Identification of fossil hairs in *Parahyaena brunnea* coprolites from Middle Pleistocene deposits at Gladysvale cave, South Africa

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1. Introduction

Hair is a unique feature of mammals (Inagaki, 1986), the identification of which provides a wealth of information to archaeology, epidemiology, ecology, criminology and forensic investigations. Hair morphology has been used to identify mammals to order, family or genus level since the beginning of this century (Hausman, 1920; Cole, 1924), and even though much is known about European mammalian hair (Brunner and Coman, 1974; Moore et al., 1974; Brothwell and Spearman, 1963; Brothwell, 1993; Teerink, 2003; Wilson et al., 2004, 2007; Wilson, 2005), relatively little research has been conducted on the morphology of fossil and modern southern African animals.

Many chemicals and biological substances that accumulate in hair can be detected and measured and this makes hair samples good resource biomaterials in forensic science and physical anthropology (Chang et al., 2005). Furthermore, the basic chemical composition of hair is not affected by changes in blood chemistry or by exposure to chemicals after hair formation (Daniel et al., 2004). Because of this, hair samples are often used for autopsy toxicology, including the detection of drug abuse, personal identification and the forensic genetic identification of relatives (Zaiats and Ivanov, 1997; Lebedeva et al., 2000). According to Wilson et al. (2007), the hair shaft does not undergo any post-keratinization biogenic change in contrast to bone and teeth, which are commonly analysed human tissues in bioarchaeology. Hair is mostly made up of the fibrous protein keratin, which is extremely resistant to decomposition (Chang et al., 2005) and enzymatic digestion (Lubec et al., 1986, 1994), owing mainly to the presence of disulphide cross linkages of the amino acid cystine (Brothwell and Spearman, 1963; Taylor et al., 1995). Such an intensely cross-linked system is extremely resistant to decay (Brothwell, 1993), leading to the preservation of hair. Hair proteins are hydrophobic in nature (Fraser et al., 1972) and this renders them insoluble in water, dilute acids

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and alkali, and various organic solvents at ambient temperatures (Taylor et al., 1995). Because of this, hair is relatively durable in the natural environment, and unlike bone, does not fragment during digestion (Keogh, 1979). While the properties of hair may enable it to survive for millennia, under unfavourable conditions, it can degrade within a few weeks (Wilson, 2005; Wilson and Gilbert, 2007).

A review of the scientific literature reveals that relatively few examples of prehistoric animal hair exist, mostly because of a lack of suitable preservation conditions (Bonnichsen et al., 2001). The oldest fossil hairs are reported from China, from Early Cretaceous (146 - 100 Ma) deposits in the Yixian Formation, where they are preserved as carbonized filaments and impressions (Luo et al., 2003), and Late Paleocene (~59–56 My) beds, where the hairs are preserved as calcium carbonate filaments in carnivore faeces (Meng and Wyss, 1997). Younger hairs are reported from Eocene (~50 Ma) deposits in the Messel Shales in Germany (Schaal and Ziegler, 1992; Schweitzer, 2011), Late Pleistocene (~50,000–17,000 BP) permafrost deposits in Siberia (Gilbert et al., 2007) and Miocene (~20–15 My) amber from the Dominican Republic (Poinar, 1988). Human hair samples over 8000 years old are associated with mummies from Peru (Benfer et al., 1978), and more recent Roman hair has been found in a lead coffin burial from Dorchester (Green et al., 1981) and a Roman Ermine street site in Cambridgeshire, England (Brothwell, 1993).

Hairs found in archaeological sites are a unique resource for capturing a snapshot of life (Chang et al., 2005), and the morphology of hair such as scale pattern, medulla, cross-section and colour patterns has provided significant information on species represented, for example, Brothwell and Grime (2003) showed that the hairs associated with the Neolithic ‘iceman’ from the Alps were that of a red deer, and that the fur armband on the Iron Age Lindow bog body was made from fox (Budworth et al., 1986). Ancient mammalian hairs also provide insight into a site’s function, the nature of the environment, species evolution, and the relation between people and animals in the past (Davis et al., 2007). Ancient human and animal hair can be an important data source for understanding palaeobiology, palaeoecology and palaeoanthropology (Bonnichsen et al., 2001), but unfortunately it is rarely preserved in the fossil record and researchers seldom attempt to find it. This study follows the recent discovery of possible human hair in a single Parahyaena brunnea (brown hyaena) coprolite from Gladysvale cave, South Africa (Backwell et al., 2009). The coprolite is part of a brown hyaena latrine preserved in calcified cave sediment dated to the Middle Pleistocene (257–195 ka) (Pickering et al., 2007; Berger et al., 2009). Element analysis showed total replacement of keratin by calcium carbonate, confirming that the Gladysvale hairs are high-resolution casts and do not preserve amino acids (Backwell et al., 2009). Nonetheless, the exceptional preservation afforded by the dolomitic cave system, and potential for expanding the range of known fauna for this time period, stimulated our interest in studying an enlarged sample of coprolites from the same deposit. Our aim was to enlarge the Gladysvale fossil hair sample and discuss the implications of our findings for Middle Pleistocene hyaena ecology and palaeoenvironment in the Sterkfontein Valley, South Africa.

1.1. Archaeological context of Gladysvale cave

Gladysvale cave is located in the Eccles Formation of the Malmani Subgroup of the Transvaal Supergroup (Berger et al., 2009) and situated on the edge of mixed savanna (Scholes, 1997) and grassland (O’Connor and Bredenkamp, 1997) biomes. The site (Fig. 1) is well known for yielding a rich Plio-Pleistocene fauna, including specimens attributed to Australopithecus africanus (Berger, 1993; Berger et al., 1993). A wealth of large vertebrate fossils (Berger, 1992; Lacruz et al., 2002) and micro-faunal remains (Avery, 1995), including diverse avian fauna (Stidham, 2004) have been reported from the site. Gladysvale is a complex cave system made up of several underground chambers reaching a depth of about 65 m (Martini and Keyser, 1989; Schmid, 2002). The cave complex is made up of a roofed system of large underground caves referred to as the Gladysvale Internal Deposits (Pickering, 2005; Pickering et al., 2007), and an outer de-roofed area known as the Gladysvale External Deposits (Lacruz, 2002; Lacruz et al., 2002). The internal deposits are clearly exposed, well preserved and stratified and this makes them unusual for caves in the region. The strata consist of clastic sediments, ranging from coarse boulder piles, through to medium grained, sandy sediment to fine grained, often laminated muds (Pickering, 2005). Flowstones that act as
chronostratigraphic markers are interbedded within the strata and are used to divide the sediments into flowstone bounded units (FBUs) (Pickering et al., 2007). The fossil hyaena latrine is preserved in FBU 14 (Fig. 1), which has well developed lower flowstones and a small stalagmite at the base of the unit, constraining the age of the latrine to between 195 and 257 ka (Pickering et al., 2007). The position of the latrine is directly under the major palaeo-drip source of the cave, providing calcium carbonate-rich water, which aided in the fossilization and preservation of the latrine and surrounding sediment (Berger et al., 2009).

2. Materials and methods

In this research, a block of the calcified latrine (Fig. 2) was taken from Gladysvale cave for laboratory analysis. From this block, 12 coprolites were studied (Table 1). The coprolites varied in size, with larger scats approximately 32 mm in diameter. The number of coprolites analysed in this study were deemed sufficient to determine the diet of *Parahyaena brunnea* considering that previous dietary descriptions were successfully achieved with 10 scats (Pontier et al., 2002; Sinclair and Zeppelin, 2002; Zabala and Zubergogoitia, 2003). Forty-eight fossil hairs were extracted from the coprolites using fine tweezers and a low magnification binocular microscope. Therefore, they were ultrasonically cleaned with analar ethanol and placed directly onto double-sided sticky stubs. The fossil hairs were sputter-coated with gold and examined using a FEI Quanta 400 E scanning electron microscope at magnifications between 461 and 2538 times. Fossil hair cross sections were obtained only from naturally occurring breaks in the specimen.

Hair identification was based on consultation of standard guides to hair identification by Hausman (1930), Lyne and McMahon (1951), Appleyard (1978), Keogh (1979, 1983), Teerink (2003), and Backwell (2009), and comparison with our own collection of samples of guard hairs from 15 taxa of indigenous southern African mammals (Table 2). The selection of these 15 animals was based on known Middle Pleistocene fauna of the Florisian Land Mammal Age (Klein, 1980, 1984) and distinct scale patterns and cross section shapes among different mammals (Keogh, 1979; Kondo, 2000), and because these are the hair types presented by other researchers (e.g. Williams, 1938; Stoves, 1942; Mayer, 1952; Stains, 1958; Keogh, 1979, 1983; Teerink, 2003; Backwell et al., 2009), hence a need to standardize for comparative purposes. Furthermore, guard hair is much more regular in shape and easier to work with than fine underhair (Homan and Genoways, 1978). Prior to examination, the hair samples were ultrasonically cleaned with a mixture of absolute alcohol and sulphuric ether in equal proportions to remove the organic and inorganic dirt from the surface of the samples. The hairs were washed in distilled water for three minutes and then air dried on a clean watch glass. To obtain cross sections, the hair samples were cut perpendicularly using a fine surgical blade. Finally, the hairs were mounted on stubs with double-sided sticky tabs, sputter-coated with gold and examined using an FEI Quanta 400 E scanning electron microscope following the same procedures as those used for the fossil specimens.

### 3. Results

3.1. Modern comparative collection

A selection of scanning electron micrographs of hairs from previously undocumented modern southern African mammal taxa is presented in Figs. 3–6. The images of hairs presented have scales between 461 and 2538 times. Fossil hair cross sections were obtained only from naturally occurring breaks in the specimen.
ranging from 30 μm to 100 μm, to permit better observation of scale features and independent assessment of hair samples. In cross section, impala hair has a diagnostic triangular shape with blunted corners. The cortex is thick and the medulla has numerous small perforations (Fig. 3a). The scales are transverse relative to the longitudinal axis of the hair. Scale pattern is irregular waved mosaic. The structure of scale margins is generally smooth and the distance between scale margins is near to distant (Fig. 3b). The cross section of eland hair (Fig. 3c) is generally circular tending to oval. The cortex is very thick and the medulla is small to medium in size. The scale pattern (Fig. 3d) is irregular waved mosaic and the scale margins are moderately rippled. The distance between scales is near. In cross section, steenbok hair (Fig. 3e) is generally reniform tending to concavo-convex. The medulla is very large and spongy. The scales are transverse and the scale pattern is irregular waved mosaic. Scale margins are smooth and the distance between scales is near to distant (Fig. 3f). The cross section of kudu hair (Fig. 4a) is generally biconvex. The medulla is large but indistinct, with a thin cortex. The scale pattern of kudu hair is irregular waved mosaic and scale margins are generally smooth (Fig. 4b). The distance between scales is near to distant. In cross section, warthog hair is oval (Fig. 4c). The scale pattern is highly irregular waved mosaic. The scale margins are rippled and the distance between scales is extremely close (Fig. 4d). The cross section of Burchell’s zebra is oblong (Fig. 4e). The scale pattern is irregular waved mosaic and the scale margins are rippled. The distance between scale margins is near to close (Fig. 4f). Scrub-hare hair cross section (Fig. 5a) is generally biconvex to oval. The medulla usually contains a few large cavities. The scales form a lanceolate pectinate (comb-like) pattern. The distance between scales is distant and scale margins are moderately rippled (Fig. 5b). Red rock hare hair cross section is dumb-bell shaped (Fig. 5c). The medulla contains large cavities. There is a broad, deep groove along the length of the hair. Both sides of the groove show a coronal scale pattern. The distance
between scales is near and the scale margins are smooth (Fig. 5d). Black rhino hair cross section is approximately oval and the medulla is ill-defined (Fig. 5e). Scales are very coarse and the pattern is irregular waved. The scale margins are moderately smooth to rippled and the distance between scales is near (Fig. 5f). Blue wildebeest hair cross section (Fig. 6a) is concavo-convex. The cortex is thick and the medulla is small to medium in size. Scale position is transversal and scale pattern is irregular waved mosaic. The scale margins are generally smooth to moderately rippled and the distance between scales is near (Fig. 6b). Rock dassie hair cross section is approximately oval although it tends to oblong (Fig. 6c). The scale pattern is ill-defined and there are cracks on the cuticular surface (Fig. 6d).

3.2. Fossil hairs

Of the 48 fossil hairs extracted from the 12 coprolites, 33 were extremely degraded with ill-defined scale patterns, rendering hair identification impossible, whilst eight were identifiable to five species, and seven could not be identified. Some fossil hairs showed reasonably clear scale morphologies but could not be conclusively matched in the comparative collections. These hairs may represent taxa for which we do not have a modern comparative sample, or the hair of a mammal now extinct. Considering that few fossil hairs are preserved in the African fossil record to enable comparison with those from Gladysvale, we are obliged to use modern taxa as a proxy for fossil forms. A selection of scanning electron micrographs and descriptions of fossil hairs is presented in Figs. 7–9. In fossil hair specimen 1, the scale pattern is imbricate, i.e. the cuticular scales overlap. The scales lie transverse to the longitudinal direction of the hair and the scale margins are generally smooth to moderately rippled (Fig. 7b). In cross section, the hair is generally oval and shows no lumen (Fig. 7a). The medulla is amorphous, lacking a definite shape, a feature of human hair. This combination of characters closely resembles those observed on modern African and European hair samples, and fossil human hairs reported by
Backwell et al. (2009) from a single coprolite from the same deposit. The scale morphology of fossil hair specimens 2 (Fig. 7c), 3 (Fig. 7d and 4 (Fig. 7e) is slightly obscured, but a closer examination shows an irregular waved mosaic pattern and smooth scale margins that are near to distant. This combination of features resembles those found in modern impala (Fig. 3a and b). Even though the cross section of fossil hair specimen 2 (Fig. 7c) could not be obtained because of the absence of naturally occurring breaks in the sample, the fossil hair specimen can be tentatively attributed to modern impala based on scale morphology. In cross section, fossil hair specimen 4 (Fig. 7f) is a triangle with blunted corners, a feature shared with modern impala (Fig. 3a). There are no clear small perforations in the fossil medulla, which is to be expected from a cast. Although ill-defined, the scale pattern of fossil hair specimen 4 (Fig. 7e) is irregular waved mosaic, and the scale margins are smooth, as in modern impala (Fig. 3b).

Scale morphology of specimens 5 (Fig. 8a and 6 (Fig. 8b) is irregular waved mosaic and the scale margins are moderately rippled. The cross section of these specimens is not available due to the absence of naturally occurring breaks in the samples. The distance between fossil hair scale margins is near to close, a scale pattern comparable to that of modern Burchell’s zebra (Fig. 4f). The hair scale morphology of fossil specimen 7 is not preserved (Fig. 8c). In cross section, it is generally biconvex to oval (Fig. 8d), a feature shared with modern kudu (Fig. 4a). Although the cross section of fossil hair specimen 8 (Fig. 8e) is distorted, it is reniform or concavo-convex, a shape similar to that of modern steenbok hair (Fig. 3e). The scale pattern of fossil hair specimen 8 is poorly preserved, but nonetheless shows an irregular waved pattern (Fig. 8f). Unlike modern steenbok scale margins, which are smooth (Fig. 3f), the fossil hair scale margins are moderately rippled. The scale morphology of fossil hair specimen 8 (Fig. 8f) could not be conclusively matched in the comparative collections, and hence an identification could not be made. Fossil hair specimens 9 (Fig. 9a) and 10 (Fig. 9b) show an irregular waved mosaic scale morphology, and the distance between scale margins is close. Scale margins are
rippled. Although the cross section of these fossil hair specimens is not available due to the absence of naturally occurring breaks in the samples, their scale morphology closely resembles that of modern warthog (Fig. 4d), being highly irregular waved. The scale morphology of fossil hair specimen 11 shows a regular waved pattern (Fig. 9c). Scale margins are smooth and the distance between scales is distant. Even though the scale morphology is well defined, it cannot be matched in the comparative collection. There is no cross section for this specimen.

4. Discussion

4.1. Fossil hair preservation

Fossil hairs were extremely difficult to identify compared to modern hairs, which record clear scale patterns and margins for the entire length of the specimen. Most of the fossil hairs were very small shaft fragments (≤ 1 mm), so only a few features were present and available for use in identification. Scanning electron microscope analysis of fossil hairs revealed that the extent of degradation varied significantly between specimens. This is most likely due to microbial activity and diagenetic processes (Martill et al., 2000), but could in part be attributed to the position from which the fossil hairs originated on the animal. This is because those from the animal’s back and tail (guard hairs) are generally more robust than those from the neck and stomach, enabling them to resist degradation. Alternatively, the hair was degraded before consumption, having been exposed to the elements for some days or weeks. Whatever the case, variable degradation between guard and under hair warrants further investigation, especially because ancient hair assemblages are known to contain a wide range of hair types such as guard hairs, under hairs, and whiskers from a variety of species (Bonnichsen et al., 2001).

Hair identification reference keys are limited to guard hairs because of their characteristic features, but this makes hair identification of less distinct or developed features challenging, especially when previous researchers have shown that there are significant differences in hair morphology between hairs taken from different sites on the animal (Riggot and Wyatt, 1981). Seasonality, age and sex differences (Brothwell, 1993) can also complicate the taxonomic identification of hair, as demonstrated by Keogh (1975), who investigated the effect of age on individual scale patterns of rodent hair, and found significant variation in the hairs of young and old animals. Many factors complicate morphological analysis, including protein degradation, abrasion, fungal and bacterial attack, all of which can obscure or alter scale and medullary features (Bonnichsen et al., 2001). This is quite evident in the fossil hairs from this research, many of which had abraded scales and obscure medullary features (e.g. specimens 7, Fig. 8c and d, e). DNA analysis could have resolved the taxonomic identity of the fossil hairs, but their age and mode of preservation do not permit it. Despite this, some fossil hairs (e.g. Fig. 7a and b) record remarkably well preserved casts of the original hair scales, providing sufficient detail to make tentative identifications of the mammal taxa represented.

4.2. Fossil hair identification

Some fossil hairs had well preserved cuticular surface and cross sectional morphology, which is rarely observed in ancient hair (e.g. specimen 1, Fig. 7a and b), and permitted visual comparison with modern hair samples. Scanning electron microscope analysis was
used for all the hair samples and resulted in relatively clear micrographs. Visual comparison of hair can be subjective and is open to interpretation (Steck-Flynn, 2009). In a study conducted by the Federal Bureau of Investigation, 11% of hairs deemed to be matches upon visual inspection were found to be non-matches after DNA testing (Saferstein, 2004). As with most forensic evidence, the information obtained from hair is expressed in terms of probabilities of a match rather than an absolute match (Crocker, 1999).

The cuticular scale surface detail of fossil hairs in this research is sufficiently intact to be of use in species identification, and on this evidence tentative identifications have been made, with eight fossil hairs identified to species level in five cases. Based on our collection of modern mammals from southern Africa, this study has established that impala, Burchell’s zebra and warthog hair predominated in the coprolites from Gladysvale cave. In accordance with Kruuk (1972), who found one taxon represented in most spotted hyaena faeces, this research showed the same pattern for brown hyaena coprolites. The only exception is in coprolite specimen 4, which preserved impala and Burchell’s zebra hairs. Skinner and van Aarde (1981) analysed hairs from scats from brown hyaena latrines from Wolfsbaai, Namibia, and found that seal and jackal hair predominated. Kuhn et al. (2008) analysed brown hyaena scats and examined faunal remains at nine dens, and concluded that brown hyaenas along the Namibian Coast predominantly feed on seals. These are only a few examples of evidence of brown hyaenas consuming locally available animals (see Faith, 2007; Kuhn et al., 2010), making them good environmental indicators. The Burchell’s zebra, impala and warthog represented in the coprolites are commonly found in savannas. Plains zebra live in open savannas and partial to open woodlands. They are a daily and seasonal migratory mammal that moves in search of better grazing areas and water supplies, but are highly dependent upon water and are never more than 10–12 km from a source (Skinner and Smithers, 1990). This species is predominantly a grazer preferring short grasses, but will also browse and feed on herbs. Warthogs are found in open grasslands, floodplains, open woodlands and open scrub. They are selective feeders, preferring short grasses growing in...
freshly burnt and damp areas. They also root for underground rhizomes and will consume sedges, herbs, shrubs and wild fruit. Warthogs are not dependent upon water, but are usually found close to it. Impala are associated with woodland, preferring light open associations. In southern Africa, they are associated particularly with *Acacia* and Mopane woodland, occurring on the ecotone of open grassland and woodland. Cover is an essential habitat requirement, but impala occasionally graze on open grassland when it is fresh and green (Skinner and Smithers, 1990). A single fossil hair exhibits features characteristic of human hair, supporting the previous tentative identification of human hair in a single coprolite from the same deposit (Backwell et al., 2009). The cuticular scale pattern on the fossil human hair (Fig. 7b) is imbricated, with a 'regular wave' morphology and the margins on the human hair scales (African and European) are smooth and moderately rippled, and relatively evenly spaced (Backwell et al., 2009). Apart from humans, the identified animals are associated with savanna grasslands, much like the Highveld environment of today. Amid a scarce fossil and archaeological record for this time period, these results contribute data to the local Middle Pleistocene fossil faunal record, and insight into the environment in which archaic and emerging modern humans in the interior of the African subcontinent lived.

On the evidence of scale morphology preserved on the fossil hairs studied here, rodents and other carnivores in general, and cats in particular, can be excluded as potentially represented. Rodent hair is typically grooved along the entire length of the hair and is usually coronal in scale morphology (Keogh, 1985). Carnivore hair scale pattern consist of closely packed scales forming an irregular pattern (Keogh, 1979), unlike that on the fossil hairs analysed in this research. In this regard, the possibility that the hyaena ingested its own hair during grooming can be eliminated. Cats, like other carnivores, have irregular waved patterns, but the scale margins are typically frilly, and none of the fossil hairs record this feature. Our results indicate that the previously undocumented scub-hare (*Lepus saxatilis*) scale pattern (Fig. 5b) closely resembles that of vlei rat hair.  

![Fig. 8. Fossil hair specimen 5 scale pattern (a), scale – 50 μm; specimen 6 scale pattern (b); specimen 7 scale pattern (c), scales – 100 μm and cross section (d), scale – 50 μm; specimen 8 cross section (e) and scale pattern which could not be matched (f), scales – 50 μm.](image-url)
(Otomys irroratus) studied by Keogh (1975). Similarities in scale pattern were also observed between red rock hare (Fig. 5d) and four-striped mouse (Rhabdomys pumilio) documented by Keogh (1975). The only difference lies in the fact that the scale pattern on either side of the groove is coronal in red rock hare (Fig. 5d) and petal mosaic in four-striped mouse. This is not surprising because of possible overlaps between mammal hair features, as discussed by Hess et al. (1985). These similarities are noteworthy because of the problem of misidentification, and thus misinterpretation of the fossil record and palaeoenvironment. Perrin and Campbell (1980) report that rock dassies have a hair cuticular scale pattern unlike most small mammals, in that it is flattened mosaic in the proximal region and changes to a waved pattern distally. The rock dassie hair studied here preserves no scales, and shows cracking of the shaft (Fig. 6d). A lack of hair scales has been documented in human hair subject to pathology (Brown and Crounse, 1980), a condition observed when studying our diabetic colleague’s hair as part of the human comparative sample. In the case of the rock dassie, a lack of scales could be due to pathology, abrasion of the hair resulting from inhabiting rock crevices, or perhaps preparation of the pelt by a taxidermist. To our knowledge, the effect of taxidermy on hair preservation is unknown, and warrants further investigation.

4.3 Parahyaena brunnea ecology and palaeoenvironment

The existence of fossil hairs in Middle Pleistocene hyaena coprolites from Gladysvale cave is attributed by Berger et al. (2009) to the activities of Parahyaena brunnea. This is based on the contents and position of the latrine in the cave, which suggests that it was used as a den for rearing pups. Spotted hyaenas (Crocuta crocuta) do not defecate in one place, and striped hyaenas (Hyena hyaena) mark a large territory around the entrance (Watts and Holekamp, 2007). In accordance with the most common foraging behaviour reported for modern brown hyaena (Skinner and Ilani, 1979; Skinner et al., 1980; Mills, 1990; Maude and Mills, 2005; Kuhn, 2001, 2005, 2006; Kuhn et al., 2009, 2010; Kuhn, 2011), the animal(s) responsible for the coprolites, scavenged the identified mammals. Brown hyaenas are reportedly inefficient predators, and their food is rarely obtained by hunting (Maude, 2005). Researchers have observed that if hunting occurs, it is targeted towards smaller mammals only (Skinner, 1976; Mills, 1978), as evidenced by brown hyaenas killing seal pups on the Namibian Coast (Wiesel, 2006; Kuhn et al., 2008). Some brown hyaenas show specialization of hunting techniques towards certain prey species (Wiesel, 2006), such as southern Kalahari brown hyaenas hunting springbok lambs (Antidorcas marsupialis) and korhaans (Eupodotis spp) as reported by Mills (1990), and brown hyaenas killing small livestock (Kuhn, 2011). They are said to be poorly equipped for running and hunting, especially of large mammals, such as the zebra and kudu represented in the coprolites. If this behaviour is true of extant brown hyaena, it should hold that Middle Pleistocene hyaena scavenged on the large mammals represented in the coprolites, which were killed by other carnivores, most likely large cats. However, according to Brain (1981), brown hyaenas are keen hunters of large mammals only when rearing pups, hence the possibility that the Middle Pleistocene hyaena(s) responsible for the coprolites actively hunted the mammals represented by the fossil hairs as part of their pup-rearing behaviour. The fact that Middle Pleistocene hyaena fed...
on the identified mammals is consistent with previous researchers who found that hyaenas accumulate a wide range of faunal remains to varying degrees and that their foraging behaviour is variable (Scott and Klein, 1981; Faith, 2007; Kuhn et al., 2010). Apart from the five mammals identified in this research, our findings show that brown hyaenas fed on at least one mammal that could not be matched in the comparative collection (e.g. specimen 11, Fig. 9c and specimen 8, Fig. 8f), suggesting that some as yet unidentified species are represented in the fossil hair samples.

5. Conclusion

Scanning electron microscope analysis of modern hair samples of known taxa revealed fine details of scale and cross sectional morphology of hair, and showed that cuticular scale pattern and cross section shape can be used as definitive criteria in species identification, and the pertinence of this technique to palaeo-ontological research. The identified fossil hairs show that between 257 and 195 ka, Parahyaena brunnea shared the Sterkfontein Valley with warthog, impala, zebra, kudu and humans. Whether the hyaena(s) responsible for the coprolites hunted or scavenged from these animals is unclear. The identification of five species of mammal represented in the coprolites in the form of fossil hairs supports the previous tentative identification of fossil human hair in a single coprolite, provides a new source of information on the local Middle Pleistocene fossil mammal community, and rare insight into the environment in which archaic and modern humans in the interior of the African subcontinent lived. Hair provides evidence of inland occupation by archaic Homo sapiens or modern humans. Amid a scarce fossil and archaeological record for this time period, these results contribute data to the ongoing debate about the role of environment in the evolution of modern humans (Mitchell, 2008; Schieg and Conard, 2006; Deacon and Deacon, 1999; Wadley, 2006; Clark and Plug, 2008; d’Errico and Banks, 2012). This study highlights the importance of researching all aspects of the fossil record, and the contribution of microscopy to palaeontology. In addition to expanding the taxonomic representation of modern southern African mammal hair samples, we propose that researchers involved in the study of hair document when possible, in addition to guard hairs, examples from different sites on the body, and from young and old individuals, factors that affect hair morphology, and motivate for the expansion of the range of features considered diagnostic of a species. We hope that the presentation of our data will assist in other fields of research and stimulate further inquiry.

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