Quaternary International 202 (2009) 14-28

Contents lists available at ScienceDirect

Quaternary International

journal homepage: www.elsevier.com/locate/quaint

A multi-disciplinary seriation of early *Homo* and *Paranthropus* bearing palaeocaves in southern Africa

Andy I.R. Herries^{a,b,*}, Darren Curnoe^a, Justin W. Adams^c

^a Human and Primate Origins Program, School of Medical Sciences, University of New South Wales, 2052 Kensington, Sydney, Australia
^b Geomagnetism Laboratory, Department of Earth and Ocean Sciences, Oliver Lodge, University of Liverpool, Liverpool L69 3BX, UK
^c Department of Biomedical Sciences, Grand Valley State University, 218 Padnos Hall, Allendale, MI 49506, USA

ARTICLE INFO

Article history: Available online 26 July 2008

ABSTRACT

Fossils of early *Homo* and *Paranthropus* have been recovered from several sites in southern Africa. Unfortunately, their precise age has historically been difficult to assess, hampering the reconstruction of their relationships to each other and to fossils from eastern Africa. Multi-dating strategies combining biochronological, archaeological, palaeomagnetic, electron spin resonance (ESR) and uranium series techniques are now clarifying their age. The following sequencing of sites is suggested: Swartkrans Member 1 (~2.0 Ma), Gondolin (~1.8 Ma), Kromdraai (1.8–1.7 Ma), Sterkfontein M5A (1.8–1.4 Ma), Swartkrans M2 (1.7–1.1 Ma), Sterkfontein M5B (1.4–1.1 Ma), Sterkfontein M5C (1.3–0.8 Ma), Swartkrans M3 (~1.0–0.6 Ma). The position of Coopers D and Drimolen is difficult to access because they only have faunal age ranges (1.9–1.6 Ma). ESR suggests mixing is a potential major problem in multi-generational sites. The oldest southern African representatives of early *Homo* and *Paranthropus* occur around 2.1–1.9 Ma in Swartkrans Member 1 and are recorded almost continuously in the palaeocave deposits until around 1.0–0.6 Ma in Swartkrans Member 3. Currently, these data suggest that *Paranthropus* and *Homo first* occur significantly later in the southern African record than the eastern African record. Moreover, *Paranthropus* persists much later in southern Africa than in eastern Africa.

© 2008 Elsevier Ltd and INQUA. All rights reserved.

1. Introduction

The geographic and temporal origins of *Homo* and *Paranthropus* (or robust *Australopithecus*) and their relationship to earlier australopithecines remain fundamental questions of palae-oanthropology. The importance of the southern African representatives of these taxa to addressing such questions has been unclear due to poor chronological resolution at the southern African palaeocave sites. The southern record of early *Homo* totals 64 craniodental fossils or more than one-third of the total African early *Homo* sample (Curnoe, in press-a), and has been recovered from five palaeo cave sites. *Paranthropus* fossils are much more numerous with almost 500 specimens having been recovered from six localities (De Ruiter et al., 2006). As in eastern Africa, fossils of early *Homo* and *Paranthropus* have been recovered together from Sterkfontein, Swartkrans, Kromdraai, Drimolen, and Gondolin (Fig. 1), while Coopers has so far only yielded Paranthropus. These

deposits are generally thought to be Plio-Pleistocene in age. In contrast the other *Homo* bearing sites in southern Africa, include Gladysvale, Cornelia and Elandsfontein, are all thought to be less than 1.0 Ma old (Brink, 2002; Lacruz et al., 2002; Klein et al., 2006).

Until recently, dating of the southern African deposits has relied heavily on faunal and archaeological comparisons with materials from radiometrically dated sites in eastern Africa. The reliability of this approach is undermined by various factors, including: (1) the view that fine-scale synchronicity of similar species and tool types can reliably be deduced in both regions, an assumption that seems to be questionable; (2) studies being undertaken of fossils and tools which were not recovered in situ (often from mining dumps) and thus of uncertain provenience; (3) complex cave stratigraphy and large-scale anthropogenic disturbance of deposits (mining activities at these sites); (4) an absence of geological materials amenable to K/Ar and $\frac{40}{\text{Ar}}$ Ar dating, and until recently a lack of absolute dating techniques applicable to these deposits and their fossils; and (5) the recovery of temporal palimpsests or time-averaged assemblages due to complicated site formation processes and histories as well as variable excavation procedures over 60 or more years of study. This has made chronological, systematic and typological comparisons between eastern and southern African fossils problematic. These problems are further exacerbated by the fact





^{*} Corresponding author. Human Origins Group, School of Medical Sciences, University of New South Wales, 2052 Sydney, Australia. Tel.: +61 2 9385 8508; fax: +61 2 9385 8016.

E-mail addresses: andyherries@yahoo.co.uk, a.herries@unsw.edu.au (A.I.R. Herries).

^{1040-6182/\$ -} see front matter © 2008 Elsevier Ltd and INQUA. All rights reserved. doi:10.1016/j.quaint.2008.05.017



Fig. 1. Location of the southern African hominin sites in the Cradle of Humankind.

that dates for some faunal deposits in eastern Africa remain open to interpretation based on stratigraphy.

In the last decade and a half a range of new geochronological approaches have been applied to these sites (Blackwell, 1994; Schwarcz et al., 1994; Curnoe, 1999; Partridge et al., 2000; Curnoe et al., 2001; Herries and Latham, 2002; Thackeray et al., 2002; Herries, 2003a; Albarède et al., 2006; Herries et al., 2006a; Adams et al., 2007; Balter et al., 2008). These have brought new insights into both the geomorphic history and dating of the cave sites. The current study reviews and synthesises these published studies as well as adding previously unpublished data and observations, along with a new biochronological analysis to create a temporal seriation of the southern African hominin palaeocave sites. The main goal is to provide current 'best apparent ages' for these palaeocave deposits and specifically for early *Homo* and *Paranthropus* in southern Africa.

2. Methods

The palaeomagnetic methodology follows the protocols of that outlined in Herries (2003a), Herries et al. (2006a,b) and Adams et al. (2007). Biochronologic methodology follows that discussed by Delson (1984, 1988) and Vrba (1982), among others (see summary in Adams, 2006; Adams et al., 2007). Electron spin resonance (ESR) dating principles and methodologies are outlined in Grün (1989, 1998, 2006a,b) and have undergone continuous development. While ESR dating appears to work at the southern African palaeocaves (i.e. results are non-random: Curnoe et al., 2001) the many variables involved in calculating ESR ages and the uncertainties in reconstructing the geomorphological history and stratigraphy of these sites makes the results prone to large errors (both random and systematic: for an explanation see Grün, 2006a,b). Some important uncertainties described by Curnoe (1999), Curnoe et al. (2001) and Grün (2006a,b) include:

- Saturation effects, recrystallization or anomalous fading in the ESR signal.
- Large scatter around the dose response curve for older enamel samples leading to large errors in the estimation of the accumulated dose.
- Diachronic changes in the sedimental and tooth (enamel and dentine) concentrations of water, U, Th and K, leading to variation in external dose rates received by teeth (assumed in ESR to have been negligible).
- Spatial variability in radioactive isotope concentrations leading to variation in the external dose rate; problematic when external gamma spectrometric measurements derive from sediment several metres from the tooth or when teeth have been recovered from a dump/museum and the original sedimentological setting is unknown or lost.
- Significant changes in the cosmic dose rate through time owing to erosion of the overlying dolomite roof and breccia deposits.
- High uranium concentrations in tooth enamel and dentine leading to large differences between the uranium uptake models (Early Uptake or EU and Linear Uptake or LU) used to calculate ESR ages.
- An actual U-uptake history which is not covered by conventional uptake models; estimates suggest that teeth from 10 to 20% of sites may fall into this category owing to leaching or strongly delayed uranium uptake.
- Uranium leaching of sediments, leading to overestimation of the age of the samples.
- Reworking of fossil materials, leading to incorrect estimation of cosmic and external dose rates and heterogeneity of tooth ages or time-averaging of palaeontological samples.

Unless indicated otherwise, we assume that the ESR linear U-uptake (LU) age is closest to the true age of samples from the

southern African palaeocaves. This seems reasonable given geomorphological evidence from these sites, including for largescale water induced erosion (esp. swallow hole: Partridge and Watt, 1991) and for their complex hydrological history incorporating periodic exposure to high intensity rains of considerable duration (Butzer, 1984). Moreover, U-series analyses on teeth from Sterkfontein and Swartkrans (Schwarcz et al., 1994; Curnoe et al., 2001) have found the activity ratio of 230 Th/ 234 U to mostly be less than unity implying secular disequilibrium. Finally, independent dating evidence in the form of palaeomagnetic, faunal and archaeological ages for these sites clearly also has a role to play in selecting U-uptake model ages. ESR dates are presented traditionally in thousands of years (ka) in the results section, but have been converted to millions of years (Ma) for the discussion and conclusions so that different methods can be more easily correlated. While single absolute dates are presented with their two sigma errors (\pm) , age ranges are presented with maximal ages for the deposit including their two sigma errors (\pm) . Confidence intervals calculated for the stratigraphic range of fossils employ the methods of Marshall (1990).

The stratigraphy of the sites is relatively simple as currently defined. All sites employ a Member system as outlined in Partridge (2000). Member 1 represents the potentially oldest deposits and Members 3, 5, etc. increasingly younger deposits. For example Swartkrans has three members discussed in this paper (Members 1–3), Sterkfontein has six members. Kromdraii and Coopers are slightly different in that they consists of more than one site which are separated as A and B, etc. Gondolin is a single cave deposit but it has been separated on the basis of stratigraphically unconnected sections or localities, GD1 and GD2 (see Herries et al., 2006a; Adams et al., 2007).

3. Sterkfontein

3.1. Stratigraphy

The history of mining and fossil prospecting activities at the Sterkfontein caves has been previously described by Brain (1981), Pickering (1999) and Partridge (2000), among others. While occasional fossil materials were likely recovered from the site around the turn of the 20th century, concentrated work did not begin until 1936 with ex situ and in situ exploration of the deposits by R. Broom and J.T. Robinson, continuing until 1947 (Brain, 1981). A series of fossil-bearing breccia deposits (Members 1–6 and post-Member 6) have been identified from both these initial phases of excavation and subsequently based on five bore cores taken across the site (Partridge, 1978, 2000; Brain, 1981; Partridge and Watt, 1991; Kuman and Clarke, 2000). Overall, the site contains hominins associated with apparently Late Pliocene to Early Pleistocene deposits including Australopithecus in Member 4 and Member 2 (STER-M4, STER-M2) and Paranthropus and Homo in Member 5 (STER-M5). The problems of chronological interpretation have been in part due to difficulties associated with understanding the complex geomorphological history of this cave complex. Published interpretations assume that a 'layer-cake' stratigraphy mostly prevails, and that similar sedimentological deposits represented in various cores and limited exposures represent identical depositional units (see Partridge, 2000). This has led to the view that vertical depth is correlated with age (Partridge, 1978, 2000). Such an interpretation persists despite the fact that sediments are currently being deposited in the active part of the system beneath the palaeodeposits leading to an at least partly inverted stratigraphy.

Many different fossil-bearing units occur, some without the exposure of surface sections allowing for the various deposits to be linked. The accessible excavated deposits can roughly be divided into surface exposed deposits (Members 4-6) and deeper cavern exposed deposits (Members 1-3). Surface exposures consist of a series of calcified deposits that have been divided into Member 4 (STER-M4) and Member 5 (STER-M5), and their various sub-units, while deep cave units Member 2; (STER-M2) consist of calcified silts inter-lavered with calcite flowstones. Recent absolute and palaeomagnetic dates (Herries, 2003a,b; Walker et al., 2006) at the site suggest that australopithecine bearing deep cave deposits (Member 2) are the same age as surface exposed australopithecine bearing deposits (Member 4) at \sim 2.2 Ma (Herries et al., in press) and this too challenges the layer-cake model of deposition. Much of the division as well as grouping of deposits that exists is based on the description of sedimentological types or inclusions, rather than discrete depositional phases. As such, a Member system as used by Partridge (1978, 2000) is questionable because stratigraphic links are not directly visible and no reliable chronological system for determining relative age has been established other than faunal comparisons and the law of superposition. Faunal comparisons have suggested a range of ages for the various deposits (McKee, 1995; Vrba, 1995) and the complex speleology of this cave suggests that the law of superposition is unlikely to be sufficient in defining its stratigraphy. Bore cores have been utilised in an attempt to bridge these gaps in the sequence but these provide very narrow glimpses of the stratigraphy and may not be representative. While, it has been argued that the various units are lithologically and taphonomically different from each other, this may simply reflect different processes in different areas of the cave, which likely had multiple entrances. This is highlighted by the fact that the Stw573 fossil was most likely deposited through a different, shear vertical entrance compared to the material deposited in STER-M4 above. The Silberberg Grotto deposits may actually represent the in-fill of a contemporaneous, but mostly unconnected deep cavern that formed at the same time as the STER-M4 deposits were being deposited in a higher cavern. Such processes have been highlighted at other sites such as Makapansgat (Latham et al., 1999, 2002, 2003). Multiple methods of dating [palaeomagnetism, fauna, ESR, Uranium-Lead (U-Pb) and cosmogenic isotopes] have been applied, but only palaeomagnetic analysis has been possible on every Member (and this too has suffered from problems in analysis and interpretation). An emphasis is therefore made herein on absolute dates for the site.

Sterkfontein Member 5 (STER-M5) has been divided into three assemblages: Stw 53 Infill (M5A), Oldowan Infill/Member 5 East (M5B), and the Acheulian infill/Member 5 West (M5C) (Pickering, 1999; Kuman and Clarke, 2000; Partridge, 2000). Review of the STER-M5 deposits, based largely on archaeological associations, led Kuman and Clarke (2000) to suggest the following ages: M5A was deposited sometime between 2.6 and 2.0 Ma, based on the presence of *Theropitheicus. Oswald*, M5B was deposited after the M5A between 2.0 and 1.7 Ma based on the occurrence of the Oldowan; and the M5C deposits between 1.7 and 1.4 Ma based on the presence of the early Acheulian.

3.2. Biochronology

Only a few specifically identified faunal remains have been described from each of these three assemblages, providing a very limited chronological context for the deposits (Pickering, 1999). The M5A assemblage includes specimens of the bovid *Makapania broomi*, as well as two extinct primate species, *Theropithecus oswaldi* and *Cercopithecoides williamsi*. Kuman and Clarke (2000) have interpreted the presence of *T. oswaldi* to indicate a depositional date for the M5A assemblage of after 2.6 Ma, but before 2.0 Ma. Given the first appearance date of this species (\sim 2.4 Ma, Jablonski, 1993) and its presence in all three Members at Swartkrans (De Ruiter, 2003; 1.0 Ma see below), the sub-KBS Tuff deposits (<1.87 ± 0.02 Ma) and

the lower part of the Okote Member at Koobi Fora (1.63–1.51 Ma; McDougall and Brown, 2006) this species could indicate ages from after 2.4 Ma to 1.5 Ma, and perhaps as young as 1.0 Ma for STER-M5A. Specimens of *T. oswaldi* have also been recovered from the M5B assemblage, along with a small collection of *Equus* sp. and *Metridiochoerus modestus* remains. Prior analysis of the *M. modestus* third molar by Cooke (1994) noted its similarity to specimens from Olduvai Bed I (2.03–1.75 Ma: Walter et al., 1991, 1992).

No identifiable non-hominin primates have been recovered from the M5C assemblage, but specimens of Dinofelis barlowi, Equus sp. and Phacochoerus cf. aethiopicus have been described. The extinct false sabretooth D. barlowi occurs in Omo Shungura Member B10 (2.95 ± 0.03 Ma: Feibel et al., 1989), the Upper Burgi Member at Koobi Fora (2.00–1.88 Ma: Feibel et al., 1989), as well as Makapansgat Member 3 (MAK-M3; 3.03-2.58 Ma, Herries, 2003a,b; Herries et al., in press) and Sterkfontein M4 (STER-M4; 2.58–2.11 Ma, Herries, 2003a,b; Herries et al., in press). It therefore has an age range of between 3.03 and 1.88 Ma. The P. cf. aethiopicus materials consist of a first phalanx and three dental specimens (Pickering, 1999), but given the great morphological similarities of species within this genus, these isolated specimens are insufficient for biochronological analysis. Although analyses of the primates from STER-M5 originally dated the assemblage as close to the age of SWART-M1 (Delson, 1984), Delson (1988) later suggested that the primate sample was too limited to infer a secure age for the deposits. Analysis of the bovids by Vrba (1982) noted that a large portion of the bovid sample excavated from the STER-M5 may actually represent intrusive fossils originally derived from STER-M4 or STER-M6. This may explain the discrepancy in the age estimates for STER-M5C (3.0–1.9 Ma) based on the presence of *D. barlowi*, perhaps being intermixed from STER-M4. The securely provenienced STER-M5 bovids are similar to those from Olduvai Lower Bed II (1.75-1.70 Ma; Blumenschine et al., 2008) and SWART-M1, which led Vrba (1982) to tentatively suggest that the deposits formed around 1.5 Ma.

3.3. Palaeomagnetism

Previous palaeomagnetic studies of the Sterkfontein deposits suffered from a number of problems, including weakly magnetised samples and sampling from unsuitable depositional contexts (Jones et al., 1986; Schmidt and Partridge, 1991). The work of Jones et al. (1986) suggested that both reversed and normal polarity periods were represented in STER-M5. However, there was little consistency between layers. Deposits formed by rapid collapse of a deposit will not record an accurate remanence direction as the magnetic minerals lack sufficient time to become oriented and locked in. As such, recent research has focused primarily on speleothem lenses within the cave deposits as these accurately record the primary remanence at the time of their deposition (Partridge et al., 1999). These data have been supplemented with directions from fine grained deposits associated with these lenses and considered to have been deposited through fluvial processes. This has suggested that speleothem and clastic depositions are penecontemporaneous. Speleothem lenses are rare in STER-M5 and only three samples could be taken: one from M5A and two from M5C. Unfortunately, no samples could be taken from M5B. One sample from M5A and one sample from M5C recorded reversed directions of polarity, while the second sample from the interface of M5C and M6 records an intermediate polarity (perhaps related to a polarity transition). As such, the reversed polarity of the bulk of STER-M4 and STER-M5 samples cannot be distinguished except on stratigraphic grounds or with the aid of absolute dates (Fig. 2). The Réunion events $(2.14 \pm 0.03 \text{ Ma})$ are recorded in a speleothem deposit forming before STER-M5 and capping STER-M4. Therefore, it is suggested that STER-M4 is older (>2.14 Ma) and STER-M5 younger (<2.14 Ma) that the Réunion events (Herries, 2003a,b; Herries et al., in press; Fig. 2).

3.4. ESR

Curnoe (1999) conducted ESR dating studies on faunal teeth from Sterkfontein which included four *in situ* teeth from STER-M4 and 10 from STER-MB5. Individual age estimates for tooth subsamples as well as weighted means and errors (1 standard deviation or 1 σ) for STER-M4 and STER-M5 (M5A, M5B and M5C) are presented in Fig. 2. A small number of teeth were excluded owing to large differences in estimates among subsamples from a single tooth (internal errors) or due to the presence of very large errors owing to high scatter in the estimation of the accumulated dose. For STER-M4, four dates from three teeth are presented providing a weighted mean of 2214 ± 220 ka for this *Austral-opithecus*-bearing deposit. These estimates are consistent with the palaeomagnetic age estimates and some faunal interpretations (Herries, 2003a,b; Herries et al., in press) but younger than other age estimates derived from faunal analysis (Vrba, 1995).



Fig. 2. Electron spin resonance (ESR) results of *in situ* derived teeth from Members 4, 5 and 6 at Sterkfontein correlated against palaeomagnetic results and the Geomagnetic Polarity Timescale (GPTS).

The ESR results of only two teeth from STER-M5A are presented here owing to large internal errors in the third tooth. One tooth produced a mean age of 1672 ± 262 ka and another a mean age of 1659 ± 213 . Together they provide a weighted mean age of 1665 ± 237 ka for M5A. The third tooth came from a decalcified deposit and has apparently undergone a complex uranium uptake history with varying age estimates from different parts of the tooth. By averaging the ages of all three teeth or the two ages from the same tooth, as is conventionally done, without considering potential errors due to stratigraphic and post-depositional factors, an erroneous age would be obtained. ESR dates for M5B show larger variation, ranging from 965 ± 147 ka to 1328 ± 87 ka (NB: one tooth is excluded there due to large internal errors). The weighted mean ESR LU age for M5B is 1223 ± 155 ka. Within M5B two teeth are associated with the hominin ulna Stw 568. A sample from the purported early Acheulian layer (M5C) provides an age estimate of 328 ± 25 ka (EU) and 502 ± 32 ka (LU). This is similar to age estimates for teeth from the MSA infill (weighted means 252 ± 41 EU and 374 ± 52 LU; EU given in Fig. 2) and likely indicate reworking of fossil material, as has also been documented for Early Stone Age tools in Lincoln Cave (Kuman, 2007; Reynolds et al., 2007). A second tooth from the M5C deposits provided an age of 1041 ± 218 ka (LU). A third tooth, from the contact between STER-M4 and STER-M5, and originally thought to have originated from the former, provided an age estimate of 1162 ± 123 ka (LU), consistent with the ages from STER-M5B and STER-M5C. As the distinction between STER-M4 and STER-M5 is not well defined in many areas this tooth may have actually derived from STER-M5 or may be further evidence of intermixing of at least the surface deposits. An age of around 1.0-1.2 Ma is therefore suggested for Member 5C.

ESR ages for the bulk of the MSA bearing (Member 6/post-Member 6 deposits) surface deposits are similar to uranium series ages for the MSA bearing Lincoln Cave South deposits between 253 ± 36 ka and 115 ± 7 ka (Reynolds et al., 2007). These deposits possess a weighted means of 252 ± 41 (EU) and 374 ± 52 (LU). Along with the dates for MSA in Lincoln Cave the Member 6 material is potentially some of the oldest MSA deposits in southern Africa. Slightly younger ages (>220 ka to ~70 ka) have been suggested for MSA bearing deposits by Beaumont and Vogel (2006) at Wonderwerk Cave in Northern Cape, while along the southern Cape coast the oldest MSA deposits are around 164 ± 12 ka (Marean et al., 2007).

Overall, the ESR estimates for Sterkfontein (Members 4 and 5) are reasonably consistent, and in most instances similar to age assessments from other methods, particularly in STER-M4. There seem to be at least four temporally distinct units evident in the surface exposures. STER-M4 dates to >2.14 Ma to 2.58 Ma (Herries, 2003a,b; Herries et al., in press) and STER-M6 dates to the middle to late Middle Pleistocene (Curnoe, 1999). There may be up to three temporally distinct units within STER-M5: (1) STER-M5A dates to around 1.67 \pm 0.24 Ma, STER-M5B to around 1.22 \pm 0.16 and STER-M5C to around 1.04 \pm 0.22 Ma. For STER-M5A and STER-M5B these distinctions hold within 1σ error of the weighted mean. However, when 2σ errors are considered, STER-M5A, STER-M5B and STER-M5C cannot be distinguished statistically, although, they overlap by only a few thousand years. However, the weighted mean age of STER-M5A is distinguishable from that for STER-M4 when considered at the 2σ error.

3.5. Discussion

Reworking of teeth seems to have occurred in the Sterkfontein deposits (as suggested by the ESR studies of Blackwell, 1994; Schwarcz et al., 1994; Curnoe, 1999) suggesting that stratigraphic units within the Sterkfontein Formation are likely to be timeaveraged. This interpretation is further supported by lithic analysis which shows Early Stone Age material intermixed with Middle Stone Age material in the Lincoln Cave South deposits (Reynolds et al., 2007). This intermixed deposit also incorporates hominin remains (Reynolds et al., 2007) and so there is no reason why intermixing of STER-M4 and STER-M5 hominin fossils may not also have occurred. Kuman and Clarke (2000) and Kuman (2007) also note mixing of lithics in surface deposits of STER-M5. At present, however, the extent and impact of this mixing on the composition and estimated age of palaeontological materials from this site is difficult to assess particularly when collections of fossils and stone tools exist from over 50 years of excavation. Moreover, faunal analysis does not allow for adequate chronological assessment of the individual parts of STER-M5 at present as too few specimens have been published and the provenience of many specimens is uncertain. A reversed magnetic polarity for M4, M5A and M5C deposits does not allow them to be distinguished palaeomagnetically as they all record a reversed magnetic polarity. As such, the dating of the deposits and the resultant magnetostratigraphic interpretation are based on stratigraphic interpretations of a highly complex cave site and chronometric dating, which is limited.

The age of the australopithecine bearing STER-M4 is the most certain. STER-M4 consists of deposits formed by the collapse of a large chamber. This deposit was then brecciated by the formation of a thick flowstone deposit that drapped over and in-filled the voids within the deposit. Both the sediments and void flowstone of STER-M4 record a reversed magnetic polarity. However, the flow-stone capping STER-M4 records a series of short normal polarity events correlated to the Rèunion at around 2.14 ± 0.03 Ma (Herries et al., in press). Therefore, STER-M4 is >2.14 ± 0.03 Ma and STER-M5 is <2.14 ± 0.03 Ma. This is further confirmed by ESR which gives an age of 2.21 ± 0.220 Ma for STER-M4 and dates of 1.67 ± 0.24 Ma, 1.22 ± 0.16 and 1.04 ± 0.22 Ma for different parts of STER-M5. The inclusion of *Equus* in STER-M4 also suggests an age of <2.36 Ma and suggests a best fit age of 2.36-2.11 Ma for STER-M4 (Herries et al., in press).

The ESR dates provide an age range between 1.91 and 0.82 Ma for STER-M5 and suggest that it is distinct from STER-M4. Much of the confusion over the ESR ages appears to have come from averaging ages in situations where uranium uptake history has been markedly different in different areas of the same tooth, in situations that have undergone extensive calcification and recalcification causing a complex uranium exchange between tooth and environment, and mixing of teeth between deposits both in the past and during mining, excavation and sampling. The presence of both Oldowan and Acheulian industries in STER-M5 suggests that it covers potentially different periods, although in certain areas of Africa such assemblages can be contemporary and the Oldowan is known in deposits as young as slightly greater than 1.43 ± 0.07 Ma at Chesowanja (Hooker and Miller, 1979). An age of 1.38-1.06 Ma for STER-M5B is therefore only slightly younger than Oldowan deposits from eastern Africa. However, the ESR data also clearly show multiple periods occurring in the STER-M5 deposit. There is some evidence that STER-M5B might have fauna suggestive of a 2.0–1.75 Ma age (M. modestus), that is also more in keeping with an older age for the Oldowan tools as suggested by Kuman and Clarke (2000). However, some fauna from STER-M5C (D. barlowi) also suggests the deposit contains fauna that is older than would be expected (3.0–1.9 Ma) for Acheulian bearing deposits, which are only known from eastern Africa after 1.65 Ma. The fauna from STER-M5 appears to be too mixed or limited to currently make an assessment of age. Moreover, as this is not eastern Africa and it is possible that the Oldowan may have lasted for 0.1 Ma years longer in the southern part of the continent. An age of 1.260.82 Ma is not unlikely for Achulean deposits, although Kuman (2007) would consider the Sterkfontein Oldowan to be early (\sim 1.6 Ma), rather than later Achulean in age (\sim 1.0 Ma). As yet, too few Acheulian sites have been accurately dated in southern Africa to identify regional trends in the industrial complex. The younger age is further supported by an intermediate polarity in STER-M5C, which might relate to a polarity transition at the Jaramillo event (1.09–0.99 Ma) or even the Bruhnes/Matuyama boundary (0.78 Ma), although the palaeomagnetic data is too limited to confirm this at present.

Kuman and Clarke (2000) have proposed that M5A (Stw 53 breccia) is actually part of an infill dated between STER-M4 and STER-M5B, although conceding that this unit is indistinguishable from the bulk of STER-M5B on sedimentological grounds. Moreover, they suggest that Stw 53 is an australopithecine, rather than a member of Homo. This view is also suggested by Ferguson (1989) and Thackeray et al. (2000). Furthermore, they have suggested that the lack of stone tools and presence of some fauna indicate an earlier date for M5A of >2.0 Ma. Firstly, the presence of *T. oswaldi* indicates an age of <2.4 Ma not >2.0 Ma and is also found in deposits as young as 1.4-1.0 Ma in eastern Africa (see above). Overall, the faunal material from STER-M5 suggests an age of between 2.0 and 1.0 Ma, with an optimal age of around 1.8-1.7 Ma. Secondly, the original excavators of Stw 53 suggested that stone manuports were present at the time of excavation (Hughes and Tobias, 1977), and most researchers have suggested that the fossil represents early Homo (see review by Curnoe and Tobias, 2006). Moreover, Pickering et al. (2000) have demonstrated the presence of cut-marks on Stw 53 indicating that tools were being used at the time that this individual died. No stone tools or manuports have been found within STER-M4 and so the presence of cut-marks may also suggest a later period of deposition, when stone tools are noted at Sterkfontein and other sites (Kuman et al., 1997; Kuman, 2007).

The stratigraphy of Partridge (2000) suggests that STER-M5A is a small pocket of material that is older than STER-M5B, but younger than STER-M4. Moreover, he suggests that a significant period of time occurred between the deposition of STER-M4 and STER-M5. With the younger age estimates for STER-M4 (2.58–2.14 Ma), an age of >2.0 Ma for STER-M5A and close to 2.0 Ma for STER-M5B, as suggested by Kuman and Clarke (2000), seem less likely. An age estimate of around 1.91–1.43 Ma for STER-M5A from ESR studies is more consistent with the view of Partridge (2000). Palaeomagnetic studies suggest STER-M5A must date to older (>1.95 Ma) or younger than (<1.78 Ma) the Olduvai event. Based on the ESR age estimates a younger age seems more likely with a combined estimate of 1.78–1.43 Ma.

In our preferred ESR based scenario the hiatus in deposition between STER-M4 (2.4-2.1 Ma) and STER-M5 (1.8-1.4 Ma) is at least 0.3 Ma. STER-M5B to STER-M5C show an increase in age with depth, the base perhaps dating to as old as 1.4 Ma and the surface dating to around 1.0 Ma. There appears to have been continuous deposition from STER-M5B to STER-M5C times. However, STER-M5A is suggested to have formed at a different period, being slightly older \sim 1.8–1.4 Ma and stratigraphically higher than the younger STER-M5B/STER-M5C deposits (1.4-0.8 Ma). This is consistent with the long held view that Sterkfontein is characterised by distinct temporal phases of deposition (Brain, 1958) and follows the stratigraphy laid out by Partridge (2000) for the surface exposed deposits. These deposits cover over 1.0 Ma of deposition, yet they have all accumulated at a similar elevation, eroding into each other successively and in some cases causing older deposits to be higher in the sequence. Further research using radiometric methods will be needed to help clarify these issues and to test the combined faunal, ESR and palaeomagnetic age estimates.

4. Swartkrans

4.1. Stratigraphy

Excavations at Swartkrans began in the late 1940s under the supervision of R. Broom, J.T. Robinson, and the University of California's Africa Expedition (Brain, 1981). Work focused primarily on *ex situ* breccia dumps and some *in situ* materials until 1953 (Brain, 1981). Excavations were resumed in 1965 by C.K. Brain, who explored further *in situ* deposits and developed extensive fossil samples from what he identified as five infillings at the site (Swartkrans Members 1–5 [here SWART-M1 to SWART-M5]; Brain, 1981, 1993, 1994). Brain (1993) visualised Swartkrans as a series of close interconnected chambers that in-filled at different periods. This was based in part on the geology of the site and biostratigraphical inferences (Brain, 1993, 1994). SWART-M1, SWART-M2 and SWART-M3 all contain fossils of *Homo* and *Paranthropus* (Grine 1993, 2005).

4.2. Biochronology

Summaries of the faunal assemblages recovered from SWART-M1 to SWART-M3 were published by Brain (1981), and later revised and expanded by Watson (1993a) and De Ruiter (2003). Although these two latter studies have produced slightly different faunal lists for the three Members, the differences in relative proportion and taxon presence or absence do not alter biochronological interpretations. We do not discuss SWART-M4 here as it consists predominantly of Middle Stone Age artefacts and does not appear to contain fossil remains (Brain, 1993), or SWART-M5 which has been dated to 11,000 yeas BP (Brain, 1993). The occurrence of these deposits, however, highlights that deposition occurred at Swartk-rans throughout much of the Pleistocene.

Species representations in the SWART-M1 to SWART-M3 faunal assemblages are very similar, leading to overlapping depositional age reconstructions using biostratigraphy. Vrba (1982) noted that the indeterminate medium alcelaphine fossils, Parmularius angusticornis, Connochaetes sp. and Syncerus cf. acoelotus from M1 are similar to those recovered from Olduvai Bed I (2.03-1.75 Ma: Walter et al., 1991, 1992) and Lower Bed II (1.75-1.70 Ma; Blumenschine et al., 2008). The cf. Damaliscus niro horn core from M2 is similar to those from Olduvai Upper Bed II (1.50-1.48 Ma; Manega, 1993), and the Tragelaphus strepsiceros dental specimens from the deposits are similar to those of Tragelaphus strepsiceros grandis from Olduvai Middle Bed II (1.7-1.5 Ma; Manega, 1993; Blumenschine et al., 2008) through Bed IV (<0.78 Ma; Manega, 1993) (Vrba, 1982). Progressive Stage III Metridiochoerus andrewsi (sensu Harris and White, 1979) craniodental specimens have been recovered from all three Swartkrans Members, and correspond to specimens from Unit 4 of Koobi Fora Areas 103 and 104 ('Upper Member' specimens above the KBS Tuff; younger than 1.869 ± 0.021 Ma: McDougall and Brown, 2006), Omo Shungura Members H-J (1.88-1.65 Ma: Feibel et al., 1989), and lower Middle Bed II from Olduvai (Tuff IIA: 1.70-1.65 Ma: Manega, 1993; Blumenschine et al., 2008). The suid species Phacochoerus antiquus was initially reported from SWART-M2 by Ewer (1956) and noted by Harris and White (1979), but has recently been reassigned simply to Phacochoerus sp. by Watson (1993a) and De Ruiter (2003). The latter authors have also reported isolated Phacochoerus sp. molar fragments and postcranial specimens from SWART-M1 and SWART-M3. If P. antiquus sensu stricto (Ewer, 1956; Harris and White, 1979) or representatives of the genus Phacochoerus (Watson, 1993a; De Ruiter, 2003) occur in all three Swartkrans Members, then all three include at least some faunal materials younger than those recovered from Olduvai Upper Middle Bed II (~1.48 Ma: Manega, 1993), and possibly younger than those from Olduvai Bed IV (<0.78 Ma: Manega, 1993; see Kromdraai A discussion below).

Biochronological analysis of the Swartkrans primates by Delson (1984, 1988) suggested that SWART-M1 to SWART-M3 were deposited between 1.9 and 1.65 Ma, based on the presence of *Papio (Dinopithecus)* ingens and Papio hamadryas robinsoni, which linked the deposits to Omo Shungura Members C-G (2.75-2.11 Ma; Hernández Fernández and Vrba, 2006) and Sterkfontein Member 4 (2.58–2.11 Ma: Herries, 2003a.b), respectively. The recovery of *C. williamsi* (M1: De Ruiter, 2003) and T. oswaldi (M1–M3: De Ruiter, 2003), however, suggested a slightly younger age for the deposits given the *T. oswaldi* FAD near 2.4 Ma (Jablonski, 1993) and their occurrence in the sub-KBS Tuff deposits ($<1.87 \pm 0.02$ Ma) and lower part of the Okote Member at Koobi Fora (1.63–1.51 Ma; McDougall and Brown, 2006), respectively (Delson, 1984, 1988). The overall composition of the Swartkrans faunal assemblages therefore suggests accumulated between 2.4 and 1.65 Ma, but with some material as young as 1.5–1.4 Ma and <0.78 Ma. The presence of progressive stage III M. andrewsi suggests a date of <1.9 Ma, while the presence of Papio (Dinopithecus) ingens and Papio hamadryas robinsoni suggests a date of >2.1 Ma.

4.3. Palaeomagnetism

Previous attempts at palaeomagnetic analysis suggested these deposits were unstable (Brock et al., 1977) with only two normal polarity directions recorded in SWART-M2 and only intermediate directions from SWART-M1. This may suggest that SWART-M2 was deposition in the Olduvai normal polarity period, between 1.95 and 1.78 Ma. The high frequency of intermediate polarities in both deposits may relate to either the 1.95 or 1.78 Ma polarity transitions with SWART-M1 dating close to 1.95 and SWART-M2 close to 1.78 Ma. However, it seems more likely that the intermediate directions indicate that the depositional environment from which the samples were taken is unsuitable. A magnetic remanence can only be locked into a sample if the magnetic grains have had time to orient themselves with the ambient magnetic field. This occurs when sediments fall out of suspension in water or if they have travelled for a period by aeolian action. However, rapid collapse will not allow time for the sediment to be oriented. As much of the Swartkrans site is in-filled with breccias, the rapid episodes of accumulation would probably not have allowed sufficient time for the magnetic remanence to have become locked in. Palaeomagnetism should therefore not be used as a reliable indicator of age unless further studies are conducted on speleothem deposits from within the various members.

4.4. ESR

Electron spin resonance studies of teeth from Swartkrans were undertaken by Curnoe (1999) and Curnoe et al. (2001). Two bovid teeth (SK2286, SK2262) and a fragment of enamel from *Paranthropus robustus* (SKW11) were studied. The bovid teeth were apparently recovered from the Hanging Remnant of M1, although the precise provenience is unknown. SKW11 was recovered from a breccia block which dislodged from the lower part of the Hanging Remnant where many hominins have been recovered. This allowed for two external gamma spectrometric readings to be taken that bracket the deposit from which SKW11 derived (one above and one below). The gamma dose rates were essentially identical, conforming to a situation of low gamma dose rate variability across the entire Hanging Remnant (Curnoe, 1999). Thus, the uncertainty associated with the external gamma dose rate is low (assuming the modern dose rate to be representative of the entire burial history of SKW11).

Curnoe et al. (2001) provided age estimates for SKW11 of 950 ± 150 (EU) and 1390 ± 180 ka (LU), which is substantially lower than faunal estimates for the Hanging Remnant (see above). ESR dates for faunal remains gave age estimates of 1430 ± 210 ka (EU) and 1920 ± 340 (LU) for SK2286 and 890 ± 140 ka (EU) and

 1210 ± 220 (LU) for SK2262. When the ESR results were combined with U-series analyses on dentine and enamel US/ESR (minimum age) and CS-US/ESR (maximum possible age) estimates were calculated. The age of SKW11 from combined analyses is between ~2020 ka (US/ESR) and 2200 \pm 260 ka (CS-US/ESR). Sample SK2286 is dated between 1420 ± 250 ka (US/ESR) and $2580\pm650\ \text{ka}$ (CS-US/ESR) and SK2262 between 1190 ± 1400 (US/ESR) and 1650 ± 440 ka (CS-US/ESR). The weighted mean age from all three samples for the Hanging Remnant of SWART-M1 is 1630 ± 160 (US/ESR) and 2110 ± 210 (CS-US/ESR). Preliminary analysis by Curnoe (1999) gave relatively consistent age estimates of 1630 ± 292 ka (EU) and 2154 ± 315 ka (LU) for SKW11 and 1564 ± 330 ka (EU) and 2170 ± 441 ka (LU) for fossil SK2286. In contrast fossil SK2262 gave younger mean ages of 991 \pm 196 ka (EU) and 1178 ± 226 ka (LU). This analysis suggests that a range of material from a range of temporally different in-fills exists in Member 1, or that mixing is a large problem. The age of Paranthropus fossil SKW11 suggests it is at least 2.0 Ma, while at least one of the faunal samples appears to be much younger 1.4-0.6 Ma.

4.5. U–Pb

Recent work by Albarède et al. (2006) and Balter et al. (2008) has attempted U-Pb dating of bovid tooth enamel from SWART-M1 to SWART-M3. These data provide the first absolute dates for SWART-M2 and SWART-M3. Albarède et al. (2006) first reported dates of 2.02 ± 0.02 Ma, 1.44 ± 0.05 Ma and 0.988 ± 0.003 Ma for SWART-M1 to SWART-M3 respectively. This was very close to faunal estimates by Vrba (1995). Recently, however, Balter et al. (2008) have reported on the full range of U-Pb dates from Swartkrans and they gained similar mean age estimates of 1.83 ± 1.38 Ma, 1.36 ± 0.29 Ma and 0.83 ± 0.21 Ma. When the errors are taken into account for the deposits they have age ranges of 3.21-0.45 Ma for SWART-M1, 1.65-1.07 Ma for SWART-M2 and 1.04-0.62 Ma for SWART-M3. While, SWART-M2 and SWART-M3 are seemingly partly distinct SWART-M1 has a huge error range that is much greater than faunal age estimates. As with the ESR analysis this method of dating is critically dependent on the modelling of the gains and losses of the involved nuclides in the tooth enamel, which is an open system. Overall, uranium and lead ratios from the three members are not markedly different and age estimates are also still very broad.

4.6. Discussion

In summarising prior geomorphological and faunal age estimates for the Swartkrans assemblages, Brain (1993, 1994) identified SWART-M1 as the single largest deposit at the site and argued that the Swartkrans caverns first opened around 2.57 Ma, with SWART-M1 deposited between 1.8 and 1.5 Ma, and Members 2 and 3 likely having been contemporaneously deposited between 1.8 and 1.0 Ma (SWART-M3 closer to 1.0 Ma). These ages for the Swartkrans infillings are broadly similar to faunal age estimates of Vrba (1995): M1 1.8–1.6 Ma; M2 1.5–1.0 Ma; M3 0.7–0.6 Ma. Both imply that the Swartkrans sequence may have formed more or less continuously over the course of more than one million years. In a contrasting view, De Ruiter (2003) has suggested that all three members are penecontemporaneous in faunal composition.

The present study suggests that while the described primate sample from Swartkrans does include taxa from deposits as old as 2.85 Ma, the recovery of *Equus sp.* specimens indicates that the deposits are likely to be no older than about 2.36 Ma (Behrensmeyer et al., 1997). A correlation of Stage III *M. andrewsi* specimens to the eastern African suid record suggests that fossil deposits from SWART-M1 are probably likely no older than 1.89 Ma and likely no younger than 1.65 Ma. The bovid sample also suggests deposition between 2.02 and 1.48 Ma. However, the presence of *Papio*

(*Dinopithecus*) ingens and Papio hamadryas robinsoni suggests an age potentially in excess of 2.11 Ma. The recovery of phacochoerines could extend the younger age range into the Pleistocene and some material from SWART-M2 suggests an age of around 1.5 Ma and some from SWART-M3 suggests an age of <0.78 Ma. The main problem is that both younger and older material appear to occur in all three members, having led to the view by De Ruiter (2003) and others that the three units are penecontemparaneous. This may be a product of the complex depositional history and mixing suggested by the ESR results, only further detailed faunal and stratigraphic analysis will clarify these problems.

Overall the fauna from SWART-M1 suggests an optimal age range of around 2.36–1.65 Ma but the presence of progressive stage III M. andrewsi (<2.0 Ma) and Papio (Dinopithecus) ingens and Papio hamadryas robinsoni (>2.1 Ma) may suggest an age closer to 2.1-2.0 Ma. Minimum ESR/U-series dates of \sim 2.0 Ma for Paranthropus fossil SKW11 from the SWART-M1 Hanging Remnant further support the faunal age estimate. Recent U-Pb isotopic composition dates (Balter et al., 2008) from in situ bovid enamel samples from SWART-M1 do not help to clarify this issue. One bovid specimen from SWART-M1 appears to come from much more recent deposits and the ESR age is consistent with U-Pb dates from SWART-M2 (1.65-1.07 Ma) and SWART-M3 (1.04-0.61 Ma). These data all suggest that SWART-M1 as currently defined represents a series of deposits covering a vast time period and with material intermixed from more recent in-fills. While the U-Pb ages of SWART-M2 and SWART-M3 may suggest that they are more temporally distinct, representing material that has accumulated at the site during later periods to SWART-M1, the fauna and ESR still suggest some mixing from material as recent as the Middle Stone Age (Member 4; 214 ± 19 and 125 ± 12 ka). These data, along with findings from Sterkfontein (Blackwell, 1994; Schwarcz et al., 1994; see also above) indicate that reworking at these sites is likely to be common and that stratigraphic units (or Members) represent time-averaged deposits. Moreover, the formation of small cavities and solution tubes with the Members has increased this intermixing to depth. It is possible that younger fauna from the SWART-M1 deposit (*Phacochoerus* sp./*P. antiquus*) that suggests an age of less then 1.5 Ma likely derives from this process. For this reason the mean estimate of 1.63 Ma for SWART-M1 as concluded by Curnoe et al. (2001) is probably an underestimate as it seems an intermixed tooth from SWART-M2 may have been sampled and averaged with teeth from SWART-M1. An age of around 2.0 Ma is suggested by the age of the ESR dated Paranthropus specimen SWART-M1, but other areas may be slightly younger.

Swartkrans contains remnants of multi-generational in-fill with Lower and Middle Pleistocene fauna occurring. Parts of the cave might represent a palimpsest of sedimentary deposits from different segments of the Pliocene and Pleistocene. This same process is seen at most of the Plio-Pleistocene palaeocave sites (Makapansgat, Sterkfontein, Swartkrans, Kromdraai, Gondolin and Gladysvale) with continuous re-use of the same palaeokarstic conduits (Herries, 2000; Herries et al., 2006a; Adams et al., 2007). The first deposits probably accumulated around 2.0 Ma, or earlier, and phases of deposition occurred for the next 1.0 Ma or more eroding former deposits and creating a highly complex series of deposits at roughly the same stratigraphic level throughout the system. If the very young age of SWART-M3 can be further supported this would be extremely important as it would represent the LAD for *Paranthropus*.

5. Kromdraai

5.1. Stratigraphy

In 1938, the first *Paranthropus* specimens were recovered from Kromdraai, a site adjacent to Sterkfontein and Swartkrans in the

Blauubank River Valley (Fig. 1; Brain, 1981). The site is divided into two separate localities: Kromdraai A ('Faunal Site') and Kromdraai B, which has produced the hominin materials including *Paranthropus* and early *Homo* (Braga and Thackeray, 2003). Both deposits consist of calcified infillings within narrow solution galleries that run parallel to each other, and may have formed within the same single cavern system; although possibly at different times (Brain, 1981). The Kromdraai B deposits have again been separated into a number of Members (KROM-M1, KROM-M2 and KROM-M3). KROM-M3 has been the focus of research as the majority, if not all of the *Paranthropus* fossils, and all of the *Homo* fossils, were recovered from this Member (Braga and Thackeray, 2003).

5.2. Biochronology

Unfortunately, biochronological dating of the Kromdraai deposits can only be conducted using a limited number of species. One extinct bovid (Antidorcas recki) from Kromdraai A has been recovered from the late Pliocene Omo Shungura Member F3 deposits $(2.34 \pm 0.04 \text{ Ma}: \text{Feibel et al., } 1989)$. It occurs in several southern and eastern African faunal assemblages with an apparent LAD of 0.6 Ma at Elandsfontein (Vrba, 1995). The dental morphology of the Kromdraai A A. recki specimens differs somewhat from those recovered from Olduvai Bed I, Swartkrans M1 and Gondolin GD2 (Vrba, 1973, 1976; Gentry and Gentry, 1978; Adams and Conroy, 2005). Vrba (1976) has, however, cautioned against using the slight morphological differences among A. recki remains to refine biochronological reconstructions of deposits. Given the broad time-span of the species across the African fossil sites and the lack of a clear morphological succession, A. recki cannot provide a restricted depositional age for the Kromdraai A faunal assemblage.

Two extinct suid species have been recovered from the Kromdraai A deposits. The *M. andrewsi* upper and lower third molars from Kromdraai A all exhibit the typical Stage III characteristics described by Harris and White (1979), and are consistent with remains recovered from Swartkrans M1, Coopers D and Gondolin GD2. Among the eastern African fossil localities, progressive Stage III M. andrewsi third molar specimens like those from the Kromdraai A deposits have also been recovered from Unit 4 of Koobi Fora Areas 103 and 104 'Upper Member' specimens above the KBS Tuff (younger than 1.869 ± 0.021 Ma: McDougall and Brown, 2006), Omo Shungura Members H-J (1.88-1.65 Ma: Feibel et al., 1989) and lower Middle Bed II from Olduvai (1.74-1.70 Ma; Blumenschine et al., 2008). The results of the biochronological correlation of the Kromdraai A Stage III M. andrewsi specimens to those from these eastern African sites suggest a biochronological date for the Kromdraai A deposits of between 1.88 and 1.65 Ma.

A second extinct suid (*P. antiauus*) has also been recovered from the Kromdraai A deposits. This species is generally considered to be ancestral to the extant warthog (P. aethiopicus), and thus has no definitive LAD (White, 1995). Determining the first appearance of the species, and its usefulness for biostratigraphy, is somewhat complicated. The probable first appearance in the eastern African fossil record occurs in the Olduvai Bed IV deposits (<0.98 Ma: Manega, 1993). However, White (1995) has noted that this FAD is probably an artefact of the fossil record. The validity of the species has been questioned by Cooke (1982) who attributes all of the P. antiquus materials to M. modestus, a species that first occurs below the Koobi Fora KBS tuff (<1.869 Ma: McDougall and Brown, 2006), and is recovered as late as the Olduvai Bed IV deposits (<0.78 Ma: Manega, 1993). Harris and White (1979) originally interpreted the occurrence of *P. antiquus* at Kromdraai to indicate that the deposits were younger than Olduvai Upper Bed II (1.48 ± 0.05 Ma: Manega, 1993), but older than Olduvai Bed IV (Bed III/Bed IV junction at ~0.98 Ma: Manega, 1993). However, given the varying systematic treatments of this species and its questionable FAD, the Kromdraai A *P. antiquus* sample can only suggest that a component of the assemblage was deposited during the Pleistocene.

Among the non-artiodactyl species recovered from Kromdraai A. *Dinofelis pivetequi* has also been recovered from eastern African sites ranging in age from the Omo Shungura Members C (2.75– 2.52 Ma: Hernández Fernández and Vrba. 2006). D (2.52–2.40 Ma: Hernández Fernández and Vrba, 2006) and F (2.36 ± 0.04 Ma; Feibel et al., 1989) to lower part of the Okote Member at Koobi Fora (1.63-1.51 Ma; McDougall and Brown, 2006). Previous biochronological analysis of the primate species from the deposit (Papio angusticeps, Papio hamadryas robinsoni, Gorgopithecus major and Cercocebus sp.) by Delson (1984, 1988) suggested that the Kromdraai A faunal assemblages are contemporaneous with Swartkrans M1, and were probably deposited between 1.9 and 1.65 Ma. One of these primates, G. major, has been recovered from eastern African deposits such as the Omo Shungura Member C (2.91-2.52 Ma; Hernández Fernández and Vrba, 2006) and the Upper Burgi Member at Koobi Fora (2.00-1.88 Ma: Hernández Fernández and Vrba, 2006) to the KBS Member (1.89-1.63 Ma; McDougall and Brown, 2006). Unfortunately this does not provide a narrow age estimate for the deposits based on this species. Overall, an age of between 1.89 and 1.63 Ma is suggested for the age of Kromdraai A based on all of the fauna.

The Kromdraai B deposits contain an even more limited number of temporally sensitive species, in part because many specimens have only been identified to the generic level (Brain, 1981). As in the Kromdraai A deposits, both A. recki and P. antiauus have been recovered, but as noted above, neither provide particularly narrow time ranges. Delson (1984, 1988) has described the presence of essentially the same primate species as occur in the Kromdraai A deposits (with G. major present and C. williamsi common), and suggested that the deposits also date to between 1.9 and 1.65 Ma (but may have been deposited before Kromdraai A). Several separate studies of the chronology of the southern African fossil assemblages have suggested that Kromdraai B was deposited prior to Kromdraai A (Vrba, 1982). McKee (1995) has further suggested that both Kromdraai assemblages had formed prior to Swartkrans M1 to M3, around the times that Sterkfontein M4 and M5 were deposited (McKee, 1995).

Delson (1988) proposed a primate-based faunal age of between 1.9 and 1.65 Ma for Kromdraai B. The Kromdraai A faunal deposits are likely no older than 1.9 Ma and no younger than 1.6 Ma given the progressive morphology exhibited by the Stage III M. andrewsi specimens from the assemblage. As stated previously, the Kromdraai B faunal assemblage likely formed just prior to, or possibly coeval, with the Kromdraai A assemblage (1.9-1.6 Ma). The recovery of P. antiquus specimens suggests that the end of the depositional period at Kromdraai A did not occur until sometime during the Pleistocene, possibly as early as 1.48–0.98 Ma. However, biochronological interpretations of the Kromdraai B deposits are more limited, and the same concerns over the use of *P. antiquus* in establishing the chronology of Kromdraai A apply equally here. An age of between 1.89 and 1.63 Ma is thus suggested for Kromdraai B and 1.89–1.51 for KROM-A, with some material potentially as young as 1.5–1.0 Ma at both.

5.3. Palaeomagnetism

Previous palaeomagnetic analyses at Kromdraai B were attempted by Jones et al. (1986), and while some of the samples showed reversed directions of polarity, the majority were intermediate. Thackeray et al. (2002) have recently conducted palaeomagnetic analyses using the hybrid demagnetization methodology (also see Herries et al., 2006a) and obtained consistent and stable



Fig. 3. Palaeomagnetic interpretations for Kromdraai B in relation to the Geomagnetic Polarity Timescale (GPTS). Data from Thackeray et al. (2002).

directions of magnetization from KROM-M1 and KROM-M2, the contact between which is uncertain. KROM-M1 exhibits a reversed direction of polarity and is correlated to the Matuyama C2r.1r chon, between 2.11 and 1.95 Ma. Samples above this record normal directions of polarity that have been correlated to the Olduvai event between 1.95 and 1.78 Ma. KROM-M2 records a normal direction of polarity in its base and is reversed at its top (Fig. 3). This reversal has been correlated to the end of the Olduvai event at 1.78 Ma. This all suggests that the KROM-M1 and KROM-M2 sequence covers the entire the Olduvai event between 1.95 and 1.78 Ma and part of the previous reversed period between 2.56 and 1.95 Ma. Sample density is probably insufficient to have detected the Réunion event at \sim 2.14 \pm 0.03 Ma. The total time range of the KROM-M1 and KROM-M2 deposit is probably between >1.95 Ma and 1.78 Ma. KROM-M3 containing Homo and most likely all of the Paranthropus fossils is therefore considered to be <1.78 Ma. However, Thackeray et al. (2002) suggest that the TM1517 type specimen of *P. robustus* derives from KROM-M1 on the basis of matrix colouration. If this were the case then this Paranthropus specimen would date to around 2.0 Ma. ESR dating also indicates the presence of younger (Middle Pleistocene) fossil-bearing layers at Kromndraai B (Curnoe et al., 2002).

5.4. Discussion

Biochronological data suggest that KROM-A most likely formed between 1.9 and 1.5 Ma, while KROM-B formed between 1.9 and 1.6 Ma. The majority of fossils from KROM-B, including those of *P. robustus* and early *Homo* derive from KROM-M3, which is suggested to have been deposited after KROM-M2 and palaeomagnetic analysis suggests this is <1.78 Ma. An optimal age range for KROM-M3-B is between 1.78 and 1.6 Ma. KROM-B-M1 dates to between 2.11 and 1.95 Ma and if the TM1517 type specimen of *P. robustus* truly derives from here it is potentially one of the oldest *Paranthropus* deposits in South Africa, penocontemporaneous with Swartktrans M1. The possible presence of *P. antiquus* and ESR dates (Middle Pleistocene) also suggest that both sites are likely to include younger material (1.5–1.0 Ma) through cycles of calcification and infilling as also suggested at Swartkrans, Sterkfontein and other palaeocave localities in southern Africa.

6. Gondolin

6.1. Stratigraphy

Initial excavations were undertaken into an in situ fossiliferous Hanging Remnant deposit near the GD2 datum point by E.S. Vrba in 1979 (Watson, 1993b). This excavation produced a rich faunal assemblage from 2 to 3 m^3 of calcified siltstone deposits (Vrba, 1982; Watson, 1993b; Adams and Conroy, 2005; Adams, 2006). After a hiatus in research, Menter et al. (1999) conducted an exploratory field season in 1997 and described two hominin teeth recovered from a miners dump at the site. The first tooth is a partial left M¹ or M² from a 'gracile' hominin (possibly *Homo*), while the second is a large left M² provisionally attributed to P. cf. robustus (Menter et al., 1999) but showing metric affinities with P. boisei (Kuykendall and Conroy, 1999; Tobias, 2000). Subsequent excavations have attempted to clarify the relationship of these ex situ hominin remains to in situ deposits in the mined Gondolin cave system (Adams, 2006; Adams et al., 2007). While they are suggested to have derived from the GD1 area of the site (based on the type of sediment from the sampled block: Kuykendall, pers comm.), this is not certain.

6.2. Biochronology

Currently, three faunal assemblages have been described from the Gondolin site: (1) the GD2 faunal assemblage produced by the 1979 excavations, which were partially analysed and described by Watson (1993b) and recently fully described (Adams and Conroy, 2005; Adams, 2006); (2) the GD A faunal assemblage, consisting of faunal remains excavated by Menter et al. (1999) from *ex situ* deposits along with the hominin specimens (Adams, 2006); and (3) the GD1 faunal assemblage, excavated in 2003 (Adams, 2006; Adams et al., 2007).

The GD2 faunal assemblage was partially analysed and described by Watson (1993b), who suggested a faunal age of 1.9–1.5 Ma based on an analysis of *M. andrewsi* specimens by H.B.S. Cooke (*ibid*; p. 37). A more comprehensive faunal analysis of the complete assemblage has recently been undertaken (Adams and Conroy, 2005; Adams, 2006), including a combined palaeomagnetic and biochronological dating of the deposits (Herries et al., 2006a). Of the specifically identified fauna from GD2, only two extinct species could potentially be used for biochronological dating. One extinct bovid species from GD2 (A. recki) has been discussed above in regards to the Kromdraai A faunal assemblage, but has little biochronological information. As in Watson's (1993b) original analysis of the GD2 faunal assemblage, Herries et al. (2006a) relied on the recovered M. andrewsi craniodental sample to provide a faunal age estimate. In contrast to the earlier study which relied on only nine molar specimens. Herries et al. (2006a) considered an expanded sample of 30 M. andrewsi craniodental specimens representing at least three individuals. The M. andrewsi upper and lower third molars from GD2 all exhibit typical Stage III characteristics described by Harris and White (1979), and are morphologically similar to third molars from Swartkrans M1 and M2, Kromdraai A and Coopers D (Adams and Conroy, 2005; Adams, 2006; Herries et al., 2006a). Progressive Stage III M. andrewsi third molar specimens like those from the GD2 deposits have also been recovered from Unit 4 of Koobi Fora Areas 103 and 104 ('Upper Member' specimens above the KBS Tuff; younger than 1.87 ± 0.02 Ma: McDougall and Brown, 2006), Omo Shungura Members H-I (1.88-1.65 Ma: Feibel et al., 1989), and lower Middle Bed II from Olduvai (Tuff IIA: 1.74-1.70 Ma; Blumenschine et al., 2008). The results of the biochronologic correlation of the GD2 Stage III M. andrewsi specimens to those from these eastern African sites, along with the last appearance of *M. andrewsi* in the lower part of the Okote Member (1.63–1.51 Ma; McDougall and Brown, 2006), suggests a maximum biochronologic date for the GD2 deposits between 1.89 and 1.51 Ma, but with a likely age range of 1.9–1.6 Ma.

The current GD1 faunal sample cannot independently support a specific date for the formation of the fossiliferous deposits, although the recovery of *Equus sp.* from the deposits minimally suggests that the fauna materials accumulated after 2.36 Ma (Behrensmeyer et al., 1997).

6.3. Palaeomagnetism

Palaeomagnetic analysis at the site shows that the GD2 faunal bearing calcified silt deposits record a normal polarity. Given the restricted age range suggested by the *M. andrewsi* remains this normal polarity period has been attributed to the Olduvai event between 1.95 and 1.78 Ma (Herries et al., 2006a; Fig. 4). Flowstone capping the deposit records a polarity transition correlated to the



Fig. 4. Palaeomagnetic interpretations for the Gondolin GD1 and GD2 localities in relation to the Geomagnetic Polarity Timescale (GPTS). After Adams et al. (2007).

end of this event at 1.78 Ma. On the basis of depositional rates it has been assessed that the GD2 fauna was probably accumulated closer to 1.78 Ma than 1.95 Ma (Herries et al., 2006a). Palaeomagnetic analysis of the GD1 and GD3 deposits shows a change from normal to reversed polarity suggested to document the same reversal at the end of the Olduvai at 1.78 Ma. The GD1 fossil deposits are therefore slightly younger than the GD2 deposits dating to just after 1.78 Ma (Adams et al., 2007; Fig. 4). Deposits underlying the GD1 basal flowstone record multiple directions of polarity and represent younger clastic deposits that have eroded and in-filled this area a number of times over the life history of the cave.

6.4. Discussion

Unfortunately, recent excavations and research at Gondolin (see Herries et al., 2006a; Adams et al., 2007) have not clarified the stratigraphic association of the *Paranthropus* and possible *Homo* fossils. However, despite this lack of clear association, palaeomagnetic analysis suggests that faunal deposition at the site is centred near the end of the Olduvai normal polarity period around 1.78 Ma. This is further supported by an optimal faunal age of around 1.88–1.65 Ma for the GD2 assemblage. The GD2 deposit most likely dates to between 1.88 and 1.78 Ma and GD1 is slightly younger than 1.78 Ma. Despite the lack of clear provenience, and the fact that no other fossil-bearing deposits have been identified in the cave system, ~ 1.78 Ma is the best current age estimate for the hominin specimens.

7. Coopers/Drimolen

The site of Coopers consists of a number of cavities that formed by the same processes forming Sterkfontein and Kromdraai. Although occasional fossil collection at Coopers began in 1938, intensive *in situ* excavations into the Coopers D deposits were not undertaken until 2001 (Brain, 1958; Berger et al., 1995, 2003). Preliminary description of the diverse faunal assemblage has noted similarities in species representation to those from Swartkrans and Kromdraai A (Berger et al., 2003). Specimens of *P. robustus* (Swartkrans, Kromdraai), *Papio hamadryas robinsoni* (Swartkrans, Kromdraai) and *T. oswaldi* (Swartkrans) have been recovered (Delson, 1984, 1988), with the latter species suggesting dates an age for the deposits similar to that of the sub-KBS Tuff deposits (<1.869 Ma; McDougall and Brown, 2006) and Okote Tuff at Koobi Fora (1.56 Ma; McDougall and Brown, 2006).

Two species of Equus (Equus burchelli and Equus capensis) are present in the deposits, indicating that the deposits are younger than 2.36 Ma (Behrensmeyer et al., 1997; Bernor and Armour-Chelu, 1999). A small sample of Sivatherium maurusium craniodental specimens exhibits some morphological similarities to those from Makapansgat M3, although the permanent molar specimen lacks a pronounced metastyle (Berger et al., 2003). More than 300 suid craniodental and postcranial specimens have been attributed to the extinct species *M. andrewsi*, with third molar specimens comparable to the Stage III specimens from Swartkrans, Kromdraai and Gondolin (Berger et al., 2003). The bovid sample is diverse and dominated by alcelaphines and antilopines, particularly A. recki. The occurrence of the extinct bovine Simatherium kohllarensi at Coopers D is somewhat unusual given the rest of the recovered species, as this taxon has only been previously described from the Upper Laetoli Beds (3.76 + 0.03 to 3.49 + 0.12 Ma; Drake and Curtis,1987) and Makapansgat M3 and M4. In general, however, the broad similarities between the Coopers D deposits and the Swartkrans and Kromdraai A assemblages suggest a faunal date for the deposits of between 1.87 and 1.56 Ma (Berger et al., 2003).Little has been published on the site of Drimolen but preliminary analysis of the fauna suggests a similar age range to Coopers (2.0-1.5 Ma; Keyser, 1998).



Fig. 5. Stratigraphy and age range (Ma = millions of years) estimates for the southern Africa *Homo* and *Paranthropus* bearing palaeocave deposits. (SWART = Swartkrans, GD = Gondolin, KROM = Kromdraai-B, STER = Sterkfontein, CopD = Coopers D, Dri = - Drimolen) (Black = age ranges and light grey = age of non-*Paranthropus* and *Homo* bearing deposits deposits). An asterisk (*) represents mean absolute ages for the deposits and a hash (#) identified palaeomagnetic reversals. The age range for *Homo* (H.) and *Paranthropus* (P) is also shown against the last occurrence of *Australopithecus* (A.) in southern Africa.

8. Discussion and conclusions

8.1. Seriation of southern African site

The long standing difficulties associated with providing accurate and reliable dates for the southern African palaeocave sites have been a major impediment to progress in palaeoanthropology. Specifically, the phylogeny of southern Australopithecus, Paranthropus and early Homo and various scenarios about their macroevolution and palaeobiogeography have been difficult to assess in the absence of a reliable chronological framework. The present contribution has brought together the results of numerical techniques such as ESR and U-series, in conjunction with palaeomagnetics, faunal and archaeological comparisons. This has been used to construct age ranges for the seven sites discussed as shown in Fig. 5. A dating framework has been compiled which provides a foundation for interpreting evolutionary scenarios during the Lower Pleistocene of this region. Further work using palaeomagnetism, U-Pb and cosmogenic isotope methods will hopefully cement this framework.

This study shows that ESR remains the primary method for constraining the age of the hominin deposits at present. While in some cases these ages are different to what was expected based on relative dating of fauna and archaeology and may be prone to high errors they cannot be discounted for a number of reasons. For example, there is a lack of systematic error; the ESR dates suggest that the material at STER-M5 is younger than traditionally suggested, while at Swartkrans, slightly older. However, ESR dates for STER-M4 appear to be correct when correlated with palaeomagnetism and this deposit is also much younger than expected (Herries et al., in press). When the geomorphological context of the ESR material is studied more closely the reason for age variations within deposits can be more easily understood and explained. The dates also provide good internal consistency and in many cases repeatability and where they exist good correlation with other methods of dating. As such, there is little systematic reason to discount them. As excavation continues faunal lists for different

Table 1

Chronological seriation (oldest top to bottom) of the southern African Paranthropus and Homo bearing sites set against hominin and archaeological associations and age ranges from the various techniques employed in this study.

	Ното	Paranthropus	Archaeology	Fauna (Ma)	ESR (Ma)	U-Pb (Ma)	Palmag (Ma)	BEST AGE
SWART-M1	Х	Х	D. Oldowan	>2.1 to <1.9	2.32-1.47* 2.46-2.02**	3.21-0.45	~ 1.95?	~2.0
KROM-B-M1	?		?				>1.95	2.11-1.95
KROM-B-M2			?				~ 1.78?	
GD1	?	?					~ 1.78	~ 1.78
GD2	?	?		1.89-1.65			~1.78	~ 1.78
KROM-B-M3	Х	Х	?	1.9-1.65			<1.78?	1.78-1.65
STER-M5A	Х		?	2.4-1.5	1.93-1.43		>1.95 or <1.78	1.78-1.43
DRI	Х	Х		2.0-1.5				2.0-1.5
COOP-D		Х		1.9-1.5				1.9-1.5
SWART-M2	Х	Х	Acheulian	1.7–1.5	1.43-0.99? 2.09-1.21?	1.65–1.07	>1.78	1.65–1.07
STER-M5B	Х	Х	Oldowan	1.9-1.5	1.38-1.07			1.38-1.07
STER-M5C	Х		Acheulian	3.0-1.9 (~1.5)?	1.26-0.82		1.78-1.07	1.26-0.82
SWART-M3	Х	Х	Acheulian	<0.78		1.04-0.62		1.04-0.62

Question marks denote unreliable data. ESR ages are presented as age ranges: * maximum and minimum mean age of all ESR samples. **Maximum and minimum age of Paranthropus fossil SKW11.

areas of the sites will hopefully allow for refinement and improvement of the dating of these deposits. This will also help in understanding the complex relationship between eastern and southern African faunal communities. All of the deposits and sites discussed here clearly represent temporal palimpsests. Thus, the question of the reworking of younger fossils requires urgent attention from chronological as well as geomorphological perspectives in order to determine the level of time-averaging in the southern African hominin record. However, there is an urgent need for more chronometric dates (e.g. U–Pb and cosmogenic nuclides) to test the ESR age estimates.

The age estimates for each deposit utalising the various methods is shown in Table 1. These have been seriated by defining the best fit age based on all methods, but weighted towards chronometric or palaeomagnetic data, over faunal and archaeological data, if they exist. The following sequencing of sites is suggested: SWART-M1 (>2.0-1.65 Ma; Paranthropus and Homo), KROM-B-M1 (2.11-1.95 Ma; Paranthropus?), Gondolin GD1/GD2 (~1.78 Ma; Paranthropus and Homo), KROM-B-M3 (1.78-1.65 Ma; Paranthropus and Homo), STER-M5A (1.78-1.43 Ma; Homo), SWART-M2 (1.78-1.07 Ma; Paranthropus and Homo), STER-M5B (1.38-1.07 Ma; Paranthropus and Homo?), STER-M5C (1.26-0.82 Ma; Homo), SWART-M3 (1.04-0.62 Ma; Paranthropus and Homo). The age of both Coopers D (Paranthropus) and Drimolen (Paranthropus and Homo) is difficult to assess given the lack of published material, however, a date of between 2.0 and 1.5 Ma has been suggested based on fauna from these two sites. The age for Swartkrans is difficult to access as the dating suggests that statigraphic interpretations may need revision. Parts of SWART-M1 appear to have occurred from at least 2.0 Ma. Our optimal ages for these sites are ranges estimates, making it possible that parts of Gondolin, Kromdraai B and STER-M5A are penecontemporaneous at around 1.8 Ma. Parts of SWART-M2, SWART-M3 and STER-M5B and STER-M5C may also be penecontemporaneous at \sim 1.4–0.8 Ma (Table 2).

8.2. Confidence intervals for hominin fossil age ranges

Paranthropus appears to have occurred in southern Africa from at least 2.0 Ma as suggested by the direct dating of a *Paranthropus* fossil from SWART-M1 and perhaps the type specimen from KROM-B-M1. *Paranthropus* persisted until at least 1.6–1.2 Ma (STER-M5B) and perhaps as young as about 0.8–0.6 Ma at SWART-M3. *Homo* may have occurred simultaneously or slightly later *Paranthropus* occurs in eastern Africa from about 2.7 to 2.3 Ma as represented by specimens of *Paranthropus aethiopicus* and later from about 2.4 to 1.4 Ma by *Paranthropus bosei* (Hooker and Miller, 1979; Feibel et al., 1989; Manega, 1993; McDougall and Brown, 2006; Wood and Constantino, 2007). By 2.5–2.3 Ma *Homo* appears to have been quite widespread, occurring in Kenya (Deino and Hill, 2002; Prat et al., 2005) Ethiopia (Kimbel et al., 1997) and perhaps also Malawi (Ramirez Rozzi et al., 1997).

Based on the age of the fossil localities found to date, both Paranthropus and Homo appear to occur in eastern Africa significantly before they occur in southern Africa. However, as the Signor-Lipps effect states the fossil record is never complete and neither the first nor last individual in a given taxon will be recorded as a fossil (Signor and Lipps, 1982). Confidence intervals give useful baseline estimates of the incompleteness of the fossil record (Marshall, 1990). Confidence intervals were calculated on the age ranges of currently known Paranthropus (and its species) and early Homo bearing horizons in southern and eastern Africa, per Marshall (1990). This method aims to create an age range (at 95% confidence level) (Table 2) for fossil genus/species that is representative of the time interval in which it is believed the species should have existed. Horizons were considered as hominin bearing layers that can be temporally distinguished at the fossil sites. For example Swatkrans Members 1-3 represent three horizons, while Gondolin represents one horizon. Results are presented in Table 1 (data from Hooker and Miller, 1979; Feibel et al., 1989; Bilsborough, 1992; Manega, 1993; Kimbel et al., 1997; Ramirez Rozzi et al., 1997; Kuman and Clarke, 2000; Tobias, 2000; Wood, 2000; Deino and Hill, 2002; Thackeray et al., 2002; Schwartz and Tattersall, 2002; Prat et al., 2005; Curnoe and Tobias, 2006; McDougall and Brown, 2006; Spoor et al., 2007; Wood and Constantino, 2007; Curnoe, 2008).

Table 2

Confidence intervals (Max CI and Min CI) for upper and lower ages of currently known fossils at the 95% confidence level and subsequent potential age ranges for the various genus and species of hominin in eastern and southern Africa.

Group	Max Age	Min Age	Max CI	Min CI
All Paranthropus	2.8	0.7	0.0140	0.0617
Eastern African	2.8	1.3	0.0170	0.0758
Paranthropus				
P. robustus	2.5	0.3	0.0905	0.4542
P. bosei	2.5	1.3	0.0234	0.1050
P. aethiopicus	2.8	2.2	0.0718	0.3493
All Homo	2.5	1.3	0.0260	0.1173
Eastern African Homo	2.6	1.2	0.0473	0.2211
South African Homo	2.5	0.3	0.0801	0.3950
(inc STER-M5C and SWART-M3)				
South African Homo	2.2	1.2	0.0801	0.3950
(exc STER-M5C and SWART-M3)				

CI Max ages for P. bosei and P. robustus are identical at 2.5 Ma, suggesting that both potentially occurred from roughly the same time period, although, this is not geographically specific. P. aethiopicus has a CI range of 2.8–2.2 Ma. Therefore, Paranthropus as a genus appears to have first occurred in eastern Africa by up to 0.3 Ma. The CI min age for the different species of *Paranthropus* is vastly different, mainly due to the very young date of SWART-M3. The CI range for *P. robustus* is 2.5–0.3 Ma, while for *P. bosei* it is 2.5–1.3 Ma. The lower age range for P. robustus seems unrealistic. Without the inclusion of SWART-M3 its age range changes to between 2.2 and 1.2 Ma and more closely parallels P. bosei. However, in this instance the CI suggests that P. robustus likely only occurred from 2.2 Ma, as opposed to 2.5 Ma, more closely following the age of the fossil record. Paranthropus as a genus in both southern and eastern Africa has a suggested CI age range of 2.7–0.8 Ma when including SWART-M3, and 2.8–1.1 Ma when excluding it. The nature of the model means that a significant increase in the number of fossil sites or refinement to the southern African chronology will improve the accuracy of the CI age estimates. However, these preliminary data show some interesting trends: (1) While Paranthropus occurs significantly later in southern Africa than eastern Africa, P. robustus most likely occurred from about the same time as *P. bosei*; (2) *Paranthropus* appears to have survived later in southern than eastern Africa.

Unlike Paranthropus, the genus Homo continues to the present day and the species-level taxonomy for early Homo is controversial for eastern and southern African fossils. The fossil material assigned to H. habilis/H. rudolfensis occur from about 2.47 until around 1.44 Ma in eastern Africa (Deino and Hill, 2002; Spoor et al., 2007). This material was used as the basis for a comparative sample of early Homo from eastern Africa. Some researches have suggested that Homo from Swartkrans M1 and M3 may represent a different species (Smith and Grine, 2008; Curnoe, 2008). As such, there is a question over including the youngest material into this CI analysis. If the youngest material from STER-M5C and SWART-M3 is included southern African early Homo has CI age ranges of 2.5–0.3 Ma, however, if they are excluded this range is reduced to between 2.2 and 1.2 Ma. In comparison, eastern African early Homo has a CI age range of 2.6-1.2 Ma. This suggests that the first occurrence of *Homo* in southern Africa may have been later than in eastern Africa by up to 400,000 years, or as little as 100,000 years. It is also interesting to note that the max age for eastern African Homo is equivalent to the age for the currently oldest known stone tools from this region at Gona, Ethiopia ~ 2.6 Ma (Semaw et al., 2003). While these CI estimates and age ranges are preliminary (in that the dating of the southern African sites is not as accurate as the eastern African sites and taxonomic assignment varies) they do show some interesting correlations that may be explored in the future.

8.3. Early Stone Age lithic assemblages

The Oldowan tradition is known from about 2.6 Ma until around 1.5 Ma in eastern Africa (Semaw et al., 2003), while the Acheulian is known from about 1.65 to 1.5 Ma (Quade et al., 2004). At some sites Developed Oldowan assemblages occur from 1.7 to 1.5 Ma (Kimura, 2002), although some (Kuman, 2007) consider these to represent early Acheulian. Kuman (2007) summarises the available data on the South African tool industries (see also Table 1) and concludes that the Oldowan is present at STER-M5B, which is dated to between 1.38 and 1.07 Ma. This would be the youngest occurrence of this tool industry, which is not generally seen after 1.5 Ma in eastern Africa. The much older material from SWART-M1 $(\sim 2.0 \text{ Ma})$ is defined as Developed Oldowan by Clark (1993) due to a lack of bifaces but larger size of the flakes from this assemblage. They further state that SWART-M2 and SWART-M3 shared closer affinities to each other than SWART-M1 and were Acheulian in character. This makes sense given their younger age. Field (1999) and Kuman (2007) partly agree with this assessment although they state that the size of the flakes at SWART-M1 suggests that it may be more Acheulian in character. Kuman (2007) defines the SWART-M1 stone tools as undetermined in her final table but if it were confirmed as Acheulian or Developed Oldowan it would potentially be the oldest example of these industries. Kuman et al. (1997) suggest that a Developed Oldowan/Early Acheulian assemblage also occurred at KROM-A, roughly dated to between 1.9 and 1.6 Ma. Kuman (2007) also states that STER-M5C could be defined as Developed Oldowan in the sense that it has few bifaces, but again classifies this material as early Acheulian. Based on our seriation this deposit dates to 1.26 Ma, at the earliest. STER-M5A lies intermediate in age between these other deposits at 1.78-1.43 Ma. Kuman and Clarke (2000) suggest that no stone tools are associated with it. However, Homo fossil Stw 53 has cut-marks which suggest the presence of stone tools (Pickering et al., 2000). Other potentially contemporary sites such as Gondolin lack tools and so this is not surprising given that the caves are not occupation sites. SWART-M3 and STER-M5C are the youngest deposits and both contain Acheulian, although Kuman (2007) suggests that the latter could again be classified as Developed Oldowan in character. This would be quite young for such an industry at < 1.26 Ma. In conclusion the typology of the stone tool industries in southern Africa do not directly correlate with age assessments from this study. However, whether this is a problem of dating, which is still tentative, mixing or typological variation, requires further analysis.

Acknowledgements

The palaeomagnetic work was partially funded by a grant made to AIRH from the Arts and Humanities Research Board (AHRB Studentship No. 99/3050). Palaeomagnetic work was undertaken at the University of Liverpool Geomagnetism Laboratory. Funding for faunal analysis and additional palaeomagnetic work was provided to JWA by the NSF (#0308014), PAST and the Wenner-Gren Foundation. Electron spin resonance dating was undertaken by DC and funded by the Australian National University as part of a PhD jointly supervised by Rainer Grün. Thanks are given to Lois Taylor for chemical analysis and to the CSIRO Black Mountain Laboratories for access to irradiation facilities. We wish to thank Kevin Kuykendall, Ron Clarke, Kathy Kuman, Francis Thackeray and Tim Partridge for access to fossils and sites and for discussion surrounding this research. This work was presented at the 2007 INQUA conference in Cairns (Australia) as part of the session organised by John Dodson (ANSTO) and entitled 'The Great Arc of Human Dispersal'. We thank the organisers of this session and conference for our inclusion. Thanks to Phil Hopley and Kaye Reed for their comments.

References

- Adams, J.W., Conroy, G.C., 2005. Plio-Pleistocene faunal remains from the Gondolin GD 2 in situ assemblage, North West Province, South Africa. In: Lieberman, D., Smith, R.J., Kelley, J. (Eds.), Interpreting the Past: Essays on Human, Primate and Mammal Evolution in Honor of David Pillbeam. Brill Academic Publishers Inc., Boston, pp. 243–261.
- Adams, J., 2006. Taphonomy and palaeoecology of the Gondolin Plio-Pleistocene cave site, South Africa. Ph.D., Washington University, St. Louis.
- Adams, J.W., Herries, A.I.R., Conroy, G.C., Kuykendall, K.L., 2007. Taphonomy of a South African cave: geological and hydrological influences on the GD 1 fossil assemblage at Gondolin, a Plio-Pleistocene paleocave system in the Northwest Province, South Africa. Quat. Sci. Rev. 26, 2526–2543.
- Albarède, F., Balter, V., Braga, J., Blichert-Toft, J., Telouk, P., Thackeray, F., 2006. U–Pb dating of enamel from the Swartkrans Cave hominid site (South Africa) by MC-ICP-MS. Geochim. Cosmochim. Acta 70, A7.
- Balter, V., Blichert-Toft, J., Braga, J., Telouk, P., Thackeray, F., Albarède, F., 2008. U–Pb dating of fossil enamel from the Swartkrans Pleistocene hominid site, South Africa. Earth Planet. Sci. Lett. 267, 236–246.
- Beaumont, P.B., Vogel, J.C., 2006. On a timescale for the past million years of human history in central South Africa. S. Afr. J. Sci. 102, 217–228.
- Behrensmeyer, A.K., Todd, N., Potts, R., McBrinn, G., 1997. Late Pliocene faunal turnover in the Turkana Basin, Kenya and Ethiopia. Science 278, 1589–1594.

- Berger, L.R., De Ruiter, D.J., Steininger, C.M., Hancox, J., 2003. Preliminary results of excavations at the newly investigated Coopers D deposit, Gauteng, South Africa. S. Afr. J. Sci. 99, 276–278.
- Berger, L.Ř., Pickford, M., Thackeray, F., 1995. A Plio-Pleistocene hominid upper central incisor from the Cooper's site, South Africa. S. Afr. J. Sci. 91, 541–542.
- Bernor, R.L., Armour-Chelu, M., 1999. Toward an evolutionary history of African hipparionine horses. In: Bromage, T., Schrenk, F. (Eds.), African Biogeography, Climate Change and Early Hominid Evolution. Oxford University Press, Oxford, pp. 189–215.
- Bilsborough, A., 1992. Human Evolution. Blackie Academic and Professional, London.
- Blackwell, B.A., 1994. Problems associated with reworked teeth in electron spin resonance (ESR) dating. Quat. Geochronol. (Quat. Sci. Rev.) 13, 651–660. Blumenschine, R.J., Masao, F.T., Tactikos, J.C., Ebert, J.I., 2008. Effects of distance from
- Blumenschine, R.J., Masao, F.T., Tactikos, J.C., Ebert, J.I., 2008. Effects of distance from stone source on landscape-scale variation in Oldowan artifact assemblages in the Paleo-Olduvai Basin, Tanzania. J. Archaeol. Sci. 35, 76–86.
- Brain, C.K., 1958. The Transvaal Ape-man-bearing Cave Deposits. Transvaal Museum, Pretoria. Memoir No. 11.
- Brain, C.K., 1981. The Hunters or the Hunted? An Introduction to African Cave Taphonomy. University of Chicago Press, Chicago.
- Brain, C.K., 1993. A taphonomic overview of the Swartkrans fossil assemblages. In: Brain, C. (Ed.), Swartkrans: a Cave's Chronicle of Early Man. Transvaal Museum, Pretoria, pp. 257–264.
- Brain, C.K., 1994. The Swartkrans palaeotological research project in perspective: results and conclusions. S. Afr. J. Sci. 90, 220–223.
- Braga, J., Thackeray, J.F., 2003. Early Homo at Kromdraai B: probabilistic and morphological analysis of the lower dentition. Comp. Rend. – Palevol., 269–279.
- Brink, J.S., 2002. Human fossil material discovered at Cornelia-Uitzoek. Culna 57, 4–7. Brock, A., McFadden, P.L., Partridge, T.C., 1977. Preliminary palaeomagnetic results from Makapansgat and Swartkrans. Nature 266, 249–250.
- Butzer, K.W., 1984. Archeogeology and Quaternary environment in the interior of southern Africa. Southern African Prehistory and Paleoenvironments, pp. 1–64.
- Clark, J.D., 1993. Stone artefact assemblages from Members 1–3, Swartkrans Cave. In: Brain, C. (Ed.), Swartkrans: a Cave's Chronicle of Early Man. Transvaal Museum, Pretoria, pp. 167–194.
- Cooke, H., 1982. Phacochoerus modestus from Bed I, Olduvai Gorge, Tanzania. Zeits. Geol. Wissenschaften (Berlin) 10, 899–908.
- Cooke, H., 1994. Phacochoerus modestus from Sterkfontein Member 5. S. Afr. J. Sci., 99–100.
- Curnoe, D., Review of Early Homo in southern Africa focussing on cranial and dental remains with the description of a new species. African Genesis: Papers in Honour of the 80th Birthday of Phillip Tobias and the 80th Anniversary of the Taung Child. University of the Witwatersrand Press; Johannesburg, South Africa, in press.
- Curnoe, D., 2008. Affinities of the Swartkrans early Homo mandibles. HOMO Journal of Comparative Human Biology 59, 123–147.
- Curnoe, D., 1999. A contribution to the question of early Homo in southern Africa: researches into dating, taxonomy and phylogeny reconstruction. Unpublished PhD thesis, Australian National University, Canberra, Australia.
- Curnoe, D., Grün, R., Taylor, L., Thackeray, J.F., 2001. Direct ESR dating of a Pliocene hominin from Swartkrans. J. Hum. Evol. 40, 379–391.
- Curnoe, D., Grün, R., Thackeray, J.F., 2002. Electron spin resonance dating of tooth enamel from Kromdraai B, South Africa. S. Afr. J. Sci. 98, 540.
- Curnoe, D., Tobias, P.V.T., 2006. Description, new reconstruction, comparative anatomy, and classification of the Sterkfontein Stw 53 cranium, with discussions about the taxonomy of other southern African early *Homo* remains. J. Hum. Evol. 50, 36–77.
- Deino, A.L., Hill, A., 2002. ⁴⁰Ar/³⁹Ar dating of Chemeron formation strata encompassing the site of hominid KNM-BC 1, Tugen Hills, Kenya. J. Hum. Evol. 42, 141–151.
- De Ruiter, D.J., 2003. Revised faunal lists for M1–3 of Swartkrans, South Africa. Ann. Transv. Mus 40, 29–41.
- De Ruiter, D.J., Steininger, C.M., Berger, L.R., 2006. A cranial base of Australopithecus robustus from the hanging remnant of Swartkrans, South Africa. Am. J. Phys. Anthropol. 130, 435–444.
- Delson, E., 1984. Cercopithecid biochronology of the African Plio-Pleistocene: correlation among eastern and southern hominid-bearing localities. Cour. Forsch. Inst. Senckenberg 69, 199–218.
- Delson, E., 1988. Chronology of South African australopith site units. In: Grine, F. (Ed.), Evolutionary History of the "Robust" Australopithecines. Aldine de Gruyter, New York, pp. 317–324.
- Drake, R., Curtis, G.H., 1987. K–Ar chronology of the Laetoli fossil localities. In: Leakey, M.D., Harris, J.M. (Eds.), Laetoli, A Pliocene Site in Northern Tanzania. Clarendon Press, Oxford, pp. 48–52.
- Ewer, R., 1956. The fossil Suidae of the Transvaal caves. Proc. Zool. Soc. Lond. 124, 565–585.
- Feibel, C.S., Brown, F.H., McDougall, I., 1989. Stratigraphic context of fossil hominids from the Omo Group deposits: Northern Turkana Basin, Kenya, Ethiopia. Am. J. Phys. Anthropol. 78, 595–622.
- Ferguson, W.W., 1989. Reappraisal of the taxonomic status of the cranium Stw 53 from the Plio/Pleistocene of Sterkfontein. S. Afr. Primates 30, 103–109.
- Field, A.S., 1999. An analytical and comparative study of the earlier stone age archaeology of the Sterkfontein Valley. Unpublished MSc. Dissertation, University of the Witwatersrand, South Africa.
- Gentry, A., Gentry, A., 1978. Fossil Bovidae (Mammalia) of Olduvai Gorge, Tanzania, Part I. Bull. Brit. Mus. Nat. Hist. (Geol) 29, 289–446.

- Grine, F.E., 1993. Description and preliminary analysis of new hominid craniodental fossils from the Swartkrans Formation. In: Brain, C. (Ed.), Swartkrans: a Cave's Chronicle of Early Man. Transvaal Museum, Pretoria, pp. 75–116.
- Grine, F.E., 2005. Early Homo at Swartkrans, South Africa: a review of the evidence and an evaluation of recently proposed morphs. S. Afr. J. Sci. 101, 43–52.
- Grün, R., 1989. Present status of ESR-dating. Appl. Radiat. Isot. 40, 1045–1055.
- Grün, R., 1998. Reproducibility measurements for ESR signal intensity and dose determination: high precision but doubtful accuracy. Radiat. Measur. 29, 177–193.
- Grün, R., 2006a. A simple method for the rapid assessment of the qualitative ESR response of fossil samples to laboratory irradiation. Radiat. Measur. 41, 682–689.
- Grün, R., 2006b. Direct dating of human fossils. Yearbook Phys. Anthropol. 49, 2–48. Harris, J., White, T., 1979. Evolution of the Plio-Pleistocene African Suidae. Trans. Am. Philos. Soc. 69, 5–128.
- Herries, A.I.R., 2000. The relationship of palaeokarst to the modern cave forming processes in the Transvaal, South Africa. Cave Karst Sci. 27, 131–132.
- Herries, A.I.R., 2003a. Magnetostratigraphic seriation of South African hominin palaeocaves. PhD thesis, Geomagnetism Laboratory, Department of Archaeology, University of Liverpool.
- Herries, A.I.R., 2003b. Palaeomagnetic seriation of South African hominid palaeocaves. Am. J. Phys. Anthropol. S36, 120.
- Herries, A.I.R., Adams, J.W., Curnoe, D., Latham, A.G., Warr, G. A multi-disciplinary perspective on the age of Australopithecus in South Africa. In: Delson, E., MacPhee, R. (Ed.) Diversity in Australopithecus: Tracking the Earliest Bipeds. Vertebrate Palaeobiology and Palaeoanthropology Series, in press.
- Herries, A.I.R., Adams, J.W., Kuykendall, K.L., Shaw, J., 2006a. Speleology and magnetobiochronologic chronology of the GD 2 locality of the Gondolin homininbearing palaeocave deposits, North West Province, South Africa. J. Hum. Evol. 51, 617–631.
- Herries, A.I.R., Reed, K., Kuykendall, K.L., Latham, A.G., 2006b. Speleology and Magnetobiostratigraphic chronology of the Buffalo Cave fossil bearing palaeodeposits, Makapansgat, South Africa. Quat. Res. 66, 233–245.
- Herries, A.I.R., Latham, A.G., 2002. Dating the depositional sequence and Australopithecine "Grey Breccia" of Makapansgat Limeworks using magnetostratigraphy. Am. J. Phys. Anthropol. S34, 84–85.
- Hernández Fernández, M., Vrba, E.S., 2006. Plio-Pleistocene climatic change in the Turkana Basin (East Africa): evidence from large mammal faunas. J. Hum. Evol. 50, 595–626.
- Hooker, P.J., Miller, J.A., 1979. K–Ar dating of the Pleistocene fossil hominid site at Chesowanja, North Kenya. Nature 282, 710–712.
- Hughes, A.R., Tobias, P.V., 1977. A fossil skull probably of the genus *Homo* from Sterkfontein, Transvaal. Nature 265, 310–312.
- Jablonski, N., 1993. The phylogeny of *Theropithecus*. In: Jablonski, N. (Ed.), *Theropithecus*: the Rise and Fall of a Primate Genus. Cambridge University Press, Cambridge, pp. 209–244.
- Jones, D.L., Brock, A., McFadden, P.L., 1986. Palaeomagnetic results from the Kromdraai and Sterkfontein hominid sites. S. Afr. J. Sci. 82, 160–163.
- Keyser, A.W., 1998. Drimolen: Excursion Guide. In: Berger, L., Keyser, A. (Eds.), Excursion Guide to Gladysvale and DrimolenIV Dual Congress, Sun City, South Africa, 28th June–4th July 1998. Desktop Creations, Pretoria.
- Kimbel, W.H., Johanson, D.C., Rak, Y., 1997. Systematic assessment of a maxilla of Homo from Hadar, Ethiopia. Am. J. Phys. Anthropol. 103, 235–262.
- Kimura, Y., 2002. Examining time trends in the Oldowan technology at Beds I and II. Olduvai Gorge Journal of Human Evolution 43, 291–321.
- Klein, R.G., Avery, G., Cruz-Uribe, K., Steele, T.E., 2006. The mammalian fauna associated with an archaic hominin skullcap and later Acheulean artifacts at Elandsfontein, Western Cape Province, South Africa. J. Hum. Evol. 52, 164–186.
- Kuman, K., 2007. The earlier stone age in South Africa: site context and the influence of cave studies. In: Pickering, T.R., Schick, K., Toth, N. (Eds.), Breathing Life into Fossils: Taphonomic Studies in Honour of C.K. (Bob) Brain. Stone Age Institute Press, Bloomington (Indiana), pp. 181–198.
- Kuman, K., Clarke, R.J., 2000. Stratigraphy, artefact industries and hominid associations for Sterkfontein, M5. J. Hum. Evol. 38, 827–848.
- Kuman, K., Field, A.S., Thackeray, J.F., 1997. Discovery of new artefacts at Kromdraai. S. Afr. J. Sci. 93, 187–193.
- Kuykendall, K.L., Conroy, G.C., 1999. Description of the Gondolin teeth: hyper-robust hominids in South Africa? Am. J. Phys. Anthropol. Supp. 28, 176–177.
- Lacruz, R.S., Brink, J.S., Hancox, J., Skinner, A.S., Herries, A., Schmidt, P., Berger, L.R., 2002. Palaeontology, geological context and palaeoenvironmental implications of a Middle Pleistocene faunal assemblage from the Gladysvale Cave, South Africa. Palaeontol. Afr. 38, 99–114.
- Latham, A.G., Herries, A., Quinney, P., Sinclair, A., Kuykendall, K., 1999. The Makapansgat Australopithecine Site from a Speleological Perspective. In: Pollard, A.M. (Ed.), Geoarchaeology: exploration, environments, resources. Royal Geological Society, London. Special Publications 165, 61–77.
- Latham, A.G., Herries, A.I.R., Sinclair, A.G.M., Kuykendall, K., 2002. Re-examination of the lower stratigraphy in the classic section, Limeworks site, Makapansgat, South Africa. Hum. Evol. 17, 207–214.
- Latham, A.G., Herries, A.I.R., Kuykendall, K., 2003. The formation and sedimentary infilling of the Limeworks Cave, Makapansgat, South Africa. Palaeontol. Afr 39, 69–82.
- Manega, P.C., 1993. Geochronology, geochemistry and isotopic study of the Plio-Pleistocene hominid sites and the Ngorongoro volcanic highland in northern Tanzania. Ph.D. Dissertation, University of Colorado.

- Marean, C.W., Bar-Matthews, M., Bernatchez, J., Fisher, E., Goldberg, P., Herries, A.I.R., Jacobs, Z., Jerardino, A., Karkanas, P., Minichillo, T., Nilssen, P.J., Thompson, E., Watts, I., Williams, H.W., 2007. Early human use of marine resources and pigment in South Africa during the Middle Pleistocene. Nature 449, 905–908.
- Marshall, C.R., 1990. Confidence intervals on stratigraphic ranges. Palaeobiology 16, 1–10.
- McDougall, I., Brown, F.H., 2006. Precise ⁴⁰Ar/³⁹Ar geochronology for the upper Koobi Fora Formation, Turkana Basin, northern Kenya. J. Geol. Soc. London 163, 205–220.
- McKee, J.K., 1995. Further chronological seriations of southern African Pliocene and Pleistocene mammalian faunal assemblages. Palaeontol. Afr 32, 11–16.
- Menter, C.G., Kuykendall, K.L., Keyser, A.W., Conroy, G.C., 1999. First record of hominid teeth from the Plio-Pleistocene site of Gondolin, South Africa. J. hum. Evol. 37, 299–307.
- Partridge, T.C., 2000. Hominid-bearing cave and Tufa deposits. In: Partridge, T.C., Maud, R.R. (Eds.), The Cenozoic in Southern Africa. Oxford Monographs on Geology and Geophysics, vol. 40. Oxford University Press, pp. 100–125.
- Partridge, T.C., 1978. Re-appraisal of lithostratigraphy of Sterkfontein hominid site. Nature 275, 282–287.
- Partridge, T.C., Latham, A.G., Shaw, J., Heslop, D., 2000. Appendix on magnetostratigraphy of Makapansgat, Sterkfontein, Taung and Swartkrans. In: Partridge, T.C., Maud, R.R. (Eds.), The Cenozoic of Southern Africa. Oxford Monographs on Geology and Geophysics, vol. 40, pp. 126–129.
- Partridge, T.C., Shaw, J., Heslop, D., Clarke, R.J., 1999. The new hominid skeleton from Sterkfontein, South Africa: age and preliminary assessment. J. Quat. Sci. 14, 293–298. Partridge, T.C., Watt, I.B., 1991. The stratigraphy of the Sterkfontein hominid deposit
- and its relationship to the underground cave system. Palaeontol. Afr. 28, 35–40. Pickering, T.R., 1999. Taphonomic Interpretations of the Sterkfontein Early Hominid
- Site (Gauteng, South Africa) Reconsidered in Light of Recent Evidence. University of Wisconsin.
- Pickering, T.R., White, T., Toth, N., 2000. Brief communication: cutmarks on a Plio-Pleistocene hominid from Sterkfontein, South Africa. Am. J. Phys. Anthropol. 111, 579–584.
- Prat, S., Brugal, J.P., et al., 2005. First occurrence of early *Homo* in the Nachukui Formation (West Turkana, Kenya) at 2.3–2.4 Myr. J. Hum. Evol. 49, 230–240.
- Quade, J., Levin, N., Semaw, S., Stout, D., Renne, P., Rogers, M.J., Simpson, S., 2004. Paleoenvironments of the earliest stone toolmakers, Gona, Ethiopia. Geol. Soc. Am. Bull. 116, 1529–1544.
- Ramirez Rozzi, F.V., Bromage, T., Schrenk, F., 1997. UR 501, the Plio-plesitocene hominid from Malawi. Analysis of the microanatomy of the enamel. Comp. Rend. l'Acad. des Sci. – Series IIA – Earth Planet. Sci. 325, 231–234.
- Reynolds, S.C., Clarke, R.J., Kuman, K.A., 2007. The view from the Lincoln Cave: midto late Pleistocene fossil deposits from Sterkfontein hominid site. S. Afr. J. Hum. Evol. 53, 260–271.
- Schmidt, V.A., Partridge, T.C., 1991. An attempt to establish a magnetostratigraphic framework for sediments deposited in Sterkfontein Cave, South Africa. Palaeoanthropology Research Unit (PARU) 25th Annual Report. University of the Witwatersrand, Johannesburg.
- Schwartz, J.H., Tattersall, I., 2002. In: The Human Fossil Record, vol. 2. Wiley, Canada. Schwarcz, H.P., Grün, R., Tobias, P.V., 1994. ESR dating of the australopithecine site of Sterkfontein, South Africa. J. Hum. Evol. 26, 175–181.

- Semaw, S., Rogers, M.J., Quade, J., Renne, P.R., Butler, R.F., Dominguez-Rodrigo, M., Stout, D., Simpson, S.W., 2003. 2.6-Million-year-old stone tools and associated bones from OGS-6 and OGS-7, Gona, Afar, Ethiopia. J. Hum. Evol. 45, 169–177.
- Signor III, P.W., Lipps, J.H., 1982. Sampling bias, gradual extinction patterns, and catastrophes in the fossil record. In: Silver, L.T., Schultz, P.H. (Eds.), Geological Implications of Impacts of Large Asteroids and Comets on the Earth. Geological Society of America Special Publication, 190, pp. 291–296.
- Smith, H.F., Grine, F.E., 2008. Cladistic analysis of early Homo crania from Swartkrans and Sterkfontein, South Africa. Journal of Human Evolution 54, 684–704.
- Spoor, F., Leakey, M.G., Gathogo, P.N., Brown, F.H., Antón, S.C., McDougall, I., Kiarie, C., Manthi, F.K., Leakey, L.N., 2007. Implications of new early *Homo* fossils from lleret, east of Lake Turkana, Kenya. Nature 448, 688–691.
- Thackeray, J.F., Kirschvink, J.L., Raub, T.D., 2002. Palaeomagnetic analysis of calcified deposits from the Plio-Pleistocene hominid site of Kromdraai, South Africa. S. Afr. J. Sci. 98, 537–540.
- Thackeray, J.F., Loth, S.R., Liang, M., Swanepoel, E., Dayal, M.R., Lubbe, K., 2000. Comparison of Sts 5 ('Mrs Ples') and Stw 53 ('Early Homo') from Sterkfontein, South Africa. S. Afr. J. Sci. 96, 21.
- Tobias, P.V., 2000. The fossil hominids. In: Partridge, T.C., Maud, R.R. (Eds.), The Cenerzoic of Southern Africa. Oxford Monographs on Geology & Geophysics. Oxford University Press, Oxford, pp. 252–276.
- Vrba, E., 1973. Two species of Antidorcas Sundevall at Swartkrans (Mammalia: Bovidae). Ann. Transvaal Mus 28, 287–361.
- Vrba, E.S., 1976. The fossil bovidae of sterkfontein, Swartkrans and Kromdraai. Transv. Mus, Pretoria. Mem. 21.
- Vrba, E.S., 1982. Biostratigraphy and chronology, based particularly on Bovidae, of southern assosiated assemblages: Makapansgat, Sterkfontein, Taung, Kromdraai, Swartkrans. Proceedings of the 1st International Congress of Human Palaeontology 2, 707–752.
- Vrba, E.S., 1995. The fossil record of African antelopes (Mammalia, Bovidae) in relations to human evolution and palaeoclimate. In: Vrba, E.S., Denton, G.H., Partridge, T.C., Burckle, L.H. (Eds.), Palaeoclimate and Evolution with Emphasis on Human Origins. Yale University Press, New Haven, pp. 385–424.
- Walker, J., Cliff, R.A., Latham, A.G., 2006. U-Pb isotopic age of the Stw 573 hominid from Sterkfontein, South Africa. Science 314, 1592–1594.
- Walter, R.C., Manega, P.C., Hay, R.L., 1992. Tephrochronology of Bed I, Olduvai Gorge: an application of laser-fusion ⁴⁰Ar/³⁹Ar dating to calibrating biological and climatic change. Quat. Int. 13–14, 37–46.
- Walter, R.C., Manega, P.C., Hay, R.L., Drake, R.E., Curtis, G.H., 1991. Laser-fusion ⁴⁰Ar/³⁹Ar dating of Bed I, Olduvai Gorge, Tanzania. Nature 354, 145–149.
- Watson, V., 1993a. Composition of the Swartkrans bone accumulations, in terms of skeletal parts and animals represented. In: Brain, C. (Ed.), Swartkrans: a Cave's Chronicle of Early Man. Transvaal Museum, Pretoria, pp. 35–74.
- Watson, V., 1993b. Glimpses from Gondolin: A faunal analysis of a fossil site near Broederstroom, Transvaal, South Africa. Palaeontol. Afr. 30, 35–42.
- White, T., 1995. African omnivores: global climatic change and Plio-Pleistocene hominids and suids. In: Vrba, E.S., Denton, G.H., Partridge, T.C., Burckle, L.H. (Eds.), Palaeoclimate and Evolution with Emphasis on Human Origins. Yale University Press, New Haven, pp. 369–384.
- Wood, B., 2000. The history of the Genus Homo. Hum. Evol. 15, 39-49.
- Wood, B., Constantino, P., 2007. Paranthropus boisei: fifty years of evidence and analysis. Yearbook Phys. Anthropol. 50, 106–132.