New Australopithecus robustus fossils and associated U-Pb dates from Cooper's Cave (Gauteng, South Africa)

Darryl J. de Ruiter, Robyn Pickering, Christine M. Steininger, Jan D. Kramers, Phillip J. Hancox, Steven E. Churchill, Lee R. Berger, Lucinda Backwell

Department of Anthropology, Texas A&M University, College Station, TX 77843, USA
Bernard Price Institute for Palaeontological Research, School of Geosciences, University of the Witwatersrand, Private Bag 3, Wits 2050, Johannesburg, South Africa
Institute for Geological Sciences, University of Bern, Baltzerstrasse 3, 3012 Bern, Switzerland
Institute for Human Evolution, University of the Witwatersrand, Private Bag 3, Wits 2050, Johannesburg, South Africa
Department of Evolutionary Anthropology, Duke University, Durham NC 27708, USA

Article history:
Received 10 September 2008
Accepted 5 January 2009

Keywords:
Australopithecus
Paleoenvironment
Cave formation
Speleothems
Uranium-lead dating

Abstract

Australopithecus robustus is one of the best represented hominin taxa in Africa, with hundreds of specimens recovered from six fossil localities in the Bloubank Valley area of Gauteng Province, South Africa. However, precise geochronological ages are presently lacking for these fossil cave infills. In this paper, we provide a detailed geological background to a series of hominin fossils retrieved from the newly investigated deposit of Cooper's D (located partway between Sterkfontein and Kromdraai in the Bloubank Valley), including uranium-lead (U-Pb) ages for speleothem material associated with A. robustus. U-Pb dating of a basal speleothem underlying the entire deposit results in a maximum age of 1.526 ± 0.088 Ma for Cooper's D. A second U-Pb date of ca. 1.4 Ma is produced from a flowstone layer above this basal speleothem; since this upper flowstone is not a capping flowstone, and fossiliferous sediments are preserved above this layer, some of the hominins might be slightly younger than the calculated age. As a result, we can broadly constrain the age of the hominins from Cooper's D to between 1.5 and approximately 1.4 Ma. Extinct fauna recorded in this comparatively young deposit raise the possibility that the Bloubank Valley region of South Africa represented a more stable environmental refugium for taxa relative to tectonically more active East Africa. The sediments of the deposit likely infilled rapidly during periods when arid conditions prevailed in the paleoenvironment, although it is unclear whether sediment deposition and bone deposition were necessarily contemporaneous occurrences. We reconstruct the paleoenvironment of Cooper’s D as predominantly grassland, with nearby woodlands and a permanent water source. The hominin teeth recovered from Cooper’s D are all from juveniles and can be confidently assigned to A. robustus. In addition, two juvenile mandibular fragments and an adult thoracic vertebra are tentatively attributed to A. robustus.

© 2009 Elsevier Ltd. All rights reserved.

Introduction

The dolomitic caves of the Bloubank Valley to the north-west of Johannesburg, South Africa have yielded rich and diverse fossil faunas and archaeological materials ranging in age from the later Pliocene to the Holocene. The faunas include abundant early hominin remains from no less than eight discrete localities. Later Pliocene hominins attributed to Australopithecus africanus are known from Sterkfontein (Broom, 1936; Clarke, 1998; Lockwood and Tobias, 2002; Moggi-Cecchi et al., 2006) and Gladysvale (Berger et al., 1993), while early Pleistocene hominins attributable to either Australopithecus robustus1 or early Homo have been recovered from Kromdraai (Broom, 1938; Thackeray et al., 2001), Sterkfontein (Kuman and Clarke, 2000), Swartkrans (Broom, 1949; Brain, 1981; Grine, 1989; de Ruiter et al., 2006), Drimolen (Keyser, 2000; Keyser et al., 2000), Gondolin (Menter et al., 1999), and Cooper’s Cave (Berger et al., 1995, 2003; Steininger et al., 2008). A lack of material suitable for radiometric dating (such as volcanic tuffs) means that, with the exception of Sw 573 from Sterkfontein (Partridge et al., 2003; Walker et al., 2006) and more recently Swartkrans (Balter

---

1 In this paper we follow a more conservative taxonomy and employ the generic nomen Australopithecus as used in de Ruiter et al. (2006), whereas elsewhere some of us have utilized the generic nomen Paranthropus (Steininger et al., 2008).
The site of Cooper’s Cave is a collection of three spatially distinct infills (Cooper’s A, B, D), all of which preserve fossil-bearing sediments with varying densities of materials. Fossils recovered from two of these infills in the 1950s, and housed in the Transvaal Museum (Pretoria), initially received accession designations of COA and COB, reflecting their sources. However, it was later discovered that these accession designations did not necessarily correspond to the actual deposits, rendering their provenience uncertain. In order to resolve this confusion, where possible we designate materials recovered from the three fossiliferous deposits as CA, CB, and CD, the latter representing the infill reported in this paper. These infills are situated partway between Sterkfontein and Kromdraai on the south flank of the Bloubank Valley (26°00′47.3″S, 27°44′43.5″E; Fig. 1). As with the other hominin sites of the Bloubank Valley, Cooper’s Cave occurs within the dolomites of the Monte Christo Formation (Malmani Subgroup, Transvaal Supergroup).

The first hominin specimen was recovered in 1938 (Shaw, 1939, 1940), although it is unclear which of the Cooper’s infills was the source of this fossil. At the time, comparative Australopithecus material was scarce, making its initial taxonomic attribution uncertain. The tooth was considered to represent an unknown fossil hominin taxon distinct from Australopithecus africanus (Plesianthropus) and Paranthropus, possibly representing “an early African human type” (Shaw, 1940: 155). Broom and Schepers (1946) and Robinson (1956), however, maintained that the specimen was most similar to Australopithecus africanus (Plesianthropus transvaalensis) and that it differed from Paranthropus and Homo. This specimen has since been lost, and all that remains is a poor quality cast, therefore neither the taxonomic affinity nor the provenience of the first hominin recovered from Cooper’s Cave can be confirmed.

A small scale excavation was undertaken at Cooper’s B in 1954 (Brain, 1958), but in subsequent decades interest in the site waned. In recent years, the discovery of additional hominin materials in collections housed at the Transvaal Museum prompted renewed interest in the site (Berger et al., 1995; Steininger et al., 2008). In 2001 we began excavations in a previously unexplored deposit at Cooper’s (Cooper’s D), and we were quickly rewarded with the first in situ hominins recovered from the cave system (Berger et al., 2003). The area of Cooper’s D that is currently under excavation extends along an east-west trend. To date, approximately 60 m² has been cleared of decalcified sediments to a depth of 2 m. A plane-table geological map of the deposits (updated here from Berger et al., 2003), an aerial photo, and section view of the site are shown in Figure 2. The decalcified component of Cooper’s D is derived from more heavily calcified sediment that is commonly, though imprecisely, referred to as “breccia.” This latter, calcified sediment is preserved in the form of a series of low pinnacles of clastic “breccia,” which contain fossils to which some decalcified specimens can be refitted. Decalcified sediments are loosened soils from which cementing CaCO3 has been leached out of “breccia” via the actions of tree roots, leaving behind fossils that are often covered with a thin layer of pyrolusite (Brain, 1958). The combined fossiliferous sediments originally filled a 3 × 20 m cave that experienced significant de-roofing, with the result that today the entirety of the Cooper’s D deposit is exposed to the surface. The presence of speleothems (here stalagmites and flowstones), which can form only in relatively closed caves, suggests that the entire series was deposited while the cave still had a fairly competent roof. Within the Cooper’s D locality, two areas of fill are recognised and termed the Cooper’s D East and West deposits (Berger et al., 2003).

The hypodigm of A. robustus currently numbers greater than 500 specimens, and as a result we know a great deal about the biology and ecology of this particular taxon (Robinson, 1956; Brain, 1981; Grine, 1981, 1988, 1989; Susman, 1989; Susman et al., 2001; Susman and de Ruiter, 2004; de Ruiter, 2004; Scott et al., 2005; de Ruiter et al., 2006; Sponheimer et al., 2005a,b, 2006). However, precise geochronological ages are only beginning to be produced for the fossil cave infills from which australopithecine fossils have been recovered. Within the Bloubank Valley, Walker et al. (2006) used U-Pb dating on speleothem material in the Silberberg Grotto of Sterkfontein to bracket the Stw 573 skeleton, producing tightly constrained age estimates above (2.17 ± 0.07 Ma) and below (2.24 ± 0.09 Ma), respectively. These dates contrast with cosmogenic 26Al/10Be dates (4.17 ± 0.14 Ma) produced for clastic cave sediments associated with the same skeleton (Partridge et al., 2003). The taxonomic affinity of this skeleton is uncertain at present (Clarke, 1998). More recently,
Balter et al. (2008) have provided U-Pb dates for bovid tooth enamel from Member 1 (1.83 ± 0.138 Ma), Member 2 (1.36 ± 0.29), and Member 3 (0.83 ± 0.21) of Swartkrans. However, their dates carry large error margins, and they must rely on the selection of an appropriate nuclide uptake model, rendering them additionally susceptible to diagenesis. In this paper, we provide a detailed geological background to a series of hominin fossils recovered from the newly investigated deposit of Cooper’s D, including U-Pb ages for speleothem material associated with *A. robustus*. In addition, we present a preliminary report on the associated fauna and paleoenvironment, including a taphonomic analysis and descriptions of recently recovered hominin material.

**Geology of the site**

**Cooper’s D East**

The sediments typical of these deposits are described in Section 1 (Fig. 3). At the base of the section, the cave floor consists of dolomite with the weathered remains of a stalagmite. Above this is a thick sediment unit, forming a fining upwards sequence of sub-angular dolomite blocks (with and without manganese staining), some quartz clasts, and abundant fossil bone in a sandy reddish-brown matrix. The sediments are well calcified with pervasive calcite and some microfaunal bone.
There is a distinct break in sedimentation at the top of the unit, representing more of an erosive contact than a flowstone marked boundary. The next unit is a coarsening upwards sequence, and like the sediments below, it is massive with no preferred orientation of clasts. This unit consists of up to 40 cm dolomite roof blocks (with clear chert layers) concentrated at the top of the section, cemented in a sandy reddish-brown matrix. Some patches of flowstone cap the sequence, though none of these are suitable for dating.

Section 2 is approximately 1.5 m away from section 1 (Fig. 2), and preserves notably different looking sediments in a pocket of fossil-bearing material against the northern cave wall (Fig. 3). The base of the section is formed by the dolomite cave wall, which is lined with flowstone. This is followed by two layers of dark brown muddy sediment containing 2–5 cm angular blocks of dolomite. This material is most likely not externally derived but is rather a residuum formed as a result of in situ dolomite weathering and break down. Similar deposits have been observed at the nearby Sterkfontein Caves (Partridge, 2000). A thick (10 cm) flowstone layer with popcorn texture caps this material. The overlying sediments form an erosive contact and are dark to moderate brown silty sands with weak horizontal layering in an east-west direction. Fossil teeth and bones are common in this section and are horizontally aligned with sediments; there are few other clasts, apart from isolated dolomite and chert clasts. As the overlying flowstone layer that fills the space between the sediments and the cave roof has no erosive contact, it is possible that the flowstone caps the sediments. Alternatively, it could be a pre-existing flowstone coating on the wall which the sediments banked up against and were then progressively calcified. Structures resembling stalactites suggest the latter is the case. Once again there is no suitable material for U-Pb dating.

**Cooper’s D West**

These fossil bearing sediments differ from those of Cooper’s D East in that they are more spatially restricted and finer grained than the eastern deposits and are extremely fossil rich. Much of the decalcified material has been excavated, leaving calcified material clung to the dolomite cave walls and a central pinnacle of “breccia,” which is notable for the suid fossils it contains. Sections 3 and 4 are taken from the northeast and southwest sides, respectively, of this “breccia” pinnacle (Fig. 2).

Section 3, as with Sections 1 and 2, begins with the dolomite cave floor, which has the remains of a large stalagmite growing up from it; a sample for U-Pb dating (CDD1) was taken from this basal stalagmite (Fig. 3). There is an erosive contact with the overlying sediments, which are reddish-brown, weakly-layered, clast and bone poor, sandy muds with some microfaunal bone. These sediments are well calcified with visible desiccation cracks running from the top surface down, which are lined with calcite cement. Above this is a poorly preserved flowstone, around 1 cm thick with a rippled surface, and which dips to the south at around 40°. On the eastern extent of Section 3, above the basal stalagmite, the sediments are massive, poorly sorted, coarse grained with angular to sub-angular 4–10 cm dolomite and chert blocks embedded in a reddish-brown sandy matrix. These two different looking sediments in Section 3 are capped by several branching flowstones, all too thin and fragmentary to be suitable for U-Pb dating. However, the presence of these flowstones allows us to group these sediments together as a single unit. Above this flowstone bounded unit is a second unit consisting of chert rich angular dolomite blocks, 5–15 cm in maximum length, randomly oriented but concentrated towards the eastern side of the section. These sediments are also bone rich, with heavily manganese (Mn) stained fossils concentrated in pockets. This entire section,
including both lower and upper units, is capped by a small, ponded flowstone.

Section 4 (Fig. 3) is on the southwestern side of the same “breccia” pinnacle as Section 3. It is generally similar to Section 3, although increasing numbers of small flowstones render Section 4 more complex. Once again, resting on the dolomite cave floor is a large basal stalagmite. There is an erosive contact between this stalagmite and the overlying sediment, the latter of which contains some rip up clasts, and is coarser grained from west to east across the section. Randomly oriented dolomite clasts fine upwards through a reddish-brown sand matrix. The unit is capped with a popcorn textured flowstone. The western extent of the section preserves a small pocket of sediment, where the lower flowstone is reasonably well developed with a small stalagmite growing up from it. We extracted a sample for U-Pb dating (CDD3) from this flowstone. The sediments overlying this flowstone have an erosive contact and fine upwards. Towards the top of the unit is a large dolomite clast, with no surface weathering and with pronounced chert layers. This is capped by a layered flowstone which splits into some thinner flowstone layers away from the clast, with intercalated reddish-brown sandy sediment; large clasts are lacking, but some fossil bone is present. These units are capped by a slightly thicker flowstone with a popcorn texture and Mn stained top surface which dips in towards the large dolomite block (i.e., to the east) at about 12° and extends around to the west where it can be seen in Section 3. In the east this flowstone is discontinuous, and the section in general is poorly calcified. Above this flowstone (in the west) and erosional contact (in the east) is another sediment unit dominated by dolomite roof blocks with a moderate reddish-brown sand matrix and some microfaunal fossil bone. The unit in general coarsens upwards and has an erosional top surface with no flowstone material preserved.

Sedimentary facies descriptions and distributions

In summary, the fossil-bearing sediments of Cooper’s D East rest on the dolomite cave floor, above a flowstone or stalagmite layer. On the northern side of the deposit (Section 2), a pocket of internally derived (free of fossil bone) sediments, believed to be dolomite residuum, represents a time before the cave was open to external infilling. The fossil bearing sediments found in the middle of Cooper’s D East form two superimposed units that are separated by an erosional contact (Section 1). Although the lower unit fines upwards towards this boundary, and the upper unit coarsens upwards away from this contact, the two units are essentially the same: massive sediment with a reddish-brown sandy matrix, dolomite clasts, and fossil bone. This type of sediment seen in Section 1 is here referred to as Facies A (see Fig. 2).

The sediments typical of the Cooper’s D West deposits consist of basal stalagmites overlain by erosive sediments consisting of dolomite blocks concentrated in a reddish-brown sandy matrix in the southeastern corner of the “breccia” pinnacle. Above this unit, a series of small flowstones, including a small stalagmite, form a break in clastic sedimentation. The next sedimentary unit is essentially similar in that it is a blocky, bone-rich, reddish-brown sandy sediment. Once again a series of small, laterally non-persistent flowstones separate this sedimentary unit from the final unit, the latter of which also consists of dolomite roof blocks in a reddish-brown, bone-rich sandy matrix. This suite of units is here defined as Facies B. They are distinct from Facies A in that they contain more, smaller, dolomite clasts and many more fossil bones and teeth.

In the northwest part of the Cooper’s D deposit, and in between the East and West sections described here, a third type of sediment is observed. This is a brownish-red, sandy sediment with distinct layering that is extremely rich in microfaunal fossils. Very few other clasts are present, with none of the dolomite blocks that characterize Facies A and B. This is termed Facies C.

The dips on the clasts in the Cooper’s D East deposit form a centripetal pattern, indicating they were deposited as a cone beneath a vertical to sub-vertical roof opening. The sediments in the western part of the deposit form a similar cone. The differences between these accumulations are subtle, but Facies A in the east is coarser grained and less fossil-rich in general than is Facies B in the west. The coarser-grained material (the dolomite blocks) accumulated directly under or close to the two entrances, while the finer-grained, more mobile material was washed further into the cave, forming the layered Facies C deposits. This hydrodynamic sorting that separated the finer-grained sediments had a similar, and in fact stronger, effect on the small and buoyant microfaunal bone, which is concentrated in Facies C. It is also possible that owls were using the cave at around this time, perhaps even perching on the fallen roof block, which could account for the density of microfaunal bones. All the microfaunal bone appears to be reworked, and this distribution pattern is also true for the other fossil bone. In general, the macrofossils are found in the finer-grained portions of the both Facies A and B.

Uranium-lead dating

Direct dating of the South African cave infills remains one of the most significant, unresolved issues in African palaeoanthropology. The geological setting in South Africa differs from that in East Africa, as no volcanic ash layers are present, thus K-Ar or Ar/Ar dating techniques and attendant bracketing of fossil-bearing horizons is not possible. Notwithstanding, using the extensive and well-dated East African faunal sequences, relative ages for the South African caves have been assigned based on correlations with the faunal assemblages recovered from these sites (Coole, 1967; White and Harris, 1977; Vrba, 1982, 1985a,b; Delson, 1984, 1988; Brain, 1993; Berger et al., 2002; Berger et al., 2003; de Ruiter, 2003). However, biostratigraphic dating has significant limitations, including an assumption of continent-wide, contemporaneous evolutionary events such as first and last appearance of taxa (Hill, 1995; White, 1995); issues involving refugia and relict populations (Vrba, 1988; Reynolds, 2007); and, the limitations imposed by the necessarily broad age ranges that must be tolerated (Berger et al., 2002). Paleo- magnetic signals recorded predominantly in the speleothem material preserved in the caves can be compared to global magnetostratigraphy (Partridge, 1973, 1982, 1986; Brock et al., 1977; McFadden, 1980; Partridge et al., 1999, 2000), but once again only relative ages are produced (Kappelman, 1993). Ideally the fossils could be dated themselves, but fossil material is notoriously difficult to date, as it does not behave as a closed system and the uptake and loss of parent and daughter isotopes must be modeled (e.g., Millard and Hedges, 1996). This is possible with U-Th dating of fossil bone (Pike et al., 2002). Electron spin resonance (ESR) dating of mainly bovid tooth enamel has produced age estimates for Sterkfontein (Schwartz et al., 1994) and Swartkrans (Curnoe et al., 2001), although problems relating to reworking of materials and uptake and loss of Uranium have not yet been satisfactorily resolved (Blackwell, 1994; Curnoe et al., 2001), and the procedure has yet to be calibrated against proven techniques such as Ar/Ar dating in Africa. A recent study used U-Pb to date tooth enamel from Swartkrans (Balter et al., 2008); this is a promising approach, although it has its limitations, especially considering that nuclide uptake must be modeled to account for possible effects of diagenesis.

Given the problems associated with directly dating fossils, two recent advances in our understanding of and ability to accurately measure radiogenic isotopes have resulted in two notable leaps in
the dating of the fossil bearing deposits. First, cosmogenic nuclides of \(^{10}\)Be and \(^{26}\)Al trapped in quartz grains record the age of burial of the crystals and can thus be used to date clastic cave sediments (Partridge et al., 2003). Second, the \(\text{in situ}\) decay of \(^{238}\)U trapped in speleothem calcite to \(^{206}\)Pb can be used to date the formation of these layers (Richards et al., 1998; Woodhead et al., 2006; Pickering et al., submitted for publication), and where flowstone layers are intercalated with fossil bearing calcitic sediments, provide age brackets for the faunal material (Walker et al., 2006). However, both methods have inherent problems and have yet to produce complementary ages for a single deposit (cf. Partridge et al., 2003). More specifically, problems associated with U-Pb dating of carbonates as young as the flowstones from Cooper’s Cave is limited by factors including: U and Pb concentrations, initial \(^{238}\)U/\(^{234}\)U ratios, obtaining a range of \(^{238}\)U/\(^{204}\)Pb ratios, and contamination from common \(^{208}\)Pb lead. Aside from these problems, speleothem material is not always closely associated with fossil bearing sediments and a detailed knowledge of the geological setting of the site is crucial in order to critically access age estimates and relate these to the fossils of interest.

The Cooper’s D West deposits (both the eastern and western extents, see Fig. 2) present a well preserved stratigraphy of basal stalagmites overlain by clastic sediments containing at least one major flowstone layer; both were sampled for U-Pb dating. The first step, critical to the success of U-Pb dating on such material, is determining the distribution and concentration of U within the samples. To this end, a Fujifilm BAS-800 beta-scanner was used to produce phosphor images showing the relative positions of radiation-emitting material (here assumed to be U) in the samples. This method has been used to find U-rich layers for U-Pb dating in Miocene tufas (Cole et al., 2003) and flowstones from Sterkfontein (Walker, 2005) and is further described in Pickering et al. (submitted for publication). Sample CDD1 has a clearly distinguishable U-rich layer (Fig. 4) and was subsequently targeted for dating.

Once layers of flowstone were selected for dating, ~0.05 g blocks were cut out using a hand held diamond wheel saw. From this stage onwards all handling of samples took place in a Picotrace® clean lab environment. These procedures are detailed in Pickering et al. (submitted for publication) and are given in brief here. A mixed \(^{206}\)Pb/\(^{208}\)U spike is added to all samples prior to separation of Pb and U via ion exchange chemistry. Large (over 0.1 g) unspiked samples from U rich layers were also measured to better constrain the \(^{238}\)U/\(^{234}\)U ratios without having to correct for the presence of these isotopes in the spike. U blanks are negligible and the total procedure blank for Pb is normally 40 pg. Pb blanks have an isotopic signature within error of common Pb and a correction is thus unnecessary.

A double focusing Nu Instruments® multicollector ICP-Mass spectrometer equipped with a fixed array of 12 Faraday cups and 2 ion counters was used for all concentration and isotope ratio determinations. Uranium standard U050 is used to tune machine settings and to bracket samples and correct for drift on the ion counters. Large unspiked samples were run in between an in-house in equilibrium standard, U Moss. The difference between the \(^{238}\)U/\(^{234}\)U ratios of the samples and bracketing U Moss runs is used to calculate the present day activity \(^{238}\)U/\(^{234}\)U ratios. Lead masses 208, 207, and 206 are measured on Faraday cups and masses 204 and 202 on ion counters in a two cycle program. Lead standard SRM 981 doped with Tl is used to tune machine setting and correct for subsequent gain on ICP by bracketing every 4–5 samples. All isotope results are summarized in Table 1.

Simple isochron age determinations using the \(^{238}\)U/\(^{204}\)Pb and \(^{206}\)Pb/\(^{204}\)Pb ratios overestimate the age of the material, as such a calculation does not take into account the initial \(^{238}\)U/\(^{234}\)U disequilibrium. In naturally occurring ground waters, \(^{238}\)U and \(^{234}\)U are not in equilibrium and thus have an activity ratio above 1. The excess of \(^{234}\)U in the ground water is due to the increased mobility of \(^{234}\)U in the weathering of the host rocks. The source of extra \(^{234}\)U is debatable but most likely derives from alpha recoil during the decay of \(^{238}\)U (Gascoyne, 1982). The speleothems (in this case flowstones and stalagmites) forming from this groundwater inherit this excess of \(^{234}\)U, which over time also decays to produce \(^{206}\)Pb. Thus an estimate of the initial \(^{238}\)U/\(^{234}\)U activity ratio is of great importance in producing accurate ages. In samples as young as these (under 2 Ma) the disequilibrium between \(^{238}\)U and \(^{234}\)U from the excess \(^{234}\)U should still be discernable, due to the long half lives of these isotopes. We measured \(^{238}\)U/\(^{234}\)U ratios in large (over 0.15 g) unspiked samples of the same material being dated to constrain the present day \(^{238}\)U/\(^{234}\)U disequilibrium (Table 1). These data were then used to calculate ages together with \(^{206}\)Pb/\(^{238}\)U ratios generated by Isolot (Ludwig, 2000). A correction is also made for the initial absence of \(^{230}\)Th in the samples. Errors are fully propagated with a Monte Carlo simulation and take into account all analytical uncertainties. The average U concentration for the dated layer of CDD1 is only 712 ppb (0.71 \(\mu\)g g\(^{-1}\)), some 15 times lower than the U concentrations published by Richards et al. (1998). Dating is made possible, however, as although Pb concentrations are low, on average 10 ppb (0.01 \(\mu\)g g\(^{-1}\)), \(^{206}\)Pb/\(^{204}\)Pb ratios of up to 23 indicate that the Pb present is radiogenic. However, it must be noted that these samples are only moderately enriched in radiogenic Pb.

Figure 4. Photograph of stalagmite from where sample CDD1 was removed (left) and close up of sample CDD1 (middle) with results from beta-scanning (right) where the black arrow shows the U-rich layer targeted for dating. Although Pb concentrations are low, most of this Pb is in the form of radiogenic daughter decay products of U. This sample produced a tightly constrained age estimate of 1.526 (± 0.088) Ma. Scale bar in middle and right images = 10 mm.
In an isochron plot of $^{206}\text{Pb}/^{204}\text{Pb}$ against $^{238}\text{U}/^{204}\text{Pb}$ for all samples for CDD1, the mean square of weighted deviates (MSWD) is large (¼ 19, see Fig. 5a), indicating that the scatter of points is not due to analytical error alone. A very similar plot presents itself if $^{208}\text{Pb}$ or $^{207}\text{Pb}$ are chosen as common denominators, which shows that the scatter is not an artifact of incorrect ion counter gain calibration or Hg correction. None of the data can be rejected on the basis of independent criteria (e.g., aberrant $^{208}\text{Pb}/^{204}\text{Pb}$ ratios).

### Table 1

Summary of U and Pb isotope data for samples CDD1 and CDD3, including ratios used in age calculations.

<table>
<thead>
<tr>
<th>Sample Name</th>
<th>Concentrations (ppb)</th>
<th>Interelement ratios</th>
<th>Pb isotope ratios summary</th>
<th>Current</th>
<th>Initial</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>U</td>
<td>Pb</td>
<td>$^{238}\text{U}/^{204}\text{Pb}$</td>
<td>$^{206}{/^{204}\text{Pb}}$</td>
<td>$^{206}/^{207}$/2SE</td>
</tr>
<tr>
<td>CDD1-1</td>
<td>47 12</td>
<td>247.20 0.96 18.530</td>
<td>0.012 1.179 0.002 0.848</td>
<td>0.001 2.065 0.002</td>
<td></td>
</tr>
<tr>
<td>CDD1-2</td>
<td>406 16</td>
<td>1675.70 9.20 18.959</td>
<td>0.051 1.205 0.002 0.830</td>
<td>0.001 2.021 0.003</td>
<td></td>
</tr>
<tr>
<td>CDD1-3</td>
<td>462 6</td>
<td>5193.73 43.37 20.264</td>
<td>0.114 1.280 0.006 0.781</td>
<td>0.004 1.916 0.005</td>
<td></td>
</tr>
<tr>
<td>CDD1-4</td>
<td>656 10</td>
<td>4323.93 23.82 19.771</td>
<td>0.059 1.252 0.002 0.799</td>
<td>0.001 1.947 0.002</td>
<td></td>
</tr>
<tr>
<td>CDD1-5</td>
<td>643 7</td>
<td>6146.67 48.71 20.442</td>
<td>0.100 1.290 0.005 0.775</td>
<td>0.003 1.881 0.005</td>
<td></td>
</tr>
<tr>
<td>CDD1-6</td>
<td>1578 7</td>
<td>14309.38 149.67 22.396</td>
<td>0.111 1.415 0.012 0.707</td>
<td>0.006 1.712 0.006</td>
<td></td>
</tr>
<tr>
<td>CDD1-7</td>
<td>934 6</td>
<td>10561.92 108.81 21.727</td>
<td>0.130 1.364 0.014 0.733</td>
<td>0.008 1.783 0.005</td>
<td></td>
</tr>
<tr>
<td>CDD1-8</td>
<td>973 7</td>
<td>8982.47 85.02 21.421</td>
<td>0.111 1.332 0.005 0.751</td>
<td>0.003 1.813 0.006</td>
<td></td>
</tr>
<tr>
<td>Average</td>
<td>712 9</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

| CDD3-3      | 655 14               | 3157.33 16.80 20.289 | 0.047 1.257 0.007 0.796  | 0.004 1.939 0.004 |          |          |          |          |
| CDD3-4      | 397 32               | 801.71 4.10 19.041  | 0.037 1.236 0.004 0.809  | 0.003 1.977 0.004 |          |          |          |          |
| CDD3-5      | 47 7                 | 409.56 4.42 19.236  | 0.143 1.210 0.005 0.827  | 0.003 1.986 0.005 |          |          |          |          |
| CDD3-6      | 39 6                 | 418.65 5.43 20.021  | 0.084 1.246 0.010 0.802  | 0.006 1.945 0.011 |          |          |          |          |
| CDD3-7      | 27 5                 | 318.99 4.90 19.724  | 0.186 1.205 0.001 0.830  | 0.000 2.029 0.001 |          |          |          |          |
| CDD3-8      | 20 7                 | 186.65 2.44 19.302  | 0.141 1.240 0.010 0.806  | 0.007 1.958 0.008 |          |          |          |          |
| CDD3-9      | 20 5                 | 281.21 4.74 19.987  | 0.184 1.204 0.003 0.830  | 0.002 2.024 0.003 |          |          |          |          |
| CDD3-10     | 17 5                 | 213.94 2.82 19.735  | 0.197 1.275 0.001 0.784  | 0.001 1.911 0.001 |          |          |          |          |
| CDD3-11     | 13 10                | 85.98 0.61 18.812  | 0.050 1.251 0.005 0.800  | 0.003 1.930 0.005 |          |          |          |          |
| CDD3-12     | 11 4                 | 181.28 2.17 19.922  | 0.145 1.221 0.006 0.819  | 0.004 1.997 0.008 |          |          |          |          |
| CDD3-13     | 10 5                 | 131.44 1.42 19.320  | 0.080 1.231 0.009 0.812  | 0.006 1.959 0.008 |          |          |          |          |
| Average     | 114 9                |                     |                          |          |          |          |          | 1.021817 0.004206 2.744 2.855 |

Figure 5. Isochron for filtered analyses of sample CDD1 and sample CDD3. See text for details on how ages were calculated.
suggesting a second, possibly detrital, common Pb component. The scatter could be due to some heterogeneity in initial Pb isotope compositions, a scatter in the initial $^{238}$U/$^{234}$U ratios, or a disturbance of the U-decay chain in some of the subsamples. We have not observed a scatter in the initial $^{238}$U/$^{234}$U ratios of any of the material analyzed from this region and believe that our sub-cm sampling scale provides a homogenous initial $^{238}$U/$^{234}$U composition. Thus we consider a disturbance in the U-decay chain to be most likely, as the scatter is greater for the more radiogenic data points than for the nonradiogenic ones. As disturbance of the chain more often takes the form of loss (e.g., of $^{234}$U or Radon) than of addition, the most radiogenic sample point CDD1–6 (Table 1; see arrow in Fig. 5a), which is below a prima facie regression line through the data, is most problematic. If a regression is made omitting this point, the MSWD is reduced to 3.5, which almost defines an isochron (in which all scatter is due to analytical error; Fig. 5b). The isochron is a good test of internal consistency of the data, indeed suggesting that only sample point CDD1–6 is suspect and its omission is legitimate. An age is then calculated using this slope (i.e., the measured $^{206}$Pb/$^{238}$U ratio) and the present day $^{238}$U/$^{234}$U ratio. The result is 1.526 ± 0.088 Ma, with an initial $^{238}$U/$^{234}$U activity ratio of 2.583 ± 0.069 (Fig. 5b; Table 1). This initial ratio is well within the range of values for other samples in the Sterkfontein area and probably reflects the accumulation of mobile $^{234}$U in soil overlying the cave during prolonged droughts (Pickering et al., submitted for publication).

CDD3 is more problematic than CDD1. However, its stratigraphic position in the flowstone above the basal CDD1 stalagmite allows us to partially bracket the fossil-bearing deposits, rendering any extricable age information especially important. CDD3 has a low U content, with some measured concentrations as low as 11 ppb; only two samples had U concentrations over 100 ppb, one of which also has a relatively high Pb content (Table 1). Pb concentrations are higher than preferred, with an average value of 0.016 ppm (Table 1). Subsamples with low $^{238}$U/$^{204}$Pb ratios show a large scatter in $^{206}$Pb/$^{204}$Pb, indicating either recent U loss (which has not otherwise been seen in this type of sample) or a heterogeneous admixture of relatively radiogenic Pb during flowstone emplacement (Fig. 5c). As we have been unable to identify reasons to exclude any data from this set, the U-Pb results remain inconclusive and we cannot extract an age from this sample. However, the $^{238}$U/$^{234}$U activity ratio for many speleothems in the region varies within a relatively narrow interval, 2.4–3.0 (Walker et al., 2006; Pickering et al., 2007; Pickering and Kramers, unpublished data), and if we assume that these limits apply to the CDD3 flowstone (with the present-day values given above), age constraints can be obtained. The upper limit of the initial value combined with the lower limit of the present-day value gives a maximum age of 1.671 Ma. Similarly, a minimum age of 1.413 Ma is imposed. Since the underlying flowstone CDD1 has an age of 1.526 ± 0.088 Ma established by U-Pb, the age of CDD3 is further constrained to between 1.413 and 1.526 Ma (at a maximum). Thus the sediments and fossils sandwiched between the flowstones must have accumulated between approximately 1.5 and 1.4 million years ago. There are sediments above the flowstone layer sampled by CDD3 that are likely to be younger than 1.4 Ma.

The U-Pb ages for the flowstones coupled with the detailed stratigraphy of the site are used to suggest a series of events in the formation, infilling, and final erosion of the cave into the present state (Fig. 6). Prior to the cave opening up to externally derived sediments and fossils, drip waters formed the stalagmites and flowstones found at the base of all the sections dated to 1.526 ± 0.088 Ma. More arid conditions led to the cessation of speleothem growth and surface weathering opened up fissures in the cave roof, through which sediments and fossils were deposited into the eastern and western sides of the cave. The collapse of large dolomite roof blocks separated the two deposits. A break in sediment accumulation is marked by a second episode of flowstone formation at around 1.4 Ma. Clastic sedimentation continued after this, ending in the complete collapse of the cave roof and present day levels of erosion.

Faunal assemblage composition

The combined faunal assemblage recovered from Cooper's D East and West is large and well preserved, with greater than 50,000 catalogued specimens. Although we can distinguish Cooper's D East and West deposits on geological grounds, the relationship between lithofacies and recovered fossils is presently unclear. This situation results from the fact that most of the faunal material so far analyzed is derived from decalcified sediments that have undergone unknown levels of sediment compaction, bioturbation, and hydrodissolution, resulting from the decalcification process. Given that there is no discernable difference between fauna recovered from the Cooper's D East and West deposits, we here consider them as a single entity pending more detailed analysis. To date, a subset of the fauna has been thoroughly analyzed, amounting to 8,488 specimens identifiable to skeletal element and taxonomic family, forming the basis of the discussion presented here. From this subset we have identified a minimum of 200 individual mammals, including primates, carnivores, hyracoids, perissodactyls, artiodactyls, rodents, and lagomorphs (Table 2). Of special interest is the rich and diverse carnivore assemblage from Cooper's D, as well as the unusual abundance of suid remains (Berger et al., 2003). As is typical of the cave infills of the Bloubank Valley, bovids numerically dominate the assemblage.

The majority of the ungulate fauna from Cooper's D are indicative of grassland habitats, including Alcelaphini, Antilopini, Equus, and Metridiochoerus. The Cercomeridae, Giraffidae, Bovini, and Tragelaphini point to the presence of a relatively wooded environment, with at least a localized existence of dense riverine underbrush. A nearby, permanent water source is indicated, likely in the form of the paleo-Bloubank River. It is difficult to determine precisely which component of the reconstructed habitat mosaic was preferred by the hominins, although a recent study has indicated that A. robustus-bearing assemblages tend to show an inverse relationship between the hominins and grassland adapted taxa (de Ruiter et al., 2008). In other words, the more grassland taxa there are in a given assemblage, the fewer hominins there tend to be. This suggests that although the Cooper's D hominins are associated with a grassland environment, they might have favored a more closed portion of the habitat mosaic. Such a suggestion is supported by isotopic studies indicating a diet of both C4 grassland and C3 woodland based foods in the diet of A. robustus (Lee-Thorp et al., 1994; Sponheimer et al., 2005b, 2006).

Taphonomic analysis

All fossil specimens were examined using a 10× magnification hand lens, and where traces of bone surface modifications were detected, they were further examined with an 8–20× magnification binocular microscope. There is no indication of hominin involvement in the Cooper's D accumulation, as there are no cut marks or hammerstone percussion marks on any of the specimens examined. Of the 8,488 specimens examined, 90 exhibit carnivore punctate depressions, including one of the hominins (CD 6807); the hominin shows a linear series of three small punctate depressions that compare favorably with those left by a small canid such as
a jackal. A further 26 specimens show gastric etching, while there do not appear to be any specimens showing porcupine gnawing. At the same time, only three coprolites were recovered. Bone breakage patterns (Villa and Mahieu, 1991) are equivocal, and thus do not aid in resolving the mode of accumulation. A ratio of carnivores to carnivores + ungulates that exceeds 20% has been cited as evidence of carnivore involvement in a fossil accumulation, specifically hyaenas (Cruz-Uribe, 1991; Pickering, 2002; Kuhn et al., in press). At 26%, the carnivores to carnivores + ungulates ratio indicates that hyaenas were likely to have been significant contributing agents in Cooper’s D. The relatively high representation of small carnivores such as viverrids, mustelids, and canids point to a probable contribution by brown hyaenas (Parahyaena brunnea; Brain, 1980, 1981). These combined factors implicate hyaenas as the predominant, though likely not exclusive, bone accumulating agent of the Cooper’s D assemblage.

Hominin fossil material

To date, four isolated teeth, two mandibular fragments, and a thoracic vertebra have been recovered (Table 3). All specimens were examined under a 8–20× binocular microscope. Comparisons were made with original hominin fossils from Swartkrans, Kromdraai, and Sterkfontein housed at the Transvaal Museum, and with original hominin fossils from Sterkfontein, Makapansgat, and Gladysvale housed at the University of the Witwatersrand. In addition, comparisons were made with casts of fossils recovered from Olduvai Gorge, Koobi Fora, and the Omo Shungura sequence in east Africa. Descriptive terminology follows Robinson (1956), Tobias (1967, 1991), Brain (1981), Grine (1984, 1989), and Wood (1991). Dental measures were recorded by us and were taken from published...
accounts of hominin materials (Robinson, 1956; Grine, 1984, 1989; Tobias, 1991; Wood, 1991; Walker and Leakey, 1993; Keyser et al., 2000; Moggi-Cecchi et al., 2006). Abbreviations used below include: ICF, interproximal contact facet; BL, buccolingual(ly); MD, mesiodistal(ly); CO, cervico-occlusal(ly); MMR, mesial marginal ridge; DMR, distal marginal ridge; C6, cusp 6. All measurements are presented in millimeters (mm).

**Isolated teeth**

CD 1634, Ldm² (Fig. 7a). This a nearly complete tooth crown lacking most of the roots. A small wedge of enamel has been broken away from the mesiobuccal corner. The tooth is estimated to measure 11.7 (MD) by 13.0 (BL). Occlusal wear is very light, with slight facet formation at the apices of the cusps, and a facet in evidence on the MMR. The mesial ICF (2.5 BL; 1.7 CO) is small and centrally positioned. There is no distal ICF. The entire crown of the tooth is extensively marked by pit-type enamel defects. Occlusally the crown displays a nearly square outline. All four principal cusps are present and well developed. The protocone is the largest cusp, followed in descending order of size by the metacone, paracone, and hypocone. The mesial face of the protocone is marked by three shallow grooves, the middle one terminating in a distinct Y-shape. The damaged MMR is thick and well developed. The fovea anterior is represented by a buccally directed limb; it is bounded distally by a low, narrow epicrista that runs transversely from the metacone to the protocone, delineating the fovea anterior from the trigon basin. The trigon basin is broad and deeply incised; the buccal limb of the trigon basin is partially interrupted at the occlusobuccal margin by a high, thin wall of enamel, though this wall is incised to the depth of the trigon basin by a narrow groove that continues onto the buccal face. The predominantly BL oriented distal trigon crest (crista obliqua) is well developed, coursing obliquely from the protocone to the metacone. The fovea posterior (talon basin) is a deep, moderately broad, transverse fissure that is continuous with the groove running between the protocone and the hypocone; the buccal limb is longer than the lingual limb. The DMR is thick and complete, and supports a faintly visible post-entoconule slightly lingual to the MD midline axis of the tooth; the DMR remains consistently thick, and achieves a moderately high confluence with the apex of the metacone.

Buccally the cervical prominence is moderate, and the cervical margin dips to form a peak of enamel between the buccal roots. The buccal groove is deep, broad, and well developed; it fines out of existence slightly more than halfway up the buccal face with no pit. Perikymata are weakly visible near the cervical margin, and the entire face is marked by numerous pit-type enamel defects.

**Table 2**

<table>
<thead>
<tr>
<th>Order</th>
<th>Family</th>
<th>Tribe</th>
<th>Genus and species</th>
<th>MNI</th>
</tr>
</thead>
<tbody>
<tr>
<td>Primates</td>
<td>Hominidae</td>
<td></td>
<td>Australopithecus robustus</td>
<td>6</td>
</tr>
<tr>
<td>Carnivora</td>
<td>Felidae</td>
<td></td>
<td>Panthera leo</td>
<td>8</td>
</tr>
<tr>
<td></td>
<td>Lagomorpha</td>
<td>Leporidae</td>
<td></td>
<td>cf. Lepus sp.</td>
</tr>
<tr>
<td></td>
<td>Carnivora</td>
<td>Fissipedia</td>
<td></td>
<td>cf. Megantereon whitei</td>
</tr>
<tr>
<td></td>
<td>Canidae</td>
<td></td>
<td>Canis mesomelas</td>
<td>5</td>
</tr>
<tr>
<td></td>
<td>Viverididae</td>
<td></td>
<td>Herpestes ichneumon</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td>Procaviidae</td>
<td></td>
<td>Procavia antiqua</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>Artiodactyla</td>
<td>Suina</td>
<td></td>
<td>Metridiochoerus modestus</td>
</tr>
<tr>
<td></td>
<td>Giraffidae</td>
<td></td>
<td>Sivatherium maurus</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td>Bovidae</td>
<td>Neotragini</td>
<td></td>
<td>Neotragus sp.</td>
</tr>
<tr>
<td></td>
<td>Alcelaphini</td>
<td></td>
<td>Megalotragus sp.</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td>Antilopini</td>
<td></td>
<td>Antilurus marsupialis</td>
<td>18</td>
</tr>
<tr>
<td></td>
<td>Hippopotamidae</td>
<td></td>
<td>Hippopotamus sp.</td>
<td>5</td>
</tr>
<tr>
<td></td>
<td>Reduncini</td>
<td></td>
<td>Redunca cf. fulvus</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td>Tragelaphini</td>
<td></td>
<td>Tragelaphus strepsiceros</td>
<td>7</td>
</tr>
<tr>
<td></td>
<td>Bovini</td>
<td></td>
<td>Syncerus sp.</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td>Peleini</td>
<td></td>
<td>Pelea sp.</td>
<td>3</td>
</tr>
<tr>
<td>Rodentia</td>
<td>Hystricidae</td>
<td></td>
<td>Hystrix africanus</td>
<td>4</td>
</tr>
<tr>
<td></td>
<td>Pedetidae</td>
<td></td>
<td>Pedetes sp.</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td>Lagomorpha</td>
<td>Leporidae</td>
<td></td>
<td>cf. Lepus sp.</td>
</tr>
<tr>
<td>TOTAL</td>
<td></td>
<td></td>
<td></td>
<td>200</td>
</tr>
</tbody>
</table>

**Figure 7.** a–d. Isolated teeth from Cooper’s D in occlusal view with mesial to top of page. Scale bar = 10 mm. a, CD 1634 Ldm²; b, CD 1638 Ldm¹; c, CD 5774 LM¹; d, CD 22619 Ldm¹.
Lingually the cervical prominence is moderate, and the cervical margin dips to form a peak of enamel adjacent to the mesial half of the lingual root. The lingual aspect of the protoconal face is inflated and vertically disposed. The lingual groove is broad, deep, and very well developed; it terminates approximately halfway along the lingual face. The terminus of the lingual groove is occupied by a small, incipient tubercle, similar to that described for *A. (P.) boisei* specimens (Grine, 1984). Originating at the terminus of the lingual groove is a distinct fissure which runs oclusomesially along the lingual face of the protocone to the mesiolingual corner of the cusp just below its apex. This fissure contacts a second fissure on the mesial face of the protocone, both of which are bounded lingually and mesially, respectively, by well-developed ridges of enamel. This feature probably represents a well-developed Carabelli’s trait.

**Taxonomic diagnosis:** CD 1634 is most consistent with *A. robustus* and can be distinguished from *A. africanus* and early *Homo* in that the DMR is thick and well developed with a moderately high oclusal confluence with the metacone apex, and the lingual aspect of the protocone face is inflated and vertically oriented. At the same time, CD 1634 can be further separated from early *Homo* by the presence of a continuous, un-incised epicrista. The lingual groove is a distinct fissure which runs oclusomesially along the lingual face of the protocone to the mesiobuccal margin is deeply though narrowly incised (though the DMR differs from the Swartkrans *A. robustus* sample in that the occlusal confluence with the metacone apex, and the lingual aspect of the protocone face is inflated and vertically oriented. A weak tuberculum molare is evident at the base of the mesiobuccal wall between the paracristid and metacone is evident), and there appears to be a strong development of a Carabelli’s trait. In crown dimensions, the tooth plots closest to the sample of *A. robustus* from Swartkrans and Drimolen (Fig. 8).

CD 1638. Ldm₁ (Fig. 7b) is a beautifully preserved tooth retaining the crown as well as the distal root plate; the crown is intact and undistorted. The tooth measures 10.2 (MD) by 8.6 (BL). The mesial root plate was lost prior to recovery of the specimen, while the distal root plate was broken off but retrieved. Occlusal wear is light, with small, pinpoint dentine exposures visible in the position of the protoconid, the hypoconid, and the entoconid. Interestingly, these exposures of dentine are not seen at the apices of the cusps but are positioned slightly towards the midline of the tooth, just below the apices. The mesial ICF (2.0 BL; 2.4 CO) is slightly oval-shaped and flat, and is positioned lingually. The distal ICF (3.1 BL; 2.7 CO) is oval and flat, and is situated slightly lingually. The crown of this tooth is marked by numerous pit-type enamel defects, in particular along the lingual face of the tooth and the occlusal aspect of the central fossa.

Occlusally the crown has an irregular rectangular outline. All five principal cusps are present and well developed; there is a faint indication of an incipient C6. The hypoconid is the largest cusp, the metaconid is the next largest, the entoconid and protoconid are about equal in size, and the hypoconulid is the smallest cusp; all cusps are broadly equivalent in occlusal height. The thick MMR presents a distinct mesioconulid, as well as a weak premetaconulid; the MMR becomes thinner lingually, being partially incised at the lingual base of the premetaconulid. The broad, deep fovea anterior is transversely oriented with minimal dental wear, appearing as a three-pronged basin owing to the delineation of the mesioconulid and premetaconulid; the fovea anterior is smaller than the central fossa. The protoconid and metaconid are transversely aligned and are joined by a relatively high distal trigonid crest that bounds the fovea anteriorly. The longitudinal fissure of the central fossa is broad and shallow, with mesiobuccal and lingual grooves arranged almost in a straight line across the tooth; there is a broad contact between the metaconid and hypoconid. The mesiobuccal and distobuccal grooves are interrupted by relatively thick, high walls of enamel between the buccal cusps, while the lingual groove is not interrupted at the oclusolingual margin. The fovea posterior is represented by a small, distinctively skewed pit that terminates near the apex of the entoconid; it is in direct contact with the fissure separating the hypoconid and entoconid. The complete, high DMR is short but very thick and well developed; it is mainly occupied by the faintly visible C6.

The mesial half of the buccal face is relatively flattened, while the distal half of the buccal face is inflated and more vertically oriented. A weak tuberculum molare is evident at the base of the

---

**Figure 8.** Scatter plots of MD vs. BL. Crown dimensions of isolated hominin teeth from Cooper’s D. Comparative measures are derived from specimens from Swartkrans, Kromdraai, Drimolen, Taung, Sterkfontein, Makapansgat, Olduvai Gorge, Omo, Koobi Fora, and West Lake Turkana (Robinson, 1956; Grine, 1984, 1989; Tobias, 1991; Wood, 1991; Walker and Leakey, 1993; Keyser et al., 2000; Moggé-Cocchi et al., 2006).
protoconid. The cervical margin of the protoconid is sub-equal to that of the hypoconid, resulting in a “stepped-down” appearance. The mesiobuccal groove is broad and deep, terminating in a (hypoplastic?) pit approximately two-thirds of the way to the cervical margin; a shallow depression continues from this groove to the cervical margin. The distobuccal groove is not evident.

The lingual face is slightly convex occlusocervically, and a moderate cervical prominence is visible. The deep lingual groove of the occlusal surface continues lingually as a weak furrow, fading to imperceptibility; a shallow depression continues to the cervical margin. The cervical margin dips to form a peak of enamel between the mesial and distal roots.

The mesial root plate has been lost, but the broken distal root plate is present. The distal root plate is straight with a distal tilt; the roots expand slightly BL towards their apical ends. The maximum length of the root plate is 10.5 from the distal cervical margin.

**Taxonomic diagnosis:** CD 1638 is most consistent with *A. robustus* and can be distinguished from *A. africanus* and early *Homo* in that the central fossa (talonid basin) is longer than the anterior fovea (trigonid basin); the protoconid and metaconid are transversely aligned; the principal cusps are all broadly equivalent in height; there is a distinct mesiobuccal cusp; the lingual extent of the MMR is thick and higher; the fovea anterior shows no lingual skewing; the lingual groove is well developed; and, the tuberculum molare is weakly developed. CD 1638 differs from other specimens of *A. robustus* in that the hypoconid is the largest cusp. CD 1638 is unusual for an African, Plio-Pleistocene hominin dm1 in that it presents a distinct premetacristid (see Grine, 1984). In crown dimensions, the tooth plots closest to the sample of *A. robustus* from Swartkrans, Kromdraai, and Drimolen (Fig. 8).

**CD 5774.** LM1 (Fig. 7c). This tooth consists of a complete and very well preserved crown that is intact and undistorted. Root formation was only just beginning. The tooth measures 14.2 (MD) by 14.4 (BL). There is no trace of occlusal wear, and no ICFs are visible; combined with the fact that root formation was in a very early phase of development, the tooth was likely unerupted at the time of death of the individual. Several pit-type enamel defects are visible encircling the crown of the tooth in a horizontal belt.

The occlusal outline of the tooth is almost square. The buccal cusps are positioned mesial to the lingual cusps; there is a slight mesiobuccal projection of the paracone, and the distobuccal crown contour is reduced. All four principal cusps are present and well developed. The protocone is the largest cusp, followed by a slightly smaller metacone; the similar-sized paracone and hypocone are slightly smaller than the metacone. The well developed MMR is thick and complete; it is occupied by a large central and a smaller buccal accessory cuspule, both of which are delineated by narrow, mesially directed furrows. The broad, deep fovea anterior is centrally positioned with longer buccal and shorter lingual limbs; it is in direct contact with the longitudinal fissure of the central fossa between the protocone and paracone. The broad trigon basin is deeply incised, presenting a crenulated appearance. The protocone is marked by three crests running from the trigon basin to the apex of the crown; the mesial one is smallest, the central one larger, and the distal one the largest. The paracone displays a broad principal crest originating in the trigon basin and running towards the apex of the cusp; this crest is separated from the apex of the cusp (“waisted”) by a shallow but distinct groove. The metacone presents a broad crest that is weakly incised by several short fissures. The hypocone exhibits a series of four short fissures on the principal crest. The buccally directed groove branching from the longitudinal fissure in the trigon basin is not interrupted at the occlusobuccal margin. The moderate distal trigon crest (crista obliqua) is deeply incised by a narrow groove between the protocone and the metacone. The shallow, narrow fovea posterior is represented by a small lingually directed limb and a larger buccally directed limb, both of which radiate from the distal end of the groove between the hypocone and the protocone. The thick DMR is low but complete; it is occupied at the midline by a moderate postentoconule.

Buccally the cervical prominence is only weakly displayed; the cervical margin dips to form a peak of enamel between the buccal roots. The narrow buccal groove is weakly developed and rapidly fines out of existence some 2.5 mm from the occlusal margin, terminating in a small pit. Perikymata are clearly visible covering the buccal face of the tooth.

Lingually the cervical prominence is weak, and the cervical margin is straight. The well developed lingual groove is narrow but deep and terminates abruptly in a small pit. A broad, low ridge courses occlusomaxillary from the terminus of the lingual fissure towards the apex of the protocone; this ridge is bounded on either side by shallow, narrow grooves. On the mesial face of the protocone a V-shaped fissure, bounded mesially by a low, inverted V-shaped ridge, represents a weakly developed Carabelli’s trait. Perikymata are evident across the lingual face.

**Taxonomic diagnosis:** CD 5774 is most consistent with *A. robustus* and can be distinguished from *A. africanus* and early *Homo* in that the cusps are low and rounded, despite being unworn; there is no epicrista joining the protocone and paracone, thus the fovea anterior directly contacts the longitudinal fissure of the central fossa; the fovea posterior is small and narrow rather than large and broad; the buccal groove is strongly developed occlusally, passing only a short distance along the buccal face where it terminates in a small pit; and, there is only a weak indication of a Carabelli’s trait. In crown dimensions, the tooth plots consistently with the sample of *A. robustus* from Swartkrans, Kromdraai, and Drimolen (Fig. 8).

**CD 22619.** Ldm1 (Fig. 7d). This tooth consists of a relatively complete crown missing a small wedge of occlusal enamel from the mesiobuccal corner; about half of the distolingual face near the cervical margin is broken away. The tooth is estimated to measure 9.6 (MD) by 10.1 (BL). The mesiobuccal and lingual roots are missing, with approximately half of the distobuccal root present. There is extensive pyrolusite (Mn) staining evident on the crown and roots. The occlusal surface is mostly unworn, with only slight smoothing of the cuspal apices evident. Although damaged, a portion of the mesial ICF is visible on the buccal half of the mesial face; there is only a faint indication of a distal ICF. What remains of the distobuccal root indicates that root formation was approximately halfway complete, and it would appear that this tooth was just coming into occlusion at the time of death of the individual.

The occlusal outline of the tooth is an irregular trapezoid, with a pronounced projection of the mesiobuccal corner. All four principal cusps are present and well developed. The protocone is by far the largest cusp, followed in descending order of size by the metacone, paracone, and hypocone. The MMR is thick and well developed, becoming thicker buccally where it expands into a well developed mesiobuccal cusp; although damaged, the mesiobuccal cusp is only slightly smaller than the hypocone. The anterior fovea is narrow and deep, with long buccal and short lingual limbs; the absence of an epicrista results in continuity with the narrow, deeply incised trigon basin, the latter presenting several small, pit-type enamel defects. The buccal limb of the trigon basin is well developed and deeply incised through the occlusobuccal margin, and there is no enamel wall joining the paracone and metacone. The protocone contacts the metacone via a thick, predominantly BL orientated distal trigon crest (crista obliqua). The posterior fovea (talon basin) is a deep, narrow fissure that is continuous with the lingual groove between the
protocone and the hypocone; the buccal limb is longer than the relatively short lingual limb, terminating near the apex of the metacone. The DMR is well developed and thick, ending in an occlusally high confluence with the metacone.

Buccally the cervical prominence is moderately developed, and it appears that the cervical margin dips to form a peak between the buccal roots. The buccal face of the paracone is damaged, although the tuberculum molare appears to be weakly developed. The buccal groove is broad, shallow, and poorly defined, slowly fining out of existence about halfway to the cervical margin. Although damaged, it appears that the groove between the paracone and the mesiostyle was about as well developed as the buccal groove.

Although a portion of the lingual face is missing near the cervical margin, we judge that the lingual protoconal face was relatively inflated and vertically oriented. The broad, deep lingual groove rapidly fines out of existence near the occlusobuccal margin; a very shallow pit appears near the terminus of the lingual groove. Numerous pit-type enamel defects are apparent on the lingual face, in particular near the apex of the hypocone.

**Taxonomic diagnosis:** CD 22619 is most consistent with *A. robustus* and can be separated from specimens of *A. africanus* and early *Homo* on the following features: the mesiostyle, although damaged, does not appear to have been significantly buccally extended; the tuberculum molare appears weakly developed; aside from the large protocone, the size disparity between the remaining cusps is not pronounced; the DMR displays a high occlusal confluence with the metacone; and, the lingual protoconal face appears inflated and vertically oriented. CD 22619 can be further distinguished from early *Homo* in that the distal trigon crest is mainly BL oriented; the mesiobuccal groove is better developed than the buccal groove; and, the hypocone is relatively well developed. CD 22619 differs from other specimens of *A. robustus* in that the buccal branch of the trigon basin is well developed and deep, and there is no enamel wall at the occlusobuccal margin. As a result, there is a V-shaped depression surrounding the groove, similar to specimens of *A. africanus*. Comparative samples are rare, although in crown dimensions the tooth plots closest to the sample of *A. robustus* from Swartkrans and Drimolen (Fig. 8).

**Mandibular remains**

CD 6807. Mandible fragment (Fig. 9a-c). This is a badly broken juvenile left mandibular fragment. Anteriorly the mandible is broken through the mesial portion of the dm2 alveolar socket; a portion of the interalveolar septum is retained on the lateral side, presenting a slightly skewed cruciate pattern. Posteriorly the mandible is broken obliquely through the developing M1 crypt. A small length of the basal contour is preserved, although the basal and mediolabial aspects of the corpus are pervaded by breccia-filled cracks.

The basal margin beneath the dm2 is gently concave inferiorly. The basal contour is broad and evenly rounded inferior to the dm2 but tapers to a thin margin as it approaches the gonial angle. The well developed and deep preangular (pregonal) incisur is continuous anteriorly with the lateral basal contour. Although broken, it is apparent that the large, developing M1 would have caused considerable bulging of the lateral face. A weak posterior subalveolar fossa lies immediately inferior to the dm2/M1. A distinct mylohyoid line is visible coursing anteroinferiorly below the dm2; its anterior extent is obscured by damage.

Near the posterior edge of the broken medial face a series of three tiny, linearly-arranged punctate depressions are visible. These marks exhibit depressed bone tables, indicating they were made while the bone was still fresh. They most likely represent carnivore activity; their size and spacing would suggest a small carnivore, perhaps a small canid.

**Taxonomic diagnosis:** only a small fragment of mandible is preserved, rendering taxonomic diagnosis difficult. This specimen is relatively robust, with a broadly rounded basal contour, and is consistent with more complete juvenile *A. robustus* mandibles known from Swartkrans, including SK 61, SK 62, SK 63, and SK 64.

CD 17796. Mandible fragment (Fig. 9d-f). This is a badly damaged juvenile right mandibular fragment. Anteriorly the mandible is broken at the position of the mesial face of the anterior root plate of the M1, leaving an almost intact M1 alveolar socket. The interalveolar septum is preserved, presenting a slightly skewed cruciate pattern. Posteriorly the mandible is broken near the mesial extent of the developing M2 crypt. The specimen is coated with a layer of pyrolusite (Mn), and the basal edge has suffered some cortical exfoliation.

The basal margin beneath the M1 is slightly convex inferiorly; despite the cortical exfoliation evident on the basal margin of the specimen, it is apparent that the basal contour was broad and evenly rounded. The M1 jugum appears as a distinct bulge on the lateral corpus. The origin of the oblique line is evident at the base of the root of the ramus. It is likely that the extramolar sulcus would have been well developed in this individual. On the medial aspect a moderately developed subalveolar fossa is positioned inferior to the M1. Towards the anterior extent of this fossa, a small, round protuberance marks a mylohyoid attachment point, while an additional short segment of mylohyoid line is visible coursing anteroinferiorly beneath the M1.

The roots of the M1 appear well developed, and were likely near complete formation. They are robust and well developed, and the anterior root appears slightly larger than the posterior. The roots taper rapidly to the apex, and both the anterior and posterior roots are doubled, with distinct longitudinal grooves evident on the
intra-alveolar septum. The crypt for the M₂ is large, indicating an advanced stage of growth for this tooth crown.

**Taxonomic diagnosis:** on a fragment this small, taxonomic assignment is problematic. Given the overall robusticity of the specimen, combined with the broadly rounded basal margin and the disposition of the alveolus for the M₁, this specimen is consistent with more complete juvenile mandibles from Swartkrans assigned to *A. robustus*, including SK 61, SK 62, SK 63, and SK 64.

**Post-cranial remains**

**CD 5773.** Thoracic vertebra (Fig. 10a-c). This is a fragment of the centrum of a hominin thoracic vertebra from an adult individual. The specimen consists of approximately one quarter of the cranial surface, the nearly complete caudal surface, the complete right lateral side, and the nearly complete ventral surface. Roughly half of the right pedicle is preserved, with the lateral portion of the centrum's dorsal wall and the ventral part of the root of the transverse process. The right lateral surface displays a large, almost circular, costal facet.

The preserved caudal surface of the centrum is intermediate between typical thoracic heart-shape and lumbar kidney-shape, more closely approximating the lumbar condition; as such, this specimen most likely represents a lower thoracic vertebra, perhaps more closely approximating the lumbar condition; as such, this specimen most likely represents a lower thoracic vertebra, perhaps a T₁₀–T₁₂. Damage at the left caudal border prevents direct measurement of the caudal transverse diameter, although what is preserved demonstrates that the transverse diameter is greater than the dorsoventral diameter. When viewed from the ventral aspect, the centrum is deeply waisted laterally. In lateral view, the centrum is markedly wedge-shaped, tapering anteriorly. The costal facet, which is elevated from the centrum's lateral wall, extends from the cranial rim halfway downward and onto the base of the pedicle. There is a small projection at the facet's cranial-ventral margin measuring about 2 mm dorsoventrally by 3 mm craniocaudally.

The surface of the costal facet displays several small osteolytic foci and a small nodule of hypertrophic bone (Franklin, n.d.). The caudal surface of the centrum exhibits approximately 2 mm of marginal lipping (spondylosis deformans) associated with the right posterior surface, adjacent to the right pedicle. Most of the cranial surface of the centrum and the majority of the left side of the element are missing, making it difficult to determine the extent of the abnormality or whether the osteophytic changes to the costal facet are present bilaterally.

**Taxonomic diagnosis:** given the rarity of comparative materials and the fragmentary nature of this specimen, taxonomic assignment is difficult. This being said, the pronounced waisting of the lateral walls of the centrum is more reminiscent of A.L. 288-1 (*A. afarensis*) and Sts 14 (*A. africanaus*) than KNM-WT 15000 (*H. erectus*) or modern humans (comparisons based on original South African fossils and casts of East African fossils). We therefore attribute this specimen to *Hominidae gen. et sp. indet.*, noting that it most likely represents the same taxon as the teeth from Cooper's D (*A. robustus*).

**Individual associations and stratigraphic positioning of hominin fossils**

All of the hominin cranio-dental remains can be attributed to juvenile individuals, raising the possibility of a common origin for at least some of the specimens. However, demonstration of inter-individual associations is rendered difficult by the fact that only two of the teeth (CD 1634 Ldm and CD 22619 Ldm¹) represent potentially contiguous specimens. In addition, linking hominins to specific stratigraphic markers is complicated by sediment compaction and bioturbation resulting from the decalcification process. Also, when bones initially entered the cave, hydrodynamic sorting likely winnowed smaller, more buoyant specimens, resulting in differential movement of materials within the cave. Notwithstanding, when we plot the hominins relative to the U-Pb samples, some level of patterning is evident (Fig. 11). Isolated molars CD 1634 and CD 1638 were recovered from above U-Pb sample CDD3, thus they are likely to be slightly younger than 1.4 Ma. The vertebra (CD 5773), two teeth (CD 5774 and CD 22619), and one mandible fragment (CD 6807) were recovered from the vicinity of U-Pb sample CDD1 (basal stalagmite) stratigraphically and thus fall somewhere between approximately 1.4–1.5 Ma in age. Mandible fragment CD 17796 was derived from an *ex situ* breccia dump and therefore cannot be related to any particular section of the deposit.

Although both teeth CD 1634 and CD 22619 are from the Cooper's D West deposit, they were recovered from above and below U-Pb sample CDD3, respectively. As a result, they are unlikely to be derived from a single individual and are probably from temporally discrete depositional episodes. The Ldm¹ (CD 1638) is the only specimen presenting visible dentine exposures; it was derived from the Cooper's D East deposit and thus is unlikely to belong to the same individual as either of the isolated teeth CD 1634 or CD 22619. The lack of occlusal wear and root formation of the Ldm¹ (CD 5774) raises the possibility that it might be associated with one of the three former individuals. However, we judge this tooth to be too well developed to be derived from the same individual as any of the aforementioned specimens; its position below...
U-Pb sample CDD1 in Cooper’s D East further distinguishes it from the remaining hominin teeth (Fig. 11). A possible association exists between the LM1 (CD 5774) and the closely proximate mandibular fragment CD 6807, although this cannot be determined with certainty. Although derived ex situ, mandible fragment CD 17796 cannot be associated with any of the isolated teeth recovered from Cooper’s D, and thus represents a unique individual. The vertebral specimen CD 5773 is clearly that of an adult, thus representing a discrete individual. Based on inter-individual associations and stratigraphic positioning, it would appear that each tooth represents a separate individual, while only one of the mandibular fragments might be associated with a tooth. We therefore conclude that at least 1 adult and 5 juvenile individual hominins are represented at Cooper’s D.

Discussion and conclusions

The taxonomic affinity of the original hominin fossil (LM3) recovered from Cooper’s Cave is unclear, having been initially assigned to Homo by Shaw (1939, 1940) and later to A. africana by Broom and Schepers (1946), the latter diagnosis being shared by Robinson (1956). Unfortunately, the tooth has been lost, although Shaw (1940) provided a thorough description and a full set of photographs. There are several features evident in the Cooper’s Cave LM3 that align it more closely with A. robustus than A. africana, including a weakly developed Carabelli’s trait, absence of any trace of a cingulum, lack of a fovea anterior, lack of a mesiostyle, a weakly developed lingual groove, and cusps that are bluntly rounded with minimal fissuring. Despite these, the tooth shares traits in common with A. africana, including the ‘waisting’ of the central ridge of the protocone which gives the appearance of an additional cuspule in the central basin of the tooth, and the small size of the tooth which is more similar to A. africana (although not outside the range of A. robustus). None of these features are exclusive to either taxon, thus in the absence of the original specimen, its taxonomic attribution must remain uncertain. Given the ambiguity over the taxonomic affinity and actual provenience of this specimen, the presence of A. africana at Cooper’s Cave cannot be confirmed.

The second hominin fossil recovered from Cooper’s Cave is an isolated incisor recovered from a box of Cooper’s A materials (COA-1); this damaged RI was attributed to either A. africana or early Homo (Berger et al., 1995). Close examination of the tooth reveals several features aligning it with early Homo as opposed to A. africana or A. robustus, including a weak cervicodentinal, a flattened lingual face, a weakly developed lingual MMR, and a weakly developed mesial lingual groove; in addition, the absence of buccal grooves and the curvature of the buccal face further identify this specimen as Homo and not A. africana. A third specimen (COB 101) was recovered from the Cooper’s Cave collections; it was housed at the Transvaal Museum in a box of materials labeled as from Cooper’s B but which were more likely derived from Cooper’s A (Steinger et al., 2008). This partial facial skeleton is most consistent with specimens of A. robustus from Swartkrans and is distinct from A. africana and early Homo. Combined with the A. robustus materials recovered during our present excavations, the presence of early Homo at Cooper’s marks this as the third South African locality with co-occurring A. robustus and early Homo, after Swartkrans (Brain, 1981; Grine, 1989) and Drimolen (Keyser et al., 2000). However, given the uncertainty over the provenience of COA-1, A. robustus is the only hominin taxon yet recorded from the in situ excavations in Cooper’s D. In other words, although early Homo and A. robustus co-occur in the Cooper’s Cave system, at present we cannot confirm their contemporaneity within any particular deposit.

Despite the problems inherent in dating our CDD3 sample, we can nonetheless determine that the Cooper’s deposits formed quickly when the cave was periodically open to the external environment for brief spans of time. We see this in other, more precisely dated sites in the region (Pickering et al., 2007), and we hypothesize that a specific set of environmental conditions must have prevailed in order for clastic sediment deposition to occur. During arid conditions, the cave openings enlarged, and clastic material was mobilized into the cave. When conditions became wetter, increasing moisture levels promoted the development of thicker mats of vegetation, possibly choking the entrances to the cave and halting sedimentation. A reversion to drier conditions would precipitate a die-back of this vegetation, promoting renewed clastic sediment deposition (Pickering et al., 2007). The implication of this is that the South African fossil cave inﬁlls might represent biased samples of animals resident in the area only during more arid conditions. This would have significant relevance to studies of the paleoenvironment and paleoecology of South Africa during the Pliocene and Pleistocene. However, it should be noted that bone deposition and sediment deposition need not be contemporaneous events, in particular when biological bone-accumulating agents are involved. Carnivores such as hyenas and leopards will utilize caves under a variety of climatic conditions, possibly depositing bones in the cave during periods when no sediments were accumulating. Therefore it is presently not possible to determine the extent of any depositional biasing that may have influenced the ecological.
composition of the faunal assemblages from Cooper’s D, high-
lighting the need for additional research in this area.

The development and infilling of the Cooper’s D deposit is broadly similar to that seen in other “breccia” caves such as Swartkrans (Brain, 1993) and perhaps Drimolen (Keyser et al., 2000). In the initial announcement of the Cooper’s D deposit we estimated the site to be 1.9–1.6 Ma, based on biostratigraphic comparison with East African deposits (Berger et al., 2003). The lower extent of this range was based on our identification of late stage Metridiochoerus andrewsi in Cooper’s D. This taxon last appears above the Okote Tuff at Koobi Fora, a deposit that has subsequently been re-dated to 1.56 ± 0.05 Ma (McDougall and Brown, 2006). More recently, a specimen of M. modestus, a taxon which goes extinct perhaps 0.78 Ma in Bed IV of Olduvai Gorge, was recognized in the Cooper’s D materials (J. Adams, pers. comm., 2008). The U-Pb dates that we report here indicate that the majority of the Cooper’s D assemblage likely falls between 1.5–
1.4 Ma, with additional materials possibly dating to even younger than 1.4 Ma. As a result, Cooper’s D possibly records the last appearance of M. andrewsi in Africa.

Additional U-Pb dates from other South African cave infills will be instrumental in determining whether there is a notable temporal disparity between the faunas and associated hominin taxa of east and South Africa. Attempts at dating fossil enamel using U-Pb are promising (Balter et al., 2008), although they are currently hampered by the necessity for modeling the uptake of nuclides, rendering them susceptible to diagenesis. More precisely constraining the ages of the hominin-bearing cave infills in the Blou-
bank Valley area will allow us to investigate the suggestion that southern Africa was less affected by tectonic, volcanic, or paleolake changes than eastern Africa (Partridge et al., 1995a,b; Bailey et al., 1994). This taxon last appears above the Okote Tuff at Koobi Fora, a deposit that has subsequently been re-dated to 1.56 ± 0.05 Ma (McDougall and Brown, 2006). More recently, a specimen of M. modestus, a taxon which goes extinct perhaps 0.78 Ma in Bed IV of Olduvai Gorge, was recognized in the Cooper’s D materials (J. Adams, pers. comm., 2008). The U-Pb dates that we report here indicate that the majority of the Cooper’s D assemblage likely falls between 1.5–
1.4 Ma, with additional materials possibly dating to even younger than 1.4 Ma. As a result, Cooper’s D possibly records the last appearance of M. andrewsi in Africa.

Acknowledgements

We would like to thank the 'Fossil Tracker' team for their efforts and expertise in the field, and the Lotz family for their support and access to the site. We would also like to thank Ingberga Hebeisen for her cheerful instruction in the lab, and Daënu Rufer and Emilie Janots for support with the Beta-scanning. Excavations were funded by the Palaeontological Scientific Trust (PAST), the South African National Research Foundation, the University of the Witwatersrand Research Council, and the National Geographic Society. This research was funded by the Swiss National Science Foundation (RP), the Texas A&M University International Research Travel Assistance fund (DJD), the Wenner-Gren Foundation (DJD), and the Duke University Paleanthropology Field School.

References

Berger, L.R., Lacroz, R., de Ruiter, D.J., 2002. Revised age estimates of Austral-
Broom, R., Schepers, G.W., 1945. The South African fossil ape-men. The Austral-
Broom, R., Schepers, G.W., 1945. The South African fossil ape-men. The Austral-
Broom, R., Schepers, G.W., 1945. The South African fossil ape-men. The Austral-
Broom, R., Schepers, G.W., 1945. The South African fossil ape-men. The Austral-