoose and meercat species (*cf. Mungos* and *Suricata*, respectively); Hyaenidae, which include the aardwolf (*Proteles* sp.), and the brown and spotted hyaenas (*Parahyaena brunnea* and *Crocuta crocuta*, respectively); and the Felidae, represented by the extinct false sabretoothed cat species, *Dinofelis barlowi*, and the extant lion, *Panthera leo* (Table 4; Pickering 1999). Recent reassessment of the Member 5 carnivores led O'Regan (2007) to suggest that this sabretoothed species does not derive from this infill. One single maxillary specimen assigned to the extinct raccoon dog, *Nyctereutes terblanchei* (SE 125) by Ficcarelli and colleagues (1984) is likely to represent a variable specimen of either *Canis mesomelas* or *C. adustus* (Reynolds 2012).

*Bovids*: Four subfamilies of the family Bovidae have been recorded from this infill: Bovinae, which contains only an indeterminate Tragelaphini; Antilopinae, which are represented by a steenbok (*Raphicerus* sp). and a springbok (*Antidorcas* sp.); the Aepycerotinae, represented by an impala (*cf. Aepyceros* sp.); and finally, the Alcelaphinae, are

represented by a blesbok (*Damaliscus* sp.), and an indeterminate Alcelaphini (Table 5; Pickering 1999).

*Other fauna*: Other fauna identified from this Acheulean infill include: the warthog (*Phacochoerus* cf. *aethiopicus*), an equid (*Equus* sp.), an extinct hyrax (*Procavia antiqua*) and specimens of the extant porcupine (*Hystrix africaeaustralis*) (Table 6; Pickering 1999). A total of 21 micromammal species are identified from the Member 5 West infill, and these are all common across the Sterkfontein deposits (Table 8; Avery 2001; Avery *et al.* 2010).

*Taphonomy*

The damage identified in the L/63 sample and in the contiguous Member 5 West sample highlights some salient differences between these deposits.

Member 5 West's relatively high incidences of carnivore damage (such as tooth scores, and gnaw marks) contrasts with that of the L/63 sample. It is possible that during the formation of the Member 5 West deposit, collapse within the site had created talus slopes of debris, which provided access for animals into the caves (Clarke 1994). Whatever the reason, the data suggest that the Member 5 West area was an attractive shelter for animals during the time of deposit formation (Pickering 1999). The main agent of accumulation in Member 5 West was probably hyaena activity, and more specifically, the brown hyaena, *Parahyaena brunnea*. While brown hyaenas may have made the largest contribution to the assemblage, the remains of porcupines and spotted hyaenas also suggest their involvement. Pickering (1999) proposes a scenario of 'serial denning' which has been noted in modern settings, based on the following: 1) the presence of carnivore damaged bones, 2) a large number of brown hyena-sized prey, 3) a sizeable number of hyena individuals (including juveniles), 4) the presence of hyaena coprolites, 5) digested

bone and 6) complete limb bone shafts are all considered supporting evidence for Pickering's (1999) conclusion that Member 5 West was a serial denning site for carnivores. Member 5 West is the only Member 5 assemblage preserving porcupine damage in conjunction with the porcupine remains themselves, thus it may also have been used as a porcupine lair during the time of deposit formation. Slopewash probably also played an additional accumulative role (Pickering 1999).

With regard to hominin accumulation of the Member 5 West fauna: the complete absence of cut-marks, chopmarks, or hammerstone percussion damage suggests that the fauna accumulated separately from the Early Acheulean archaeological assemblage found in this deposit. The isolated chop-marked bone recovered by Brain (1981) does not point to extensive modification of the fauna in Member 5 West. Pickering concludes that the Early Acheulean tools 'are in no way causally linked to the animal remains, and thus the bones are not archaeological in derivation' (Pickering 1999: 162).

### Palaeoenvironments

Fauna from the Member 5 West Early Acheulean appears to indicate open or wooded grassland or open savanna (Vrba 1975; McKee 1991; Reed 1997; Kuman & Clarke 2000). Certainly, isotope data appear to suggest Member 5 fauna being from a drier, grassland environment, compared with earlier Member 4 times (Luyt 2001; Luyt & Lee-Thorp 2003), and this is in keeping with drier conditions after 1.7 Ma and the onset of the Walker Circulation, as has been proposed by Hopley and colleagues (2007).

## Member 6

### Stratigraphy

Member 6 is a small hanging remnant, presumed to be mid- to late Pleistocene in age, which is exposed on the north wall of the West Pit excavation in the Member 5 West (Kuman & Clarke 2000; Fig. 2). Almost all of Member 6 has been eroded, and from what little remains, it appears that this infill does not contain artefacts, and very little fossil material (Kuman & Clarke 2000).

## Post-member 6
## The L/63 Infill

### Stratigraphy

Within the main excavation of breccias exposed at the surface of the Sterkfontein cave system, the youngest breccia has been called the Post-Member 6 Infill by Kuman and Clarke (2000). Although this infill lacks datable materials, it is markedly different from the contiguous deposits around it (Fig. 2). Instead, it appears to be an intrusive, younger deposit that separates the older Acheulean breccias into Member 5 West and Member 5 East. Unlike the older deposits that both dip to the west, the infill area is horizontally bedded, poorly calcified and similar in appearance to the deposit in the neighbouring Lincoln Cave (Kuman & Clarke 2000).

### Dating

Electron spin resonance ages on fossils from postMember 6 give an age spread of between 684 and 251 ka (Herries & Shaw 2011). A Correspondence Analysis of fauna in Member 5 West, and the two Lincoln Cave deposits indicates that the fauna and hominin species found in the L/63 infill is more similar to the Upper Pleistocene deposits (Table 1; Reynolds *et al.* 2007). Dates are shown in Fig. 4.

### Taxonomy

*Primates*: This group is represented by two primate species, both extant, that include an archaic *Homo sapiens* and a baboon (*Papio cynocephalus*) (Table 3; Reynolds *et al.* 2007). The isolated human specimen (StW 585) is a right upper canine (Kuman & Clarke 2000).

*Carnivores*: Three families of the order Carnivora are represented and none of the species identified are extinct. The family Felidae is represented by an indeterminate cat (*Felis* sp.); Canidae, specifically the black-backed jackal (*Canis mesomelas*) and Viverridae represented by the meercat (*Suricata* sp.), and the grey mongoose (*Herpestes ichneumon*) (Table 4; Reynolds *et al.* 2007). In contrast to the Member 5 West infill, no large carnivores have been recovered from this infill, suggesting that large carnivores may have been less common in the Sterkfontein area during the mid- to late Pleistocene (Reynolds *et al.* 2007).

*Bovids*: Five tribes of the family Bovidae are represented in the L/63 fossil assemblage, and as with the carnivore assemblage, there are no extinct species. These include: the Alcelaphini, represented by an indeterminate blesbok (*Damaliscus* sp.) and an indeterminate Alcelaphine; the Reduncini, represented by the steenbok (*Raphicerus* sp.); Antelopini, represented by the springbok (*Antidorcas* sp.); Cephalophini, represented by the grey duiker (*Sylvicapra grimmia*), and finally, the Peleini, represented by the grey rhebok (*Pelea capreolus*) (Table 5; Reynolds *et al.* 2007).

*Other fauna*: Other fauna represented within the L/63 infill include the Plains zebra (*Equus burchellii/ quagga*), the hyrax (*Procavia capensis*), the porcupine (*Hystrix africaeaustralis*), the springhare (*Pedetes capensis*) and the Cape Hare (*Lepus capensis*) (Table 6; Reynolds *et al.* 2007).

### Taphonomy

The L/63 solution cavity the main excavation has earned the nickname 'The Porcupine Lair', due to the large numbers of porcupine-gnawed bone observed there. The preliminary study indicated that, although present, the incidence of porcupine damage was not high enough to indicate a porcupine lair (O'Regan, pers. comm.). The L/63 area has the lowest incidence of non-rodent mammalian modification to the fauna, with 1.1%, contrasting markedly with the neighbouring Member 5 West totals for the same category (3.3%). A total of 1.86% of the L/63 sample was modified by porcupines and other rodents. Although this is the highest percentage of porcupine and rodent damage in all the samples compared, it does not suggest significant porcupine/rodent involvement in the damage of the sample (Reynolds *et al.* 2007).

In contrast to the Member 5 West pattern, the L/63 area has the highest incidences of porcupine/rodent gnawing, but also the lowest incidence of non-rodent mammalian (presumably carnivore) damage. In both cases the low percentages of damage, along with the fact that no large carnivore species were identified from the L/63 area, would suggest that there was probably no carnivore dens in the area during the deposition of the L/63 material, but that porcupines were probably more active in the area during the time the L/63 fauna was accumulating (Reynolds *et al.* 2007). Only one hyaena coprolite has been recovered from the sample studied for this analysis, but further excavations being conducted by Clarke have produced more hyaena coprolites (Clarke, pers. comm.). As with Member 5 West, the fauna of the L/63 sample were most probably not accumulated by humans, since no cut-marked, chop-marked bone or burnt bone have been identified in the L/63 sample.

*Palaeoenvironments*

The L/36 fauna differ from that of the Member 5 West deposit (Reynolds *et al.* 2007). Instead of the large carnivore species found in Member 5, this infill preserves smaller carnivores, such as the black-backed jackals and viverrids. No extinct species are represented, and the overall faunal composition is very similar to the fauna present in the area today (Reynolds *et al.* 2007).

**Lincoln Cave**

*Stratigraphy*

The Lincoln-Fault cave system lies adjacent to the Sterkfontein Cave system, approximately seven metres from the northernmost limit of the main excavation (Fig. 2). There are two fossil deposits within the Lincoln Cave: a hard and a soft, poorly calcified breccia. The South deposit contains both hard breccia and soft breccia, and these grade into each other and are difficult to separate clearly, but the bulk of the artifacts are contained in the softer breccia. The Lincoln Cave North and South deposits were systematically excavated from early 1997 until 1998 (Reynolds *et al.* 2003, 2007).

*Dating*

Uranium Series dating of the capping and lower flowstones in the North profile yielded age estimates of between 252 600 ± 35 600 years and 115 300 ± 7700 and (Table 1; Reynolds *et al.* 2003, 2007; indicated in Fig. 4).

*Taxonomy*

*Primates*: Hominins are represented by four specimens assigned to *Homo ergaster* (Reynolds *et al.* 2007). The three teeth from Lincoln Cave South represent a minimum of two individuals; a child of roughly three years of age (represented by StW 591 and StW 592), and an adult (StW 593). StW 594 from Lincoln Cave South is a hominin cranial fragment, which is likely to also represent the same species (Table 3).

*Carnivores*: Four carnivore species are represented, and all four are extant species: the Felidae, represented by an indeterminate cat (*Felis* sp.) Canidae, by a jackal (*Canis*

sp.); and the Viverridae by the meerkat (*Suricata* sp.) and Hyaenidae by an indeterminate hyaena specimen (Table 4; Reynolds *et al.* 2007).

*Bovids*: Four bovid tribes are represented: Alcelaphini by the extinct giant hartebeest (*cf. Megalotragus* sp.); the Hippotragini by an antelope (*Hippotragus* sp.); Tragelaphini by the bushbuck (*Tragelaphus scriptus*) and Cephalophini by an indeterminate small duiker (Table 5; Reynolds *et al.* 2007).

*Other fauna*: Other fauna recovered from the Lincoln Cave include: the Plains zebra (*Equus burchellii/quagga*), the hippo, (*Hippopotamus amphibius*), the warthog (*Phacochoerus africanus*), the extant hyrax (*Procavia capensis*), the porcupine (*Hystrix africaeastralis*), the springhare and Cape Hare (*Pedetes capensis* and *Lepus capensis*, respectively) (Table 6; Reynolds *et al.* 2007).

*Taphonomy*

Relatively higher percentages of canivore damage in Lincoln Cave North and rodent gnawing in L/63 may suggest that these agents were more active in the surface catchment area during the time of deposition of the fauna. Low proportions of hyaena remains (only one piece in Lincoln Cave North) and the lack of hyaena juveniles or subadults would seem to discount a primary carnivore den accumulation for the younger deposits.

*Palaeoenvironments*

The majority of the fauna are extant forms which are common in the area today. In contrast with the Member 5 West assemblage, the younger deposits are dominated by small carnivore species, suggesting that larger carnivores (such as lions, leopards and hyaenas) moved out of the Sterkfontein area during the Upper Pleistocene (Reynolds *et al.* 2007, Reynolds 2010).

**ARCHAEOLOGY**

The presence of Earlier Stone Age (ESA) and Middle Stone Age (MSA) lithic assemblages indicate that hominins favoured the catchment area around the site of Sterkfontein for tool manufacture. Kuman (1994a,b, 2007) has proposed that the combination of available raw materials, shelter provided by the dolomite outcrops and the likely presence of shade-trees would have created an attractive locale for hominins to gather raw materials and knap tools. The abundance of artefacts, particularly for the Oldowan assemblage indicates that the accumulation occurred over a long period, as opposed to single-event sites found elsewhere.

**Member 5 East Oldowan**

The Oldowan tools, which derive from the lowest excavated levels of the Sterkfontein surface excavation, are one of the oldest known lithic assemblages from South Africa. Other Oldowan assemblages recently published from southern Africa include Wonderwerk Cave, in the Northern Cape Province, and these deposits date to ~0.78–1.96 Ma (Chazan *et al.* 2008). The Sterkfontein Oldowan deposit contains a near-complete accumulation profile (Kuman 1994a,b, 1996; 2003; Kuman & Clarke

2000). The assemblage comprises 3245 pieces, of which 84% are less than 20 mm in length (Kuman 2007). Since the full range of artefact sizes are represented, as well as the high levels of small pieces, this assemblage is assumed to be representative of a primary or near-primary context (Kuman 2007). The majority of the material is in a fresh condition, with only a small portion showing signs of weathering and abrasion.

The assemblage shows that hominins used simple manufacturing methods, with the emphasis on easily flaked stone types, especially quartz (Kuman 1994a,b, 2007). Quartz was the most important raw material; with 94% of all Oldowan artefacts and 68% of all cores made on quartz (Kuman 2003). Because quartz fractures so easily, the assemblage is dominated by chunks, flakes and chips which commonly result from quartz-knapping (Kuman 1994a,b). Other utilized raw materials are quartz-ite and, less commonly, chert. There is evidence of direct percussion, and also some use of bipolar flaking (i.e. hammer and anvil) techniques. The most commonly recovered core-types are: simple cores, chopper-like cores, discoid-like cores, at least one protobiface, casual, irregular and quartz polyhedral cores (Kuman 1994a,b, 2007).

## Member 5 West Acheulean

At Sterkfontein, percentages of small flaking debris differentiate between the Acheulean and the Oldowan levels. The Early Acheulean assemblage of Member 5 West is composed of 701 pieces, but only 2.7% of the assemblage is small flaking debris ≤ 20 mm in length (Kuman 1994a,b 1998; Field 1999). Larger flakes (complete, incomplete and flaked) make up just 8.4% of that assemblage, whereas cores contribute 36.8% to the total. Manuports make up 29.7% of the assemblage (Field 1999). The relatively high percentages of small flaking debris in the Lincoln Cave South and L/63 area deposits suggest that these assemblages were not deposited during Member 5 West times, when such elements were eroded from the surface before deposition into the infill (Kuman 1994a,b; Field 1999).

Manuports and polyhedral cores are typical of the Acheulean assemblage at Sterkfontein (Kuman 1994a,b; Field 1999). Manuports are river cobbles with the cortex intact and without signs of utilization, such as battering. Hominins selected the cobbles from the gravels that lie within 300 m of Sterkfontein and brought them to the site for later use. In Member 5 West, manuports comprise 29.7% and cores 37% of the assemblage, which has lost most of its small material through erosion (Kuman 1998). However, the absolute number of manuports is also very high, a pattern which is often noted in Developed Oldowan/Early Acheulean assemblages (Schick 1987; Potts 1991).

## The L/63 Infill and Lincoln Cave deposits

Prior to the Lincoln Cave excavation, the only MSA lithics derived from excavations of overburden deposits near Member 4 and material recovered from mixed or decalcified deposits (Mason 1962a,b; Kuman 1994a,b). The excavation of Lincoln Cave South deposit yielded an assemblage of 69 artefacts and manuports, of which the majority appear to have been deposited during the MSA. Specifically, the *in situ* recovery of diagnostic artefacts, including a diabase blade and flakes with facetted platforms, suggest an MSA industry was present at Sterkfontein (Reynolds *et al.* 2007). However, the recovery of a bifacial chopper core also from the Lincoln Cave South deposit is more characteristic of the Early Acheulean industry, suggesting incorporation of some older artefacts into the deposit, along with some manuports. Manuports recovered from the L/63 area deposit suggest much the same process of erosion and redeposition (Reynolds *et al.* 2007). The Lincoln Cave North assemblage does not have any small flaking debris elements, and only a small sample of non-diagnostic core tools. Raw material proportions and artifact typologies suggest that Lincoln Cave South and L/63 area are more closely related and that both these deposits are younger than the Member 5 West Early Acheulean deposit.

In contrast to the L/63 deposit, diagnostic MSA artefacts present in Lincoln Cave South indicate that this deposit was formed during the Middle Stone Age. However, the presence of a bifacial chopper core and manuports most closely resembling ESA material strongly suggest mixing between the Lincoln Cave South and material deriving from an older deposit, probably Member 5 West. When the L/63 assemblage is compared to the Lincoln Cave deposits, both the small flaking debris and raw material distributions suggest these deposits are more similar in age (Reynolds *et al.* 2007). The L/63 area assemblage contained only 50 artefacts, of which none are diagnostic of a specific industry. However, the high proportions of small flaking debris and flakes, combined with the low proportions of manuports and polyhedral cores, suggest an age younger than the contiguous Member 5 West deposit, where these elements are abundant (Field 1999; Table 1).

Now that we have reviewed the fauna and artefacts from the individual Sterkfontein deposits, we progress in the next section to a discussion of pertinent debates about the Sterkfontein material.

## DISCUSSION

### Complexity of karst deposits and their interpretation

One of the ongoing debates at Sterkfontein is the range of dates produced by diverse methods (see Table 1), and the lack of agreement between faunal/archaeological dates and absolute dating methods (e.g. Clarke, in press). The complexity of the karst deposits lies at the heart of this debate. These deposits result from various processes, each acting on different scales, from large-scale climatic cycles right down to the prevailing conditions at the individual site catchment area. At the very largest scale, climate conditions are linked to planetary orbital variations (Milankovitch cycles) and more local effects created by circulation patterns and variation in the Earth's surface (de Menocal 1995, 2004; Hopley *et al.* 2007). At a smaller scale, the floral communities are composed of different

**Table 11**. Summary of palaeoenvironmental reconstructions for Sterkfontein Members 2 to Post Member 6 deposits.

| Sterkfontein Member | Palaeoenvironmental reconstruction | Data source and references |
| --- | --- | --- |
| Jacovec Cavern | Mosaic habitat of open and closed habitats, with a riverine gallery forest, with bushland and open country in close proximity. | Fauna (Kibii 2004) |
| Member 2 | Presence of open grassland with rocky outcrops, permanent water supply, and riverine gallery forest wetter habitats | Fauna (Pickering *et al.* 2004a) |
| Member 4 | Mosaic habitats with forest fringe environment and grassland habitats close by. | Fauna (Vrba 1974, 1975, 1980) <br> Fossil wood (Bamford 1999) <br> Micromammals (Avery 2001) <br> Stable carbon isotopes and Sr/Ca ratios (Sponheimer *et al.* 2005a,b) |
| Member 5 StW 53 infill | Open, drier, grassland conditions | Fauna (Kuman & Clarke 2000) |
| Member 5 East | Drier, more open environments, but with a significant amount of tree cover present | Fauna (Pickering 1999) <br> Ecomorphology (Bishop *et al.* 1999) |
| Member 5 West | Open grassland and/ or wooded grassland | Fauna (Vrba 1975; McKee 1991; Reed 1997; Kuman & Clarke 2000). <br> Stable carbon isotopes (Luyt 2001; Luyt & Lee-Thorp 2003) |
| Post Member 6 (L/63); Lincoln Cave deposits | Similar to modern environments | Fauna (Reynolds *et al.* 2007) |

proportions of C$_3$ (trees) and C$_4$ (grass) vegetation and support fauna associated with these types of habitats (e.g. Vrba 1974, 1975; Reed 1997; Andrews & Bamford 2008). Taphonomic processes, (animals, slope wash) control how bones enter the fossil record, but the time taken by deposition means several types of processes and habitats are probably represented in a single deposit (Pickering 1999; Hopley & Maslin 2010). Finally, within breccias there is increasing evidence for cycles of deposition, erosion and redeposition (de Ruiter 2003; Reynolds *et al.* 2007; Herries *et al.* 2009). A recent study by Hopley & Maslin (2010) suggests that southern African cave deposits sample more than one processional cycle (~7000 years), and are therefore likely to be 'climate-averaged', showing a mix of species characteristic of both open, grassland-dominated periods of the climate cycle, as well as woodland-dominated extremes. Mixing may also have implications for the dating difficulties and may compounded difficulties in sampling procedures for the dating of cave sediments. Given the complexities of cave formation processes, it is not surprising that different techniques applied to the same Sterkfontein Member may provide different dates (as has been suggested by Pickering & Kramers 2010 and Herries & Shaw 2011).

In summary, the complexity of the karst formations affects all other aspects of interpretation, including evidence of climate change, understanding fossil communities, dating possibilities and identifying possible new species (e.g. O'Regan & Reynolds 2009; Hopley & Maslin 2010; Herries & Shaw 2011). As a result, the evidence for the various patterns observed in the fossil record is best viewed as having been filtered by numerous processes. Thus the consideration of all aspects (specifically the dates

in the light of the stratigraphy and artefacts and faunal material contained within them) remains the most reliable means of interpretation for karst deposits (Kuman & Clarke 2000; Reynolds *et al.* 2007; Clarke, in press).

**Varying environmental reconstructions for Sterkfontein Member 4**

Sterkfontein Member 4 is an important deposit, due mainly to the large sample of *Australopithecus africanus* specimens that has been recovered from this Member (Lockwood & Tobias 1999, 2002; Pickering *et al.* 2004b; Moggi-Cecchi *et al.* 2006 and others). The hominins and the associated abundant faunal assemblage have the potential to reveal the preferred habitats of *Australopithecus africanus* (and possibly also of the proposed *Australopithecus* 'Second species'), as well as the environmental context prior to the appearance of early *Homo, Paranthropus* and the earliest stone tool industries in southern Africa (Oldowan and Early Acheulean Industries). One of the most important debates is exactly what type of environments are represented by the fauna, flora and sedimentological evidence, and the results of various studies indicate differing habitat types.

Sterkfontein Member 4 was previously characterized as representing closed, forested environments (e.g. Vrba 1975) but later studies have indicated that the environmental context is more complex. Some part of Member 4 fauna appears to sample grassland environments, so these are likely to have been present at least some of the time during Member 4 accumulation. Indeed, several recent studies have identified a significant grassland signal within the Member 4 fauna, based on a variety of environmental proxies, ranging from hominin diets (van

der Merwe *et al.* 2003); through to micromammals (Avery 2001; Avery *et al.* 2010), primate postcranial morphology (Elton 2001) and in-depth isotopic work (Luyt 2001; Luyt & Lee-Thorp 2003), which all indicate that a significant grassland component was already present during Member 4 times. While Member 5 deposits preserve numerous species more typically associated with grasslands, including the extinct gelada baboon (*Theropithecus oswaldi*) and ostrich bones and eggshell (*Struthio*), this does not necessarily mean that Member 5 represents exclusively dry, grassland environments, nor that Member 4, in contrast, sampled only moister, more forested environments. Except for the fossil wood analysed by Bamford (1999), all other studies indicate high levels of habitat variability in Member 4, but each study suggests a slightly different mix of these habitat types. This is equally true of studies focusing on taxonomy (e.g. primates, Kibii 2004); taxon-free ecomorphological techniques (e.g. Elton 2001), and stable light isotope results of fauna and hominin tooth enamel (van der Merwe *et al.* 2003; Lee-Thorp *et al.* 2007). Likewise, high habitat variability over the same time period has been reported from Laetoli, based on vegetation evidence (Andrews & Bamford 2008).

This revised paleoenvironmental reconstruction has bearing on the occurrence of *Equus* in Sterkfontein Member 4, fossils of which have previously thought to be intrusive from a later Member 5 infill (Kuman & Clarke 2000). The first appearance of the equids in the eastern African fossil record at $2.33 \pm 0.03$ Ma (lower Member G of the Shungura Formation, Ethiopia) combined with the relatively younger age estimates for Member 4 suggested by combined palaeomagnetic, uranium-lead and ESR studies (Schwarcz *et al.* 1994; Pickering & Kramers 2010; Herries & Shaw 2011), show that there is no *a priori* reason why *Equus* could not occur in the later, upper beds of Sterkfontein Member 4, which date to less than 2.36 Ma. The ESR ages in particular, supported by palaeomagnetism and U-Pb suggest that Member 4 formed over a very long time period, perhaps as much as 600 ka (2.6–2.0 Ma).

Of particular relevance to this question is the in-depth isotopic study of a sample of 10 Sterkfontein Member 4 hominins, sampling specimens assigned both to *Australopithecus africanus* and to Clarke's (1988) 'second' species (van der Merwe *et al.* 2003). Not only do van der Merwe and colleagues report a significant $C_4$ component in the diets, but they conclude that *A. africanus* 'had the most variable dietary behaviour of all the early hominin species we have investigated' (van der Merwe *et al.* 2003: 593).

So, the question remains: does Member 4 represent a consistent mix of gallery forest that fringed the Blaaubank river, with close proximity to open grassland areas through time? Or is it perhaps a sampling of closed, wetter habitats (interglacials), interspersed with drier, open episodes (glacials)? Overall, the majority of the evidence points towards a mosaic habitat (a combination of open grassland with closed, forested areas in close proximity), which is in keeping with the speleothem signal reported from the Limeworks Member 1 Collapsed Cone and Buffalo Cave speleothem in the Makapansgat Valley

(Hopley *et al.* 2007). However, this apparent combination of habitats may equally represent distinct environmental shifts between closed, forested conditions, and cooler, drier grassland conditions, which have become time-averaged in the fossil record. This process, referred to as 'climate-averaging' (Hopley & Maslin 2010) may characterize deposits which accumulate over more than one climatic cycle. Recent studies of the structure of carnivore guild community (O'Regan & Reynolds 2009) and studies of the relationship between large-scale climate changes and karst deposition (Hopley & Maslin 2010) strongly suggest that time-averaging played an important role how certain different types of habitats appear together in Member 4. An alternative hypothesis regarding the existence of Member 4 mixed environments is the Tectonic Landscape Model (TLM, Reynolds *et al.* 2011). Geomorphological evidence suggests the presence of a fault close to Sterkfontein, which would have created and sustained heterogeneous habitats consistently at Sterkfontein (Bailey *et al.* 2011; Reynolds *et al.* 2011). Modern analogies of how tectonics affects diversity are the tectonically-controlled wetlands of the Nysvley (South Africa) and Okavango (Botswana) regions; in both cases, a close proximity to faults in the presence of surface water creates high habitat diversity and promotes a wide range of plant, animal, fish and insect diversity (Ramberg *et al.* 2006; Havenga *et al.* 2007). This type of habitat creation, facilitated by tectonic motions, may have increased the biodiversity of plants and animals as has been observed in Sterkfontein Member 4

**Taphonomic differences between Sterkfontein Members**

Certain fossil accumulations at Sterkfontein may represent death traps, where animals have fallen into steep shafts or avens from which they could not escape (Pickering 1999). The presence of several species of carnivores within Member 2 suggests that they too fell prey to the same death trap which appears to have trapped the StW 573 hominin (Pickering *et al.* 2004a). No tooth marks have been observed on the exposed surfaces of the StW 573 bones, and this, combined with evidence of at least partial mummification of the left-hand and forearm bones of the specimen, suggest that it was not accumulated by carnivores (Pickering *et al.* 2004a). The recovery of extinct carnivores, specifically of the genera *Chasmaporthetes, Homotherium* and *Megantereon,* suggest that they were common in the area during the time of accumulation. The sabretoothed species are rare in the fossil deposits of the Cradle of Humankind, and appear spatially restricted mainly to the southern end of the Cradle of Humankind area, concentrated around the site catchment areas of Sterkfontein, Swartkrans and Kromdraai (Reynolds 2010). However, the new *Australopithecus* site of Malapa has also yielded species of extinct carnivores, such as *Dinofelis* sp., and *Megantereon whitei* at around 1.95 Ma (Dirks *et al.* 2010).

Little is known about potential bone accumulating behaviour of these extinct carnivore taxa, but the Friesenhahn site in Texas (USA) studied by Marean and Ehrhardt

(1995) has been interpreted as a *Homotherium* den. In this case, the sabretooths appear to have specialized upon juvenile proboscidean prey. In addition, this species may have damaged the bones with similar tooth-mark frequencies as has been observed in modern hyaena and leopard den assemblages (Marean & Ehrhardt 1995; Pickering *et al.* 2004b). The lack of carnivore tooth damage supports the overall interpretation that Member 2 was not accumulated by carnivores, extinct or otherwise. In the Jacovec Cavern there is only one *Australopithecus* clavicle with gnaw-marks (Partridge *et al.* 2003). There is no evidence apart from this to suggest that Jacovec was a carnivore den or a death trap accumulation. The majority of the fauna appear to have been washed into the cavern from the catchment area at the surface (Kibii 2004).

Member 4 shows a different pattern of accumulation. This Member contains the largest numbers of *Australopithecus* specimens, co-occurring with a large carnivore guild totalling 14 species (Table 4). It has been suggested that there may be a bias towards females and immature males of *Australopithecus africanus,* which may in turn reflect the prey selection of large carnivores active at the cave during the accumulation of Member 4 (Lockwood & Tobias 2002). Based on modern prey spectra, and body size estimations of fossil carnivores, the majority of the carnivores would be preying on medium-sized prey, including hominins (O'Regan & Reynolds 2009). Studies of bone surface modification suggests that the Member 4 fossils were accumulated by carnivore activity, natural death trap accumulations and slope wash (Brain 1981; Kibii 2004).

By Member 5 times (StW 53 infill, Member 5 East and West), virtually all large extinct carnivores have disappeared, and the faunal assemblage is dominated by extant medium and larger-sized carnivores such as lions (*Panthera leo*), leopards (*Panthera pardus*) and several species of hyaenas (Table 4). From the presence of coprolites, and specimens of juvenile carnivores, it appears that these species were using the cave as a denning site (Pickering 1999). The presence of cut marks on the StW 53 hominin cranium, suggests that hominins were using the site, both as an area for the manufacture of stone tools and for certain butchery activities in early Member 5 times (Pickering *et al.* 2000). This is further corroborated by an abundance of Oldowan and Acheulean stone tools in the other two Member 5 infills (Kuman & Clarke 2000). However, the dearth of chop- or cutmarked bone argues against a significant role for hominins in Member 5 faunal accumulation (Pickering 1999).

By Member 6 and Post Member 6 times (L/63 and Lincoln Cave), the only carnivores recovered in the deposits are small carnivores, such as the black-backed jackal and bat-eared fox (*Canis mesomelas* and *Otocyon megalotis,* respectively). While large carnivores become scarcer at the site through time, small canids and viverrids appear abundant in later deposits than in Member 4 or Member 5 assemblages. This pattern suggests that both canids and felids may have varied their use of areas of the Sterkfontein caverns through time, most likely for denning purposes (Reynolds *et al.* 2007). Fossils associated with the

Lincoln Cave (located in a nearby miner's dump, called 'Dump 7') are dominated by small carnivores (in particular, jackals *Canis* cf. *mesomelas*), with several juveniles of more than one carnivore species, suggesting that the Lincoln Cave was commonly used as a small carnivore den at some point during the Pleistocene (Reynolds 2010). Possibly, the larger carnivore species moved out of the Sterkfontein area as humans became more technologically competent and competitive towards the Upper Pleistocene (Reynolds *et al.* 2007; Reynolds 2010).

## CONCLUSIONS

The initial stages of study of many African cave sites, including Sterkfontein, suggest simple environmental differences between deposits and through time. Over time, subsequent studies revise these early, simple models by recognizing complexity of various kinds: climatic, stratigraphic, taxonomic and environmental, that was not fully appreciated before, such as the three separate infills in Sterkfontein Member 5 (e.g. Kuman & Clarke 2000).

Even after 75 years of excavation and study of the Sterkfontein deposits, the telling of the Sterkfontein story is not finished. Many researchers have all contributed to our understanding of the site and its significance (Tobias 2002). Fortunately, the use of novel techniques and new approaches continue to yield exciting insights into the cave and its remains. All we are able to present here is the Sterkfontein story as it stands so far, knowing that many chapters are yet to be written.

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