Taphonomic interpretations of the Haasgat HGD assemblage: A case study in the impact of sampling and preparation methods on reconstructing South African karstic assemblage formation

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ARTICLE INFO

ABSTRACT

The Haasgat fossil-bearing karstic system is situated within the Skurweberg Mountain range in the northeastern portion of the Fossil Hominids of South Africa UNESCO World Heritage Site in South Africa. As is the case for the nearby Gondolin hominin locality, Haasgat occurs in an area of substantial modern topographic relief that contrasts with the low-relief landscape of the southwestern extent of the World Heritage Site surrounding the Blauubank Stream Valley sites (e.g., Sterkfontein, Swartkrans, Kromdraai, Bolt's Farm). This suggests differential landscape formation processes during the Neogene and potentially novel palaeoecosystems and taphonomic processes governing karstic fossil assemblage composition across even a small geographic region. This is particularly critical given the overall paucity of taphonomic data from the region, the substantial cercopithecoid primate assemblage that is uniquely dominated by the basal baboon species *Papio angusticeps,* and the recent announcement of the first hominin specimen from Haasgat.

Here we provide the first comprehensive taphonomic analysis of the Haasgat HGD faunal assemblage that was developed from *ex situ* calcified sediment blocks in the 1990s. There is direct evidence for biotic activity (e.g., large-bodied carnivores and porcupines) mediating the formation of parts of the HGD faunal assemblage, including at least part of the primate craniodental and postcranial sample. There is minimal evidence for pre-depositional element UV exposure and weathering or winnowing of the assemblage, but there is abiotic distortion and crushing of elements. Our analysis has equally found that taphonomic data from the HGD assemblage is compromised by a modern 'overprint' of damage through mechanical preparation and a lack of documentation generated during sampling, processing, and initial curation. Nearly half the cortical surfaces and many dental specimens in the assemblage exhibit evidence of substantial preparation damage rendering many purported biotic modifications ambiguous or suspect. Element proportions may be artificially skewed towards craniodental specimens and more reflective of block selection and/or selective processing rather than original deposition composition. As a result, the Haasgat HGD sample provides only limited data on the depositional processes mediating karstic assemblage formation in the region, and ultimately serves as a cautionary tale of the impacts of palaeontological sampling strategies on subsequent analysis and research.

1. Introduction

Haasgat is a fossil-bearing karstic system that formed in the Eccles Formation of the Malmani Subgroup dolomites, and is situated on the western slope of a narrow north-south trending valley within the Skurweberg Mountain range (Adams, 2012; Herries et al., 2014; Fig. 1). The modern landscape surrounding Haasgat, like the region surrounding Gondolin, is defined by substantial

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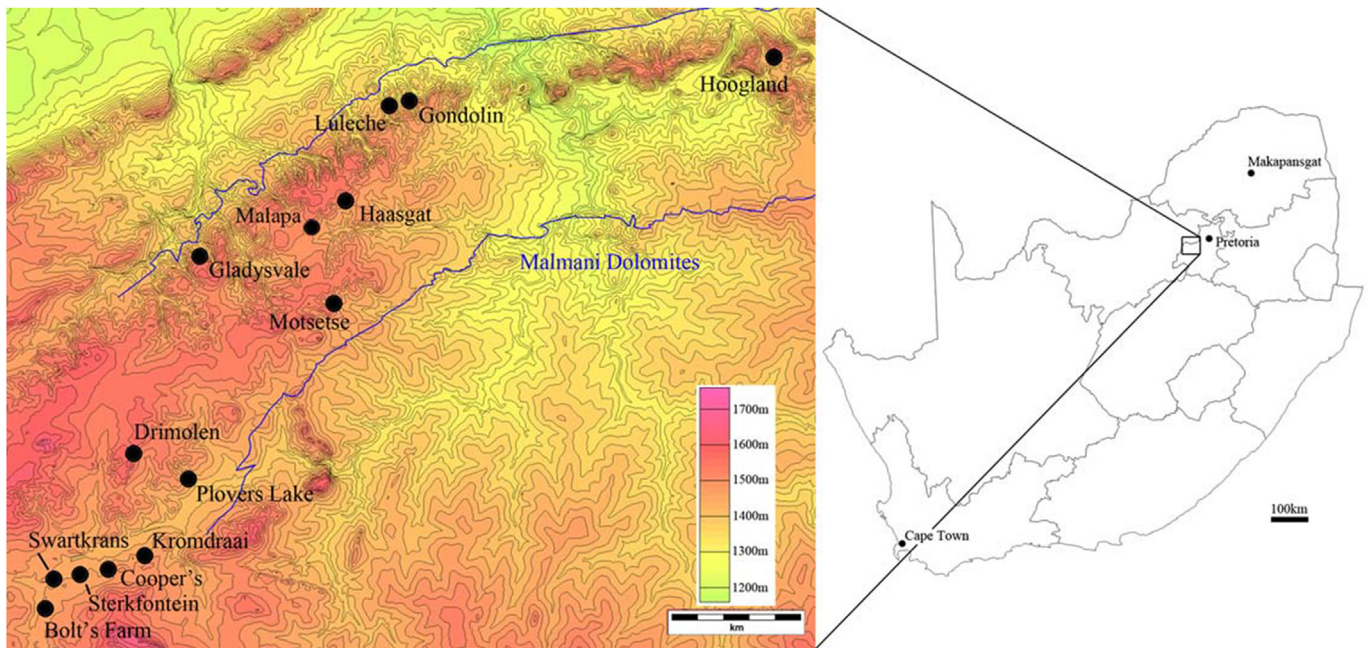
Fig. 1. Map of South Africa (left) with topographic inset (right) of the Haasgat and other major late Pliocene and early Pleistocene fossil-bearing localities.

topographic relief that sharply contrasts with the low-relief modern topography surrounding other penecontemporaneous sites (e.g., Sterkfontein, Swartkrans, Kromdraai, Bolt's Farm) of the Blauubank Stream Valley (Brain, 1981; Adams, 2006; Adams et al., in press). Haasgat is also one of few localities in this more mountainous portion of the northern UNESCO Fossil Hominids of South Africa World Heritage Site with richly fossiliferous and hominin-bearing early Pleistocene deposits, and the only site in the region with a substantial non-hominin primate fossil record (Adams, 2012; Leece et al., 2016).

During the early 20th century lime miners excavated a large amount of the original paleokarst deposits from the cave, forming a secondary modern system comprising a large horizontal tunnel with fossiliferous bands of calcified sediments on the walls and ceilings (Herries et al., 2014). In the course of mining the calcified sediments adhering to the dolomitic roof of the cave collapsed onto the modern cave floor, and a massive dumpsite of calcified sediments that presumably represents material spanning the entire depositional history of the system was generated that extends from the modern cave entrance to the valley floor. Fossiliferous calcified sediment blocks collected from this *ex situ* dumpsite in the early 1990s (Keyser and Martini, 1991; Keyser, 1991) was processed to produce the HGD assemblage and ultimately found to yield a diverse faunal sample, including three species of extinct primate (*Cercopithecoides haasgati, Cercopithecoides williamsi,* and *Papio angusticeps*) (McKee and Keyser, 1994; McKee et al., 2011; Kegley et al., 2011; Adams, 2012). Subsequent sampling of the same *ex situ* deposits has also yielded the first hominin specimen (representing either *Australopithecus* or *Homo*; Leece et al., 2016). Magnetobiostratigraphic analysis has indicated that the primary Haasgat fossil deposits are dated to between 2.3 and 1.9 million years ago (Ma; Herries et al., 2014). This age places the overall Haasgat deposits during a critical period in South African fossil history that records significant ecological changes (deMenocal, 2004; Dupont et al., 2005; Hopley et al., 2007), and overall faunal community turnover including hominin and other primate migration, speciation and extinction (Vrba, 1995; Reed, 1997; Adams, 2006; Herries et al., 2009; Werdelin and Sanders, 2010; Herries

and Shaw, 2011; Pickering et al., 2011a, b; Adams et al., in press).

In the initial publications the cave system was envisioned as a shallow pit, with a wide depression funneling into the cave, which potentially had a discrete upper chamber separate from the portion of the cave system that eventually served as a depositional area for skeletal elements (Keyser, 1991; Keyser and Martini, 1991). A long post-mortem, pre-depositional history for elements in the HGD assemblage was suggested based on the occurrence of significant cortical damage, distortion and/or extreme weathering prior to fossilization. This suggested that the skeletal elements had likely been exposed, either outside the karstic system or within the light zone of the cave, prior to being hydrologically transported farther into the cave system (Keyser, 1991; Keyser and Martini, 1991). Formation of the majority of the assemblage was attributed to active accumulation by large carnivore (potentially leopard) and porcupine based on element modifications on recovered fossil specimens (Keyser, 1991; McKee and Keyser, 1994; Plug and Keyser, 1994).

The entire Haasgat HGD assemblage was recently reevaluated, revealing that only 1475 of the 2413 *ex situ* specimens processed in the early 1990s had been considered in prior publications on the faunal assemblages, and several critical specimens had been misidentified or had gone missing from the collections (Adams, 2012). This reanalysis of the HGD assemblage has significantly altered the faunal composition of the sampled cave deposits and, alongside results of comprehensive geomorphological study and sampling, has necessitated reconsideration of the previously offered interpretations of the depositional history and assemblage taphonomy of Haasgat (Adams, 2012; Adams et al., 2013; Herries et al., 2014). This paper provides the first taphonomic analysis of the HGD assemblage that includes all faunal material as recently revised and expanded by Adams (2012), and specifically addresses the taphonomy of primates in the HGD sample. We also present the first listing and counts of elements as Adams (2012) focused on taxonomic reassessment rather than detailed craniodental and postcranial composition. We also provide the first quantitative assessment of prior, largely qualitative statements regarding assemblage taphonomy by Keyser (1991), McKee and Keyser

(1994), and Plug and Keyser (1994) on assemblage deposition and composition of the analyzable fossil sample.

2. Materials and methods

2.1. Historical issues with the Haasgat HGD assemblage

The entire HGD assemblage of 2414 individual specimens described by Adams (2012) is curated by the Council for Geosciences (Silverton, South Africa). As noted in the Adams (2012) reanalysis, there are several limitations to analyzing and interpreting the HGD assemblage due to the known issues with the preparation and curation history of the assemblage that we summarize here as they are directly relevant to taphonomic analysis and interpretation.

First, no basic database information exists regarding the number or geomorphology of the collected sediment blocks that yielded the assemblage or the original in-block associations of individual specimens. The historic Haasgat HGD catalogue only lists some of the specimens by number, their basic taxonomic and element identification, and their original storage location within the curation cabinets. As such, it is impossible to assess the density of elements in the sampled blocks, element associations, or the homogeneity or heterogeneity of the deposits sampled from the *ex situ* dumpsite. This confounds broad assemblage interpretations by introducing an unknown degree of collection-phase temporal and spatial averaging in the sample, and taphonomic and depositional data from a single element or subsets of the assemblage may not be applicable to other elements or subsets.

Second, there is established and unknown degree of specimen loss. Several specimens, including two *Cercopithecoides haasgati* crania (HDG 1166 and 1167; McKee et al., 2011; Adams, 2012), and the only carnivore specimens, represented by a *Chasmaporthetes nitidula* maxilla (Keyser, 1991: Fig. 7; Keyser and Martini, 1991, Plate 4) and the *Canis* sp. mandible (Keyser, 1991; Keyser and Martini, 1991), have not been located since reassessment of the HGD sample began in 2010 (Adams, 2012). These previously described and figured examples aside, there is an unknown level of potential specimen loss due to incongruities in the counts between the catalogue, the published lists (Keyser and Martini, 1991; McKee and Keyser, 1994; Plug and Keyser, 1994), and the revised specimen list (Adams, 2012). As previously noted, out of the 2413 HGD specimens, only 1475 were ever listed in the published literature (Keyser, 1991; Keyser and Martini, 1991; McKee and Keyser, 1994; Plug and Keyser, 1994; McKee et al., 2011) prior to re-description of the assemblage. Of those 1475 specimens, only 946 had been physically labeled and only 740 (30.7%) had entries in the Council for Geosciences HGD catalog (Adams, 2012). The most striking example of potential loss is the disparity of 254 individual specimens between published and located numbers of hyraxes (*Procavia* sp.) between Plug and Keyser (1994) and Adams (2012). This is particularly important for this taphonomic analysis as the element representation and damage patterns to hyrax remains were used by Plug and Keyser (1994) to argue for the involvement of leopard (or leopard-like felid) in accumulating the sampled HGD assemblage.

Third, aspects of the sampling and processing strategy employed in the production of the HGD assemblage are unknown. Although Keyser (1991) notes that blocks were selected from the *ex situ* dumpsites, the criteria used (e.g., random sampling, selection of all blocks with visible fossils, selection of blocks with a certain density, selection of blocks with a certain sediment matrix) was never defined. The primary, and apparently exclusive, method for fossil extraction was mechanical preparation using air scribes and the heavy use of the cellulose nitrate polymer Glyptal G 1276 (cellulose nitrate polymer) as a stabilizing agent/consolidant

(Keyser, 1991; McKee and Keyser, 1994; Plug and Keyser, 1994). This processing method has had two major impacts on our ability to assess specimen/assemblage taphonomy: the heavy application of the semi-opaque Glyptal consolidant obscures parts of the external cortex on many of the individual specimens, and there is physical damage to the elements (scribe marks, processing-induced breaks, poorly executed regluing) present on 1090 specimens (45.2% of the assemblage; see section 3.2; Fig. 2). In addition, although Glyptal was commonly used in vertebrate palaeontology in the 20th century (e.g., see Brink, 1957; Wilson, 1965; Chinsamy and Raath, 1992; and discussions in Shelton and Chaney, 1994; Brown, 2012), it is currently avoided, usually replaced by acrylic resins such as Paraloid B-72. Glyptal consolidant is manufactured utilizing highly concentrated nitric acid and using sulfuric acid as a catalyst, is highly unstable, especially without a plasticizer or other fixative, and readily undergoes photochemical degradation which releases nitrous oxide, which promotes the production of nitric acid (Koob, 1982). These degradation products, as well as chemical impurities remaining from manufacture can irreversibly deteriorate coated surfaces and deeper structures in fossil specimens. We cannot confidently establish whether the use of Glyptal not only simply obscured surface features or has actually altered cortical surfaces. As such, the combination of obscured surfaces, caustic chemical application and processing-induced mechanical damage has necessitated an extremely conservative approach to coding and interpreting potential abiotic and biotic modifications to individual specimens.

2.2. Study methodology

Our methods for evaluating the pre-, peri- and postdepositional taphonomic features of the HGD assemblage follow those described in detail in Adams (2006, 2010: Table 1) and described in the supplementary online material (SOM) including assessment of: assemblage composition demographics, biotic and abiotic element modification, indices of consumption/utility/transport, and assemblage comminution and attrition. All statistical analyses were performed in SPSS 23 (IBM SPSS Statistics, Inc.). Comparative fossil and modern taphonomic data sources are as detailed in Adams (2010). Although we have followed the size class categories as defined by Brain (1981), these classes were defined by live weights that overlap in the transitions between adjacent classes (e.g., large class I bovids overlap with the body masses exhibited by small class II bovids; noted by Brain, 1981: p.9). In contrast to the original revision of the bovid listing provided in Adams (2012), which did attribute a collection of 'transitional' postcranial elements (likely derived from *Oreotragus* sp. and *Antidorcas* sp.) to class I, analysis for this study has been ultimately unable to attribute these materials to organisms clearly under the 23 kg live-weight threshold that defines class II (or the class II *sensu lato* lower boundary of 18 kg given reported live weights for *Antidorcas marsupialis* provided in Brain, 1981: Table 1). Simultaneously we emphasize that the class II remains analysed here are nearly exclusively from organisms at the lower boundary of the 18 kg–84 kg live-weight range established by Brain (1981; Table 1; and below the 104 kg live weight maximum boundary listed for class II taxa).

3. Results

3.1. Assemblage composition and demographics

Of the 2414 identifiable remains in the Haasgat HGD *ex situ* sample, two (the uncatalogued purported *Chasmaporthetes nitidula* maxilla, and the single purported *Canis mesomelas* mandible) could not be located or confirmed and is not included in subsequent
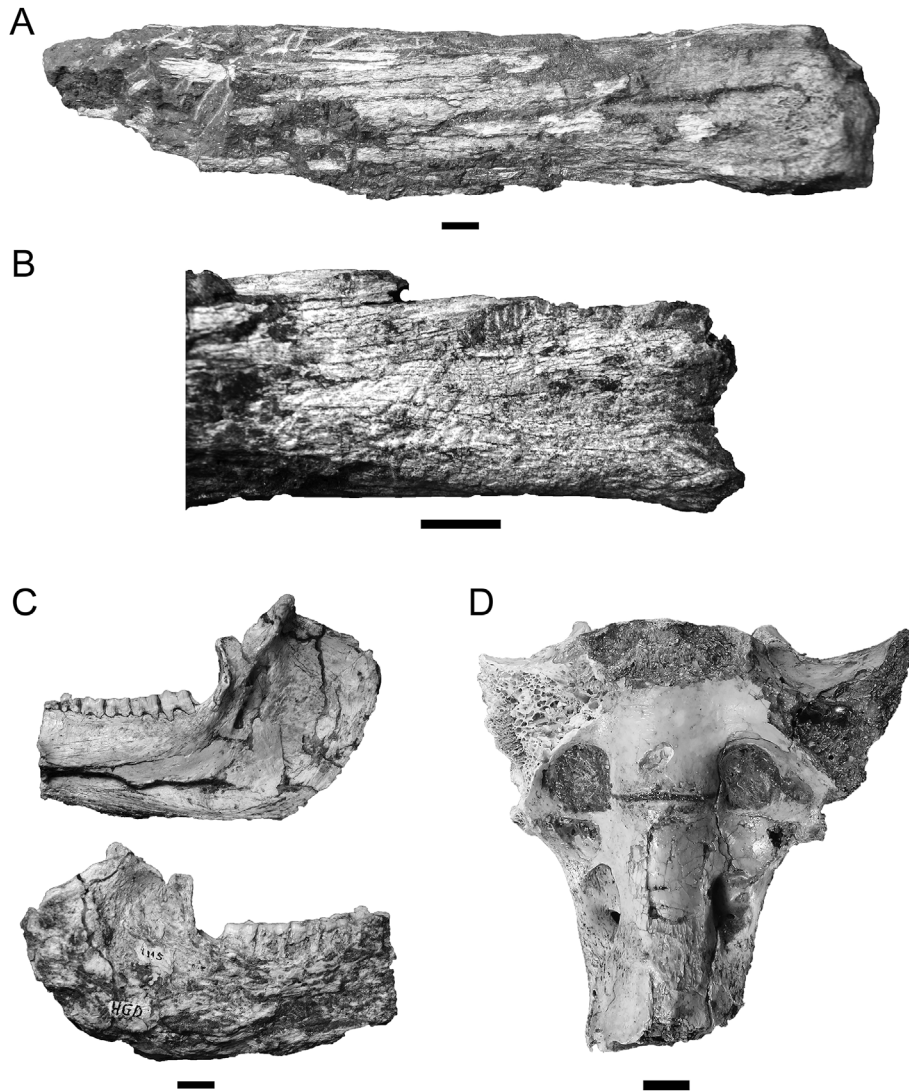
Fig. 2. Examples of Haasgat HGD assemblage fossil specimens with preparation damage. A, HGD 1009 *Equus* sp. indeterminate side metatarsal diaphysis and distal metaphysis with combination of weathering and mechanical preparation damage that has largely removed most of the external cortical surface. B, HGD 710 *Equus* sp. indeterminate side metacarpal diaphysis with strong air-scribe gouging across the element that has heavily altered the external cortical surface. C, HGD 1145 *Procavia transvaalensis* right mandible. The lingual surface (top) preserves an intact external cortex (if distorted and crushed) and surfaces of the dentition, while the buccal surface (bottom) has been heavily damaged through mechanical preparation. D, HGD 1073 Bovidae gen. et sp. indet. (Class II) sacrum with surface damage to the external cortex of the margins of the element from mechanical preparation and an ambiguous central depression that is unlikely carnivore-derived. Scale bars equal 1 cm.

taxon-based analyses (as casts of the two currently missing *Cercopithecoides haasgati* crania exist and could be directly studied they were included). A total of 1446 specimens (59.93%) could be taxonomically identified, while the remaining 968 specimens were only identifiable as mammalian craniodental (number of individual specimens (NISP): 49), postcranial (NISP: 692), or indeterminate origin (NISP: 227) remains. The taxonomically identifiable remains are derived from a minimum of 154 individuals (MNI), with the majority representing bovids (40.9%) and primates (35.06%), with only hyracoids (13.64%) and *Hystrix africaeaustralis* (5.84%) represented beyond one or two individuals of other groups (Adams, 2012). The HGD primate assemblage includes a large, ontogenetically diverse sample of the extinct basal baboon species *Papio angusticeps* (NISP: 88, MNI: 37) and the only described sample of the extinct colobine *Cercopithecoides haasgati* (NISP: 22, MNI: 12) in the African fossil record. The bovid assemblage is composed almost entirely of klipspringer (*Oreotragus* sp.; NISP: 158, MNI: 24; see discussion in Adams, 2012) or indeterminate alcelaphins (NISP: 116,

MNI: 10) in bovid size classes I and II (<84 kg estimated live-weight). As a result, the HGD assemblage is more taxonomically homogeneous (as reflected by the low McIntosh evenness value of 0.73) than most penecontemporaneous fossil localities (excepting Gondolin GD 2 and Sterkfontein Member 4), and is most similar to that reported from Sterkfontein Oldowan Infill (Table 1). This value contrasts with the McIntosh values for fossil and modern hyaena dens (*Crocuta crocuta* and *Parahyaena brunnea*; $\overline{x}$: 0.87, s.d. 0.059) and modern leopard dens (*Panthera pardus*; $\overline{x}$: 0.88, s.d. 0.458, range: 0.09). Simultaneously there is a low carnivore-ungulate ratio (2.99%) given the identification of only two single individuals of cf. *Dinofelis* sp. and an indeterminate hyaenid, placing Haasgat HGD in the lower ranges of the South African fossil localities and previously described modern hyaenid den localities (Table 2).

The distribution of bovids across size classes (with *Oreotragus* sp. treated as class II after metric data presented in Adams, 2012) in the HGD assemblage is dissimilar from the distribution of bovids from most comparative fossil and modern deposits (Table 3). That

Table 1
McIntosh evenness statistic values for fossil and modern comparative assemblages.

Site	Evenness
Fossil Sites	
Haasgat HGD	0.73
GD A	0.90
GD 1	0.79
GD 2	0.60
Gladysvale	0.92
Kromdraai A	0.83
Kromdraai B	0.77
Makapansgat 2	0.93
Makapansgat 3	0.81
Makapansgat 4	0.84
Makapansgat 5	0.78
Sterkfontein Member 4	0.70 (0.69)[a]
Sterkfontein 53 Breccia	0.87
Sterkfontein Olduwan Infill	0.75
Sterkfontein Member 5 West	0.84
Swartkrans Lower Bank	0.81
Swartkrans Member 2	0.82
Swartkrans Member 3	0.81
Fossil Hyaena Dens	
Equus Cave 2b	0.81
Equus Cave 2a	0.92
Equus Cave 1b	0.93
Swartklip	0.86
Modern Hyaena Dens	
Deelpan	0.89
Syokimau	0.85
Amboseli	0.77
Botswana	0.94
Kasperdraai	0.92
Kannaguass	0.89
Roikop	0.90
Kwang	0.77
Fossil Felid Den (_Homotherium_)	
Friesenhahn Cave	0.71
Modern Leopard Dens	
Hakos	0.92
Portsmut	0.89
Quartzberg	0.83

[a] The statistic value in parentheses is that using an updated hominid MNI count from Pickering (1999); the other is based on MNI counts published in Brain (1981).

said, the broad trend of dominance of smaller class II bovids, followed by larger class III and minimal class I/IV is shared with several deposits (Kromdraai A, Swartkrans Members 2–3), observed spotted hyaena kills in Kruger Park, and most observational data on leopard predation patterns. The summed age category data for bovid individuals recovered from the HGD assemblage is provided in Table 4. A similar proportion of immature (juvenile and/or sub-adult) to adult individuals occur in the class II and III bovids; and although a higher proportion of immature individuals occurs in the class IV group, this is based on a small MNI (four total individuals) and cannot be views as a 'trend'. Likewise, the low MNIs for other taxa make demographic interpretation speculative, although it is worth noting the single large suid (likely _Metridiochoerus_ sp.; Adams, 2012) is a very young juvenile, and there are many immature porcupines (_Hystrix africaeaustralis_; immature MNI: 4; 44.4% of total) and fossil hyraxes (_Procavia transvaalensis_ and _Procavia antiqua_; immature MNI: 2 and 5, respectively; 15.5% and 62.5% of totals). There is no evidence for juvenile or subadult equid individuals in the assemblage as no deciduous teeth were recovered and all postcranial elements exhibiting full epiphyseal-

diaphyseal fusion. In addition, the moderate occlusal wear to equid dental specimens does not support either of the minimally two equid individuals in the sample representing adults of advanced age (Adams, 2012).

The demographics of the substantial primate sample can be reconstructed with somewhat greater detail given sample size and the preservation of sexually dimorphic craniodental features. Most of the 17 colobine individuals assigned to _Cercopithecoides haasgati_, _Cercopithecoides williamsi_ and _Cercopithecoides_ sp. are adults either with full third molar eruption or sufficient molar wear to indicate full skeletal maturity. Only minimally three _C. haasgati_ individuals from four specimens are immature (HGD 1167: deciduous M2 erupted; HGD 1172: deciduous M2 erupted; HGD 1174: m1 erupted; HGD 1193: m1 erupted), with a further immature _Cercopithecoides_ sp. individual represented by the HGD 1184 edentulous mandible (Kegley et al., 2011). The sex demographics of the colobine sample are more evenly divided: _C. haasgati_ is represented by minimally four male and three female individuals, _C. williamsi_ by a single male and single female individual, and a single male indeterminate _Cercopithecoides_ (Kegley et al., 2011). The large _Papio angusticeps_ sample (MNI: 37) is also demographically diverse with minimally ten adult male individuals, nine adult female individuals, and three further adult individuals of unknown sex. There are three subadult females (lacking fully erupted third molars or premolar occlusal wear) and 12 subadult individuals of unknown sex representing young juveniles with deciduous second molars erupted (e.g., HGD 634) to the third molar just erupting (e.g., HGD 632).

Finally, the distribution of skeletal elements recovered from HGD (Table 5) varies across the three bovid size classes recovered from the assemblage, and between the bovids, equids and cercopithecoids - the only non-bovid taxonomic groups with sizable skeletal samples in the HGD assemblage. In the postcrania, long bone element epiphyses are more commonly recorded than diaphyses, and appendicular elements are better represented than axial elements. Although the class II and class III bovid element distributions mirror each other in terms of the element portions recovered, the proportions of class III element portions are depressed by a strong representation of craniodental elements. Most striking is the extreme paucity of cercopithecoid postcranial elements relative to craniodental specimens in the HGD assemblage. The equid sample is also very craniodentally dominated, and the postcranial sample contrasts with that of the only other large ungulates (class IV bovids) in the high proportion of carpals, tarsals and distal limb elements and element portions (Table 5).

3.2. Ante-, peri-, and postmortem element modification

A total of 1159 specimens (48.0% of the total HGD assemblage) exhibited signs of modification by carnivores, rodents, insects or human activity during preparation (Table 6; Figs. 2–3). Insect boring damage and small rodent gnawing was infrequently identified. Carnivore-induced modification (exclusively tooth scoring and small diameter punctures; Fig. 3A–B) was noted on a total of 41 specimens (1.7% of the total assemblage), roughly equally recorded across cranial (NISP: 13) and postcranial (NISP: 28) elements, and within the latter category mostly identified on bovid long bone epiphyses (NISP: 12). As expected given the dominance of bovids in the HGD assemblage, most carnivore and porcupine-induced modification was noted on bovid specimens, with few equid and primate specimens recording diagnosable damage attributable to these two agents. Craniodental specimens of _Cercopithecoides haasgati_ (HGD 1179a right mandible), _Cercopithecoides williamsi_ (HGD 1180 left mandible), _Papio angusticeps_ (HGD 613 partial cranium, HGD 636 left mandible, HGD 1243 left mandible), _Papio_ sp. (HGD 695 left mandible, HGD 1223 partial cranium), and

Table 2
Carnivore-ungulate ratios from fossil and modern comparative assemblages.

Fossil assemblages	Carnivore-ungulate ratio
Haasgat HGD	2.99%
GD 2	0.054%
GD A	0.081%
GD 1	0.0%
Makapansgat Member 2	60.0%
Makapansgat Member 3	11.73%
Makapansgat Member 4	30.0%
Makapansgat Member 5	3.57%
Sterkfontein Member 4	23.14%
Sterkfontein Member 5 West	33.96%
Swartkrans Member 1 (Lower Bank + Hanging Remnant)	25.0%
Swartkrans Member 2	19.51%
Swartkrans Member 3	23.74%
Kromdraai A	18.54%
Kromdraai B	30.0%
Swartklip 1	24.0%
Equus Cave	30.0%
Sea Harvest	42.0%
Hoedjies Punt	31.0%
Elandsfontein Bone Circle	30.0%
Deelpan	31.0%
Ysterfontein	35.0%
Archaeological Sites	
Klasies 1 (Middle Stone Age)	9.0%
Die Kelders (Middle Stone Age)	11.0%
Nelson Bay (Late Stone Age)	8.0%
Boomplaas I (Middle & Late Stone Age)	12.0%
Border Cave (Middle & Late Stone Age)	10.0%
Modern brown (B) and striped (S) hyaena dens	
Botswana (B/S)	30.0%
Kasperdraai (B/S)	77.0%
Kannaguass (B/S)	25.0%
Rooikop (B/S)	30.0%
Kwang (B/S)	57.0%
Boekenhoutskloof (B/S)	40.0%
Leuufontein (B/S)	0.0%
Tweeputkoppies (B/S)	13.0%
Uniab (B/S)	13.0%
Arad A & B (B/S)	24.0%
Koobi Fora Den I (S)	4.0%
Kasperdraai (S)	0.0%
Syokimau (S)	4.0%
Amboseli (S)	10.0%
Kruger Park 1 (S)	0.6%
Kruger Park 3 (S)	0.0%
Kruger Park 5 (S)	5.0%
Urikaruus (S)	0.0%

indeterminate cercopithecoid postcrania (HGD 956 right proximal ulna, HGD 1238 right distal femur) exhibit light carnivore tooth scoring and small diameter puncture marks (Fig. 3A–B). Only a modest sample of specimens preserved porcupine damage (Fig. 3C–D), with the majority taxonomically indeterminate postcranial element fragments (NISP: 27; 1.1% of the total assemblage) and a single *P. angusticeps* left mandible with a gnawed ascending ramus (HGD 639); but representing the most frequently observed biotic modification to the equid specimens (Table 6). Of note, only a single specimen (HGD 1503, 14–15 cm segment of indeterminate diaphysis) records damage from multiple biotic agents (wide, porcupine-induced gouging and narrower rodent-induced gnawing). Complicating the interpretation of these primary biotic modifications is the 'overprint' of human-induced preparation damage, which was noted on nearly half of the entire HGD sample (NISP: 1090; 45.2%) and occurs on 22 of the 41 specimens that also record carnivore tooth marks, small punctures, and gnawing damage (Fig. 2). This preparation damage ranges from cortical gouging from mechanical air scribes to heavy application of consolidant obscuring cortical surfaces, and frequent examples of preparation damage to elements with inaccurate repair attempts. The ubiquity of damage raises questions regarding some cortical modifications (e.g., Fig. 2D) that superficially resemble carnivore-mediated damage but in the larger context of noted preparation damage cannot be confidently attributed.

Weathering stage data were collected from 1714 specimens (71.0% of the total HGD assemblage; necessarily excluding specimens with preparation damaged cortices preserving insufficient external cortex to stage) and underscores the limited cortical exfoliation in the sample (Stage 0: 956 (55.8%); Stage 1: 480 (28.0%)). Only 15.9% of the sample exhibited evidence of moderate cortical exfoliation (Stage 2: 168, Stage 3: 104), and only 6 specimens were in a more advanced degree of exfoliation (Stage 4). The minimal cortical exfoliation to elements in the assemblage makes it unlikely that alteration to element cortices substantially influenced the identifiability or preservation of primary biotic cortical

Table 3
Percentage of total bovid individuals (MNI) by size category for the Haasgat HGD and comparative assemblages.

Assemblage	Class I	Class II	Class III	Class IV
Haasgat HGD	0	55.55	38.1	6.35
Fossil assemblages				
GD 2	29.89	50.57	18.39	1.15
GD A	10.71	46.43	39.29	3.57
GD 1	7.69	30.77	61.54	0
Gladysvale	9.10	27.30	51.90	11.70
Kromdraai A	5.50	61.54	28.57	4.40
Kromdraai B	24.00	40.00	32.00	4.00
Makapansgat Member 3	13.40	53.80	22.40	10.50
Makapansgat Member 4	5.30	36.80	42.10	15.80
Makapansgat Member 5	26.10	4.30	60.90	8.70
Swartkrans Member 1	2.86	41.43	52.86	2.86
Swartkrans Member 2	2.47	49.38	43.21	4.94
Swartkrans Member 3	4.29	47.14	45.00	3.57
Sterkfontein Member 5 West	47.83	43.48	8.70	0
Sterkfontein Olduwan Infill	27.03	48.65	18.92	5.41
Sterkfontein STW 53 breccia	21.43	21.43	28.57	28.57
Modern spotted hyaena kills				
Kruger Park	0.55	63.39	34.97	1.10
Serengeti	0	34.90	64.58	0.52
Ngorngoro Crater	0	4.76	94.71	0.53
Modern leopard kills				
Kafue Flats	18.80	47.90	16.60	0
Serengeti (1)	0	59.90	10.80	0
Serengeti (2)	0	81.10	10.30	0
Matopos	15.70	44.80	26.20	5.30
Kruger Park (1)	3.80	83.10	8.60	0.20
Kruger Park (2)	2.00	96.00	2.00	0
Sabi-Sands (1)	0	90.88	9.12	0
Sabi-Sands (2)	26.90	54.97	18.13	0
Timbavati	0	93.37	6.63	0
Umfolozi	11.11	48.15	40.74	0

modifications. This pattern of minimal cortical exfoliation is similar to that present in the Gondolin GD 2 (62.7% Stage 0, 30.1% Stage 1, 7.1% Stages 2—5; Adams, 2010) and Sterkfontein Member 5 West (63.3% Stage 0, 27.1% Stage 1 & 2, 9.6% Stages 3—5; Pickering, 1999). A substantial number of specimens (NISP: 111; 4.6% of the total assemblage) evinced morphological distortion and crushing damage that can be attributed to geological processes within the depositional environment; in many cases only remaining a single specimen through arresting mechanical processing before fragments would become dissociated (Fig. 4A—B). Other abiotic element modifications were infrequently encountered in the sample, with only three specimens exhibiting cortical smoothing (fine-

sediment abrasion marks under magnification) and fracture margin rounding consistent with substantial hydrological/geological abrasion and 36 specimens with a manganese-stained patina.

3.3. Predepositional consumption sequences, element utility and transportability

Neither the calculated proportions of bovid class II skeletal elements, aggregated bovid class elements, nor primate elements (% MAU) from the HGD assemblage resemble either the normal or inverse carnivore consumption sequences (Blumenschine, 1986). A positive, moderate and significant correlation was found between the Haasgat HGD cercopithecoid assemblage %MAU values and the skeletal element refuse %MAU values for baboons (r_S: 0.661, p < 0.001; Pickering and Carlson, 2004). Although reporting a significant correlation, evaluation of the graphed data highlights the absence of elements in the HGD primate sample that are well-represented in the Pickering and Carlson (2004) baboon refuse assemblage (e.g., carpals, ribs, phalanges, vertebral elements) and the substantial scatter of datapoints relative to the regression line (Fig. 5). No significant correlation was found between the HGD cercopithecoid %MAU values and the scat assemblage (e.g., elements consumed and voided by leopards; r_S: 0.174, p = 0.407). Regression of the HGD class II bovid %MAU values on percentage meat utility index values (%MGUI) found no significant relationship between the two variables (r_S: 0.162, p = 0.409), and the scatterplot does not resemble any of the patterns described by Binford (1978). There was also no significant relationship between the HGD class II bovid %MAU and food utility index (FUI) values (r_S: 0.177, p = 0.367) and no visible trend within a scatterplot of the datapoints.

The minimum number of elements (MNE) ratio $MNE_{femur} + MNE_{humerus}/MNE_{metapodial}$ ratio (0.27) from the Haasgat HGD class II bovid sample indicates a strong bias towards the recovery of the low flesh-bearing metapodials. This value contrasts with the flesh-bearing element-driven ratios from Gondolin GD 2 (1.27), Swartkrans Members 1 and 2 (1.31/1.39), Sterkfontein Member 5 West and 53 Breccia (1.13/1.14), the Olduvai Gorge MNK assemblage (1.45) and a modern hyaena den from Koobi Fora (1.32); and even the Sterkfontein Oldowan Infill (0.95), Swartkrans Member 3 (0.91), and Olduvai HWK E 1—2 (0.66) assemblages that have a paucity of high flesh-bearing elements (Adams, 2010). A slight bias towards elements with lower marrow yields is indicated by the $MNE_{femur} + MNE_{tibia} + MNE_{metatarsal}/MNE_{humerus} + MNE_{radius} + MNE_{metacarpal}$ ratio (0.91) class II bovid sample, also contrasting with values from the GD 2 assemblage (1.30), Swartkrans Member 1 (1.52), Olduvai MNK (1.08), and Olduvai BK (1.0); but similar to that of Sterkfontein Member 5 West

Table 4
Percentage of total bovid individuals (MNI) by age categories for the Haasgat HGD and comparative assemblages.

Assemblage	Class I		Class II		Class III		Class IV	
	Immature	Adult	Immature	Adult	Immature	Adult	Immature	Adult
Haasgat HGD	—	—	19.4%	80.6%	13.3%	86.7%	50%	50%
GD 2	34.6%	65.4%	48.9%	51.1%	42.9%	57.1%	100%	0%
GD A	33.3%	66.7%	21.4%	78.6%	35.7%	64.3%	0%	100%
GD 1	0%	100%	25%	75%	12.5%	87.5%	—	—
Sterkfontein Type Site[a]	—	—	45.5%	54.5%	36.4%	63.6%	38.9%	61.1%
Sterkfontein Extension[a]	0%	100%	15.4%	84.6%	16.7%	83.3%	0%	100%
Sterkfontein D16[a]	40%	60%	43.33%	56.7%	66.7%	33.3%	0%	100%
Kromdraai A[a]	0%	100%	42.3%	57.7%	43.5%	56.5%	50%	50%
Kromdraai B[a]	—	—	16.7%	83.3%	66.7%	33.3%	—	—
Swartkrans Member 1	0%	100%	46.2%	53.8%	30%	70%	50%	50%
Swartkrans Member 2	0%	100%	72.2%	27.8%	16.7%	83.3%	33.3%	66.7%
Swartkrans Member 3	11.1%	88.9%	22.2%	77.8%	26.7%	73.3%	50%	50%

[a] As described in Vrba (1976).

Table 5
Primary counts of skeletal remains from the Haasgat HGD deposits (NISP/MNE/MNI/MAU/%MAU).

Element	Bovid II*	Bovid III	Bovid IV	Bovidae Indet. Size	Equidae	Cercopithecidae
Craniodental	219/48/35/35/100	153/24/24/24/100	6/4/4/4/100	5/1/1/1/100	27/2/2/2/100	152/54/54/54/100
Astragalus	28/28/21/14/40	3/3/2/1.5/6.3	2/1/1/0.5/10	–	3/3/3/1.5/75	2/2/2/1/1.9
Calcaneus	17/15/12/7.5/21.4	3/3/3/1.5/6.3	–	–	2/2/2/1/50	6/6/3/3/5.6
4th Carpal	–	1/1/1/0.5/2.1	–	–	–	–
2nd Carpal	–	–	–	–	2/2/2/1/50	–
Intermediate Carpal	1/1/1/0.5/1.4	2/2/1/1/4.2	–	–	–	–
Radial Carpal	2/2/2/1/2.8	–	–	–	–	–
Distal Femur	24/24/18/12/34.3	1/1/1/0.5/2.1	–	–	–	6/6/4/3/5.6
Femur MSHF	9/9/7/4/11.4	2/2/1/1/4.2	–	–	–	2/2/2/11.9
Proximal Femur	18/18/13/9/25.7	–	–	1/1/1/0.5/50	–	10/10/7/5/9.3
Distal Humerus	28/28/24/14/40	5/4/4/2/8.4	–	–	–	5/5/3/2.5/9.3
Humerus MSHF	6/6/6/3/8.6	6/4/4/2/8.4	–	–	–	2/2/2/1/1.9
Proximal Humerus	33/33/26/16.5/47.1	2/2/2/1/4.2	–	2/2/2/1/100	–	6/6/5/3/5.6
Metacarpal I	–	–	–	–	–	1/1/1/0.5/0.9
Metacarpal IV	–	–	–	–	–	1/1/1/0.5/0.9
Metatarsal II	–	–	–	–	–	1/1/1/0.5/0.9
Metatarsal III	–	–	–	–	–	2/2/1/1/1.9
Metatarsal V	–	–	–	–	–	1/1/1/0.5/0.9
Distal Metacarpal	15/15/13/37.1	3/3/3/1.5/6.3	–	–	3/3/2/1.5/75	–
Metacarpal MSHF	12/12/11/6/17.1	1/1/1/0.5/2.1	–	–	2/2/2/1/50	–
Proximal Metacarpal	22/22/28/11/31.4	1/1/1/0.5/2.1	–	–	6/4/2/2/100	–
Distal Metatarsal	16/16/13/37.1	3/3/2/1.5/2.1	–	–	3/3/2/1.5/75	–
Metatarsal MSHF	15/15/14/7.5/21.4	5/3/2/1.5/2.1	1/1/1/0.5/10	–	–	–
Proximal Metatarsal	28/27/23/13.5/38.6	2/2/2/1/4.2	–	–	1/1/1/0.5/25	–
Distal Metapodial	7/7/7/1.75/5	–	2/2/1/0.25/5	–	6/2/2/1.5/75	3/3/1/0.15/0.3
Metapodial MSHF	3/3/3/0.75/2.1	–	–	–	1/1/1/0.25/12.5	–
Proximal Metapodial	1/1/1/0.25/0.7	–	–	–	–	–
Patella	–	1/1/1/0.5/2.1	–	–	–	–
Pelvis	36/12/12/11.5/32.9	1/1/1/0.5/2.1	–	1/1/1/0.5/50	1/1/1/0.5/25	2/2/2/1/1.9
Phalanx 1	33/28/6/3.5/10	8/7/2/0.88/3.8	1/1/1/0.125/2.5	–	1/1/1/0.25/12.5	–
Phalanx 2	25/24/12/3/8.6	2/2/1/0.25/1	–	–	3/3/2/0.5/25	–
Phalanx 3	16/16/10/2/5.7	2/2/1/0.25/1	–	–	4/4/2/2/100	–
Distal Radius	13/13/11/6.5/18.6	5/5/5/2.5/10.4	–	–	2/2/2/1/50	4/4/3/2/3.7
Radius MSHF	12/10/9/5/14.3	3/2/2/1/4.2	–	–	–	2/2/2/1/1.9
Proximal Radius	8/8/6/4/11.4	1/1/1/0.5/2.1	–	–	1/1/1/0.5/25	2/2/2/1/1.9
Scapula	13/12/8/6/17.1	4/4/2/2/8.4	1/1/1/0.5/10	6/3/2/1/100	–	2/2/2/1/1.9
Proximal Sesamoid	8/8/1/0.5/1.4	1/1/1/0.06/0.3	–	–	–	–
Distal Sesamoid	–	–	–	–	2/2/2/–/–	–
Sternebrae	–	–	–	7/5/3/–/–	–	–
2/3 Tarsal	3/3/2/1.5/4.3	–	–	–	1/1/1/0.5/25	–
Central/4th Tarsal	10/10/9/5/14.3	3/3/2/1.5/6.3	–	–	2/2/2/1/50	–
Lateral Malleolus	2/2/1/1/2.3	–	–	–	–	–
Distal Tibia	4/4/3/2/4.6	4/4/4/2/8.4	1/1/1/0.5/10	–	2/2/1/0.5/25	6/6/5/3/5.6
Tibia MSHF	15/11/10/5.5/15.7	4/2/2/1/4.2	–	–	–	3/3/3/1.5/2.8
Proximal Tibia	13/11/7/5.5/15.7	2/2/2/1/4.2	–	–	–	2/2/2/1/1.9
Distal Ulna	–	–	–	–	–	2/2/2/1/1.9
Ulna MSHF	3/3/3/2.5/7.1	1/1/1/0.5/2.1	–	–	–	4/3/3/1.5/2.8
Proximal Ulna	8/8/7/4/11.4	1/1/1/0.5/2.1	1/1/1/0.5/10	–	–	5/5/3/2.5/4.6
Atlas	8/8/8/8/22.8	2/2/2/2/8.4	–	–	1/1/1/1/50	–
Axis	4/4/4/4/11.4	1/1/1/1/4.2	–	1/1/1/1/100	–	–
Cervical Vertebrae	13/12/3/1.2/3.4	9/5/1/1/4.2	–	2/2/1/0.4/40	–	1/1/1/0.2/0.4
Thoracic Vertebrae	41/34/3/2.5/7.1	3/3/1/0.23/1	–	1/1/1/0.8/80	–	2/2/1/0.16/0.3
Lumbar Vertebrae	45/43/8/6.14/17.5	–	–	–	–	1/1/1/0.16/0.3
Sacrum	3/3/3/3/8.6	–	–	–	–	–
Caudal Vertebrae	–	3/3/1/–/–	–	11/11/–/–	–	–
Vertebrae Fragments	2/–/–/–/–	–	–	–	–	–

Table 6
Distribution of biotically modified elements by taxonomic group from Haasgat HGD.

| Taxon Grouping	Insect	Small Rodent	Porcupine	Carnivore	Preparation
Bovidae	1	1	17	24	585
Equidae		1	5	1	50
Primates			1	5	149
Other				2	57
Indeterminate		2	21	9	249
Total	1	4	23	41	1090

(0.95) and Swartkrans Member 2 (0.93) (Adams, 2006).

There is no significant correlation between the rank-ordered disarticulation sequence (Hill, 1979) and either the HGD class II bovid (r_S: −0.340, p = 0.143) or cercopithecoid (r_S: −0.329, p = 0.251) %MAU values. There is also no apparent bias or trends in the representation of either the class II bovid or cercopithecoid skeletal elements in the HGD assemblage relative to the transportation potential groups identified by Voorhies (1969); however, the highest %MAU values for both groups are within the Group III category commonly representing lag deposits post-winnowing. Simultaneously, there is a positive and significant correlation between the HGD class II bovid %MAU values and class II *Redunca* saturated weight index values (SWI; Behrensmeyer, 1978), indicating a trend for the increased recovery of skeletal elements as their transport potential decreases (r_S: 0.484, p = 0.031). It is worth
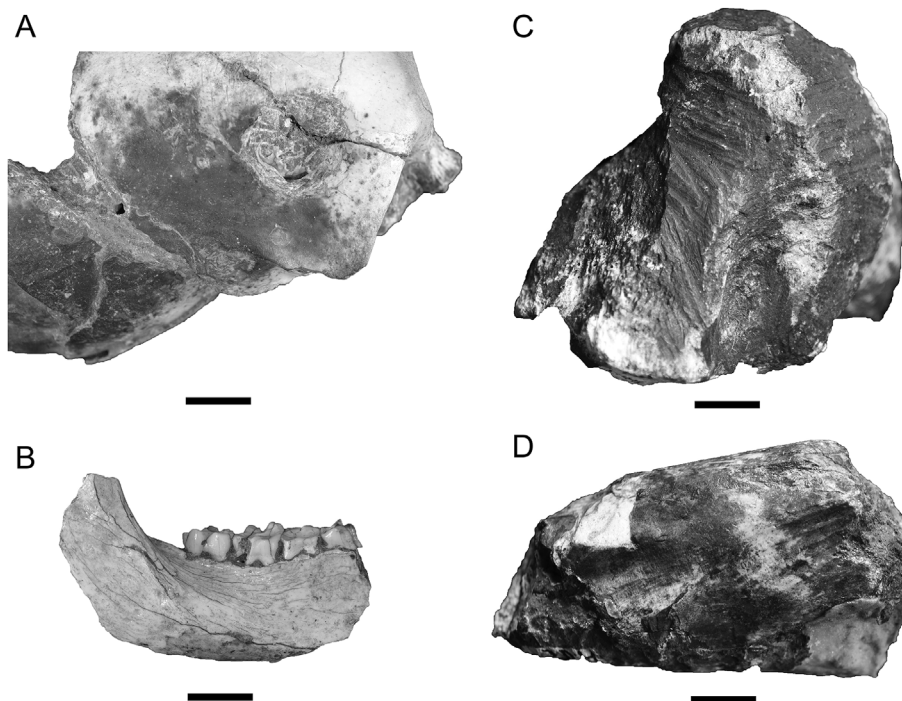
Fig. 3. Examples of Haasgat HGD assemblage fossil specimens with biotic modifications. A, HGD 613 *Papio angusticeps* crushed female cranium with large matrix-filled depression and small-diameter shallow puncture near the right supraorbital torus. B, HGD 1179a *Cercopithecoides haasgati* indeterminate sex right mandible with shallow tooth marks and scoring along the ascending ramus. C, HGD 1104 *Equus* sp. left astragalus with heavy porcupine gnawing. D, HGD 1956 indeterminate diaphyseal fragment (5–6 cm overall length) with porcupine gnawing parallel to the element long axis on both portions of the segment. Scale bars equal 1 cm.
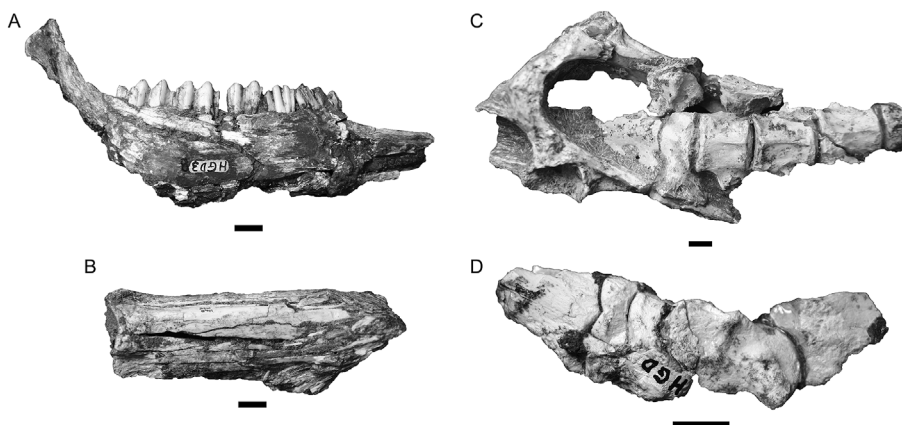
Fig. 4. Examples of Haasgat HGD assemblage fossil specimens exhibiting crush damage and preserving articulations post-processing. A, HGD 38 Reduncini gen. et sp. indet. left mandible that has been crushed and distorted within the calcified matrix. B, HGD 1465 Bovidae gen. et sp. indet. (Class III) left proximal metatarsal that has been crushed and distorted around a solid sediment core. C, HGD 964 Bovidae gen. et sp. indet. (Class II) articulated partial pelvis, sacrum and lumbar vertebrae. D, HGD 1054 Bovidae gen. et sp. indet. (Class II) articulated distal tibia, tarsals and proximal metatarsal. Scale bars equal 1 cm.

noting there are 17 sets of articulated skeletal element sets retained in the HGD assemblage that were not separated during processing (largely vertebral series or carpal and tarsal bundles; Fig. 4C–D); the original number of originally articulated remains is unknown given the lack of cataloguing data of block or specimen associations during processing.

3.4. Fragmentation, shaft attributes and pre- and postdepositional destruction

Overall element size category data were taken from the entire catalogued HGD assemblage and demonstrate a relatively even representation of elements across categories between 1-2 cm and 5–6 cm in overall length; collectively representing 76.5% of all specimens in the sample (Fig. 6). There are very few specimens under 1 cm (10; 0.4% of the sample) or over 12 cm (51; 2.1% of the sample) in overall length in the assemblage. This contrasts with the GD 2 assemblage which is dominated by small fragments (45.0% of all specimens under 1 cm and 97.7% under 5 cm), and somewhat contrasts Kromdraai B and Swartkrans Members 1 and 2 that have a peak in overall specimen size around 2–3 cm (Adams, 2006; Note: specimens under 1 cm were not reported by Brain (1981) for assemblages other than Kromdraai B). The most comparable of the fossil assemblages to HGD is that from Swartkrans Member 5, with
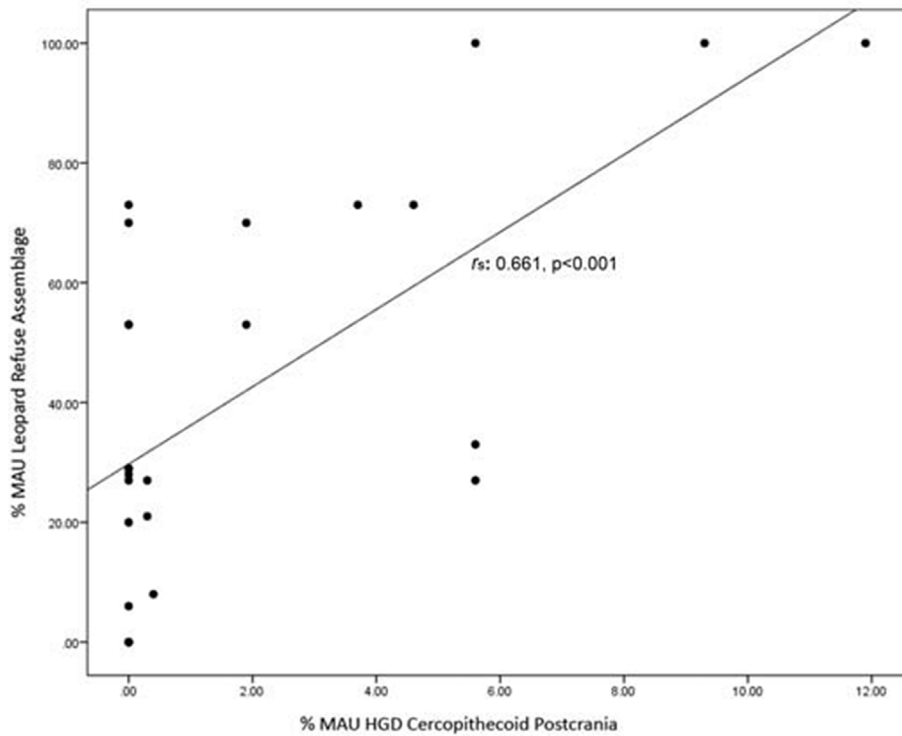
Fig. 5. Scatterplot of percentage minimal animal unit (%MAU) values from a modern leopard-produced refuse assemblage after baboon carcass consumption on %MAU values of cercopithecoids from the Haasgat HGD assemblage. Data from Pickering and Carlson (2004).
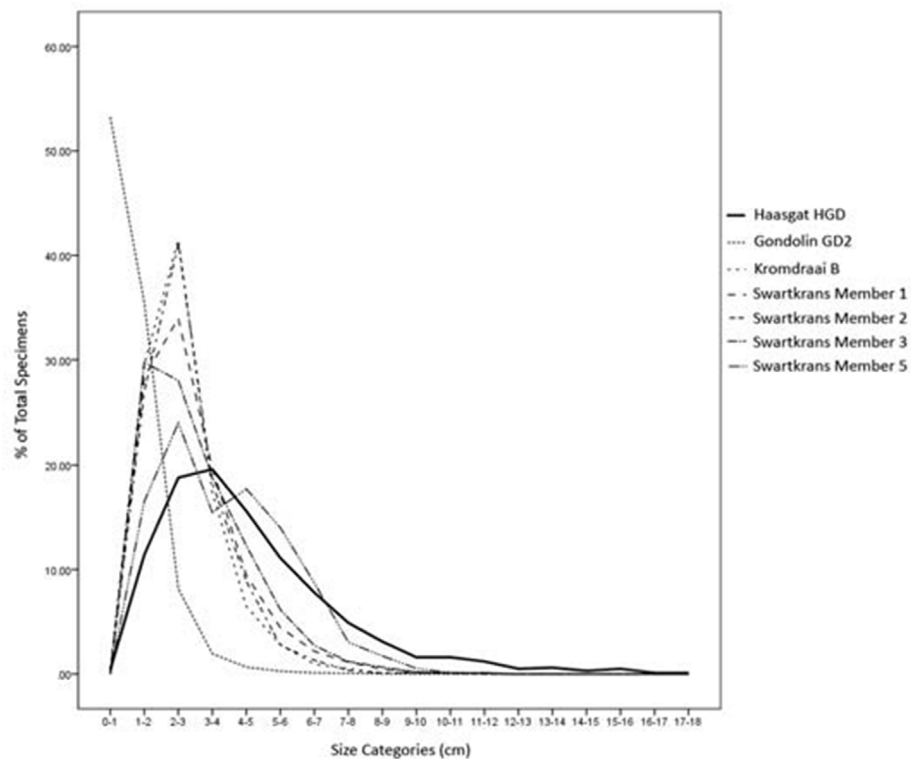

Fig. 6. Line graph of percentage size category data for the Haasgat HGD assemblage and comparative fossil assemblages. Data from Brain (1981).

a similar proportion of the specimens above 5 cm in overall length (33.4% in HGD, 28.3% in Member 5).

Long bone fracture features were coded from a total of 107 postcranial specimens from the HGD assemblage and are summarized (both as an assemblage total and major taxonomic group) in Table 7. A series of χ^2 analyses (d.f. 2, $\alpha = 0.001$) failed to detect any
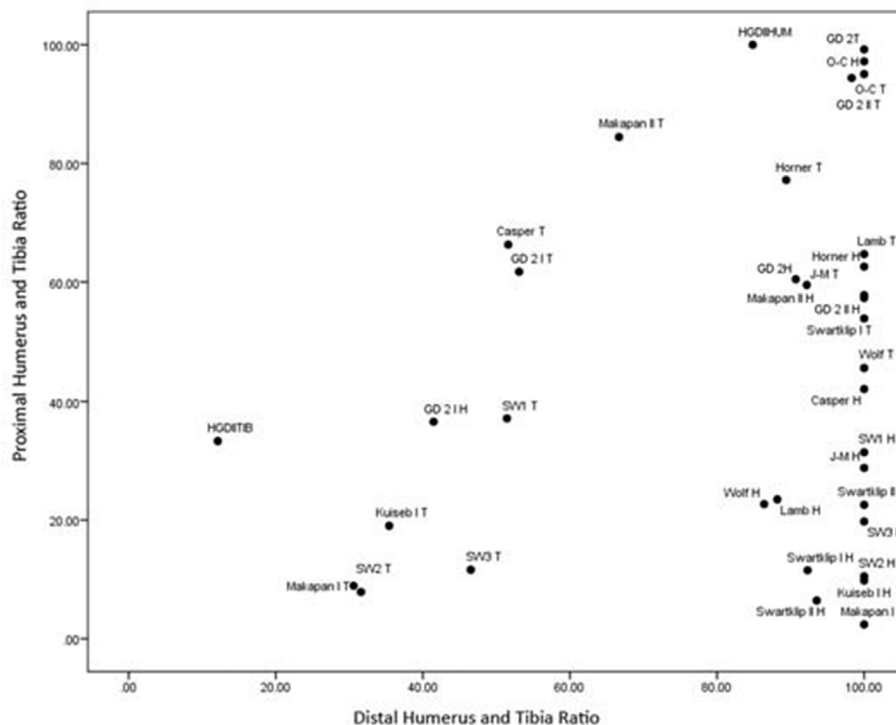
Fig. 7. Scatterplot of proximal humerus and tibia ratio values on distal humerus and tibia ratios for the Haasgat HGD bovid class II humeri (HGDIIHUM) and tibiae (HGDIITIB) and comparative fossil and modern assemblages. Comparative data as reported in Todd and Rapson (1988), Binford (1981) and aggregated in Adams (2006). T: Tibia, H: Humerus, I: class I bovid, II: class II bovid, GD 2: Gondolin GD 2, J–H: Jones Miller, O–C: Olsen-Chubbuck, Lamb: Lamb Spring, Makapan: Makapansgat Member 3, SW1: Swartkrans Member 1, SW2: Swartkrans Member 2, SW3: Swartkrans Member 3, Wolf: Wolf kills.

significant differences in the distribution of fracture features among the three well-represented taxonomic groups (class II bovids, equids, and cercopithecoids), except between class II bovid and cercopithecoid fracture outlines (χ^2: 18.811, p < 0.001); with the latter group recording a higher proportion of intermediate fracture outlines. Analysis of fracture features of the aggregated total HGD sample (initial sequentially-reductive Bonferroni $\alpha = 0.0029$) revealed significant differences in fracture angle and circumference with all three comparative assemblages reported by Villa and Mahieu (1991), except preserved circumference from the Sarrians assemblage (χ^2: 2.928, p = 0.231), and no significant difference in fracture outline. The fracture angle and preserved circumference of the HGD assemblage differed significantly from that of all Sterkfontein Member 5 comparative assemblages, except for fracture angles in the STW 53 breccia (χ^2: 3.687, p = 0.158); with

no significant differences in proportions of fracture outlines.

The standardized bovid class II proximal:distal ratio values for tibiae and humeri fall within the 'Zone of No Destruction' (*sensu* Binford, 1981, Fig. 7), with the tibiae isolated and the humeri closest to the Gondolin GD 2 class II tibiae and bovid humerus and tibia values from the Olsen-Chubbuck site (Todd and Rapson, 1988). The distribution of NISP:MNI ratio values for the HGD Bovid class II elements are significantly correlated to those from Gondolin GD 2 (r_s: 0.729, p < 0.001), El Juyo Cave Layer 6 (r_s: 0.442, p = 0.016) and Equus Cave (r_s: 0.461, p = 0.018); but not with the NISP:MNI ratio values from El Juyo Cave Layer 4 (r_s: 0.179, p = 0.354; Klein and Cruz-Uribe, 1984; Adams, 2010). Finally, no significant correlations exist between the Haasgat HGD class II bovid %MAU values (by element portion) and bovid element-portion bone mineral density values (BMD; Lam et al., 1999) (r_s: 0.161, p = 0.302).

Table 7
Fracture feature data from the Haasgat HGD assemblage.

HGD Total Assemblage				Bovid Class II			
Category	Angle	Outline	Circumference	Category	Angle	Outline	Circumference
1	47	33	9	1	30	20	2
2	34	54	11	2	13	32	4
3	26	19	87	3	15	11	57

Equidae				Cercopithecidae			
Category	Angle	Outline	Circumference	Category	Angle	Outline	Circumference
1	3	2	0	1	5	3	0
2	1	2	1	2	3	5	2
3	2	2	5	3	1	0	7

Category Legend: Angle: 1 - oblique, 2 − right, 3 − oblique and right; Outline: 1 − transverse, 2 − curved/V-shape, 3 − intermediate; Circumference: 1 - <50%, 2 - >50%, 3−100%.

4. Discussion

In the original publications on the Haasgat HGD assemblage, Keyser (1991), McKee and Keyser (1994), and Plug and Keyser (1994) provided broad and largely anecdotal suggestions of the taphonomic history of the assemblage ancillary to site description, faunal description, and analysis of the primate craniodental remains. In an overview article on the palaeontology of Haasgat (Keyser, 1991, p. 30) stated that 'virtually all the fossil specimen from the sediment blocks on the dumps were badly broken and weathered prior to fossilization. Bones in all stages of weathering according to the scale of Behrensmeyer (1978) are encountered. A very large number have, however, weathered to stage 5.' This observation was used (tentatively in Keyser (1991); more fully in Plug and Keyser [1994, p. 142]) to support the occurrence of an upper cave within the Haasgat karstic system that would have allowed for extensive cortical exposure (within the 'light zone' of the system) with subsequent washing and accumulation into the lower (main) chamber. Interrelated to this process of intrakarstic movement was breakage prior to fossilization (Keyser, 1991, p. 30; unclear if implying the entire assemblage or exclusively pre-fossilization breakage) and some post-depositional destruction (e.g., flattening and distortion of the HGD 620 *Papio angusticeps* cranium; McKee and Keyser, 1994).

The allochtonous contributions by porcupines and carnivores were also highlighted across these three early publications. Keyser (1991, p. 30) figured two specimens (including HGD 1073; Fig. 2D) and noted that 'There can be no doubt that porcupines and carnivores were important accumulators of bones in the cave sediment'. This was expanded and clarified by Plug and Keyser (1994), who noted porcupine activity was noted on 0.2% of the sample, and carnivore gnaw marks on 7% of the bone fragments ('mostly hyrax skulls and bones', Plug and Keyser, 1994. p. 142); leading them to conclude that 'The greater part of the assemblage, particularly the hyrax and klipspringer remains, appears to have been accumulated by large carnivores' and 'Hyaenas contributed to the assemblage as well since their tooth marks are present on some of the larger bones' (Plug and Keyser, 1994, p. 144). Simultaneously, an argument (based largely on frequent recovery of hyrax and klipspringer remains) was made for the specific involvement of leopards in producing the assemblage. The only primate-specific discussion of potential accumulative agent(s) was in noting the presence of a large, puncture-type mark on the HGD 613 female *Papio angusticeps* cranium (Fig. 3A) and that the smaller primate body masses (like the smaller bovid body masses) in the HGD sample may indicate 'The predator may have been limited to catching smaller primates. On the other hand, most of the individuals were adults, usually the most difficult to catch.' (McKee and Keyser, 1994, p. 840).

The results of the analyses presented here contradict many of these prior anecdotal interpretations, but equally highlight the substantial challenge for direct interpretation of the taphonomy of the Haasgat HGD assemblage; both in total and the primate component in particular. In order to parse out what data can be interpreted given our results and the caveats about the collections noted in section 2, and some of the methodological limitations noted in the SOM, we will first address the prior specific suggestions offered by these initial publications and then address what can be reasonably established from our analyses.

First, recent geomorphological revision and direct sampling of the Haasgat karstic system by Herries et al. (2014) has failed to support the original speleological interpretations offered in Keyser (1991) and Keyser and Martini (1991), including the occurrence of separate 'upper' and 'lower' chambers. Second, we have been unable to document advanced cortical exfoliation consistent with substantial sub-aerial environmental exposure, nor is there unambiguous evidence of cortical abrasion or element patterning suggestive of substantial hydrological transport of the sampled assemblage within the karstic system. Although we can only speculate as no counts or data were encoded in the original publications or catalogue, we suspect that Plug and Keyser (1994) may have misinterpreted physically crushed and cracked specimens (that superficially resemble the deep cracks of heavily weathered elements but lack diagnostic cortical exfoliation of the external bone surfaces), or the substantial mechanical preparation damage to the external cortical surfaces, with the cortical damage introduced through environmental exposure. Although what 'weathering' means in karstic assemblages with taphonomic histories that may include both sub-aerial exposure (outside and potentially within the karstic system) and sub-surface exposure within deposits is still unresolved, the minimal indications of cortical exfoliation do not support the original interpretations by Plug and Keyser of 'heavy weathering' (see SOM; reviews in Lyman and Fox, 1997; Junod and Pokines, 2014). While there are a large number of craniodental specimens consistent with a bias towards Voorhies Group III (suggesting sampling of a lag deposit) and a higher recovery of low-transport potential elements, it is important to note that most of the craniodental remains are in fact isolated teeth and fragmentary remains (Adams, 2012), as evinced by a high NISP:MNE ratio across the major taxonomic groups (e.g., class II and III bovids, cercopithecoids; Table 5). The transport potential of isolated dental or partial craniodental elements is understandably substantially different than intact crania and/or mandibles, which are the elements that are addressed by both Voorhies (1969) and Behrensmeyer (1975). Equally, the retention of a number of articulated specimens (particularly small remains like carpal and tarsal sets with high transport potential) even after mechanical preparation does not support interpreting the HGD assemblage (uniformly) as a lag deposit. And finally, direct interpretation assumes minimal element sampling bias during the preparation of the HGD assemblage such that these proportions have high fidelity to composition of the original deposits they were sampled from; an issue we will explore further below.

Third, our analyses do suggest some *in situ* element communition but cannot identify the timing of element breakage or fragmentation across the pre-to postdepositional (and sampling) phases of the sample. Neither the intra-element ratios (e.g., MNE based, NISP:MNI), assessment of density-mediated attrition, or overall specimen size category data support interpreting extensive post-depositional fragmentation or density-mediated element attrition. The mix of statistically significant and insignificant differences in coded fracture features and preserved circumferences of elements between HGD and other modern and fossil reference samples does not provide a readily interpreted signal of the timing or context for long bone element fracturing. This may, however, simply reflect the expected result for an aggregated, non-homogenous *ex situ*-derived fossil sample: element fracturing occurred to different parts of the sample at different phases from original deposition through to preparation. Simultaneously, there is direct evidence for *in situ* crushing and distortion of craniodental and postcranial elements within the deposits. Unfortunately, we again encounter the issue of the lack of catalogue data allowing for potential association between specimens to be established to assess depositional communition, as well as the overall fidelity of sampled assemblage relative to the composition of the original deposits; particularly whether the preparation strategy was inclusive of diaphyseal fragments or postcranial elements which play a critical role in assessing the timing and extent of assemblage communition.

Fourth, we can clearly demonstrate biotic modifications of elements in the assemblage which may reflect allochthonous assemblage formation for at least parts of the HGD assemblage; however,

identifying specific agencies (e.g., hyaenas, leopards) and the extent of their role in producing the sample is beyond the available data. Both porcupine and carnivore damage was infrequently encountered, but the 'overprint' of mechanical preparation to the cortical surfaces of elements makes the observed proportions a minimum count rather than an accurate assessment of occurrence. The presence of carnivore damage to all three species of primate and across the hyrax and antelope remains does suggest some degree of carnivore involvement in either primary accumulation and/or subsequent modification of individuals of these taxonomic groups. The significant relationship between the cercopithecoid assemblage and a modern leopard-produced refuse assemblage may also be indicative of carnivore-mediated aggregation of the HGD primate sample, although there are major points of difference in element presence/absence (particularly in smaller sized elements). As noted in section 3.4 in regards to fragmentation, however, as an aggregated *ex situ* sample we would expect heterogeneous primary agents underlie the introduction and modification of the skeletal elements in the deposits sampled in the HGD assemblage.

Unfortunately, we conclude that the issues regarding the HGD assemblage highlighted in Adams (2012) and summarized in section 2 – namely the lack of catalogue data and documentation on sampling, fossil preparation, potential specimen loss - have only expanded through the results of this analysis and ultimately limit moving beyond addressing historical suggestions of the taphonomy of the Haasgat HGD assemblage. The identification of preparation-induced damage to nearly half the fossil specimens in the sample means that the counts of biotic and abiotic cortical modifications and fracture features are immediately questionable. Equally, this evidence for lack of care during preparation coupled with an unknown dumpsite collection and processing strategy raises serious questions about the fidelity of any of the taxonomic and element counts presented as representative of the original deposit(s) the assemblage was sampled from. Most notable is whether the taxonomic proportions (like the large primate sample), or the proportion of craniodental remains relative to other skeletal elements, is an accurate reflection of the Haasgat deposit(s) or reflect excavator/preparation biases that shaped the analysable assemblage.

As we are approaching the assemblage *a posteriori* we cannot precisely gauge where the Haasgat HGD assemblage falls on a theoretical continuum of taphonomic interpretations from 'terminally compromised' to 'high fidelity to the original deposits' other than to reinforce two points. First, that the use of mechanical preparation of fossils from calcified sediment blocks is an inherently selective process of preparation, particularly when removing fossils from blocks with dense aggregations of individual specimens, relative to more 'global' processing methods like acetic-acid processing. Second, there are striking differences in the noted element damage, the presence of smaller elements and identifiable element fragments, recovery of smaller mammal postcrania, and recovery of microfauna between HGD and other penecontemporaneous South African fossil assemblages that were excavated from naturally decalcified or acetic-acid prepared calcified sediments (e.g., Brain, 1981; Pickering, 1999; Adams and Conroy, 2005; Adams, 2006, 2010; Adams et al., 2007a,b; Adams et al., 2010; Rovinsky et al., 2015; Adams et al., 2016).

Because of this unknown level of excavation and preparation bias, we offer the two extremes of potential taphonomic interpretations for the Haasgat HGD assemblage. If the Haasgat HGD sample is treated as representative of skeletal element assemblages interred at Haasgat there are several unique features of the site relative to other penecontemporaneous South African localities. The HGD assemblage is dominated by smaller-bodied bovids and cercopithecoids, and is more taxonomically homogenous than nearly every other previously described locality in the region. In contrast to the more homogenous (and geographically nearby) Gondolin GD 2 assemblage, Haasgat has an extremely large primate sample (completely absent at GD 2) and substantially biologically different klipspringer (*Oreotragus*) population sample (Adams and Conroy, 2005; Adams, 2006, 2012). This may represent several different interrelated factors, ranging from different accumulative agencies, extremely localized palaeohabitat differences, differences in time averaging, and different depositional ages of the deposits (Herries et al., 2006; Adams et al., in press). Relative to the other Blaauubank localities, Haasgat is unique in recording multiple species of *Cercopithecoides* and the largest early assemblage of the basal *Papio* species *Papio angusticeps* in Africa (Jablonski and Frost, 2010; Herries et al., 2014). Both the *Cercopithecoides* and *Papio angusticeps* samples are notably sex- and age-category balanced, and do not deviate strongly from an attritional mortality profile to suggest selective integration of specific individuals (e.g., males, females, immature, older, or prime age adults). The presence of carnivore modifications, constraint in taxon body masses represented in the assemblage, reduced flesh-bearing element portion representation and correlation between the HGD cercopithecoid element proportions and modern leopard-produced refuse assemblages support some level of carnivore-mediated accumulation within the sampled deposits. Attributing the HGD assemblage to a specific carnivore accumulator is speculative and unwarranted, however we do note that the low carnivore:ungulate ratio and minimal carnivore cortical modification across the sample is not consistent with most modern and attributed fossil hyaenid-accumulated assemblages (Pickering, 1999; Adams, 2006). As noted previously, there is minimal evidence for element exposure prior to deposit internment, an unclear source and timing of element fracturing, and an overall minimal degree of non-density mediated comminution of elements. The strong bias towards the recovery of craniodental elements may reflect sampling a lag deposit where winnowing or selective transport shaped the assemblage within the karstic system; however, the persistence of articulated small element sets (even post-preparation) and the fact that most of the craniodental specimens are isolated teeth or partial cranial fragments their transport potential may be artificially depressed by consideration of the broad Voorhies Group and SWI analyses.

Alternatively, if Haasgat HGD is viewed as an assemblage compromised by a highly selective sampling and processing strategy that favored the recovery and cataloguing of specific taxonomic groups and elements - and suffered subsequent data loss through imprecise cataloging and processing methods - then a more limited taphonomic interpretation of the Haasgat locality can be supported. While the exact proportions may be distorted, the recovered *Cercopithecoides* and *Papio angusticeps* craniodental samples are well-preserved and the demographic homogeneity is likely an accurate reflection of remains interred relatively intact and without strong sex- or age-mediated bias. Equally, the simple presence of carnivore- and porcupine-induced modifications supports an allochthonous origin within the original deposits for at least some of the sampled HGD assemblage, including all three primate species that all show evidence of carnivore modification. Beyond these two very broad statements, however, the lack of confidence in the precision of the taxon- and element-based assemblage counts (and substantial evidence of preparation-induced element damage) lead us to advocate no additional interpretations of the pre-, peri- and postdepositional taphonomic processes that occurred in the Haasgat deposits sampled in the HGD assemblage.

This open-ended set of alternative interpretations leads to the rather standard concluding position of advocating for the development of an expanded fossil record from Haasgat to circumvent these historic limitations; a suggestion that is unfortunately

frequently implicit (or explicit) at the end of many analyses of the South African Neogene fossil record from cave sites (Brain, 1981; McKee, 1991; Reed, 1996; de Ruiter, 2001; Adams, 2006). Even taking the best-case scenario, the issues with the HGD assemblage raised previously by Adams (2012; particularly the missing block-based specimen associations) and highlighted by the data presented here mean that we cannot confidently treat the sample as a homogenous unit for the purposes of taphonomic, palaeoecologic, or even palaeobiologic analyses; at least not without substantial circumspection and caveats. We therefore ultimately view the Haasgat HGD assemblage as a cautionary tale of what can arise when developing fossil data from South African karst deposits without precautions in place to document methodology, primary data, and limit the effect of sampling and processing bias on subsequent analyses. Although study of individual specimens of the Haasgat HGD primates and faunas will continue to provide critical, perhaps largely heuristic, data – particularly the unique cercopithecoid primate sample critical to understanding the evolution of colobines and *Papio* in South Africa, to the recent recovery of a hominin specimen that makes it one of few hominin-bearing localities in the northern Cradle – the absence of key contextual information make integration of data into larger analyses of the record difficult-to-unwarranted. Developing a new fossil sample from Haasgat would allow for more confidence in the qualitative and quantitative palaeontological data than we can place in the HGD assemblage, but only if generated with a carefully articulated sampling and processing strategy that minimises collection and preparation biases - and takes the decades of potential palaeontological research within such samples into consideration when cataloguing and archiving the steps made in developing fossil assemblages.

Acknowledgements

Appendix A. Supplementary data

Supplementary data related to this article can be found at https://doi.org/10.1016/j.quaint.2018.01.036.

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