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

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Abstract

Occasional excavation of in situ and ex situ deposits at the formerly mined Gondolin paleocave system has yielded large and diverse samples of Plio-Pleistocene faunas, including isolated hominin and non-hominin primate remains. In 2003, new excavations into naturally decalcified, in situ sediments near the GD 1 datum point near the northwest corner of the cave system were undertaken. This paper describes the recovered faunal remains, taphonomy of the assemblage, and the geological and paleomagnetic context of the GD 1 deposits. The deposits represent a series of inter-stratified speleothem, in-washed sediments and talus deposits we suggest date to a time period prior to, and just after, the Olduvai normal-polarity event at around 1.7–1.8 Ma. Surface sediments and clasts were introduced into the cave by rain water runoff entering a vertically-oriented entrance that had formed along a rift in the area of GD 1. The faunal assemblage consists primarily of fragmentary diaphyseal fragments and isolated teeth. Taxonomically, the small collection of specifically identifiable bovid and equid fossils is generally consistent with remains previously excavated from in situ deposits in the Gondolin paleocave system (GD 2) and dated to around 1.8 Ma; however, the depositional histories of these two assemblages from Gondolin are remarkably different. The preservation and relative proportions of recovered skeletal elements at GD 1 is consistent with these materials having been initially accumulated outside the karstic system near the vertical cave entrance, and then later hydrologically sorted and deposited inside the cave. The sporadic to continuous water flow into the northwest corner of the cave system during the Pleistocene gradually decalcified the excavated fossilbearing breccias and further modified the composition and spatial distribution of the fossil assemblage by introducing potentially younger deposits and skeletal materials. This study highlights the variation in taphonomic processes that can occur within a single cave system, and the complex pre- and postdepositional geological and hydrological processes that can influence the taphonomic history of South African Plio-Pleistocene karstic fossil assemblages.

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1. Introduction

The formerly mined paleocave system known as Gondolin first came to the attention of the scientific community after E.S. Vrba and D. Panagos (then of the Transvaal Museum, Pretoria, Republic of South Africa) excavated highly fossiliferous breccia blocks from exposed in situ deposits adhering to the northeastern cave wall in 1979 (Watson, 1993b). Preliminary analysis and publication by Watson (1993b), and later comprehensive faunal, taphonomic and paleoecological analyses (Adams and Conroy, 2005; Adams, 2006) have highlighted several unique aspects of the 1979 (GD 2) faunal assemblage relative to those from other South African Plio-Pleistocene paleocave systems, including the numerical dominance of smaller bovid species like reedbuck (\textit{Redunca} sp.) and...
klipspringer (*Oreotragus oreotragus*), the lack of primates and other hominins, and the excellent preservation of articulated, and generally rare, skeletal elements. Many of these unique features of the GD 2 assemblage resulted from both a combination of specific taphonomic factors during assemblage formation and the influence of local paleoecosystems on faunal communities near the site at around 1.8 million years ago (Adams, 2006; Adams, in prep.; Herries et al., 2006b).

Excavation of a test trench (Trench A) cut into one of the ex situ breccia dumpsite deposits at the site in 1997 produced a faunal assemblage (GD A) containing the first identifiable hominin and non-hominin primate specimens recorded from Gondolin, including a left mandibular M1 or M2 from a ‘gracile’ hominin (possibly *Homo*), and an extremely large left mandibular M2 provisionally attributed to *Paranthropus cf. robustus* (Menter et al., 1999) but showing metric affinities with *Paranthropus boisei* (see also Kuykendall and Conroy, 1999). Exploration of the Gondolin paleocave system by Menter et al. (1999), and subsequent research by Herries (2003), described several fossiliferous in situ deposits at Gondolin that had likely contributed to the sampled dumpsite faunal assemblage. New excavations were conducted in a series of exposed paleocave deposits near the GD 1 datum point, which was established for the geological survey conducted by Menter et al. (1999) on the northwestern rim of the cave (hereafter referred to as the GD 1 deposits; Fig. 1) in an attempt to clarify the relationship of the hominin-bearing GD A trench breccias to the in situ sequence of infillings still preserved at the site. The selection of these GD 1 deposits was guided by several factors: the identification of a gray, clastic breccia analogous to the Conglomerate Unit breccias described from GD A (Menter et al., 1999), the presence of exposed surface fossils in the immediate area, and being a location amenable to surface-down excavation methods. Furthermore, the exposed calcified sediments of the GD 1 deposits were interspersed with fossiliferous decalcified sediments in a region undergoing continuing erosion thereby facilitating the rapid excavation, recovery, processing and analysis of fossil specimens.

This paper provides a description and taphonomic analysis of the excavated GD 1 faunal assemblage excavated during a four week field season in 2003, along with Fig. 1. Plan view of the excavated GD 1 deposits. Each grid is 1 m².
with geologic and paleomagnetic analyses of the deposits. These results are discussed in the context of previous research on other roughly contemporaneous southern African faunal assemblages generally, and deposits from the GD 2 region of the Gondolin paleocave system specifically. In doing so, we will attempt to highlight the variation in geological and taphonomic processes that can occur within karstic deposits of the same cave system, and how geological and hydrological processes can influence the composition of South African Plio-Pleistocene faunal assemblages prior to recovery.

2. Materials and methods

2.1. Faunal and taphonomic analysis

A field season was conducted between September 12th and October 11th, 2003. A 1 m grid system was erected over the site, established in reference to the GD 1 datum point to the south-west of the deposits (Fig. 1). Excavation into the decalcified sediments proceeded in 10 cm levels in case any of the original stratigraphy was present in the decalcified sediments, and all recovered fossil specimens cataloged by both the grid unit and 10 cm level they were originally derived from. The extent of the excavation was restricted by the presence of several sinkholes and an unstable rim along the more southern extent of the cave rim that abuts a vertical drop-off to the modern floor of the site (Fig. 1). The grid system and unit levels at GD 1 were mapped with a theodolite in reference to the datum point. A 1 mm mesh screen was used to sift the approximately 50 m³ of surface soils and decalcified sediments removed during the field season.

All fossil specimens recovered from the GD 1 assemblage were sorted and identified following the protocols established in Brain (1974, 1980, 1981, 1993), Klein and Cruz-Uribe (1984) and Pickering (1999). Each specimen was physically marked with a catalogue number and listed in a Microsoft Excel XP computer database following the coding system from Gifford and Crader (1977) as modified by Blumenschine (1988) and Pickering (1999). Identifiable elements were also assigned as either a ‘Left’, ‘Right’ or ‘Indeterminate’ side where possible. Unidentifiable specimens were denoted in the database as either long bone fragments (defined as preserving less than 50% of original circumference and preserving no articular surface [after Pickering, 1999]), metaphyseal fragments, epiphyseal fragments (defined as preserving less than 50% of original circumference and preserving no articular surface [after Uribe, 1984] and Pickering, 1999), and long bone segments. Minimum number of elements (MNE) was calculated using a modified manual overlap approach (Bunn, 1982; Bunn and Kroll, 1986; Marean et al., 2001; see more detailed discussion in Adams, 2006).

Taxonomic identifications of the craniodental specimens were based on direct comparisons to Plio-Pleistocene faunas from Swartkrans, Kromdraai, Sterkfontein Type Site (Transvaal Museum, Pretoria); Makapansgat (Bernard Price Institute, University of the Witwatersrand, Johannesburg); and Cornelia, Vaal River Gravels and Florisbad (National Museum, Bloemfontein). Additional comparisons of the GD 1 craniodental materials to modern faunas were made in reference to collections housed at the Transvaal Museum, National Museum, and the Bernard Price Institute and School of Anatomical Sciences (University of the Witwatersrand, Johannesburg). Postcranial specimen identifications were based, in part, on fossil and modern comparative museum collections already noted, as well as in reference to descriptions of postcranial materials in the literature (Walker, 1985; Peters, 1986; Peters et al., 1997).

Maximum linear length was measured from each specimen using Mitutoyo 150 mm Digital Calipers (Model #500–672; Mitutoyo Corporation, Tokyo), with specimens placed into 1 cm size categories (e.g. 1–2 cm, 2–3 cm, etc.). There is an ongoing debate about the proper statistical tests for ordinal data that exhibits features more typical of interval data (see Knapp, 1990; Kuizon et al., 1996; Jamieson, 2004). The size category data are minimally ordinal, but given the large number of equivalent categories and large sample size, a case can be made to treat this data as interval and therefore treated as a parametric statistic. Visual analysis of the Gondolin size category data, however, indicates that there is a very strong positive skew in the size category distribution. As non-parametric statistics (like Kolmogorov–Smirnov) rely on comparisons of independent sample medians, the positive skew does not influence the accuracy of the statistic as strongly as it would if a parametric (mean-based) test were used (Motulsky, 1995; Sokal and Rohlf, 1995). As such, we treat the data as ordinal and use a series of non-parametric Kolmogorov–Smirnov (K–S) tests (α = 0.05) to statistically compare the size category datasets. Because of the potential for increased experiment-wise error rates with multiple comparisons, probability values for all K–S analyses were evaluated using the sequentially reductive Bonferroni method described by Holm (1979; also Rice, 1989). Intersite statistical comparisons were restricted to a consideration of broad size category trends between sites because of differences in prior reporting methods that did not consider specimens <1 cm (Brain, 1981; Watson, 1993a). All statistical tests were performed using SPSS 14.0 (SPSS Inc., 2005).

Specimens over 1 cm in overall length with a sufficiently preserved cortex were assigned to weathering stage categories after Behrensmeyer (1978). Weathering stage data was analyzed using a series of K–S tests (α = 0.05), with complications arising through multiple comparisons mediated by using the sequentially reductive Bonferroni method (Holm, 1979; Rice, 1989).

Each individual specimen was examined under natural and artificial light conditions, as well as under a 16x hand lens, for indications of biotic and/or abiotic modification. Modifications to fossil surfaces were assigned to different categories after definitions in Maguire et al. (1980), Bunn (1982), Blumenschine and Selvaggio (1988, 1991), etc. There is an ongoing debate about the proper statistical tests for ordinal data that exhibits features more typical of interval data (see Knapp, 1990; Kuizon et al., 1996; Jamieson, 2004). The size category data are minimally ordinal, but given the large number of equivalent categories and large sample size, a case can be made to treat this data as interval and therefore treated as a parametric statistic. Visual analysis of the Gondolin size category data, however, indicates that there is a very strong positive skew in the size category distribution. As non-parametric statistics (like Kolmogorov–Smirnov) rely on comparisons of independent sample medians, the positive skew does not influence the accuracy of the statistic as strongly as it would if a parametric (mean-based) test were used (Motulsky, 1995; Sokal and Rohlf, 1995). As such, we treat the data as ordinal and use a series of non-parametric Kolmogorov–Smirnov (K–S) tests (α = 0.05) to statistically compare the size category datasets. Because of the potential for increased experiment-wise error rates with multiple comparisons, probability values for all K–S analyses were evaluated using the sequentially reductive Bonferroni method described by Holm (1979; also Rice, 1989). Intersite statistical comparisons were restricted to a consideration of broad size category trends between sites because of differences in prior reporting methods that did not consider specimens <1 cm (Brain, 1981; Watson, 1993a). All statistical tests were performed using SPSS 14.0 (SPSS Inc., 2005).

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Lyman (1994), Blumenschine and Marean (1993) and Blumenschine et al. (1996). Additional evidence for predictable biotic influences on the sampled GD 1 assemblage were assessed through comparisons of %MAU values (sensu Binford, 1981; Lyman, 1994) to the typical carnivore consumption sequence described by Blumenschine (1985, 1986, 1988) using Spearman’s rank-order correlation coefficient (z = 0.05; Lyman, 1994), and relative to measures of carcass utility including the modified general utility index (MGUI; Binford, 1978, 1981) and the unstandardized food utility index (FUI; Metcalfe and Jones, 1988).

Abiotic taphonomic processes, such as the action of hydrological systems, can introduce allochthonous faunal materials into karstic systems. Such assemblages would therefore be a reflection of the skeletal elements introduced to the karstic deposits after natural mortality or carnivore consumption, and as winnowed based on the transport potential of the surviving elements. We evaluate the potential primary or secondary effect of abiotic element transport into the GD 1 deposits through both consideration of the physical condition of recovered remains for signs of transport-related abrasion, through a consideration of the spatial distribution of recovered specimens within the deposits relative to the established grid system, and through three separate statistical analyses. First, the proportion of recovered elements (%MAU) was compared to a bovid disarticulation sequence (Hill, 1979) using Spearman’s rank-order correlation coefficient (z = 0.05) to assess the potential relationship in the proportion of recovered elements to those most readily transported from landscape carcasses. Second, recovered skeletal elements were assigned to transportability groups (Voorhies, 1969) to evaluate any trends between potential element transportability and representation in the assemblage. And third, possible relationships of the recovered elements in the Gondolin assemblage (%MAU) and saturated weight index values (Behrensmeyer, 1975) were made using the Pearson product-moment correlation coefficient (z = 0.05), to assess the effect hydrological transport may have had on the sampled accumulation.

Finally, it has long been recognized that the variation in the bone mineral composition of individual skeletal elements might influence their relative survival and recovery from modern and fossil faunal assemblages (Brain, 1981; Lyman, 1994; Lam et al., 1999, 2003; Lam and Pearson, 2005). While early descriptive studies made implicit connections between skeletal element distribution patterns and density-mediated attrition among South African assemblages (e.g. Brain, 1981), more recent studies of South African and other assemblages have found little to no relationship between the two (Lam et al., 1999; Pickering and Carlson, 2002). Here, %MAU values from the Gondolin assemblages were plotted against CT-derived, bone mineral density (BMD) values for an extant Class III bovid (wildebeest, Connochaetes taurinus; Lam et al., 1999). Shape-adjusted density values (BMD2) were preferentially used here, although in cases where BMD2 values were unavailable, we have used the BMD1 values (that were not shape adjusted). Percentage MAU values were log10 transformed prior to plotting and a regression of %MAU on BMD was performed using the least-squares criterion (z = 0.05) (after Pickering and Carlson, 2002).

2.2. Paleomagnetic analysis

Nine paleomagnetic samples were oriented in situ using a Suunto clinometer and magnetic compass. Subsequent corrections were made for the declination of the local field according to the International Geomagnetic Reference Field accessed through the British Geological Survey (available at http://www.geomag.bgs.ac.uk/gifs/igrf.html). As the GD 1 samples came from blocks from exposed and weathered deposits, the top portion of each drilled core was discarded so as to limit the possible effects of weathering and modern detrital contamination on the samples. Heavily brecciated areas were avoided if possible without compromising the overall potential for recovering as complete a polarity sequence as possible. Samples were drilled in a zero field cage at the Liverpool University Geomagnetism Laboratory to remove the influence of the Earth’s magnetic field and stop the acquisition of a drilling induced magnetization, both of which have been problems at other South African Plio-Pleistocene sites (Partridge et al., 2000; Herries, 2003).

Paleomagnetic methods employed here followed the protocols established in Butler (1992). Measurements were made using a Molspin (Ltd.) minispin magnetometer. Magnetic cleaning to identify the characteristic remanent magnetization (ChRM; main remanence preserved in the sample after the removal of any secondary magnetization) was undertaken by 3 methods: (1) stepwise alternating field demagnetization in 2.5–5 mT stages using a laboratory-built alternating field demagnetizer capable of imparting fields as high as 100 mT; (2) 11-step thermal demagnetization of sister-specimens between 100 and 550 °C using a Magnetic Measurements thermal demagnetizer; and (3) subjecting a further set of sister-specimens to an 11-point thermal demagnetization, with an initial alternating field cleaning step of 12 mT. This was undertaken to remove any viscous magnetization and decrease the temperature to which highly calcified samples or calcite needed to be heated during subsequent thermal demagnetization.

After magnetic cleaning, ChRMs were determined using principle component analysis (Kirschvink, 1980) with vector and stereographic projections to determine declination (orientation in horizontal plain) and inclination (orientation in the vertical plane). The polarities of sub-samples were assigned to normal (or reversed) polarity according to whether their declinations were within a 40° cone of the normal (0°) or reversed (180°) field and had inclinations above ±20°. Those outside this range of variation were determined as intermediate normal or
reversed if they fell within an 80° cone of declination variation or if their inclinations fell below 20°. If the values fell outside this range, but a stable direction of magnetization could still be isolated, the samples were designated as intermediate. Samples were considered successful if they had a MAD (Mean Angular Deviation) value of < 10. This produced a sequence of polarity intervals and reversals that were then correlated to the Geomagnetic Polarity Time scale (GPTS; Ogg and Smith, 2004), to produce potential age ranges for the various deposits and site as a whole.

Mineral magnetic measurements were undertaken on sister sub-samples from the various paleomagnetic block samples to determine the magnetic mineralogy, magnetic grain size and concentration of remanence carrying minerals (see Walden et al., 1999 for a more detailed description of the methodology). This is important for establishing if the magnetic polarity preserved within the speleothems and sediments is primary (formed at the time of deposition), secondary (formed from secondary chemical alteration, i.e. chemical remanent magnetization; CRM), or from the relaxation of low coercivity, viscous magnetic grains that do not hold a stable remanence over the time period represented by the age of the deposits (a viscous remanent magnetization; VRM). Magnetic susceptibility measurements (K_{LF}; Low Frequency, K_{HF}; High Frequency, K_{LT}; Low Temperature) were undertaken using the Bartington MS2B and χ/T system for frequency dependant room temperature and low temperature analysis down to −196 °C. Isothermal Remanent Magnetization (IRM) acquisition curves and backfields, hysteresis loops and Curie curves were run on a Magnetic Measurements Variable Field Translation Balance (VFTB). Stepwise demagnetization was undertaken using a laboratory built alternating field demagnetizer capable of imparting fields as high as 100 mT.

3. Results

3.1. Geology and paleomagnetism of the GD 1 deposits

The area near the GD 1 datum point identified for excavation centered on a naturally formed central channel that runs from the northwest to the southeast, extending to the present-day rim of the mined center of the Gondolin site (Fig. 1). This channel formed along a fault that provides the least resistance to water flowing through the site and is likely to have done so in the past, causing the formation of an entrance in the area of GD 1. This central channel, and the area immediately surrounding it, has been heavily eroded by meteoric waters that flow from the crest of the hill (that lays upslope to the northwest) and by tree roots that have caused the formation of makondos (solution tubes formed due to increased acidity around tree roots). These makondos and meteoric water flow will preferentially flow into and dissolve the calcite-rich calcified sediments and breccias rather than the less soluble dolomite. As such, the same paleokarstic conduits are used to flow into the channel and then flows off the excavated rim as a waterfall into the excavated floor of the mined center. While it is unknown how long runoff in the area has been directed through the deposits, it is probable that this has been occurring for a substantial period of time given the volume of decalcified and partially decalcified sediment in the area. The resulting channel-cut, exposed GD 1 calcified deposits consist of a series of inter-stratified speleothem, in-washed sediments, and talus deposits. Geological interpretations of such cave deposits are necessarily complex, in part because they are ‘relief’ karstic features and appear to preserve multiple phases of sediment infilling, undercutting, and reworking of material over a long period of time. At GD 1, stratigraphic sequences are inverted due to the presence of thick flowstone layers that acted as false floors, under which sediment and breccias were eroded out and redeposited at much later periods. Our excavation into such deposits has therefore likely sampled fossils from a variety of extremely different depositional phases that have come to lie at the same stratigraphic position. Despite our proceeding with excavation in 10cm levels, no evidence of the original depositional stratigraphy was present in the decalcified sediments, which have apparently been so reworked that the sediments appear homogenous.

Calcified and decalcified sediments in the GD 1 deposits contain a number of large diameter, in-washed and weathered chert-lag debris that are derived from surface exposed outcrops. These extrinsic clasts entered the cave system through a nearby vertical entrance near the crest of the hill, which would have permitted at least intermittent water flow into the GD 1 cave region (also Menter et al., 1999; Herries, 2003; Herries et al., 2006a). The occurrence of cave pearls in layers below the GD 1 deposits further suggests a relatively wet, but low energy hydrological environment with small standing pools in this portion of the cave. These lower deposits also contain small rounded pebbles, which suggest that a small, low-energy stream entered the cave, possibly where water ran over the lip of the dolomite rear wall and into the rift below. In contrast, the sediments of Vrba’s original GD 2 sequence consist mainly of laminated, but sloping, siltstones underlain and overlain by flowstone deposits (Herries et al., 2006a). The fossils from GD 2 are densely aggregated, partly articulated, and exhibit strong body size and taxonomic biases and other factors suggesting element accumulation in a
carnivore den with animals entering via a lower, lateral entrance (Adams, 2006; Adams, in prep.; Herries et al., 2006a).

Two main depositional sequences are exposed in the GD 1 region and were paleomagnetically sampled (Fig. 2). Thick flowstone layers occur in both sequences but their relationship to the fossil bearing clastic deposits is different. In the GD 1 eastern sequence (GD1-e) the flowstones (paleomagnetic samples GD1-01 to -04) have been heavily eroded and undercut, with younger infillings of both siltstone (GD1-05) and breccia (GD1-06). This is a classic example of an inverted cave sequence with the older deposits overlying younger infills due to the presence of a calcite false floor. The GD 1 East flowstone sequence probably represents some of the oldest deposits in the cave, although the stratigraphic breaks that occur in the sequence make conformation of this difficult. The GD 1 East flowstone is overlain by a second sequence of interstratified flowstones and siltstones termed GD 1 West (GD1-w). The basal flowstone of GD 1 West (paleomagnetic sample GD1-10) lies over the GD 1 East flowstone but is not part of the same sequence. There is a major truncation of the GD 1-e deposits before deposition of the GD1-w deposits. Calcified silts (GD1-08 to -09) are sandwiched between two flowstone layers (GD1-10, GD1-07), with partial truncation of the flowstones suggesting that a partial hiatus occurs between deposition of these two layers. All fossil specimens excavated from the GD 1 deposits described below are derived from the decalcified silt layers of the GD 1 West sequence (Fig. 3).

Results of the paleomagnetic analysis of the sampled GD 1 sequences are summarized in Table 1 and displayed in Fig. 2 (along with results from a prior analysis of the GD 2 depositional sequence; Herries et al., 2006a). The samples all show good stability of remanence to all three magnetic cleaning methods and better stability than seen at other South African paleocave sites (e.g. Herries et al., 2006b). While the final results show good consistency of polarity for sister samples cleaned by different methods, the actual data values from sample to sample from each block show lower consistency than would be useful for secular variation studies, as is also the case at other South African paleocave sites (Herries et al., 2006a, b). Mineral magnetic data shows that the samples are dominated by low coercivity magnetite and maghaemite minerals in the superparamagnetic (SP; ultra-fine grained) to stable-single (SSD; fine grained) domain grain size. The greater stability
of remanence found in the Gondolin samples, when compared to other South African hominin paleocaves, is due to a greater proportion of the remanence being held in larger, more stable, SSD grains. However, median destructive fields for alternating field (AFd) cleansings are still fairly low and show that the samples have suffered significant relaxation of more viscous grains since their deposition. Despite this partial overprinting of the primary remanence and cross over in the AFd remanence spectra the consistency of data between different cleaning methods and stability of remanance at higher fields and temperatures suggests that the primary polarity of the sample at or close to its time of deposition is being successfully isolated.

Samples from the GD 1-w section show a gradual change in polarity from normal (GD1-10d-e), through intermediate normal (GD1-10b-c), intermediate (GD1-10a, 9c-d) and intermediate reversed (GD1-09a-b, 8d) directions, to a reversed polarity (GD1-08a-c, 07a-c). This suggests that this sequence was deposited at various intervals over a continuous time period covered by a polarity reversal from normal to reversed polarity. Samples from the GD 1-e section show a dominance of intermediate directions (GD1-01/02) of polarity for the flowstone layers but with normal polarity at its base (GD1-01 to -04), perhaps suggesting deposition close to a polarity transition. In contrast, underlying deposits record varied directions of polarity that suggest they are not deposited at the same period. Siltstone deposits (GD1-05) have a reversed direction of polarity and sample GD1-06 records intermediate and intermediate normal directions of polarity that are mostly due to the brecciated nature of the deposit. No definite interpretation can be made about the age of the GD 1e section other than that the paleomagnetic data support the geological interpretation of the deposits as representing different time periods.

### 3.2. The GD 1 faunal assemblage

A total of 4843 individual fossil specimens were recovered during the 2003 excavation, of which 1349 are

<table>
<thead>
<tr>
<th>Sample</th>
<th>Deposit</th>
<th>Demag type</th>
<th>MDF</th>
<th>SF</th>
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<th>Inc</th>
<th>MAD</th>
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<td>I</td>
</tr>
<tr>
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<td>FS</td>
<td>AF</td>
<td>12.5 mT</td>
<td>20–40 mT</td>
<td>219.1</td>
<td>−63.2</td>
<td>2.3</td>
<td>I</td>
</tr>
<tr>
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<td>AF</td>
<td>12.5 mT</td>
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<td>39.6</td>
<td>−12.9</td>
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<td>7.2</td>
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<td>10–45 mT</td>
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</tr>
<tr>
<td>GD1-01b</td>
<td>FS</td>
<td>TH</td>
<td>250 °C</td>
<td>100–450 °C</td>
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<td>−67.1</td>
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</tr>
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<td>275 °C</td>
<td>100–450 °C</td>
<td>256.4</td>
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<td>4</td>
<td>I</td>
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<tr>
<td>GD1-02b</td>
<td>FS</td>
<td>AF-TH</td>
<td>250 °C</td>
<td>150–500 °C</td>
<td>268</td>
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<td>N</td>
</tr>
<tr>
<td>GD1-04b</td>
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<td>300 °C</td>
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<td>250–550 °C</td>
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</tr>
<tr>
<td>GD1-05c</td>
<td>CS</td>
<td>AF-TH</td>
<td>150 °C</td>
<td>200–550 °C</td>
<td>282</td>
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<tr>
<td>GD1-06a</td>
<td>BR</td>
<td>TH</td>
<td>300 °C</td>
<td>250–500 °C</td>
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<td>2.7</td>
<td>1.9</td>
<td>I</td>
</tr>
<tr>
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<td>BR</td>
<td>AF-TH</td>
<td>300 °C</td>
<td>100–500 °C</td>
<td>12.3</td>
<td>−4.6</td>
<td>2.1</td>
<td>I</td>
</tr>
<tr>
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<td>AF</td>
<td>12 mT</td>
<td>12–40 mT</td>
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<td>−12</td>
<td>2.6</td>
<td>IN</td>
</tr>
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<td>AF</td>
<td>12 mT</td>
<td>12–30 mT</td>
<td>93.1</td>
<td>−53.1</td>
<td>–</td>
<td>I</td>
</tr>
</tbody>
</table>

Deposit (CFS = contaminated flowstone, CS = calcified silt, FS = flowstone), Demagnetisation type (AF alternating field, TH = thermal, AF-TH = hybrid method), MDF = median destructive field, SF = stable field range in milli Tesla (mT) and degrees centigrade (°C), Dec = declination (°C), Inc = inclination (°C), MAD = mean angular deviation (quality parameter) and P = Polarity (N = normal and R = reversed).
identifiable craniodental and 39 identifiable postcranial elements. Of the identifiable remains, only 75 craniodental specimens could be taxonomically identified below the Family level (Table 2). The remaining 3455 unidentifiable specimens are mainly diaphyseal long bone fragments. We wish to emphasize that, given the complex mix of depositional phases that have been sampled through excavation, the faunal assemblage described here is an aggregation of fossil specimens from multiple periods of interment. As such, the GD 1 assemblage described here does not represent faunas incorporated during a single depositional event, and therefore may not be directly comparable to other in situ faunal assemblages.

Of the total fossil sample removed, 1195 specimens (24.63%) were recovered from the first 10 cm of excavation consisting mainly of overburden soils, of which only one craniodental specimen from was specifically identifiable. Once this overburden layer had been removed, fossil specimens were found to be unequally distributed throughout the decalcified deposits. The majority of the sediments excavated at the site were sterile, with fossil materials primarily recovered from isolated, dense ‘pockets’ within the deposits. While two of these concentrations (Pocket A [Grid square E3]: NISP = 10; Pocket C [Grid squares K3 and L3]: NISP = 125) were relatively small, Pockets B and D (that started at two separate units and merged through excavation; Grid squares H3 and I3) yielded 1686 total specimens (34.76% of the recovered remains). Pocket C produced four identifiable craniodental and postcranial specimens, while Pocket B/D yielded 21 identifiable specimens. The remainder of the fossil specimens came from the ‘Northern Extension’ (Grid squares L6-L11, M6-M11), which yielded a total of 1732 specimens (35.70% of the total) within the first 30 cm of excavation (at which point excavation in the extension was terminated due to safety concerns at the cave edge). This unit of the GD 1 excavation yielded 81 identifiable cranial and postcranial remains.

A total of 38 alcelaphine specimens have been recovered from the GD 1 deposits. Because of fragmentary and isolated nature of the remains, and the strong overlap in dental morphologies among genera and species within the tribe, none of these specimens could be reliably attributed to even the generic level. The collection of specimens could, however, be separated into those derived from small-to-medium (Class II/III) and large (Class III) alcelaphines.

Of the 33 smaller alcelaphine dental specimens, eight (GD 3014, 3016, 3017, 3034, 3035, 3038, 3047, and 3050) are generally comparable in overall size and morphology to the *Damaliscus* sp. 1 or *Parmaluris* sp., and *Damaliscus* sp. 2 (*niro*?) from Swartkrans, Kromdraai and Sterkfontein (Adams, 2006). The other 25 medium sized alcelaphine specimens are consistent in size with larger extant *Alcelaphus buselaphus*, and smaller/female individuals within the genus *Connochaetes*. Of these 25 alcelaphine dental specimens, four were unworn, four were lightly worn, and the remaining 17 exhibited moderate occlusal wear. In sum, minimally two individuals are derived from the smaller subset of the medium alcelaphine grouping; and minimally three individuals are represented by the remaining medium alcelaphine sample.

Five isolated specimens (GD 3018, 3019, 3032, 3036 and 3057) are derived from a large bodied alcelaphine taxon and are comparable in size to individuals from species within the genus *Comnochaetes*. Of these 25 alcelaphine dental specimens, four were unworn, four were lightly worn, and the remaining 17 exhibited moderate occlusal wear. In sum, minimally two individuals are derived from the smaller subset of the medium alcelaphine grouping; and minimally three individuals are represented by the remaining medium alcelaphine sample.

Five isolated specimens (GD 3018, 3019, 3032, 3036 and 3057) are derived from a large bodied alcelaphine taxon and are comparable in size to individuals from species within the genus *Comnochaetes*, and are smaller than *Megalotragus* specimens from Swartkrans Member 1 (Adams, 2006). One specimen (GD 3032) is a right m3 lacking any occlusal wear and is comparable in size to m3 specimens derived from large extant male specimens of *Comnochaetes gnou*. The lack of occlusal wear on the specimen indicates that the individual was no more than 30–33 months of age (about one year prior to obtaining full adult body weight; van Zyl, 1972).

<table>
<thead>
<tr>
<th>Taxon</th>
<th>NISP</th>
<th>MNI</th>
</tr>
</thead>
<tbody>
<tr>
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<td></td>
</tr>
<tr>
<td>Bovidae</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Alcelaphini</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Medium sized</td>
<td>33</td>
<td>5</td>
</tr>
<tr>
<td>Large sized</td>
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<td>2</td>
</tr>
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<td>Antilopini</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Antidlocas cf. recki</td>
<td>4</td>
<td>1</td>
</tr>
<tr>
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<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Neotragini</td>
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<td></td>
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<td>1</td>
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<tr>
<td>Reduncini</td>
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</tr>
<tr>
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<td>1</td>
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<tr>
<td>Bovid I Indet.</td>
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<tr>
<td>Bovid II Indet.</td>
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<tr>
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<td>Equidae</td>
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</tr>
<tr>
<td>Indet.</td>
<td>9</td>
<td></td>
</tr>
<tr>
<td>Lagomorpha</td>
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<tr>
<td>Indet.</td>
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<td>1</td>
</tr>
<tr>
<td>Indet.</td>
<td>259</td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>1388</td>
<td>16</td>
</tr>
</tbody>
</table>
Tribe Antilopini

*Antidorcas* cf. *recki*

Four specimens (GD 3025, 3031, 3037 and 5626) are minimally identifiable to the tribe Antilopini. The GD 3031 lower molar fragment preserves cusp morphology consistent with the species *Antidorcas recki*, but is only provisionally assignable given the amount of crown preserved. The other three specimens are attributable to *Antidorcas* and are all comparable to the extinct species *Antidorcas recki* previously described from GD 2, Swartkrans Members 1 and 2, and Kromdraai A deposits (Adams and Conroy, 2005; Adams, 2006). If a developmental and occlusal wear schedule for extant *A. marsupialis* is used to gauge the age of *A. cf. recki* represented by GD 3025 m1, it would likely be just older than 9 months and maximally below 3.5 years of age (between class II and IVb; Rautenbach, 1971).

Tribe Hippotragini/Tribe Reduncini

A single partial m3 specimen, GD 3048, may represent a hippotragine. The specimen is generally consistent with mandibular third molars of *Hippotragus*, but the preserved surfaces overlap in both size and morphology with the third molars of large-bodied reduncines, such as *Kobus ellipsiprymnus*. Although the specimen is more consistent with a hippotragine, the incomplete preservation of this single specimen and the possibility that the specimen might represent a large reduncine precludes a more specific interpretation.

Tribe Neotragini

*Oreotragus oreotragus*

A single *Oreotragus oreotragus* P2, GD 3091, is identical in size and morphology to extant and extinct *O. oreotragus* upper second premolars, including those recovered from the GD 2 deposits (Adams and Conroy, 2005; Adams, 2006). Given the occlusal wear state, this specimen is derived from a fully adult individual.

Tribe Reduncini

*Redunca* sp.

A small collection of ten isolated dental specimens from the tribe Reduncini were recovered from the GD 1 deposits. Although the sample is small, there is no indication that more than one reduncine genus or species is represented. The morphology of isolated molars and the single p4 specimen (G 3085), are consistent with an assignment to the genus *Redunca* rather than *Kobus*. The recovered specimens are comparable in size and morphology to the GD 2 *Redunca* (Adams and Conroy, 2005; Adams, 2006).

Tribe Tragelaphini

A single enamel fragment (GD 1497) may be from a (minimally) medium-sized tragelaphine, but can only be provisionally assigned to the tribe. The specimen preserves part of the buccal enamel near the cervical margin, including a small, spire-like ectostylid analogous to those that occur on many tragelaphine lower molars.

**Indeterminate Bovid Class I, II and III**

A small collection of nine bovid craniodental specimens were not identifiable below the family level. These include two bovid Class I petrosals (GD 968 and 978, likely antimeric) and an indeterminate upper molar (GD 3077, possibly neotragine or antilopine); an indeterminate bovid class II left i2 (GD 3095) and left m3 (GD 3042, a possible alcelaphine); and a bovid Class III indeterminate premolar fragment (GD 2609) and left i1 (GD 1897). In addition, there were 1012 indeterminate bovid craniodental fragments, including one horn core (GD 178, bovid Class II or III), one lower molar (GD 3080), three lower premolars (GD 3068, 3080, 3083), one cranial fragment (GD 3155) and 1006 indeterminate bovid enamel fragments. Of these indeterminate bovid enamel fragments, 24 may have been derived from alcelaphines, four from tragelaphines, and one from a reduncine. Only a limited collection of identifiable bovid postcranial remains were recovered from the GD 1 deposits and are summarized in Table 3.

In sum, the total GD 1 bovid assemblage is comprised of minimally one Class I individual (NISP = 6), four Class II individuals (NISP = 31) and eight Class III individuals (NISP = 45).

**Order Perissodactyla**

**Family Equidae**

*Equus* sp. and Equidae Indet.

A total of 18 craniodental and one postcranial specimen could be attributed to the family Equidae. One of the (minimally) two *Equus* individuals is a juvenile, as
indicated by the recovery of deciduous dental remains and unfused postcrania. Despite the large number of individual specimens relative to the other taxa identified from the deposits, most of these specimens are associated enamel fragments and therefore derived from a much smaller number of individual teeth. Two sets of equid specimens (GD 5627 and 5628; GD 5629–5632) are derived from two individual upper premolars or molars whose crowns are still set within calcified sediments within the Northern Extension section of the GD 1 deposits. Two other sets of enamel fragments (GD 5637 and 5638; GD 5633–5635, 5639–5640) represent two further isolated premolars or molars recovered from Pocket D.

The overall size and morphology of the equid remains from the deposits suggest that only members of the genus *Equus* are represented. One of the more complete specimens, GD 3045, is an upper deciduous premolar that is comparable in morphology to the GD 2 G 2026 specimen (Adams and Conroy, 2005; Adams, 2006). The specimen is similar in overall size to deciduous premolars of modern *Equus* species, although the extinct *Equus capensis* is a possible identification for the specimen.

The only equid postcranial specimen, GD 5574, is an isolated 3rd metapodial distal epiphysis that preserves a small portion of the metaphyseal surface. While the articular surface is poorly preserved, it is consistent in size with the unfused epiphyses of modern *Equus* juvenile 3rd metapodials.

If a modern *E. burchelli* developmental schedule is used, the GD 3045 lightly worn *Equus* deciduous upper premolar was derived from an individual under three years of age, as this is when the tooth is heavily occluded and shed (Klingel, 1965). The occlusal wear on the specimen suggests that the individual was likely under a year in age at death.

**Order Lagomorpha**

*Lagomorphidae indet.*

One complete calcaneus (GD 2228) preserves analogous morphology to the lagomorph calcaneal remains recovered from the GD 2 deposits (Adams and Conroy, 2005; Adams, 2006), being most similar to modern *Pronolagus rupestris*.

### 3.2.1. Indeterminate and postcranial specimens

A further 255 craniodental specimens from GD 1 were unassignable with any degree of certainty to a taxonomic level. Included are three cranial fragments (GD 942, 2490, 2939), one heavily occluded incisor (GD 3089, possibly suid), and 251 enamel fragments. Of the enamel fragments, one is a probable indeterminate artiodactyl (GD 1855), five are possible suids (GD 1240, 2639, 5591, 5692, 5693), 61 specimens are possible bovids or equids, and two specimens are possible equids (GD 2033, 2935). A further isolated enamel fragment (GD 2927) may be from a porcupine incisor.

In addition to the bovid, equid and lagomorph postcranial specimens already discussed above, six further postcranial specimens were recovered. Included in this group are four specimens derived from either a large artiodactyl (e.g. bovid Class III or larger) or perissodactyl: a proximal humerus articular surface (GD 5572), a postzygapophysis from a cervical vertebra (GD 954), and two vertebrae fragments (GD 959, a prezygapophysis; GD 2474, a vertebral body portion); and two indeterminate fragments, including a rib shaft portion (GD 3046) and a small, unfused proximal articular surface, likely from a femur (GD 2572).

### 3.3. Taphonomy of the GD 1 deposit fossils

Fossils recovered from the GD 1 deposits are predominately manganese-stained, poorly preserved, and comminuted (Fig. 3). Weathering stage data was gathered from 1683 specimens (66.81% of the non-dental cranial and postcranial specimens > 1 cm; n = 2519; Table 4). Of the
fossils that could not be coded for this variable, 421 of the non-dental cranial and postcranial specimens (16.71%) preserved rounded break edges and/or exhibited heavily abraded/artificially smoothed cortical surfaces that were consistent with movement within a hydrological system. A series of K–S tests ($\alpha = 0.05$; modified by the sequentially reductive Bonferroni method to $\alpha = 0.003$) found no significant differences in preserved weathering stages between 10 cm excavation levels within each of the major units of the excavated GD 1 assemblage (Table 5; Adams, 2006). Similarly, a second K–S test series ($\alpha = 0.05$; modified to $\alpha = 0.0011$) revealed no significant differences in the distribution of preserved weathering stages between any of the major units of the GD 1 assemblage (all interunit comparisons $D = 1.0$, $p = 0.011$; except Northern Extensions vs. Pocket B/D, $D = 0.5$, $p = 0.5344$).

The majority of specimens recovered from the GD 1 excavations exhibit minimal or no weathering (68.45% stage 0 or 1); however, the GD 1 fossils have a greater proportion of heavily weathered (stage 3 or above; 16.76%) than in the GD 2 assemblage (0.56%; Fig. 4; Adams, 2006). The distribution of GD 1 specimens across weathering stages is similar to that reported from the Olduvai FLK ‘Zinj’ floor assemblage (Fig. 4; Potts, 1988), but differs from the landscape and hyaena den assemblages reported by Potts (1988) in the smaller proportion of heavily weathered specimens above stage 3 (Fig. 4). Despite these proportional differences amongst these Gondolin and comparative assemblages, no statistical differences were detected (all intersite comparisons $D = 0.667$, $p = 0.077$). Finally, no statistical differences were found between the GD 1 assemblage and the Sterkfontein Member 5 assemblages (Pickering, 1999; grouped as ‘Fresh’ [stage 0], ‘Cracked’ [stage 1 to early stage 2] and ‘Exfoliated’ [late stage 2–stage 5]) groupings (Fig. 5; GD 1 vs. Sterkfontein Member 5 West and STW 53 Breccia, $D = 0.333$, $p = 0.976$; GD 1 vs. Olduvan Infill, $D = 0.667$, $p = 0.319$); despite the GD 1 assemblage including a far greater proportion of more advanced, ‘Exfoliated’ stage specimens (31.55%) than among any of the Sterkfontein assemblages (Olduvan Infill: 8.82%, STW 53 Breccia: 16.33%, Sterkfontein Member 5 West: 9.58%; Pickering, 1999).

![Fig. 4. Percentage of the total number of specimens across weathering stage categories from the GD 1, GD 2, Olduvai FLK floor, and two modern bone assemblages (data from Potts, 1988; Adams, 2006).](image_url)

![Fig. 5. Percentage of the total number of specimens across weathering stage categories from the GD 1 and Sterkfontein Member 5 assemblages (data from Pickering, 1999).](image_url)

### Table 6
Size category data from fossils recovered from the GD 1 deposits

<table>
<thead>
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<th>Size (cm)</th>
<th>GD 1 total</th>
<th>Overburden</th>
<th>Pocket B/D</th>
<th>Pocket C</th>
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<td>1055</td>
<td>540</td>
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<td>486</td>
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<tr>
<td>1–2</td>
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<td>85</td>
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</tr>
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<td>2–3</td>
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<td>–</td>
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<td>2</td>
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<td>–</td>
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<tr>
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<td>13–14</td>
<td>1</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>Total</td>
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<td>910</td>
<td>1387</td>
<td>126</td>
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</tbody>
</table>
The size category data gathered from the GD 1 assemblage is summarized in Table 6. A series of K–S analyses (\(z = 0.05\), modified to \(z = 0.006\)) indicated that none of the major unit divisions of the total assemblage exhibited significant difference in the size category distributions from one another (Table 5; Fig. 6). Although no statistically significant differences were detected, fossil materials from the overburden layer appears to be more heavily fragmented than among the other major divisions of the GD 1 deposits, with a greater percentage of 0–1 cm specimens (59.34%) than found among the other major excavation units (Northern Extension: 29.56%; Pocket B/D: 0%; Pocket C: 17.46%). As is the case in the GD 2 and Swartkrans Members 1–3 assemblages, nearly all recovered specimens from GD 1 are smaller than 5 cm in overall size (GD 1: 99.12%; GD 2: 99.50%; Swartkrans Member 1: 91.43%; Member 2: 95.26%; Member 3: 88.91%). The Swartkrans Member 5 assemblage differs somewhat in having a greater proportion of specimens above 5 cm in overall length (28.27%). By way of contrast, the majority of specimens recovered from three modern hyaena den accumulations fall above 5 cm in length (Kalahari brown hyaena den: 94.22%; Kalahari spotted hyaena den: 92.69%; Kruger spotted hyaena den: 67.52%; Brain, 1981).

3.3.1. Pre- and postmortem biotic element modification
A total of 191 specimens (3.94% of the total GD 1 sample; 5.46% if dental specimens are excluded) exhibited signs of pre- or postmortem modification by carnivores, rodents, borer beetles, or tree roots. There were no potentially hominin-modified specimens and none of the recovered remains showed indications of premortem pathology.

Carnivore-induced modification was noted on a total of 169 specimens, although 94 of these were classified as only ‘probably’ modified by carnivores. The total breakdown of carnivore modification types is as follows: 82 specimens exhibited small-diameter shallow pitting, 55 specimens preserved tooth marks, 17 specimens showed signs of gnawing, 10 specimens had combined shallow pitting, tooth marks and/or gnaw marks, and five specimens showed deep puncturing. All carnivore modifications were located on unidentifiable diaphysis fragments, except for a single Class II bovid proximal femur (GD 5571) that was gnawed, and three bovid Class II specimens with shallow punctures (GD 951, astragalus; GD 3055, first phalanx; GD 953, proximal humerus).

Small rodent gnawing was noted on seven unidentifiable diaphysis fragments. One of these specimens also exhibited edge-rounding. Porcupine gnawing was noted on 10 specimens. One of these was a Class II bovid distal radius (GD 952), while the others were unidentifiable diaphysis fragments (one of which exhibited edge-rounding).

Borer beetle perforations were found on three specimens, of which two were indeterminate diaphysial fragments and one was an indeterminate sized (minimally Class II) bovid horn core pedicle (GD 178). Two specimens were acid-etched by plant roots (GD 50, 1028), although two others may have been root etched and/or tooth marked by carnivores (GD 40, 745).

There are no significant correlations between the %MAU values from the GD 1 fossil assemblage and the typical carnivore consumption sequence reported by Blumenschine (1986), nor does the proportion of elements resemble either the direct or inverse consumption sequence. Several elements from GD 1 were not recorded within the consumption sequence (e.g. carpals, tarsals, etc.), because they are not primary parts of the first cycle (fleshy portions) or second cycle (marrow-filled elements) of consumption (Blumenschine, 1986). Those elements that were recovered from GD 1 and occur in the described consumption sequence include those that are often damaged or consumed during the first cycle (e.g. proximal limb epiphyses), and include elements from early and late in the typical sequence. Marrow-bearing element portions, such as identifiable or complete diaphysial portions, are notably absent from the deposits. In addition, there is no significant relationship between the GD 1 total bovid %MAU values and %MGUI (\(r_S = 0.021, \ p = 0.950\)) or FUI values (\(r_S = -0.088, \ p = 0.798\)) reported by Metcalfe and Jones (1988), and the proportions of recovered elements does not resemble any of the patterns previously identified by Binford (1978) based on modern human meat foraging strategies.

3.3.2. Transport and density mediated attrition
Total bovid %MAU values do, however, exhibit a significant, negative correlation (\(r_S = -0.861, \ p = 0.013\)) with the rank-ordered disarticulation sequence described by Hill (1979a), with the highest proportion of specimens...
from the early to the middle of the disarticulation sequence. Although there is no significant correlation between the total bovid %MAU values and the saturated weight index values (SWI) for Redunca skeletal remains ($r_s = -0.178$, $p = 0.647$), most of the recovered elements have SWI values below 50 (suggesting a higher than average transportability potential for the elements in the assemblage; Behrensmeyer, 1975). The identifiable skeletal elements from GD 1 also fall only within the group I, I/II, or II transportability groups described by Voorhies (1969).

No significant correlation exists between log transformed GD 1 postcranial %MAU values and bovid element-wise bone mineral density values ($r_s = -0.214$, $p = 0.505$), and a plot of standardized residual values on predicted values of the dependent variable indicated that the variation was homogeneously distributed.

4. Discussion

4.1. Dating of the GD 1 deposits

The current sample of GD 1 fauna cannot independently support a specific date for the formation of the fossiliferous deposits. The occurrence of Equus throughout the deposits minimally suggests that these specimens accumulated after 2.36 Ma (Behrensmeyer et al., 1997). The GD 1 Antidorcas cf. recki materials are most similar to the A. recki specimens from Gondolin GD 2, Swartkrans Members 1 and 2 and Kromdraai A, which would suggest an age for the specimens near 1.8 Ma. The species is known from deposits ranging in age from the 2.5 Ma to around 0.6 Ma (Vrba, 1995); however, Vrba (1976) has cautioned against using morphological differences among A. recki remains to refine biostratigraphic reconstructions of deposits.

The GD1-w section shows a change from normal polarity at the very base of the section, with reversed polarities recorded for the rest of the overlying section. This suggests that this section represents deposition during, and soon after, a polarity transition from a normal to reversed direction. The occurrence of Equus in the deposits suggests that the base of the deposit is unlikely to date to an earlier normal polarity period such as the Gauss at >2.58 Ma, given the first appearance date for this genus in Africa at around 2.36 Ma (Behrensmeyer et al., 1997).

While the GD 1 fossils could also have been deposited during the Réunion events at $\sim 2.14 \pm 0.03$ Ma, this is a less likely option given the expected depositional rates for flowstone from which the normal polarity is recorded and our past experience with the duration of this episode at other South African sites (Herries, 2003). We tentatively suggest that the normal polarity flowstone at the base of the sequence represents the very end of the Olduvai normal polarity period (1.95–1.78 Ma), with the overlying deposits postdating the end of the event at 1.78 Ma. Although the current GD 1 faunal sample does not allow us to eliminate the possibility that the deposits formed at the end of and after the Jaramillo event (0.99 Ma), the Olduvai normal polarity period (1.95–1.78 Ma) is the only major period in the faunal time range of the site and has been recorded within the stratigraphy of the GD 2 deposits (Herries et al., 2006a). Under this dating scheme, the GD 1 fossil deposits are dated to soon after 1.78 Ma, making them slightly younger than those from GD 2, which are dated to slightly older than 1.78 Ma (Herries et al., 2006a).

The GD-1e section preserves a mixture of both normal and reversed polarities. Normal polarities in the flowstone could at the very least be dated to the Gauss normal polarity epoch ($>2.58$ Ma) based on our suggested age of the overlying GD1-w section. The stratigraphically underlying clastic deposits show normal and reversed directions and cannot be ascribed to a particular polarity period, as they represent deposits infilling an area of previously eroded deposits beneath the base flowstone and could therefore date to almost any time period after deposition of this flowstone ($>2.58$ Ma).

4.2. Taphonomy of the GD 1 deposits

The complex geology of the Gondolin cave system near the GD 1 datum point precludes a simple interpretation of the taphonomy of the fossil deposits as might be possible in other in situ-derived samples; however, our reconstruction of the original geological context of the cave provides several important indicators for interpreting the depositional history of the fossil materials.

The modern dolomite caves of South Africa generally develop along joints and bedding planes forming either large interconnected caverns or complex maze caves. The Gondolin paleocave may have developed initially as two independent cavities that were later joined by collapse and increased solution. The western cavity (GD 1/3) developed from a small fault cavity which developed along a mineralization vein that can be seen in the area of GD 1. This rift provided the path of least resistance through the rock and was enlarged by percolating water and later captured and enlarged by small phreatic conduits to produce a major conduit for water drainage through the hillside. The initial entrance to the cave system most likely occurred uphill of the GD 1 area where speleogenesis initially took place. The top part of the paleocave has since been removed by subsequent erosion but a study of modern caves suggests that a vertical entrance most likely occurred directly from the surface rather than via a small upper chamber.

With a lowering of the local piezometric surface (local groundwater level), the cave was moved from the phreatic zone (water filled) into the vadose zone (air filled) of the rock. Percolating water would then have enlarged the routes directly to the surface. Large-scale collapse then occurred due to lack of support from water during the phreatic phase, and the cave would have enlarged laterally into a large cavern. This area of the dolomite has a very high degree of chert banding. High frequency, thin chert banding would have caused
instability after dissolution of the interlayered dolomite and would have resulted in a chert-rich, small-scale, block-brecia deposit. Such deposits are noted at the base of the sedimentary sequence where large chert blocks are cemented by speleothem. In the area of locality GD 4, the large amount of basal collapse rubble stands as evidence to this process of enlargement and collapse that filled the central area of the cavern. This basal collapse forms a breccia mass that constitutes the base upon which subsequent sedimentation took place.

The GD 1 area contains a number of different depositional deposits that represent in-washed material from several different phases. These deposits contain exogenous, weathered chert and large clasts that, given their size, suggest that the hydrological system was relatively high energy (at least intermittently), perhaps due to flash flooding with heavy runoff from the hillside. The continuous local occurrence of generally mesial conditions surrounding the Gondolin cave system is supported by the high organic content in the carbonate component of speleothem samples from throughout the Gondolin system, which suggests extensive vegetative cover around the cave during flowstone formation (Hopley, 2004). Water flowed into the GD 1 entrance and along with breakdown of the ceiling and walls caused the formation of breccia deposits. Fine-grained silt was later winnowed from these deposits and deposited as thick mud floors in the GD 3 and GD 2 areas of the cave. The presence of cave pearls directly below the GD 1 depositional area, however, suggests that the energy of the hydrological system was greatly reduced by the time water entered this portion of the cave system. Paleomagnetic measurements show that the basal flowstones in different areas of the cave were not formed at the same period.

The morphology of the nearby cave entrance and the associated hydrological system appear to have been the two primary contributing factors that both introduced and shaped the composition of the fossil ‘assemblage’ sampled from the GD 1 in situ sediments. Biotic modifications noted on skeletal elements recovered from the GD 1 deposits indicate that carnivores, porcupines, and small rodents initially contributed and/or modified at least some of the skeletal materials that were eventually interred within the sediments. Carnivore modifications to elements consist primarily of shallow pitting or isolated tooth marks and were generally restricted to unidentifiable diaphyseal fragments. None of the modified elements are sufficiently diagnostic enough to identify a specific carnivore taxon that was responsible for accumulating the remains; although an apparent bias towards the recovery of Class III bovids that comprise 61.5% of the bovid individuals from the deposit is more consistent with the typical bovid prey size preferences of modern hyaenas (Kruuk, 1972; Bearder, 1977; Cooper, 1990; Cooper et al., 1999) than modern leopards (Kruuk and Turner, 1967; Bothma and Le Riche, 1986; Kruuk, 1986; Bailey, 1993; Radloff and du Toit, 2004).

Several lines of evidence beyond the geological reconstruction above suggest, however, that carnivores, porcupines, or other rodents did not directly occupy the GD 1 cave area as a feeding retreat, den or lair. The first is the composition of the fossil materials excavated from the GD 1 deposits, which includes only a limited number of identifiable craniodental or postcranial remains. Identifiable elements are uniformly small, consisting primarily of isolated teeth, epiphysial fragments, and/or dense elements like carpals, tarsals and phalanges. Although long bone diaphyseal fragments comprise the majority of the recovered fossil remains, they were so comminuted that they generally retained no diagnostic characteristics. While based on a limited number of elements, the strong, negative correlation between the proportion of identifiable bovid elements in the GD 1 sediments and the typical bovid disarticulation sequence (Hill, 1979) indicates that elements recovered from the GD 1 deposits are those that most readily naturally disarticulate from bovid carcasses. Elements recovered from the GD 1 deposits also have saturated weight index (SWI) values below 50, indicating that these elements had a higher than average transport potential. The only exception to this trend in the assemblage is the recovery of partial tibiae and femora from the deposits, which have higher SWI values (and therefore lower potential to be transported within a hydrological system). However, the SWI values for elements listed by Behrensmeier (1975) were calculated based on whole elements, and thus the transport potential of these elements may have been considerably greater if they were reduced before transport. In addition, only elements from the first three Voorhies (1969) element groupings (I, I & II, and II) were recovered from the deposits. The recovery of elements solely from these groups indicates that the GD 1 materials represent a collection of elements that had been winnowed away from the original point of collection.

The second important, if somewhat confounding, line of evidence for taphonomic interpretation of the deposits is the poor preservation of the recovered fossil materials. The recovery of specimens with artificially smoothed cortices and smoothed break-edges supports our contention that some hydrological transport of specimens from the initial accumulation site occurred prior to deposition. In his interpretation of the Sterkfontein Member 5 West assemblage, Pickering (1999) suggested that some of the recovered fossil remains had been transported, with the lack of hydrological-modifications to specimens possibly due to either transport over only a short distance, or episodically, prior to final deposition. The recovery of these transported elements from the GD 1 deposits could indicate that these specimens were transported over a great distance from the original accumulation. An alternative, and more likely scenario given the likely close proximity of the original cave entrance, is that specimens had been transported only a relatively short physical distance, but that this movement occurred over a long period of time in
constant contact with sediments. This transport could readily occur during both the predepositional phases of the history of the assemblage in a low-energy hydrological system, or during intra-depositional shifting in a decalcified, postdepositional phase (see below).

The GD 1 fossil sample has a far greater proportion of heavily exposed (e.g. Stage 3 or above) specimens than the Gondolin GD 2 or Sterkfontein assemblages and preserves only a slightly lower proportion of such specimens than reported from landscape and hyaena den assemblages (Potts, 1988). It can be difficult, however, to interpret such weathering stage data as it is unclear what the tempo or even the initial source of such signs of environmental exposure are for karstic-interred skeletal specimens. A simple interpretation of the GD 1 weathering stages data would suggest that the specimens exhibiting low weathering stages were either directly interred in the deposits, washed into the deposits from outside the cave environment relatively soon after having been accumulated, or sufficiently shaded by local vegetation such that even longer-term exposure did not affect the specimens (Behrensmeyer, 1978). Conversely, the more heavily weathered specimens would again suggest that some skeletal materials were transported into the karstic environment only after significant surface exposure.

It seems unlikely that a scenario where specimens were discontinuously interred would have resulted in the uniform proportions of specimens across weathering stages deposited throughout the sampled GD 1 sediments, with no significant differences detected between major excavation units or 10 cm levels within units. Although the weathering stage system was developed based on observed changes to the external table of skeletal elements due to UV and general environmental exposure (Behrensmeyer, 1975, 1978), and subsurface weathering has been assumed to be an insignificant source of cortical erosion (Lyman, 1994), it is currently unknown to what degree postdepositional geological processes could influence cortex preservation in fossils. The GD 1 sediments underwent at least one cycle of natural calcification and decalcification prior to excavation, as evidenced by the presence of the heavily mineralized fossil specimens partially imbedded in calcified sediments and partially within loose matrix. It is possible that multiple cycles might have occurred since the initial deposition of the skeletal materials, particularly given the active hydrological system within the depositional area. As decalcification is an anataxic process, where the calcium component of sediments and their constituents are leached and removed, it has the potential to erode or otherwise further modify the cortices of fossilized specimens. Such a scenario, where the pattern of cortical preservation has been influenced throughout the deposits by decalcification, would better explain the observed uniformity of recovered specimens in this respect.

An unknown taphonomic factor is the extent to which subsequent postdepositional processes further modified the fossil materials after their initial postdepositional processes introduced exogenous skeletal materials into the GD 1 deposits. This is particularly important for assessing whether the heterogeneous spatial distribution of fossil materials in the GD 1 deposits reflects significant and/or selective removal of fossil materials from the in situ sediments. The notably discontinuous spatial distribution of recovered fossil specimens could relate to the long-term, natural action of the regional hydrological system. Under such a scenario, fossils originally deposited within the main drainage pathway would have been gradually transported out of the GD 1 sediments, leaving only a subset of the original fossil materials to be recovered in situ. This would explain why the fossil-rich pockets sediments were only identified adjacent to, but not within, the direct gravity-driven path of water drainage from above the deposits to the modern cave system floor. The majority of the GD 1 fossil sample was recovered from the Northern Extension (35%) and Pocket B/D (35%), with neither area directly inline with the central cut that channels water directly from above the deposits (Fig. 1). At the same time, if mining activity during the early part of the 20th century assisted in de-roofing the cave over the sediments there may have been only minimal hydrological removal of fossil materials in the intervening decades. The heterogeneous spatial distribution of fossil materials in the deposits could thus be a direct reflection of the initial postdepositional in-washing that introduced materials into the system, rather than any subsequent hydrological re-working of the assemblage.

A final notable feature of the fossil assemblage is the uniform linear length of specimens, with the only apparent variation from the typical GD 1 fragment size distribution pattern being those fossils recovered from the soil overburden layer. A predominance of small, isolated skeletal elements would be expected for a hydrologically-sorted fossil assemblage, where small elements or element portions (like isolated teeth or diaphysis fragments) are readily moved by even low-energy streams. As discussed above relative to the weathering stage data, however, the homogeneous distribution of specimen lengths across units and levels of the deposits appears somewhat inconsistent with a scenario where fragmentation occurred primarily before deposition and the interment of elements occurred sporadically and/or over a potentially long period(s) of time.

Although simple specimen length data cannot identify the phase during which fragmentation occurred, other observations from the recovered specimens suggest that both pre- and postdepositional fragmentation of elements has taken place. Among the identifiable craniodental and postcranial remains, the only complete elements recovered were carpals, tarsals and/or other small, relatively dense elements. The craniodental sample was comprised entirely of isolated teeth, with not even a partial mandible recovered. Similarly, long bones are represented solely by isolated epiphyseal fragments and the diaphyses are heavily reduced to the point where they are now undiagnostic. If fragmentation of craniodental or postcranial materials...
occurred solely postdepositionally, we would have expected more associated fragments or elements/element portions to have been recovered in situ. We would also have expected to recover more diaphyseal fragments with relatively fresh break edges. Instead, break edges on specimens (both identifiable and unidentifiable) were either moderately eroded or had significant edge-rounding, suggesting fragmentation prior to hydrological transport.

Both the predominance of extremely small (e.g. 0–1 cm) and eroded fragments recovered from the soil overburden layer, and the relative uniformity of specimen sizes recovered from the deposits, may be explainable by the same process of natural, in situ decalcification discussed above in reference to the weathering stage results. Previous research by Brain (1981) at Kromdraai B suggested that natural decalcification can lead to small, uniform fragment sizes within these karstic sediments. The combination of the meteoric water drainage through the GD 1 region and natural acids released by tree and grass roots within the overburden soils and makondos has exposed the GD 1 breccias and fossils to a highly caustic environment. This would potentially explain the extreme comminution of fossils from the overburden, as this is the layer that surface waters and organically-produced acids would affect first. The unbiased postdepositional leaching of calcium from fossil specimens would progressively reduce specimens to small, relatively homogenous fragments (and likely dissolve them completely over time).

5. Conclusions

To summarize, fossil materials recovered from the GD 1 deposits (a) have carnivore and other biotic damage that is consistent with these groups having been involved in the initial accumulation of at least some of the eventually interred skeletal materials; (b) exhibit cortical surfaces that are generally more weathered than is typical for other assemblages deposited in cave sediments, as well as signs of having been abraded during transport; (c) consist of elements that rapidly disarticulate from exposed carcasses after the death of the organism (and are thus readily available for transport); and (d) are those with both high transport potential and those typically found in deposits that form some distance downstream from hydrologically-sorted carcasses. When combined with the geological evidence for an active hydrological system and a cave entrance morphology that may have limited direct entry, we feel that the most likely taphonomic scenario for the accumulation of fossil materials into the GD 1 deposits is as follows. Carnivores, porcupines, or other rodents used either the dense vegetative cover surrounding the cave system, or the area directly near the vertical cave entrance (that may have had a small lateral entrance followed by a vertical drop or talus cone) as a feeding retreat/den. These agents produced bone litter which collected either on the surface near the cave entrance or just within the entrance itself. The seasonal to continuous water flow through this entrance to the cave system then washed surface debris (including surface clasts and skeletal materials) from outside the cave environment into the sampled GD 1 area, where the material was interred within the in-washed sediments during a series of depositional periods, rather than in a single event.

The predepositional history of the sampled GD 1 faunal assemblage was more complex than the processes that formed the Gondolin GD 2 assemblage (Adams, 2006; Adams, in prep.). If our interpretation of the depositional dates of the GD 1 fossil materials are correct, this suggests that two very different taphonomic processes were operating in different regions of the Gondolin cave system in the late Pliocene and early Pleistocene (Adams, 2006; Herries et al., 2006a). It is somewhat more difficult to assess the duration and influence of the postdepositional phase on the composition of the sampled GD 1 assemblage. The heavily exposed and weathered elements in the deposits, as well as their overall physical length, may reflect processes that acted on fossil specimens either pre- or postdepositionally, although we suggest that postdepositional processes have strongly influenced the sampled assemblage. The heterogeneous spatial distribution of fossils throughout the deposits could reflect the initial hydrological sorting of the skeletal materials where specimens were deposited in isolated pockets. Alternatively, the sampled distribution may be an artifact of later (possibly very recent) movement of fossils through the deposits because of the continued drainage of meteoric water through this part of the cave system. As natural decalcification of the deposits occurred by the percolation of water through the brecciated deposits, fossils within the pockets may have been further aggregated; specimens in the primary path of drainage may have been progressively moved through the deposits and eliminated by dropping out of the sampled area to the modern cave floor.

The overall results presented here highlight the complex geological and hydrological processes that can underlie the taphonomic history of some South African karstic fossil assemblages. We strongly suggest that future analyses of South African cave systems integrate geologic and hydrologic data when evaluating the biotic and abiotic taphonomic processes that may have mediated the pre- and postdepositional history of recovered fossil assemblages. Furthermore, our results from GD 1, when compared to those from GD 2 (Adams, 2006; Adams, in prep.), stress the variation in underlying taphonomic processes that can occur between fossil-bearing deposits that form within the same cave system over a relatively short geological time span. The potential for such variation suggests that caution be used when offering simple taphonomic interpretations of South African Plio-Pleistocene karstic fossil accumulations, particularly for those assemblages aggregated from ex situ sediments that may represent accumulations that originally formed discretely and/or asynchronously within the cave system. The analysis of fossils from ex situ calcified blocks only provides a blunt assessment of the
faunas, depositional processes, and the history of the cave as a whole. Only an analysis of in situ fossil deposits, with careful consideration of multiple geologic and taphonomic factors, can provide the resolution necessary to begin to interpret the depositional processes underlying the formation of the South African Plio-Pleistocene fossil record.

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