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Identification of mammalian species represented by fossil hairs in Parahyaena Brunnea coprolites from middle pleistocene deposits at Gladysvale Cave, South Africa

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CHAPTER ONE

INTRODUCTION

1.1 Background

Hair is a defining feature of mammals (Bower and Curry, 1983; Inagaki, 1986; Amman *et al*., 2002), the biological structure of which is well known (Montagna and Ellis, 1957; Lyne and Short, 1965; Montagna and Dobson, 1967; Hardy, 1992; Robbins, 1994; Schweitzer, 2011). Numerous coats of mammals, except for humans and sheep, consist of several types of hair, the main components being the guard hair and under fur (Kondo, 2000; Teerink, 2003). Guard hair is that long and stiff hair with a thickening in the distal part, called the shield and a thinner proximal part, the shaft (Teerink, 2003). The differing hair characteristics among mammals are recognized by the differences in guard hair, based on the colour and morphological characteristics of the cuticle and medulla (Kondo, 2000). Underhair is thinner, less stiff and has an undulating appearance (Teerink, 2003).

By combining the main features of cuticular scales, medulla, and transverse sections of hair, researchers have managed to develop keys to identify hairs to taxon (Keller, 1978, 1980, 1981a, 1981b; Keogh, 1979, 1983, 1985; Taylor, 1985; Thompson *et al*., 1987; Oli, 1993; Wallis, 1993; Teerink, 2003). Hair morphology has been used to identify mammals to order, family, or genus level since the beginning of the last century (Hausman, 1920; Cole, 1924), and even though much is known about European mammalian hair, relatively little research has

been conducted on the morphology of modern and fossil southern African animals.

Hair identification provides a wealth of information in criminology, epidemiology, archaeology, ecology and forensic investigations. 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 (Pichini *et al.*, 1996; Palmeri *et al.*, 2000; 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 (Miller *et al*., 1997; 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.

In addition to the benefits of studying modern hair, the scientific study of ancient hairs can contribute evidence important for addressing questions about the past (Bonnichsen *et al*., 2001). Hairs found in archaeological burials 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 present at these sites (Appleyard,

1978; Budworth *et al*., 1986; Brothwell and Grime, 2003). 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.

1.2 Hair development

The hair follicle initially produces cells which give rise to hair growth. The cells gradually ascend to the neck of the hair bulb where they begin to elongate and change in cellular structure (Brothwell, 1993). The cells increase in size into the the keratogeneous zone, and beyond that become more and more elongated and compressed (Matoltsy, 1958). In the mature cortex above the skin surface, the elongated cells are tightly packed and the hair appears as a horny mass (Brothwell, 1993) .Over the surface is the unpigmented cuticle, appearing as a series of overlapping scales towards the hair tip (Wildman, 1954; Brothwell, 1993; Kondo; 2000; Teerink, 2003). The mature hair mainly consists of a water insoluble component, which is largely in the form of keratin, built up of amino acids in different sequences and groupings (Brothwell, 1993).

1.3 Preservation of hair

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; Yu *et al*., 1993; Macho *et al*., 1999), owing mainly to the presence of disulphide cross linkages of the amino acid cystine (Brothwell and Spearman, 1963; Taylor, 1994; 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 and alkali, and various organic solvents at ambient temperatures (Barnett and Sognnaes, 1962; 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). Although hair can survive for millennia, it may also degrade within a few weeks (Wilson, 2005; Wilson and Gilbert 2007). Soil conditions and fungal attack can cause various forms of hair decay (Brothwell, 1993).

A review of the scientific literature reveals that relatively few examples of prehistoric animal hair exist (e.g. Benfer *et al*., 1978; Massa and Fuhrman, 1978; Bryan, 1979; Bonnichsen and Bolen, 1985; Lubec *et al*., 1986; Poinar, 1988; Schaal and Ziegler, 1992; Brothwell, 1993; Lubec *et al*., 1994; Bonnichsen *et al*., 1994; Wilson *et al*., 1995; Chrisman *et al*., 1996; Meng and Wyss, 1997; Allen *et al*., 1998; Loy and Dixon, 1998; O'Connell and Hedges, 1999; O'Rourke *et al*., 2000; Baker *et al*., 2001; Wilson *et al*., 2001; Ji *et al*., 2002; Gilbert *et al*., 2007; Backwell *et al*., 2009), mostly because of a lack of suitable preservation

conditions (Bonnichsen *et al*., 2001). Fossil hairs reported in the Early Cretaceous mammals of the Yixian formation of China are preserved as carbonized filaments and impressions around the torso of the holotype, and the pelage appears to have both guard hairs and denser underhairs close to the body surface (Luo *et al*., 2003). Certainly, this presents an exceptionally different preservational mechanism to that of Gladysavale fossil hairs which are preserved as high resolution casts (Backwell *et al*. 2009) of external and not internal morphology.

Other examples of fossilized mammalian hairs are from carnivore faeces from Late Palaeocene (~59 - 56 My) beds in China (Meng and Wyss, 1997). Other early examples come from 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). Schweitzer (2011) reports that hair has been identified morphologically in exceptionally preserved mammal fossils (~50 million years in age) from the Messel Shale (Schaal and Ziegler, 1992), and in fossils contained in Eocene amber (Poinar 1988), illustrating its relatively high preservation potential.

Medullar and scale patterns of hair are well known for a variety of mammal species, but the effects of long term burial or exposure to hazardous conditions on the internal and external morphology of hair may be marked, and therefore misleading when it comes to making unequivocal identifications (Quadros and Monteiro-Filho, 1998). Morphological changes that occur in hair during long term

burial can be understood by considering changes in histological morphology of the hair caused by various factors (Chang *et al.*, 2005).

In Kangneung, Korea, Chang *et al*. (2005) made ultramicroscopic observations on morphological changes in human hair shafts during 25 years of weathering and concluded that long term burial can cause significant morphological and histological changes in hair, which undoubtedly impacts on the results of forensic and archaeological investigations. Besides the destructive taphonomic agents associated with subterranean conditions, aerial environmental factors such as sunlight, air pollution and wind, have also been found to induce histological changes in the hair cuticle and cortex, ultimately leading to the destruction of the hair shaft (Dawber and Comaish, 1970; Venning *et al.*, 1986; Tobin *et al.*, 1990; Georgalas and Dowbrands, 1993).

1.4 Previous mammal hair research

Ancient mammalian hair has been of interest to scientists since the 19th century when human mummy hair from South America was examined (Browne, 1860: in Brothwell and Spearman, 1963). Thereafter, Pruner-Bey (1877) analysed pigmentary and structural variation between Egyptian and Peruvian mummy hair specimens. Scientific publications on mammalian hair are available from the end of the 19th century when De-Meijere (1894) first studied hair morphology (Keogh, 1979). The identification of modern European mammal hair has been extensively studied, with the first important contribution coming from Hausman (1920, 1924,

1930). A detailed description of 73 species of west European mammals is now published by Teerink (2003). There is also great interest in the use of hair from archaeological contexts in key research (Wilson *et al*., 2001).

A considerable number of researchers from different disciplines, including veterinary anatomy (Feder, 1987; Meyer *et al.*, 1997), wildlife biology (Wolfe and Long, 1997; Bahuguna and Mukherjee, 2000; Phan *et al*., 2000; Teerink, 2003; Sahajpal *et al*., 2008, 2009), the textile industry (Wildman, 1954; Appleyard, 1960; Anderson and Lipson, 1970; Haly *et al*., 1970; Langley and Kennedy, 1981; Wortmann *et al*., 1986; Phan and Wortmann, 1987; Kadikis, 1987; Wortmann *et al.*, 1989; Cheng and Huang, 1992; Hall *et al*., 1992; Rollins and Hall, 1999) and forensic medicine (Stoves, 1942; Hausman, 1944; De Boom and Dreyer, 1953; Meyer *et al.*, 2000), have investigated the micromorphological characteristics of various hair types of mammals to identify hair samples. Many scientific investigations published by Hausman (1920, 1920a, b, 1924, 1930) paved the way for a vast array of research on the attributes of mammalian hair. Scientists have also examined the commercial aspects of hair produced by domestic breeding of mammals (Appleyard, 1978) and focused on hair identification of stomach or scat contents (Day, 1966; Cypher *et al.*, 1994).

Van den Broeck *et al*. (2001) researched the micro architecture of cover hairs, wool hairs and tactile (sinus) hairs of feral New Zealand White and Angora rabbits. Their research confirms species-specific characteristics, individual and

breed-dependent variations of the structural hair components in rabbits. Other scientists have concerned themselves with hair evolution, for example Korhonen *et al*. (1991) who studied the insulation of raccoon dog *(Nyctereutes procyonids)* coats in Finland, and that of raccoon dogs in Japan, where the climate is milder. The investigation revealed that the coat of the Japanese raccoon dog has very limited insulating ability compared to that of the Finnish raccoon dog which has adapted to the cold climate. The Finnish racoon dog has a thick fur coat with high insulation. It has a good ability to alter its body energy reserves seasonally.

Hess *et al*. (1985) was one of the first to use scanning electron microscopy to examine surface scale patterns, cross and longitudinal sections and sanded hairs from selected species and subspecies of the families Tayassuidae and Suidae. From this research as well as investigations by other scientists (Adorjan and Kolenosky, 1969; Riggot and Wyatt, 1980, 1981), it was concluded that there are significant differences in hair morphology between hairs taken from different sites on the body of the animal.

Brazej *et al*. (1989) used scanning electron microscopy to observe the hair of 50 kinds of fur animals and contributed important data for the identification of fur skins. Kondo *et al.* (2000) focused on the morphological structure of mink pelage in the telogen (resting) phase using scanning electron microscopy. Bahuguna and Mukherjee (2000) also used scanning electron microscopy to recognize Tibetan

antelope hair and blending in wool products. Tibetian antelope are a threatened species known for their fine wool, and their trade is illegal.

In Brazil, both scanning and light microscopy were used to test the occurrence of structural alteration in white-eared opossum (*Didelphis albiventris*) hair morphology due to taxidermy, digestion, and putrefaction processes (Quadros and Monteiro-Filho, 1998). Brunner and Coman (1974) focused on the morphology of hair on 77 species of mammals including 36 species of marsupialia.

Hair morphology has been extensively studied under a light microscope (Blomstedt, 1989, 1992, 1995). Maurel *et al*. (1986) looked at the differences in hair bundles among three fur bearing mammals: European badger *(Meles meles)*, red fox *(Vulpes vulpes)*, and mink *(Mustela vison)*. Both light and scanning electron microscopy were used to study hair morphology of 36 species of the family Heteromyidae including the genera *Dipodomys, Perognathus, Microdipodops* and *Liomys* (Homan and Genoways, 1978). Furthermore, Rollins and Hall (1999) used both light and scanning electron microscopic methods to differentiate Ibex goat and Tibetian antelope fibers.

In France, hairs from Caucasian and sub-Saharan descendants were analyzed for their elemental composition of melanin granules and other components of human hair shaft using multi-isotope imaging mass spectrometry (Hallegot *et al*.,

2004). The recovery and analysis of mitochondrial DNA from ancient hairs now enables researchers to genetically confirm taxonomic identifications based on scale morphology (Bonnichsen *et al*., 2001; Gilbert *et al*., 2004).

Although numerous researchers in South Africa have focused on investigating the pelt and hair of modern mammals in relation to thermoregulation (Riemerschimid and Elder, 1945; Bonsma, 1949; Bonsma and Louw, 1963), very few studies on hair identification have been undertaken. The microstructure of hair of modern southern African carnivores is well documented by Keogh (1979), however, limited examples have been drawn from a wider field. The other animal taxa that Keogh studied using scanning electron microscopy include some bovids such as the bontebok, cattle and clun forst sheep, as well as diurnal rodents, bats, and elephants. Recently, Backwell *et al*. (2009) used scanning electron microscopy to document modern indigenous primate hairs from southern Africa. There is a notable gap when it comes to comparative hair samples for perrisodactyls, lagomorphs, hyracoidea, tubulidentata and many artiodactyls.

This research 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 (195 000 to 257 000 years ago) (Berger *et al*., 2009). This aroused my interest in identifying the mammal species represented by fossil hairs in an enlarged sample of

coprolites from the same deposit. Because of the general shape of the latrine, its confined nature, the shape and size of the coprolites, and the fact that they contain bone fragments and microscopic traces of hair, Berger *et al*. (2009) confidently ascribes it to *Parahyaena brunnea*. The correct identification of hair in the coprolites is relevant to interpreting Middle Pleistocene hyaena ecology and palaeoenvironment in the Sterkfontein Valley, as well as ancient hyaena behaviour and that of its prey. Furthermore, the research is an expansion of Keogh's modern comparative hair samples of southern African mammals.

1.5 Objectives

The aims of the study are to:

1. Identify fossil hairs in a sample of *Parahyaena brunnea* coprolites from Gladysvale cave using scanning electron microscopy.

2. Discuss the implications for Middle Pleistocene hyaena ecology and palaeoenvironment in the Sterkfontein Valley based on the identified fossil hairs.

1.6 Hypotheses

1. Fossil hairs in the coprolites are identifiable to genus and possibly species.
2. Fossil hairs in the coprolites provide data on a range of Middle Pleistocene fauna in the Sterkfontein Valley.

3. Fossil hairs in the coprolites provide data on Middle Pleistocene *Parahyaena brunnea* palaeoenvironment, behaviour, diet and ecology in the Sterkfontein Valley.

1.7 Study site

Gladysvale cave is located approximately 13 km north-northeast of Sterkfontein on the John Nash Nature Reserve (Fig 1.1). The site 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 Gladysvale cave. Currently, Gladysvale cave is on the edge of mixed savanna (Scholes, 1997) and grassland (O'Connor and Bredenkamp, 1997) biomes. The cave is surrounded by trees, shrubs, and grass, while higher ground above the cave is grass-dominated (Pickering *et al*., 2007). It is a complex cave system made up of several underground chambers reaching a depth of about 65 metres (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 (Fig 1.2) and this makes them unusual for caves in the

region.

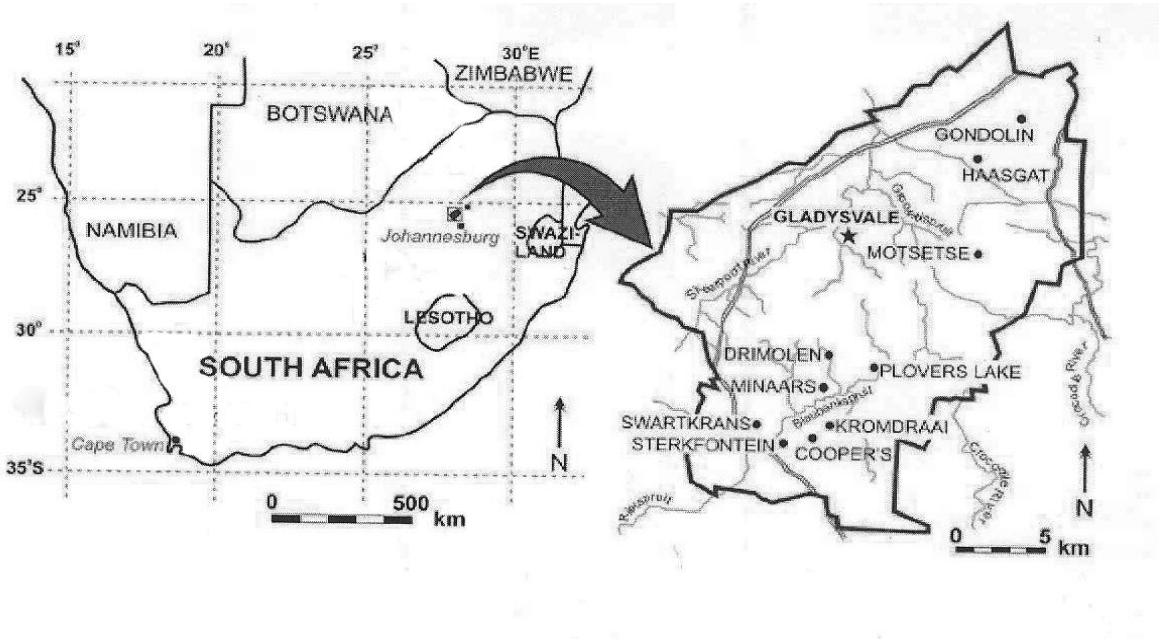


Fig 1.1: Map showing the location of Gladysvale cave (modified after Berger *et al*., 2009).

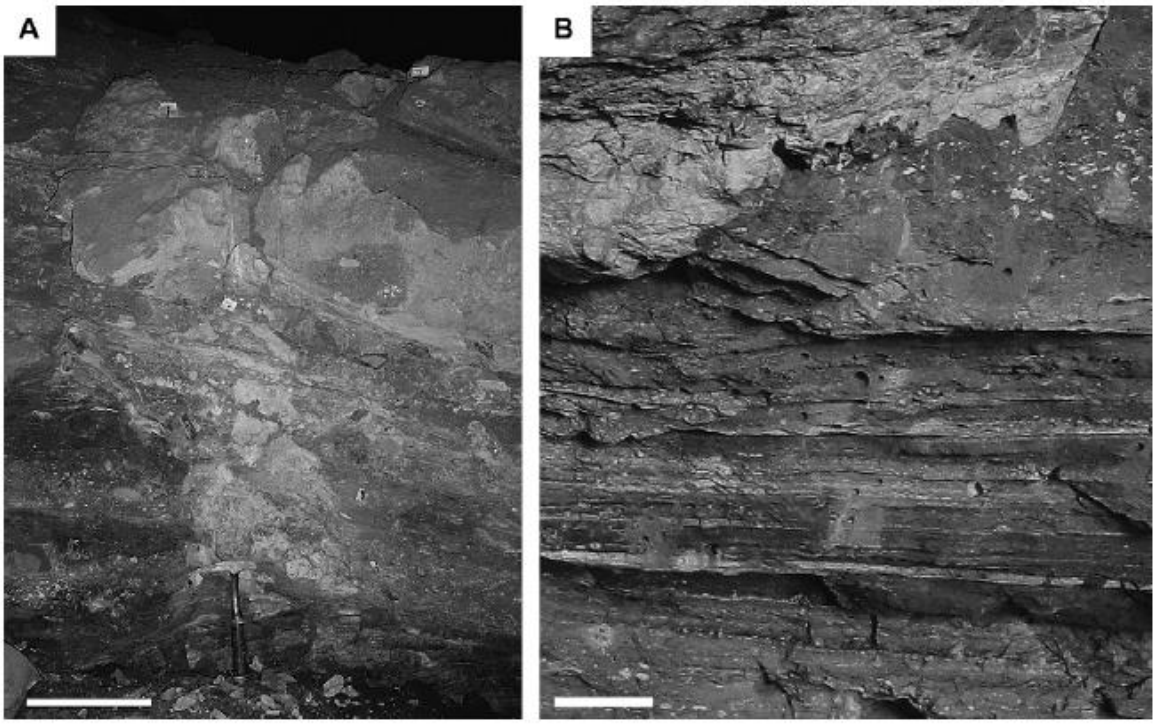


Fig 1.2: Clearly exposed, well preserved and stratified clastic sediments from the Western Face 1 (A) and the Peabody Chamber (B) in Gladysvale cave. Both scale bars are 30 cm (after Pickering *et al.*, 2007).

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 1.3), which has well developed lower flowstones and a small stalagmite at the base of the unit, constraining the age of the latrine to between 195,000 and 257,000 years old (Pickering *et al*., 2007).

The position of the latrine is directly under the major palaeo-drip source of the cave (Fig 1.4), providing calcium carbonate-rich water, which aided in the fossilization and preservation of the latrine and surrounding sediment (Berger *et al.*, 2009). The remains of stalactites on the cave roof is an indication of the close proximity of the palaeo-drip source.

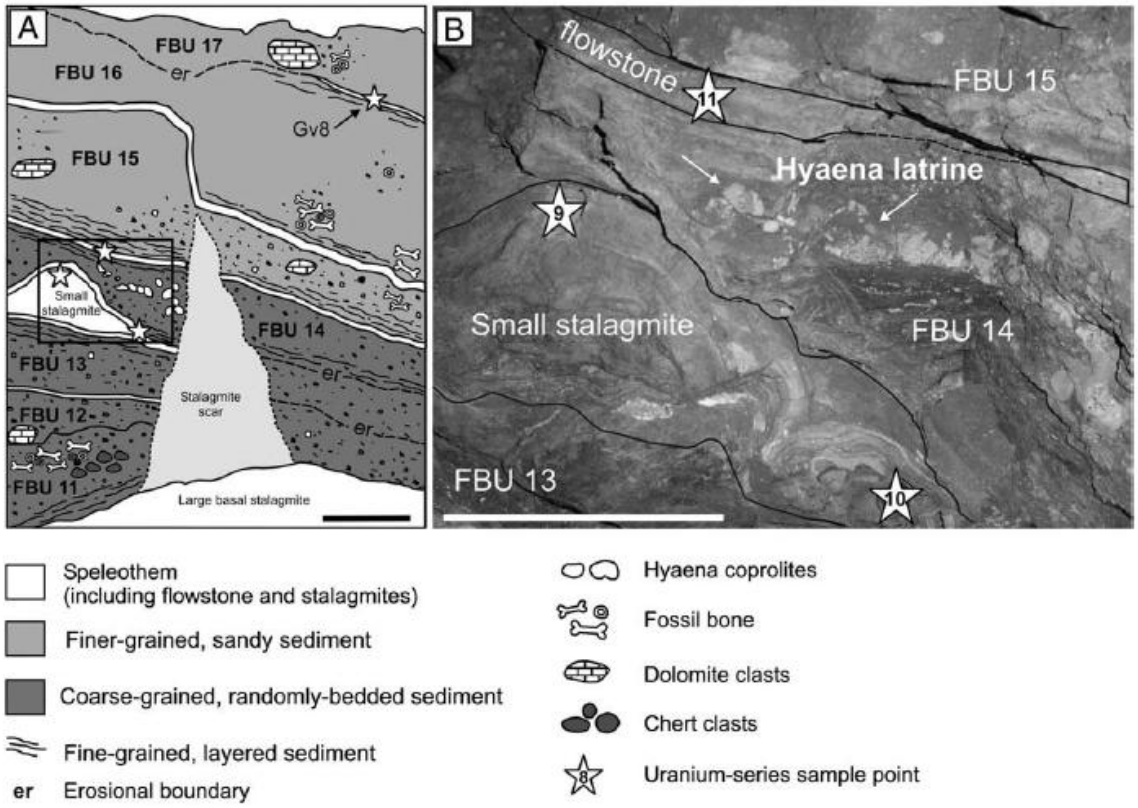


Fig 1.3: (A) Geological section of Gladysvale deposits showing the position of the latrine within flowstone bounded unit 14. (B) Photograph of the area showing details of the section containing coprolites and the dated flowstone layers. Both scale bars = 30 cm (after Backwell *et al.*, 2009).

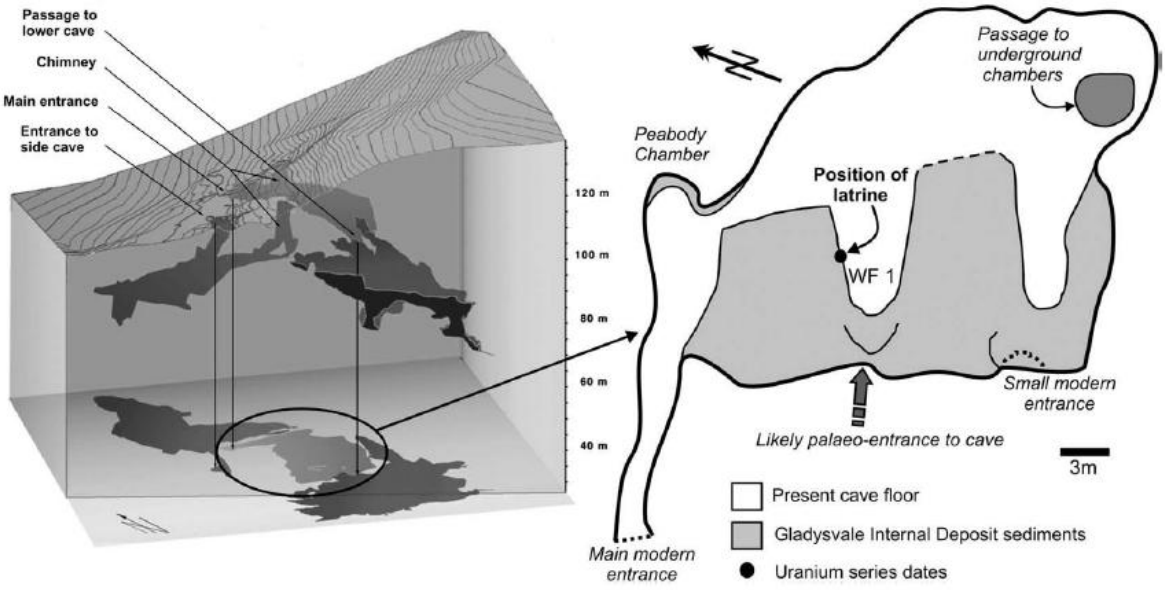


Fig 1.4: Map indicating the position of the latrine in the cave system (after Berger *et al.*, 2009).

1.8 Coprolites

The term coprolite was first introduced by Buckland (1829). It refers to preserved faeces and mummy intestinal contents (Callen and Cameron, 1960; Callen, 1965; Heizer and Napton, 1969; Fry, 1977, 1980, 1985; Turpin *et al*., 1986). It includes faecal material preserved either by mineralization or desiccation, from both palaeontological and archaeological contexts (Reinhard and Bryant, 1992).

Coprolites often contain a wide range of macroscopic and microscopic remains that form interrelated data sets that are relevant in reconstruction of diet (Reinhard and Bryant, 1992). Researchers analyse carnivore coprolites because they contain skeletal inclusions (Chin, 2002). Significant information on animal diet (Siegfried, 1984) and past animal-human relationships (Horwitz and Goldberg, 1989) can be obtained from contents of hyaena coprolites. Analysis of faecal material aids in the determination of diet choice (Day, 1966; Stuart, 1976; Putman, 1984), and has been used in several different habitats to establish feeding ecology of several carnivore species (Hoppe-Dominik, 1984; Henschel and Skinner, 1990; Mukherjee *et al*., 1994; Karanth and Sunquist, 1995; Hart *et al*., 1996; Kruger *et al*., 1999).

Many investigators have analysed hyaena coprolites focusing particularly on pollen spectra analysis (Girard, 1987; Scott, 1987; Mills, 1989; Vivent, 1989; Carrion *et al*., 2001; Gonzalez-Samperiz *et al*., 2003; Scott *et al*., 2003). At least

ten hyaena sites in South Africa and four in Spain have been subjected to palynological examination of coprolites (Scott *et al*., 2003). Pollen in hyaena coprolites has also been investigated in other regions such as Israel, Sicily, France and Britain (Sutcliffe, 1969, 1970; Horwitz and Goldberg, 1989; Larkin *et al*., 2000). Pollen analysis of hyaena coprolites has yielded valuable palaeoenvironmental data (Scott and Klein, 1981; Scott, 1987; Gonzalez-Samperiz *et al*., 2003).

In addition to the determination of diet from pollen, some researchers have critically analyzed coprolites for palaeophamacological purposes (Dean, 1993; Chaves and Reinhard, 2006). Other studies have focused on the chemistry, mineralogy and texture of coprolites to infer their biological source and taphonomy (Hollocher *et al.*, 2005). Much more recently, researchers in Brazil have taken a new dimension and embarked on archaeoparasitological analysis of human coprolites (Araujo *et al*., 2000). Analysis of hair in the coprolites revealed a variety of diseases, including head louse infestation. Louse eggs were found on isolated hair shafts dating to over 10,000 years ago (Araujo *et al*., 2000). Numerous scientists have focused on macroscopic and microscopic remains from European human coprolites. In Tehuacan, Mexico, Callen (1967) identified a large number of animals that were consumed basing upon the hairs present in human coprolites. Similar data from southwest Texas coprolites has been documented (Williams-Dean, 1978; Sobolik, 1988). Deer and antelope hairs in human coprolites from Danger cave in Utah were also reported by Jennings (1957).

The existence of hairs from several extinct mammals has been reported from a rich accumulation of fossil excrement from the Late Palaeocene beds of Inner Mongolia, China (Meng and Wyss, 1997). Hundreds of mammalian carnivore coprolites have been reported from this highly unusual depositional occurrence (Hunt, 1992) and fossil hairs from at least four mammalian taxa have been identified with the most notable being the multituberculate *Lambdopsalis bulla* (Chow and Qi, 1978). Fossil hairs in hyaena coprolites were reported in Dabie cave, Jordan, but were not identified (Kempe *et al.*, 2006).

It is unfortunate that fossilized mammalian faeces are rarely recorded, and isolated occurrences are reported in the pre-Pleistocene palaeontological record (Hunt *et al*., 1994). Studying fossil faecal deposits has recently gained popularity as a palaeoecological tool (Poinar *et al*., 1998; Pearson and Betancourt, 2002; Davis, 2005). The analysis of coprolites gives useful indications on palaeoclimate, palaeovegetation and even palaeoethnology (Bryant and Holloway, 1983; Davis, 1990; Scott and Cooremans, 1992; Carrion *et al*., 2000).

1.8.1 *Parahyaena brunnea* scats

Hair is a common feature observed in modern *Parahyaena brunnea* scats (Skinner and van Aarde, 1981). Details of the contents of extant *Parahyaena brunnea* scats are reported by Skinner and van Aarde (1981). They argue that the scats of *Parahyaena brunnea* contain a higher percentage of hair than those of *Crocuta crocuta*, and other researchers suggest that this may be behaviourally linked (Berger *et al*., 2009). Unlike *Parahyaena brunnea*, *Crocuta crocuta* are efficient hunters and scavengers (Kruuk, 1972; Tilson *et al.*, 1980; Henschel and Skinner, 1990; Mills, 1990). *Parahyaena brunnea* scats contain much more hair (Berger *et al*., 2009) because they do not regularly regurgitate indigestible residues of prey. Larkin *et al.* (2000) recognised that the high inorganic content (calcium phosphate) of *Crocuta crocuta* droppings leads to their frequent preservation in the fossil record.

Information on coprolites of *Crocuta crocuta* is abundant in scientific literature. Faeces of modern *Crocuta crocuta* are widely reported, and detailed studies of their content have been made (Skinner, 1976; Mills, 1978; Skinner and van Aarde, 1981; Mills, 1990; Larkin *et al*., 2000). Analysis of hair in modern spotted hyaena scats for the purpose of identifying prey species was first undertaken by Kruuk (1972), who reported human hair scavenged from recently buried corpses. Thereafter, analysis of hair in modern brown hyaena scats was conducted by Skinner (1976), and further investigated and developed by Keogh (1979) in an atlas of hair from southern African carnivores. Unfortunately, hair from scats

contains no information on age, sex or size of the species, hence no further classification is possible (Skinner *et al.*, 1992). Furthermore, faecal analysis is not conclusive on whether the animal was hunted or scavenged.

1.9 *Parahyaena brunnea*

1.9.1 Physical description of extant *Parahyaena brunnea*

The brown hyaena is medium in size, with adults weighing around 40kg (Mills, 1982b). It has long legs with well developed fore-quarters, weak hindquarters and a sloping back (Mills, 1982; Watts and Holekamp, 2007). It is widely regarded as a carnivore (Kuhn, 2011), though it includes some unusual food items in its diet, as discussed later on. Although it is sympatric with the spotted hyaena (*Crocuta crocuta*), it is surprisingly not with its closest relative, the striped hyaena (*Hyaena hyaena*) (Eaton, 1981; Mills, 1982). Brown hyaenas usually have large pointed ears, with their bodies often covered with coarse, brown hair (Skinner, 1976). Length of individual hairs varies. Their legs are striped and the mane around the neck is lighter in colour (Fig 1.5). They live in clans of up to 10 adult animals (Mills, 1990). Their cubs are raised in dens to which they remain partially attached until they are 15 months old (Mills, 1981). The dens are considered to be a social meeting point of the clan members (Wiesel, 2006). Other than at their dens, brown hyaenas are mostly not seen in groups (Wiesel, 2006).



Fig 1.5: An adult male brown hyaena (after Wiesel, 2006).

Fossil remnants of brown hyaenas are reportedly confined to southern Africa (Turner, 1990; Skinner and Chimimba, 2005). The hyaenidae family is remarkable for its ecological and social diversity (Watts and Holekamp, 2007). The distribution, diet, ecology and behaviour of extant *Parahyaena brunnea* have received considerable attention in the scientific literature. The species ecology and its coexistence with *Crocuta crocuta* in the southern Kalahari has been well studied (Mills and Mills, 1978; Mills *et al*., 1980; Mills, 1982a, 1982b, 1983, 1984, 1989, 1990). In the agricultural areas of the Transvaal in South Africa, a detailed account of the species ecology is given (Skinner, 1976; Skinner and Ilani, 1979; Skinner and van Aarde, 1987), while its feeding habits in the central Karoo is reported (Maddock ,1993). *Parahyaena brunnea* ecology has been researched in central Kalahari (Botswana) with particular focus on feeding habits and aspects of its behaviour (Owens and Owens, 1978). This research explores the diet,

behaviour and ecology of Middle Pleistocene *Parahyaena brunnea* in the Sterkfontein Valley between 257 - 195 ka.

1.9.2 Reproduction of extant *Parahyaena brunnea*

Brown hyaenas are born with their eyes closed, their ears bent sharply forward and with the same body colour as an adult, but with shorter hair (Schultz, 1966). Sexual maturity is reached after about 3 years (Mills, 1990). The mean litter size is usually three cubs and all clan members supplement the cub's diet by carrying food back to the den (Mills, 1983). Female brown hyaenas cooperate in raising the cubs by occasionally suckling (Fig 1.6) each other's cubs (Owens and Owens 1979; Mills, 1981) although they give priority to their own offspring (Watts and Holekamp, 2007). Young females usually start breeding at a later stage (Wiesel, 2006) and it is common practice for only one female per clan to have litter at a time. Male brown hyaenas normally remain in the clan or become nomadic, although they are still believed to reproduce with clan females (Mills, 1990). The brown hyaena's lifespan in the wild has not been reported, but can reach over 20 years in captivity (Crandall, 1964, in Mills 1982b).



Fig 1.6: Female hyaena suckling its cubs (after Mills and Hofer, 1998).

1.9.3 *Parahyaena brunnea* territory

Brown hyaenas define their territories with paste marks (Watts and Holekamp, 2007) that are often deposited on grass stalks, bushes or rocks and through defecating in latrines (Fig 1.7). Mills *et al*. (1980) reported that the paste marks are of two types, a white paste, with a long lasting odour, and a black paste with a less long lasting odour. Paste marks and latrines are distributed throughout the brown hyaena's territory and are often used to communicate with other clan members and to warn off intruders (Mills *et al*., 1980; Mills, 1990).



Fig 1.7: Brown hyaena paste mark showing the black and white paste (left) and a brown hyaena latrine on the right (after Wiesel, 2006).

1.9.4 Modern *Parahyaena brunnea* diet

Brown hyaenas are solitary nocturnal foragers that feed on a vast array of food items (Mills and Mills, 1978; Owens and Owens, 1978). They eat almost anything (Sutcliffe, 1970; Kruuk, 1972), although their diet is almost exclusively mammals when these are in abundance (Kruuk, 1972; Mills, 1989). Brown hyaenas are effective scavengers in most ecosystems (Mills and Mills, 1978; Owens and Owens, 1978; Skinner and Smithers, 1990; Lacruz and Maude, 2005; Kuhn, 2006; Kuhn *et al*., 2009, 2010; Kuhn, 2011), where food is patchily distributed and where other large carnivores occur (Wiesel, 2006). They are keen hunters of baboons and other large mammals when rearing cubs (Brain, 1981). Despite this, they are not habitual hunters and their diet usually consists of fruit, insects, reptiles, birds and scavenged mammals (Skinner, 1976; Mills and Mills, 1977; Skinner and van Aarde, 1981; Mills, 1990; Lacruz and Maude, 2005; Maude,

2005; Maude and Mills, 2005), though ostrich eggs (Fig 1.8) are also reported to form part of the brown hyaena diet (Mills and Mills, 1977; Skinner and van Aarde, 1991; Skinner *et al*., 1995).



Fig 1.8: Brown hyaena scavenging an egg from an ostrich nest (photo by Gus Mills in Watts and Holekamp, 2007).

Cape fur seals (*Arctocephalus pusillus pusillus*) were found to be the most important food item for brown hyaenas in the coastal areas of the Namib Desert (Stuart and Shaughnessy, 1984; Skinner and van Aarde, 1991; Skinner *et al*., 1995; Wiesel, 2006). Brown hyaenas on the Namibian coast sometimes kill seal pups (Kuhn *et al.*, 2008; Kuhn, 2011) in the seal colonies (Fig 1.9a and b). They usually kill seals up to a size of a yearling with only one bite to the head (Skinner *et al*., 1995; Wiesel, 1998). Kruuk (1976) has recognised that hunting is often poorly developed and a rather "primitive chase and grab affair" for brown hyaenas.



Fig 1.9: (a) Brown hyaena hunting a seal pup (after Kolar, 2004).



(b) Brown hyaena lifting a hunted seal pup away from a seal colony (after Wiesel, 2006).

Although they depend heavily on seals as a primary food source, both as carrion and by killing seal pups (Skinner *et al*., 1995; Wiesel, 2006), brown hyaenas

sometimes supplement their diet with other food items washed up along the beaches. Their diet can also consist of any food items found in the inland areas of their home range, especially outside the seal pupping season. Brown hyaenas along the west coast of southern Africa are reported to feed on marine animals such as crabs, fish, birds and any other mammals which have been cast up on the seashore (Roberts, 1954; Shortridge, 1934).

In the Makgadikgadi National Park (Botswana), carcasses of zebra, wildebeest and springbok were found to be their most important food source (Maude, 2005). Common ungulates (gemsbok, wildebeest, hartebeest, springbok and steenbok), spring hare, bat eared fox, and black-backed jackal are predominantly eaten by brown hyaenas in the southern Kalahari (Mills and Mills, 1978). The diet of brown hyaenas in the central Kalahari is similar to that in the southern Kalahari, except that giraffe occurs there and is often scavenged (Owens and Owens, 1978). In the Transvaal agricultural areas of South Africa, cattle in the form of carrion and small indigenous mammals are highly consumed by brown hyaenas (Skinner, 1976).

1.10 Summary

Hair identification provides a wealth of information in many fields of research, with scale patterns and hair cross sectional shapes being important defining features in the identification of taxa. Ancient mammalian hairs can be an important data source for understanding palaeobiology, palaeoecology and

palaeoanthropology, but fossil hair identification is complex and involves many ambiguities, mostly caused by destructive taphonomic processes that may alter or obliterate diagnostic features. Nevertheless, in light of the fact that numerous researchers have successfully identified the taxonomic origin of ancient hair from different preservation contexts, this research seeks to identify fossil hairs extracted from well-preserved *Parahyaena brunnea* coprolites, from Middle Pleistocene deposits in Gladysvale cave, South Africa.

Coprolites are the most notable dietary remains recoverable from archaeological contexts. They are of critical importance because they contain remains that were actually consumed and defecated, hence significant information on past animal-human relationships and animal diet can be obtained from their contents.

CHAPTER TWO

MATERIALS AND METHOD

2.1 Background to hair morphology and identification

The hair scale patterns formed by the cuticle, and hair cross sectional shapes formed by the cortex and medulla, are important characteristics that are utilized by researchers in the identification of mammalian species. Longitudinal section has also been shown to be an important distinguishing feature (Hess *et al*., 1985), but cannot be applied to most fossil hairs as these are preserved as high resolution casts of external structure only.

The correct identification of hair is done using determination keys that are based on macroscopic features such as size, shape, profile and colour of the hair, as well as microscopic characteristics of the cuticle, cortex and medullar (Teerink, 2003). The identification is however difficult because of the presence of considerable variation caused by differences in species, breed and gender of the animals, environmental conditions (climate, habitat, nutrition) and possibly by the body region from which the hairs derive (Wildman, 1954; Appleyard, 1960; Herrmann *et al.*, 1996a; Herrmann *et al*., 1996b; Meyer *et al.*, 2000). Hair identification is further complicated because of the variety of hair types produced by a single animal. There are also structural variations along a single hair and dissimilar animals may have hairs with a similar structure (Marshall *et al*., 1977).

Most hair types consist of three layers of keratinized cells (Day, 1966; Homan and Genoways, 1978). These are the cuticle which is the outer layer, the cortex forming the middle layer, and the medulla resulting in the inner layer (Ryder and Stephenson, 1968; Teerink, 2003). These morphological regions form the hair structure patterns and cross sectional shapes that are of taxonomic significance in hair identification of mammals. The basic structure of hair is shown schematically in Fig 2.1

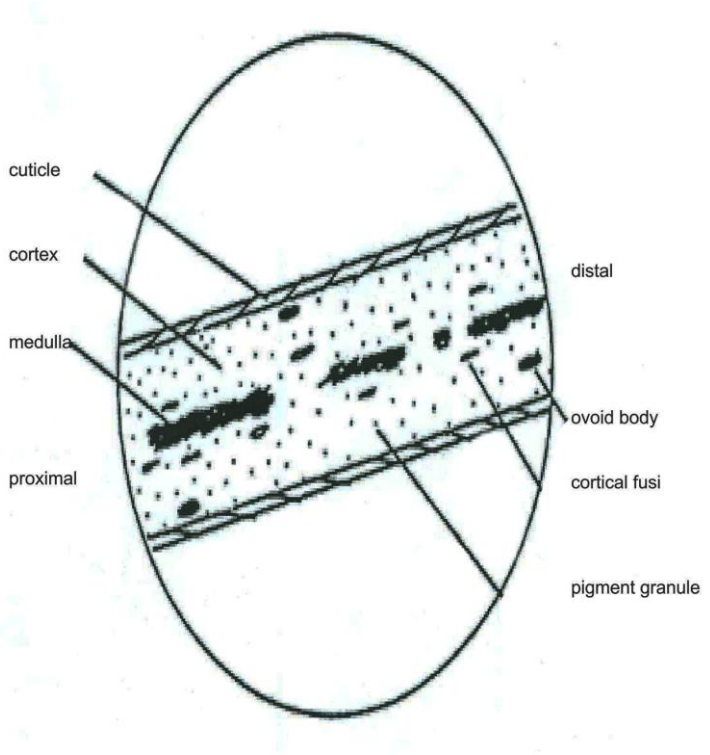


Fig 2.1: Basic structure of hair (after Deedrick and Koch, 2004).

The hair cuticle consists of an overlapping single layer, although it may appear to have multiple layers in cross or oblique section (Morioka, 2009). Furthermore, keratinization of the hair cuticle proceeds with the accumulation of highly

electron-dense granules at the distal side of the cytoplasm (Morioka, 2009). The hair cuticle appears to have a "stone-wall" construction and is sometimes called the exocuticle (Powell and Rodgers, 1997). The primary function of the cuticle is protection of the hair (Rudall, 1941). The medulla occurs in most mammals (Bradbury and Leeder, 1970) but is absent in some types of hair (Inagaki, 1986) such as vellus (fine body) hair from humans (Bisbing, 2002), fine wool fibres from sheep (Bacha and Wood, 1990) and pig hair (Fawcett, 1986). The medulla is the central portion of the hair shaft and is made up of cells of various shapes, which are often interspaced with air pockets (Homan and Genoways, 1978). The presence and patterns of these cells have been used to distinguish various kinds of hair (Hausman, 1920, 1944; Day, 1966; Mayer, 1952). The cortex is the main body and middle layer of the hair shaft composed of elongated and fusiform (spindle-shaped) cells (Hausmann, 1932; Homan and Genoways, 1978). The fusiform or spindle-shaped cells interdigitate with each other along the long axis of the hair shaft (Homan and Genoways, 1978).

2.2 Cuticular scale features

The cuticular scale features of mammalian hair have been widely studied (Hausman, 1930). Hair cuticular scales can vary greatly between taxa in many ways, and can be of taxonomic significance, thus aiding identification (Backwell *et al*., 2009). Brunner and Coman (1974) reviewed the subject of hair scale patterns and described in detail their own replica methods in a large number of indigenous Australian mammals.

Hair scale patterns provide most of the diagnostic characteristics for identifying hair samples (Bower and Curry, 1983) but Short (1978) argues that these cuticular scale patterns are only important as an accessory to other characters he considered of greater diagnostic importance. Among these characters are cross sectional form and medullar form. Short (1978) also reports that identification to species level cannot be achieved using scale form alone, but only if a variety of characters are used. Hence in this study, I employ both scale patterns and details from the cross sections when these were available.

Teerink (2003) recognizes that the scale position in relation to the longitudinal direction of the hair may be transversal, longitudinal or intermediate, whilst the scale patterns can be varyingly petal-shaped, wavy, mosaic or transitional (Fig 2.2). Keogh (1983) reports that the most common hair scale patterns of southern African mammals are mosaic, chevron, coronal and petal-shaped. The scale margins are described as smooth, rippled or frilled, and relative to hair width, the scales could be large and few, or many and closely packed. The texture of these patterns varies greatly between species of mammals and may also vary along a single hair (Perrin and Campbell, 1980).

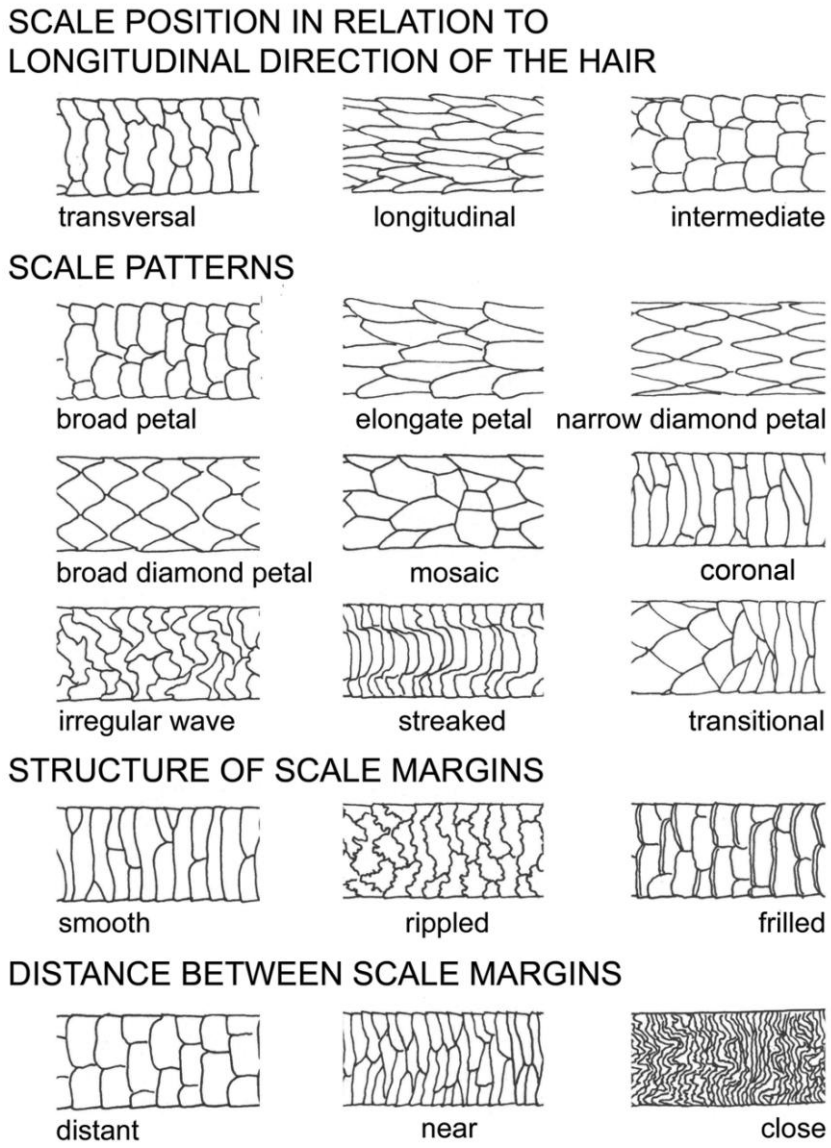


Fig 2.2: Cuticular scale features used in identifying hair (modified after Teerink, 2003).

2.3 Cross-sectional shapes

The most common cross sectional shapes are circular, oval, oblong and concavo-convex (Fig 2.3). These different shapes, together with scale patterns are used to identify fossil hairs from *Parahyaena brunnea* coprolites in this research.

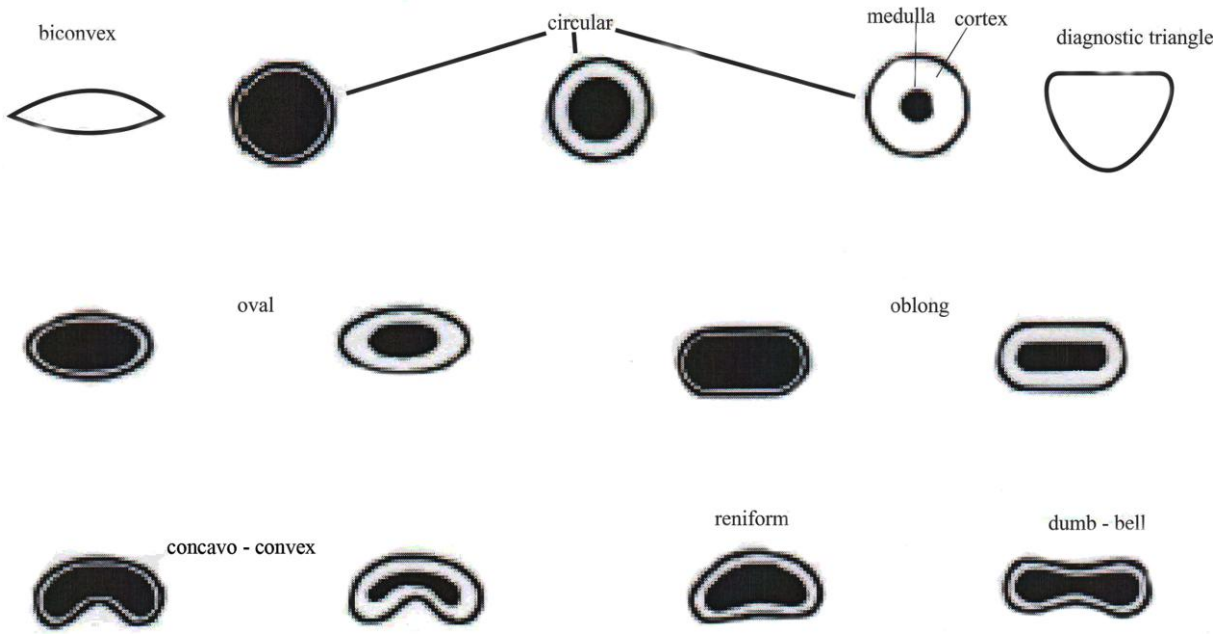


Fig 2.3: Common hair cross sectional shapes (modified after Keogh, 1983).

The recovery of mitochondrial DNA from single ancient hairs has recently enabled the genetic identification of specimens (Bonnichsen *et al*., 2001; Gilbert *et al*., 2004). Despite this, a significant number of researchers have continued to rely on hair scale patterns, among them are Van den Broeck *et al*. (2001), Dove and Peurach (2002), Chang *et al.* (2005), Backwell *et al.*(2009) and Sahajpal *et al*. (2008, 2009).

Definitive taxonomic identification is usually difficult because of variations in hair structure along the length of individual hairs (Keogh, 1979), as well as different hair types on an individual animal (long stiff guard/overhair, versus thinner undulating underhair). Nevertheless, correct identification of hair is possible by studying hair morphological features, which are quite distinct and

characteristic in several species (Feder, 1987; Langley and Kennedy, 1981; Wortmann *et al*., 1989; Teerink, 2003).

2.4 Techniques for studying hair morphology

The examination of scale patterns of the cuticle and medullary shapes of hairs usually involve conventional histological sectioning and specific techniques such as cuticular casting and medullary impregnation (Wildman, 1954; Teerink, 2003). Most studies on mammalian hair identification were done using plastic impressions of cuticular scales and direct observation of whole mounts using light microscopy (Mayer, 1952; Benedict, 1957; Dweyer, 1962; McFadden, 1968; Brunner and Coman, 1974; Homan and Genoways, 1978; Valente, 1983; Oli, 1993; Wallis, 1993) whilst others have used transmission electron microscopy (TEM) (Birbeck and Mercer, 1957a, 1957b; Nakai, 1964; Hayat, 1985; Morioka, 2009).

The use of optical light microscopy (OLM) gives poor topographic resolution of hair features. TEM provides better resolution (Verhoeven, 1972) which is however sometimes affected by spherical aberrations resulting in imperfection of images. It requires constant upkeep by maintaining voltage, current to the electromagnetic coils and cooling water. However, many previous investigators have successfully used the scanning electron microscope (SEM) to observe the surface structure and scale patterns of the cuticle (Dziurdzik, 1978; Short, 1978;

Vogel and Kopchen, 1978; Homan and Genoways, 1978; Riggot and Wyatt, 1983; Hess *et al*., 1985; Quadros and Monteiro-Filho, 1998; Kondo, 2000; Kondo *et al*., 2000; Dove and Peurach, 2001; Van den Broeck *et al*., 2001; Amman *et al*., 2002; Chang *et al*., 2005; Sahajpal *et al*., 2008; Backwell *et al*., 2009; Sahajpal *et al*., 2009). The scanning electron microscope allows direct observation at high magnification permitting imaging specimens with high level of detail (Teerink, 2003). This technique is also relatively simple and fast, and shows unique three-dimensional information (Van den Broeck *et al*., 2001).

Recently, attempts have been made in using pattern recognition computer programmes to aid in the identification of species from hair scale patterns. While methods relevant to this application are found in other fields such as aquaculture (Yang and Chou, 2000), medicine (Forero *et al*., 2004) and biometrics (Sanchez-Avila and Sanchez-Reillo, 2005), current hair pattern recognition programmes lack the necessary comparative hair data, so at this stage cannot be used as a hair identification technique.

DNA extraction is one of the most reliable techniques used to identify hair samples. However, compared to other tissues, the DNA content of hair (Higuchi *et al*., 1984; Allen *et al*., 1998) is typically low because hair cells undergo dehydration and catabolic breakdown of nucleic acids during keratinisation (Forslind and Swanbeck, 1966). In addition, levels of amplifiable mitochondrial DNA decrease as the hair degrades (Gilbert *et al*., 2004). Because of this, ancient

hair specimens have not been widely used as a source of ancient DNA. Furthermore, ancient DNA studies have been plagued by problems and limitations that have made gaining insights into the past rare and sometimes very controversial (Gill *et al.*, 1994; Krings *et al.*, 1997; Greenwood *et al.*, 2001; Orlando *et al.*, 2003; Mohandesan *et al.*, 2008). After decades of research using biomolecules, authentic ancient sequences could not be produced because of many reasons including low DNA concentrations in the samples, problems of contamination and DNA damage (Greenwood, 2009).

Despite this, researchers have successfully extracted mitochondrial DNA from degraded and ancient hair samples from century old native American Indian populations (Baker, 2001), including burnt specimens (Baker *et al.*, 2001), wool from a 9,400 year old Bighorn sheep (Bonnichsen *et al.*, 2001) and permafrost-preserved bison (*Bison bison*) dating to over 64,800 years old (Gilbert *et al.*, 2004). Because of this, hair is a promising source of DNA for both forensic and ancient DNA studies (Thomas *et al.*, 2006).

2.5 Analytical protocol used in this study

2.5.1 Scanning electron microscopy

In accordance with previous studies, scanning electron microscopy (SEM) was used in this research to document modern hair samples and facilitate taxonomic identification of fossil hair specimens (Reinhard and Bryant, 1992). The use of

scanning electron microscopy for mammalian hair studies has numerous advantages which far surpass other techniques. It provides the best topographical resolution of hair features. It is also renowned for its ability to elucidate any peculiarities of the surface structure of hair (Homan and Genoways, 1978), and is efficient to the extent of determining variation of scale patterns along the length of a single hair (Meng and Wyss, 1997). For these reasons, the FEI Quanta 400 E SEM in the Microscopy and Microanalysis Unit at the University of the Witwatersrand was used in this research to observe the scale patterns of the cuticle and the cross sectional shapes of the medulla and cortex.

2.5.2 Operation principle of the scanning electron microscope

The scanning electron microscope uses a focused beam of high-energy electrons to generate signals at the surface of the specimen (Goldstein, 2003). The signals that derive from electron-sample interactions reveal information about the sample, in this case the external morphology of hair. Accelerated electrons in the scanning electron microscope carry significant amounts of kinetic energy which is dissipated as signals produced by electron-sample interactions when the incident electrons are decelerated in the solid sample (Voutou and Stefanaki, 2008). These signals include secondary electrons which produce images and backscattered electrons which escape from the surface of the sample having energy of ≥ 50 eV (Voutou and Stefanaki, 2008).

It should be noted, however, that scanning electron microscopy has its own share of problems that lie in the mechanism of contrast production. The contrast effects in the scanning electron microscope are due to differences in secondary electron emission or to contour effects on the surface of the specimen (Carr, 1970). Back scattered electrons cause background radiation and thus a smaller degree of contrast. However, the contrast can be slightly increased electronically.

2.5.3 Fossil hair analysis

In this research, a 75 x 30 x 15 cm block of the calcified latrine was taken from Gladysvale cave for laboratory analysis. From this block, 12 coprolites were studied (Table 2.1). The coprolites varied in size, with larger scats approximately 32 mm in diameter (Fig 2.4). The number of coprolites analysed in this study is sufficient to determine the diet of *Parahyaena brunnea* because previous diet descriptions were successfully attained with as few as 10 scats (Bartoszewicz and Zalewski, 2003; Olesiuk *et al*., 1990; Patterson *et al*., 1998; Pontier *et al*., 2002; Sinclair and Zeppelin, 2002; Zabala and Zuberogoitia, 2003).

Table 2.1: Coprolites from Gladysvale cave analysed in this study.

Coprolite specimen number	Diameter (mm)	Shape	Number of fossil hairs extracted
C1	21	ovoid	4
C2	19	ovoid	5
C3	8	ovoid	2
C4	11	spherical	4
C5	10	spherical	3
C6	15	spherical	5
C7	20	spherical	4
C8	32	spherical	7
C9	19	spherical	4
C10	18	spherical	4
C11	10	ovoid	3
C12	8	spherical	3

Key: C1 - C12 refers to coprolite specimen number 1-12.

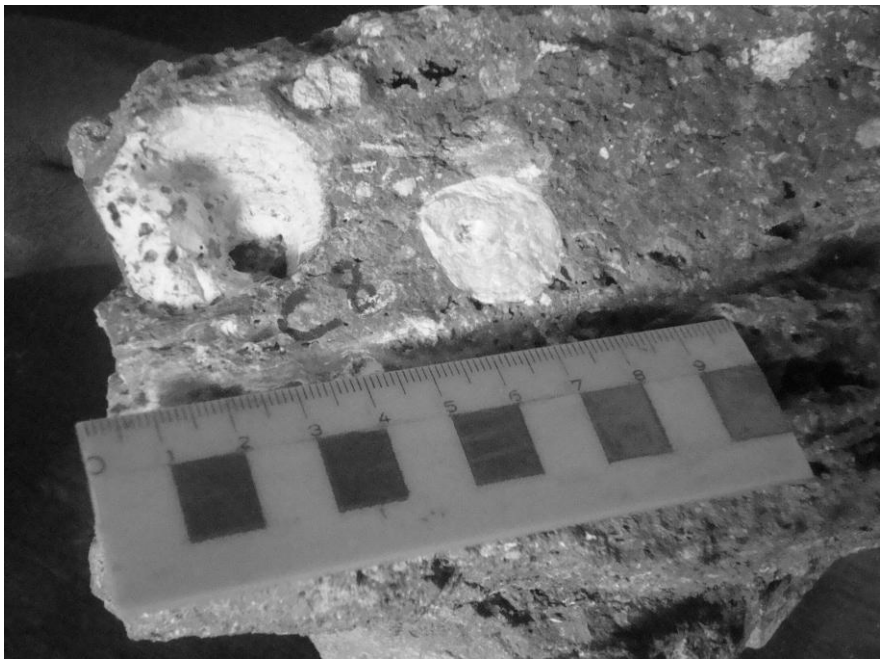


Fig 2.4: Block of calcified cave sediment containing part of the hyaena latrine, showing the largest coprolite analysed in this study (C8). Scale bar = 10 cm.

Forty-eight fossil hairs were extracted from the coprolites using fine tweezers and a low magnification binocular microscope. Thereafter, they were ultrasonically cleaned in analar ethanol and placed directly onto double-sided sticky stubs. The fossil hairs were sputter-coated with gold and examined using an FEI Quanta 400 E scanning electron microscope. Gold is an electrically conductive coating which is most effective for high resolution electron imaging applications. Carbon coating was not done because it is most desirable during elemental analysis of samples. Fossil hair cross sections, where permitting, were obtained from naturally occurring breaks in the sample and could not be obtained by cutting perpendicularly using a sharp surgical blade because the hairs were preserved as casts of external and not internal morphology and could easily break. The coprolitic residues were kept safely for possible further analysis. Table 2.2 gives a summary of coprolites analysed in this research as well as the fossil hairs that were extracted from these coprolites and whose scanning electron micrographs are shown in the Results Chapter. Because previous investigations detected no protein in fossil hairs from *Parahyaena brunnea* coprolites from Gladysvale cave (Backwell *et al*., 2009), DNA analysis was not attempted as part of this research.

Table 2.2: Coprolites from which fossil hairs were collected.

Coprolite specimen number	**Fossil hair specimen number**
C1	F_1
C2	F_2 and F_3
C3	F_4
C4	F_5 and F_6
C5	F_7
C6	F_8
C7	F_9
C8	F_{10}, F_{11} and F_{12}
C9	F_{13}
C10	F_{14}
C11	F_{15} and F_{16}
C12	F_{17}

Key: C1 - C12 refers to coprolite specimen number 1-12, and $F_1 – F_{17}$ refers to fossil hair specimen number 1-17.

Previous researchers have extracted hairs from long dried faecal samples using a softening agent (Sodium hydroxide and disodium EDTA) (Samuels, 1965), while others soaked coprolites in a 0.5% aqueous solution of trisodium phosphate (Callen and Cameron, 1955). Soaking for a week or more frequently allows the coprolite to fall apart naturally (Callen, 1963). However, softening agents have the potential to further degrade the cuticula scale pattern, thereby presenting difficulties in identification. For this reason, I deliberately excluded softening

agents in extracting fossil hairs from *Parahyaena brunnea* coprolites from Gladysvale cave.

2.6 Modern hair analysis

2.6.1 Modern comparative collection

Guard hair samples occurring on the animal's back were collected from 15 modern mammals housed at the Ditsong National Museum of Natural History (formerly Transvaal Museum) in Pretoria, and from the Johannesburg Zoo. The selection of these 15 animals (Table 2.3) was based on known Middle Pleistocene riverine forest-fringe and open grassland fauna of the Florisian Land Mammal Age (Klein, 1980, 1984) reported for the Sterkfontein Valley (Lacruz *et al.*, 2002; Lacruz *et al.*, 2003), which may have been preyed upon by hyaenas and which are not represented in hair identification literature. Reference keys are limited to fully grown guard hairs (Bonnichsen *et al*., 2001; Teerink, 2003), so these were sampled from the various pelts, and stored in labelled sealed containers.

Table 2.3: Modern comparative mammals from which guard hair samples were collected.

Order	Genus	Species	Common Name
Perrisodactyla	*Diceros*	*bicornis*	Black rhinoceros
	Equus	*quagga (formerly burchelli*)	Burchell's zebra
Artiodactyla	*Antidorcas*	*marsupialis*	Springbok
	Aepyceros	*melampus*	Impala
	Tragelaphus	*strepsiceros*	Greater kudu
	Connochaetes	*gnou*	Black wildebeest
	Connochaetes	*taurinus*	Blue wildebeest
	Syncerus	*caffer*	Cape buffalo
	Taurotragus	*oryx*	Eland
	Phacochoerus	*aethiopicus*	Warthog
	Raphicerus	*campestris*	Steenbok
Lagomorpha	*Lepus*	*saxatilis*	Scrub hare
	Pronolagus	*crassicaudatus*	Red rock hare
Hyracoidea	*Procavia*	*capensis*	Rock dassie
Tubulidentata	*Orycteropus*	*afer*	Aardvark

2.6.2 Cleaning of modern hair samples

A variety of techniques have been employed for cleaning, drying and mounting modern hair samples for the purpose of examining the cuticular scale patterns, and

this varies from one researcher to another (Keogh, 1979). Trevor-Deutch (1970) as reported by Keogh (1979), washed hairs in carbon tetrachloride. Brunner and Coman (1974) used an alcohol-ether mixture to clean hairs and dried them between absorbent paper. Some researchers have used acetone (Homan and Genoways, 1978; Hess *et al*., 1985; Takizawa *et al.*, 1998; Bahuguna and Mukherjee, 2000), whilst others have used graded ethanol series and isoamyl acetate (Chang *et al*., 2005) to clean modern hair samples. Wilson *et al* (2007) obtained hair samples from both field and laboratory 'burials' and simply rinsed them in 70% alcohol before examining them using scanning electron microscopy.

According to Keogh (1979), the most satisfactory method of cleaning hairs is by washing them in a mixture of absolute alcohol and sulphuric ether in equal proportions. Following Keogh, a mixture of absolute alcohol and sulphuric ether in equal proportions was used for cleaning the modern comparative samples in this research. The hairs were washed in distilled water for about three minutes and then air dried on a clean watch glass. Finally, the hairs were mounted on stubs, sputter-coated with gold, and examined using an FEI Quanta 400 E scanning electron microscope at magnifications between 400 and 4,050 times. This range falls comfortably within that used by previous authors (e.g. Keogh, 1979 ; Perrin and Campbell, 1980; Keogh, 1983, Backwell *et al*., 2009), so comparison is to scale. To obtain cross sections, the modern hair samples were put on a clean watch glass and cut from a perpendicular position using a sharp surgical blade. All

samples were clearly labelled, details recorded and stored in sealed dust-proof containers for future use and reference.

2.7 Hair identification features and definitions

Hair identification was based on consultation of standard guides to hair identification by Appleyard (1978), Keogh (1979) and Teerink (2003), as well as the work by Backwell *et al.* (2009) on southern African primates and my own collection of 15 taxa of modern mammal hairs (Table 2.3). Descriptions of scale and cross-sectional morphology of hair follow those of Hausman (1930), Lyne and MacMahon (1951), Appleyard (1978), Keogh (1983; Figure 2.3) and Teerink (2003; Figure 2.2). Table 2.4 provides definitions of the most common scale patterns used in the literature.

Table 2.4: Descriptions of scale patterns used in the text. Adapted and modified from Keogh (1979) and Teerink (2003).

Scale pattern	**Description**
Coronal	Scale pattern is often composed of a single scale but can occasionally be two or more across hair width. The scales are usually evenly spaced.
Mosaic	This is a pattern made up of a number of scales which can be regular or irregular. In a regular mosaic, the scales are nearly the same size. In an irregular pattern, the scales are randomly distributed and are of different size.
Elongate petal (also known as Lanceolate-pectinate)	This is a comb like pattern in which the scales are long and narrow, and the pattern is in between the broad and diamond petal pattern

It is important to mention that the majority of scale patterns are generally waved but to different extents. The waved patterns are described as regular or irregular waved. Keogh (1975) defines a regular waved pattern as one in which the waves nearly have the same amplitude and wavelength, and an irregular wave pattern as the one in which the amplitude and wavelength are different and there is an abrupt change on the wave sequence. Although the distance between scale margins is a distinguishing feature, it is difficult to quantify and is only a qualitative measure (Keogh, 1979). Brunner and Coman (1974) define scale margin form as the free distal edge of an individual scale. The form of scale margin can be smooth in which the scales show no indentations and appear as a smooth line or rippled in which there are small indentations along the margins, usually close together (Teerink, 2003).

CHAPTER 3

RESULTS

3.1 Introduction

This chapter presents the scanning electron micrographs and descriptions of 15 previously undocumented modern southern African mammal hair taxa (Fig 3.1 to Fig 3.15), as well as those of fossil hairs from coprolites in Gladysvale cave (Fig 3.16 to Fig 3.33). For comparative purposes, all the images shown have scales ranging from 10 µm to 100 µm. Using exactly the same scale for each hair specimen did not always result in clear images of the scale patterns. During scanning electron microscopy analysis of the hair samples, I learnt that this range of scale (10 µm to 100 µm) allows for fair independent assessment of various hair samples. Taxonomic identification of fossil hairs is mainly based on scale pattern and where available, cross sectional data, following the terms used to describe modern hairs (see Table 3.1).

3.1.1 Scanning electron micrographs of modern comparative hair samples

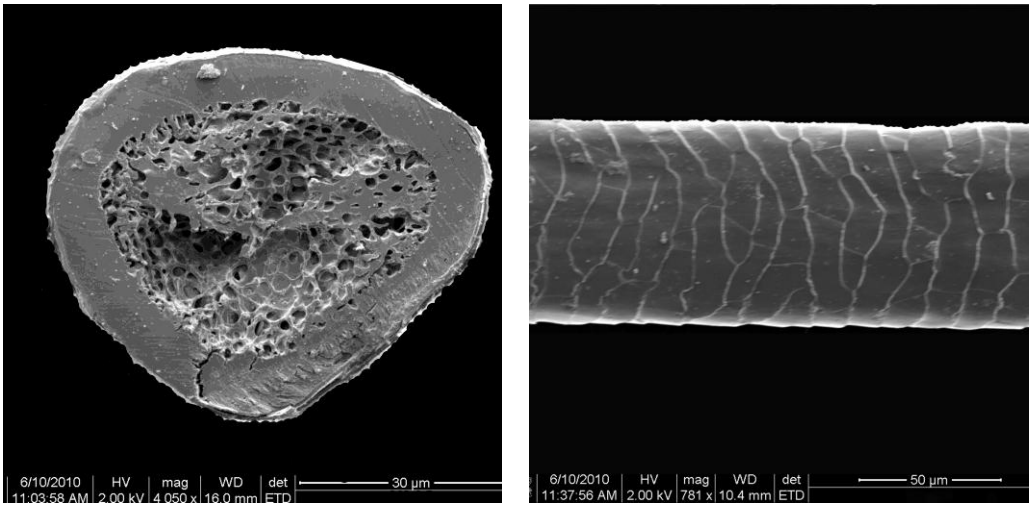


Fig 3.1: Impala hair cross section (left, scale = 30 µm) and scale pattern (right, scale = 50 µm). Unlike the common shapes used in identification, the cross section is a diagnostic triangle with blunted corners. The cortex is thick and the medulla has numerous small perforations. The scales are transverse 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.

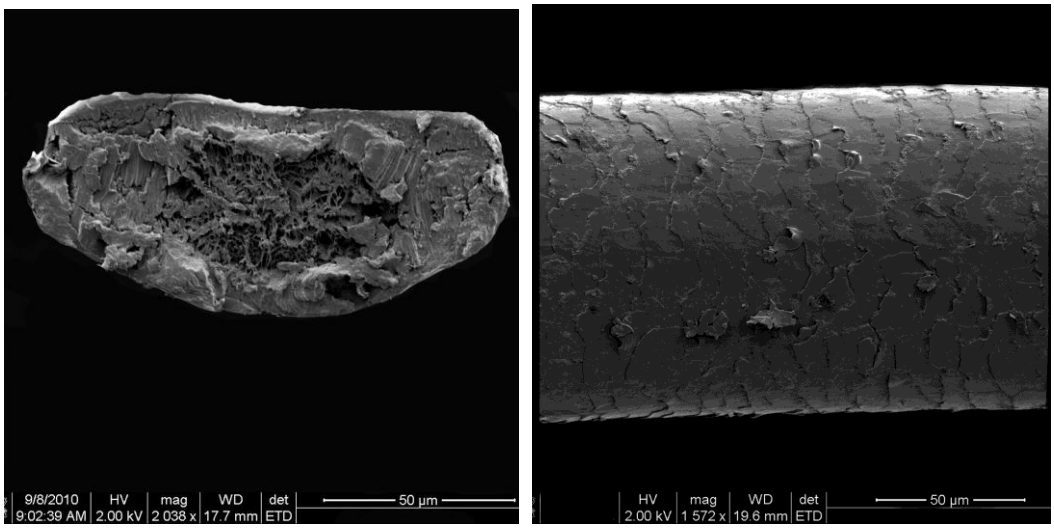


Fig 3.2: Blue wildebeest hair cross section (left, scale = 50 µm) and scale pattern (right, scale = 50 µm). The cross section is concavo-convex. The cortex is thick and the medulla is small to

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.

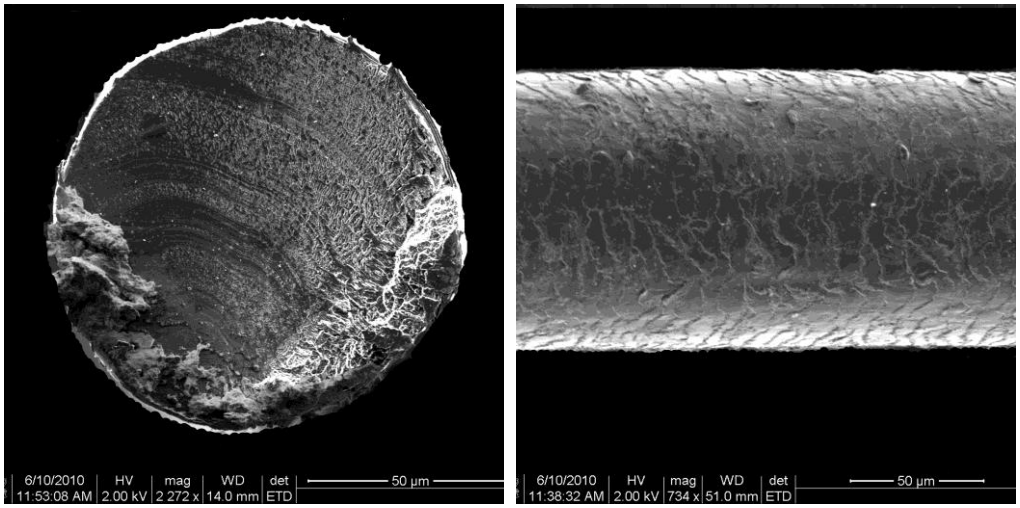


Fig 3.3: Black wildebeest hair cross section (left, scale = 50 µm) and scale pattern (right, scale = 50 µm). The cross section is circular and the cortex is thick with no distinct medulla. The scale position is transversal and the pattern is irregular waved. Scale margins are moderately rippled and the distance between scales is near.

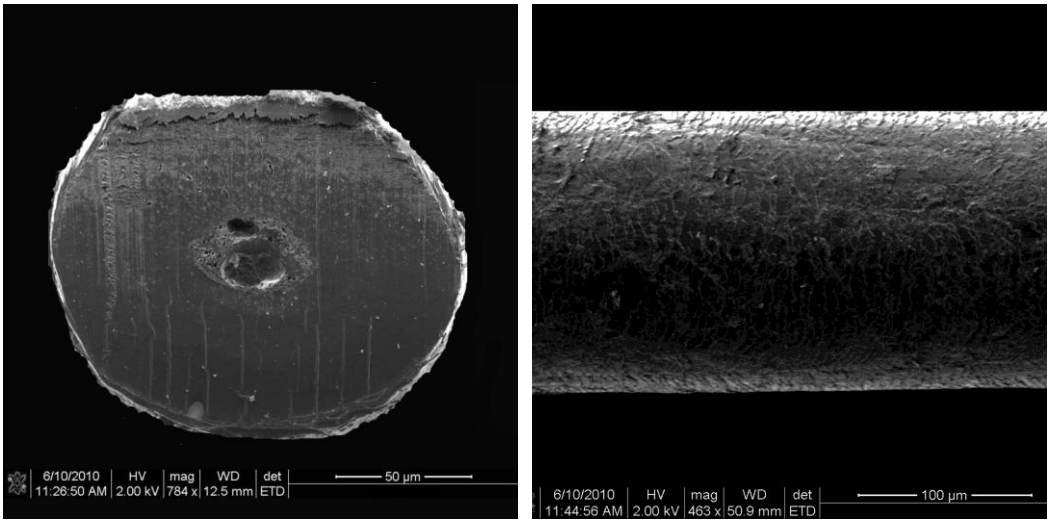


Fig 3.4: Buffalo hair cross section (left, scale = 50 µm) and scale pattern (right, scale = 100 µm). The cross section is circular and there is a relatively small medulla. The scales have a highly irregular waved pattern and the scale margins are rippled. The distance between scales is close.

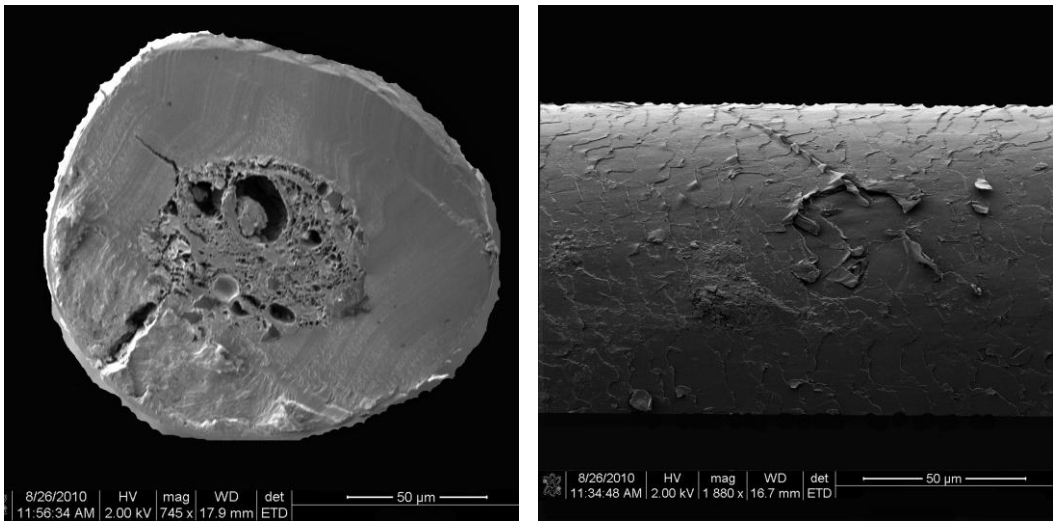


Fig 3.5: Eland hair cross section (left, scale = 50 µm) and scale pattern (right, scale = 50 µm). The cross section is generally circular tending to oval. The cortex is very thick and the medulla is small to medium in size. The scale pattern is irregular waved mosaic and the scale margins are moderately rippled. The distance between scales is near.

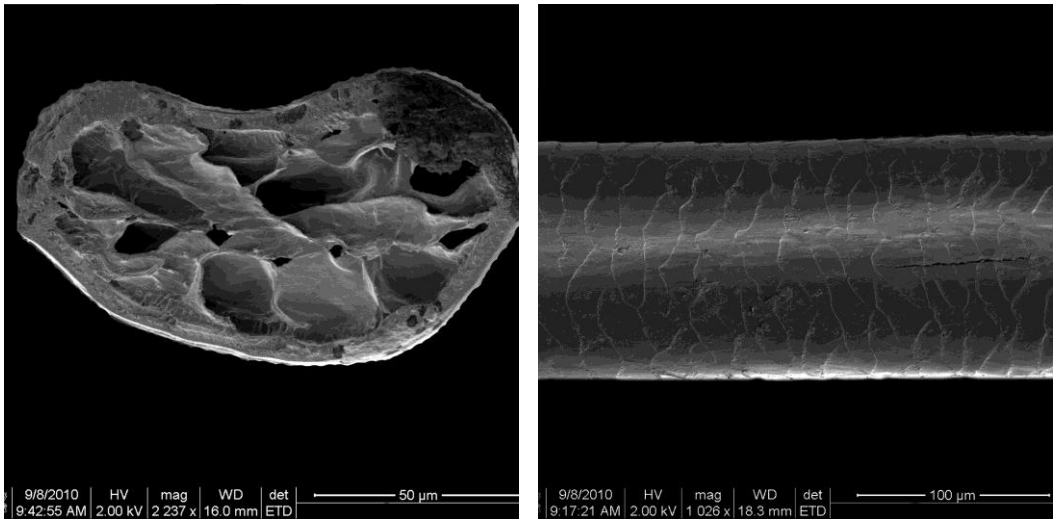


Fig 3.6: Steenbok hair cross section (left, scale = 50 µm) and scale pattern (right, scale = 100 µm). The cross section is generally reniform tending to concavo-convex. The medulla is very large and spongy. The scales are transversal and the scale pattern is regular waved mosaic. Scale margins are smooth and the distance between scales is near to distant.

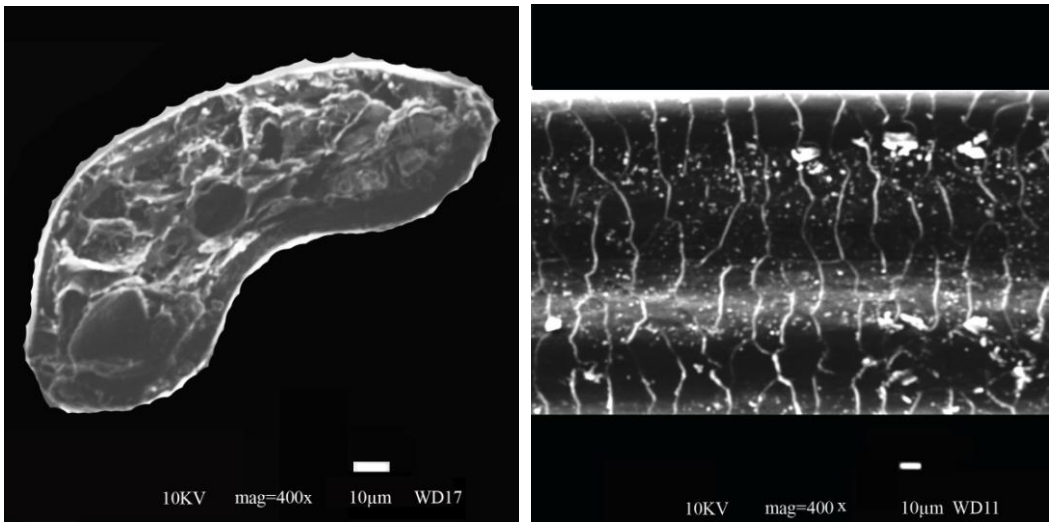


Fig 3.7: Springbok hair cross section (left, scale = 10 µm) and scale pattern (right, scale = 10 µm). The cross section is concavo-convex and the medulla is large. Scale pattern is regular waved mosaic and the scale margins are smooth. The distance between scale margins is near.

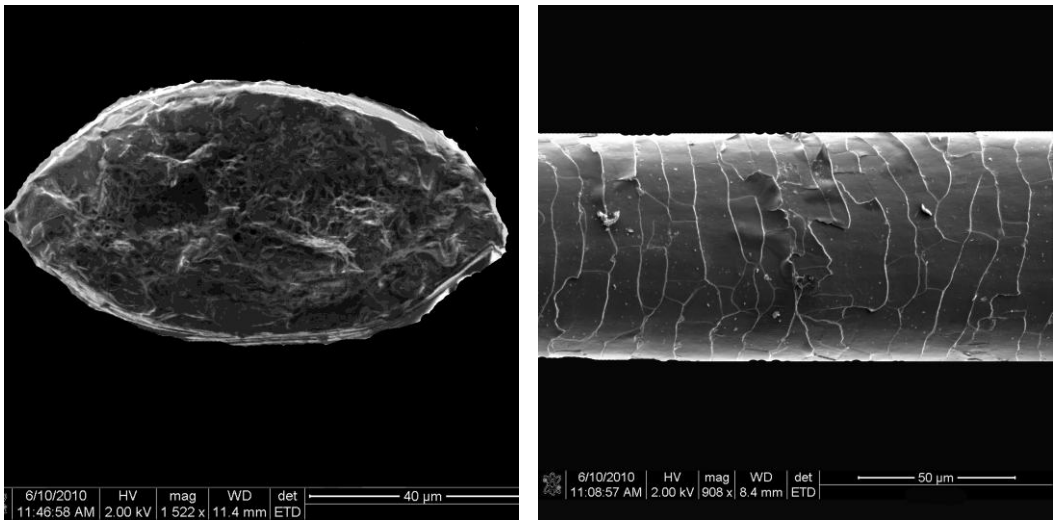


Fig 3.8: Kudu hair cross section (left, scale = 40 µm) and scale pattern (right, scale = 50 µm). The cross section is generally biconvex. The medulla is large but not distinct. The cortex is thin. Scale pattern is irregular waved mosaic and scale margins are generally smooth. The distance between scales is near to distant.

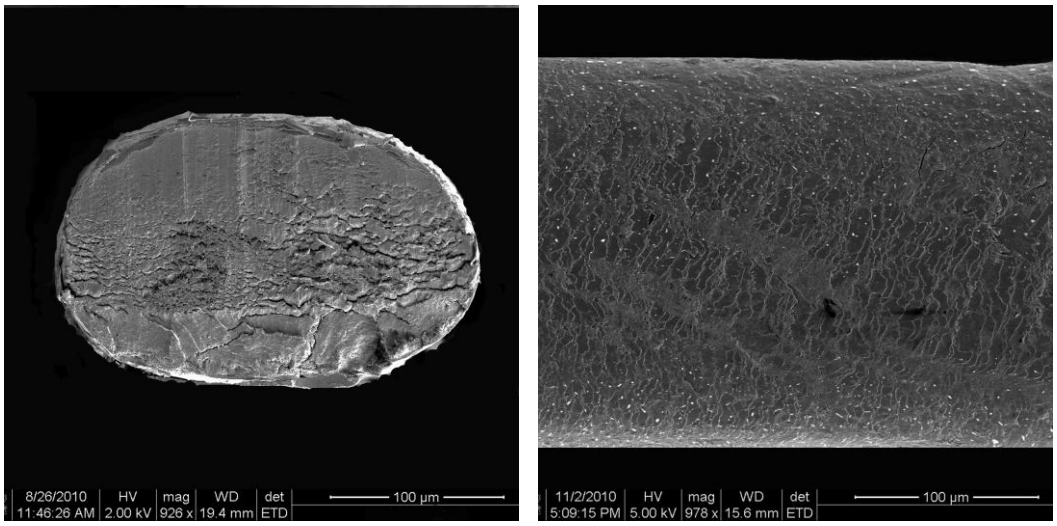


Fig 3.9: Warthog hair cross section (left, scale = 100 µm) and scale pattern (right, scale = 100 µm). The cross section is oval. Scale pattern is highly irregular waved mosaic. The scale margins are rippled and the distance between scales is close.

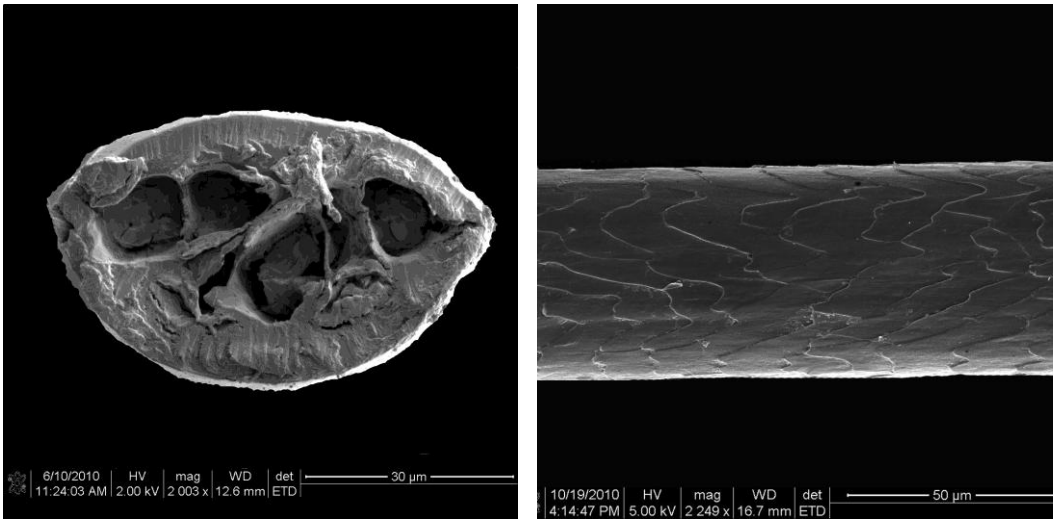


Fig 3.10: Scrub-hare hair cross section (left, scale = 30 µm) and scale pattern (right, scale = 50 µm). The cross section is generally biconvex to oval. The medulla usually contains a few large cavities. The scales form a comb-like pattern called lanceolate pectinate. The distance between scales is distant and scale margins are moderately rippled.

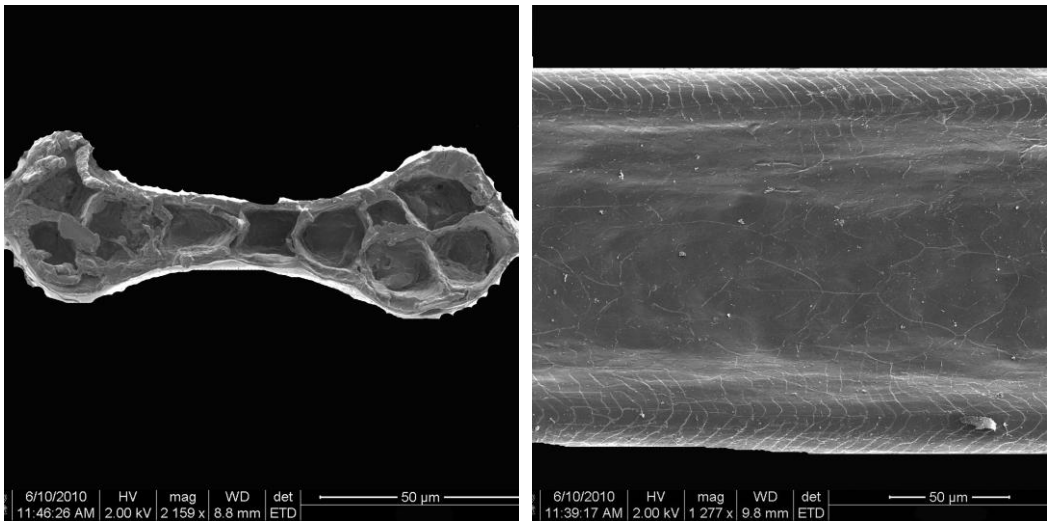


Fig 3.11a: Red rock hare hair cross section (left, scale = 50 µm) and scale pattern (right, scale = 50 µm). The cross section is dumb-bell shaped. The medulla usually contains ten large cavities and occasionally more (see Fig 3.11b). There is a broad, deep groove along the length of the hair. Both sides of the groove show a coronal scale pattern. The distance between scales is near and the scale margins are smooth.

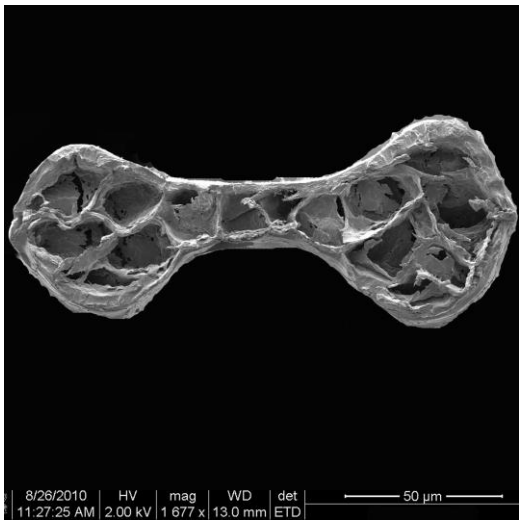


Fig 3.11b: Red rock hare hair cross section containing more than ten perforations (scale = 50 µm).

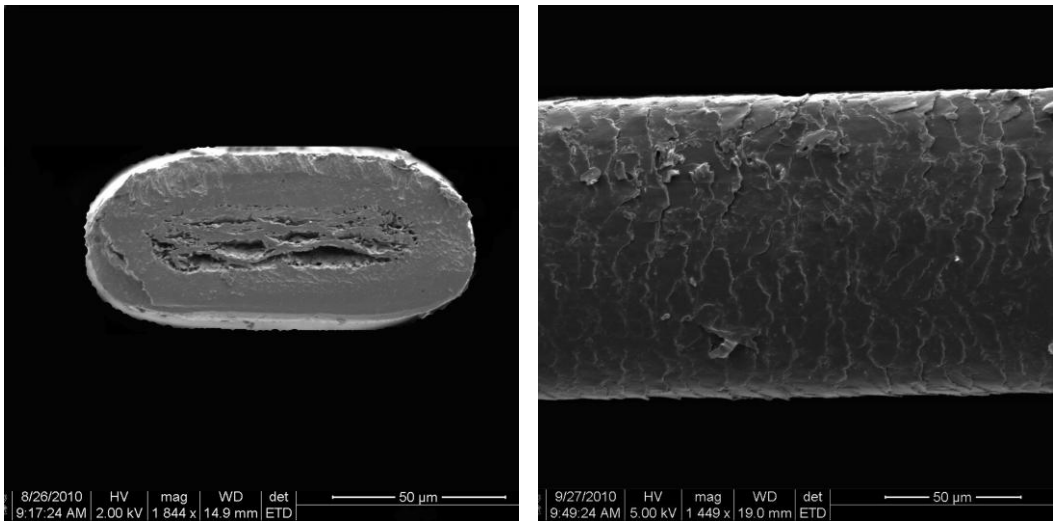


Fig 3.12: Burchell's zebra hair cross section (left, scale = 50 µm) and scale pattern (right, scale = 50 µm). The cross section is oblong. Scale pattern is irregular waved mosaic and the scale margins are rippled. The distance between scale margins is near to close.

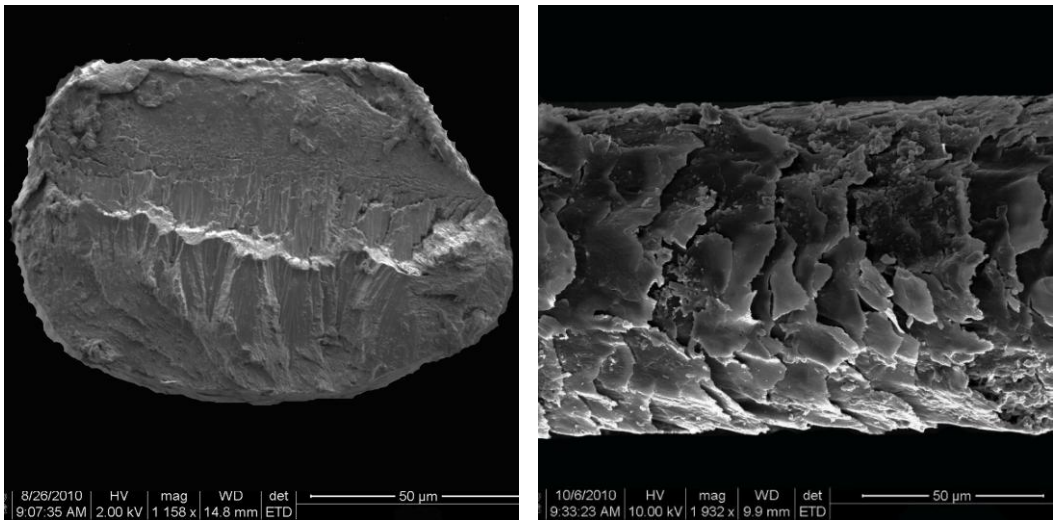


Fig 3.13: Black rhino hair cross section (left, scale = 50 µm) and scale pattern (right, scale = 50 µm). The cross section is approximately oval. The medulla is not well defined. Scales are very coarse and the pattern is irregular waved. The scale margins are moderately smooth to rippled and the distance between scales is near.

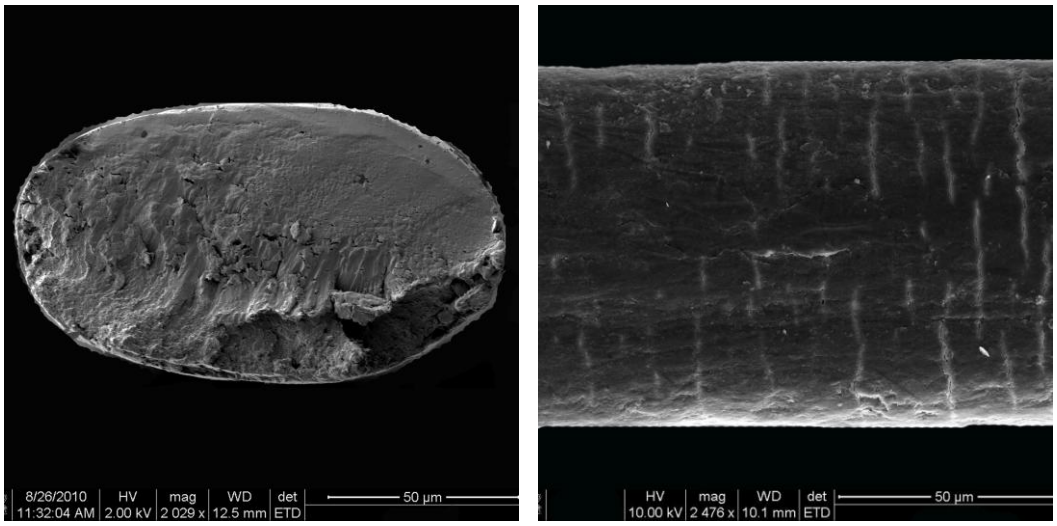


Fig 3.14a: Rock dassie hair cross section (left, scale = 50 µm) and scale pattern (right, scale = 50 µm). The cross section is approximately oval although it tends to oblong. Scale pattern is not defined although the marks on the cuticular surface show an approximate coronal shape. The cuticular surface of the same piece of hair at two different positions along the length of the hair also shows no defined scale pattern (see Fig 3.14b).

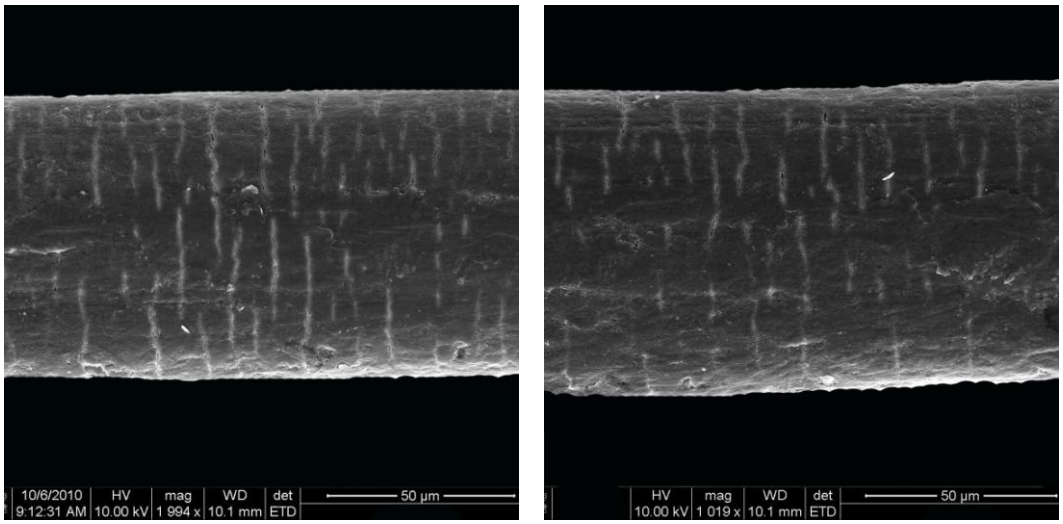


Fig 3.14b: Rock dassie hair scale pattern at two positions along the length of the hair (left, scale = 50 µm) and (right, scale = 50 µm). The cuticular surface of this piece of hair at two different

positions along the length of the hair shows no defined scales except for the cut marks that depict an almost coronal pattern.

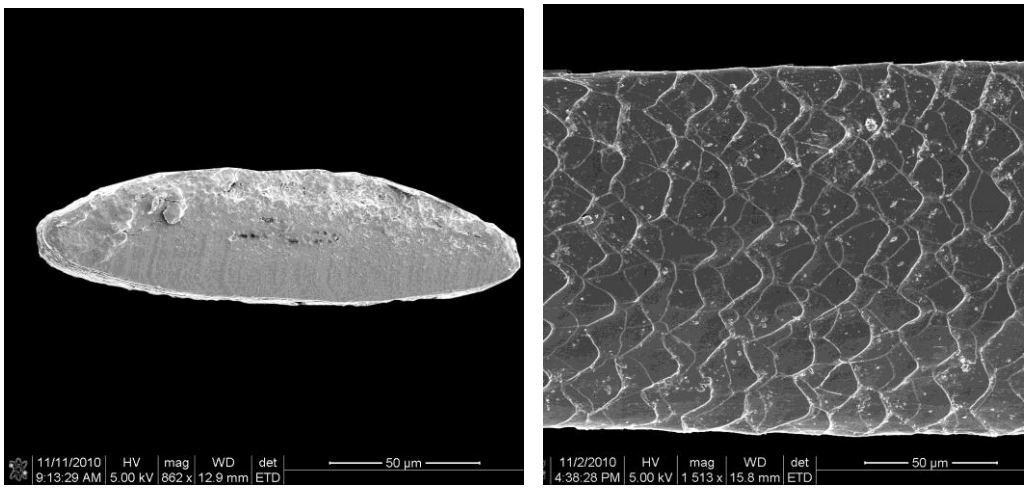


Fig 3.15: Aardvark hair cross section shape (left, scale = 50 µm) and scale pattern (right, scale = 50 µm). The cross section is clearly biconvex. The scale pattern shows overlapping petals and is described as broad diamond petal. Scale margins are generally smooth and the distance between scale margins is near to distant.

3.1.2 Summary of modern hair morphological characteristics

The table below shows a summary of the major morphological characteristics of 15 modern hairs analysed by scanning electron microscopy (Table 3.1).

Table 3.1: Morphological characteristics of 15 modern hairs analysed by scanning electron microscopy.

Mammal	**Scale pattern**	**Cross section**	**Distance between scale margins**	**Structure of scale margins**
Impala	Irregular waved mosaic	Triangle with blunted corners	Near to distant	Smooth
Blue wildebeest	Irregular waved mosaic	Concavo-convex	Near	Smooth to rippled
Black wildebeest	Irregular waved	Circular	Near	Moderately rippled
Buffalo	Highly irregular waved	Circular	Close	Rippled
Eland	Irregular waved mosaic	Circular to oval	Near	Rippled
Steenbok	Regular waved mosaic	Reniform to concavo-convex	Near to distant	Smooth
Springbok	Regular waved mosaic	Concavo-convex	Near	Smooth
Kudu	Irregular waved mosaic	Biconvex	Near to distant	Smooth
Warthog	Irregular waved mosaic	Oval	Close	Rippled
Scrub-hare	Lanceolate-pectinate	Biconvex to oval	distant	Rippled
Red rock hare	Grooved with coronal pattern on both sides of the groove	Dumb-bell	Near	Smooth
Burchell's zebra	Irregular waved	Oblong	Near to close	Rippled
Black rhino	Irregular waved	Oval	Near	Moderately smooth to rippled
Rock dassie	Coronal	Oval to oblong	Near to close	Smooth
Aardvark	Broad diamond petal	Biconvex	Near to distant	Smooth

3.1.3 Scanning electron micrographs and descriptions of fossil hairs

A selection of scanning electron micrographs of fossil hairs is shown in figure 3.16 to 3.33. From these, it was possible to tentatively identify 10 of the fossil hairs, although seven could not be identified. Some fossil hairs preserved both the cuticular scale pattern and cross sectional shapes, whilst others showed severe degradation of both, as shown in Fig 3.16 below. Others showed several cracks and no scale pattern at all, rendering hair identification impossible.

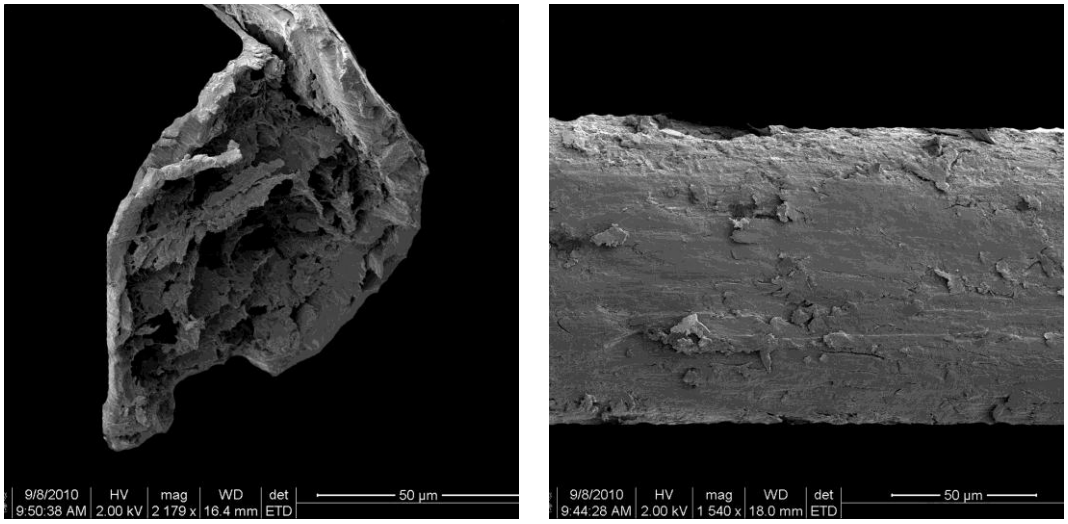


Fig 3.16: Distorted cross section of an unidentified fossil hair (left, scale = 50 µm) and severely degraded cuticular scales (right, scale = 50 µm). Although the cross section is highly degraded, it clearly shows that the cortex is medium to large in size. There is also evidence of a large lumen present. The cuticular surface shows no interpretable pattern.

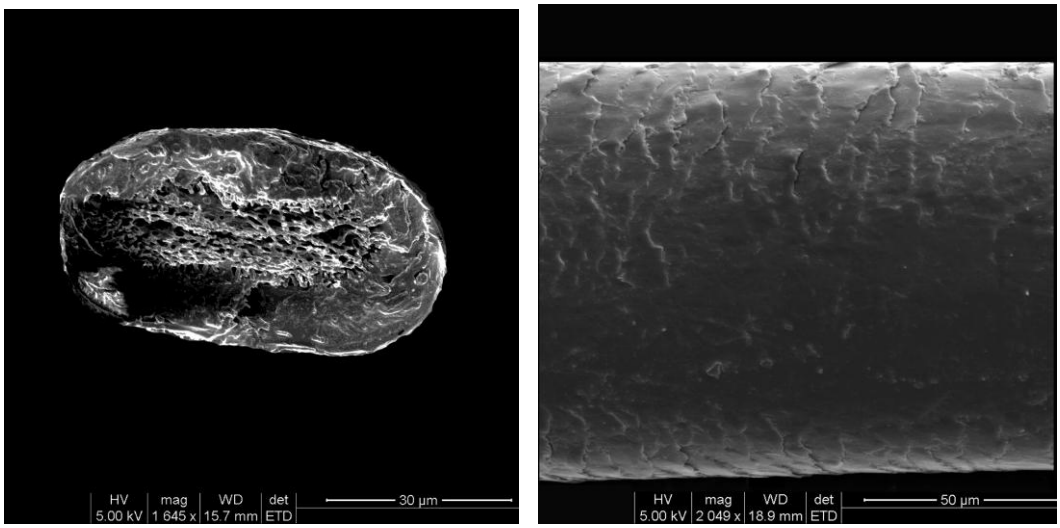


Fig 3.17: Fossil hair specimen 1 cross section (left, scale = 30 µm) and scale pattern (right, scale = 50 µm). The cross section is oval. There is no lumen in the medulla. The medulla shows no clear shape or form (armophous). The scales show an imbricate pattern. The scales lie transverse to the longitudinal direction of the hair and the scale margins are generally smooth to moderately rippled.

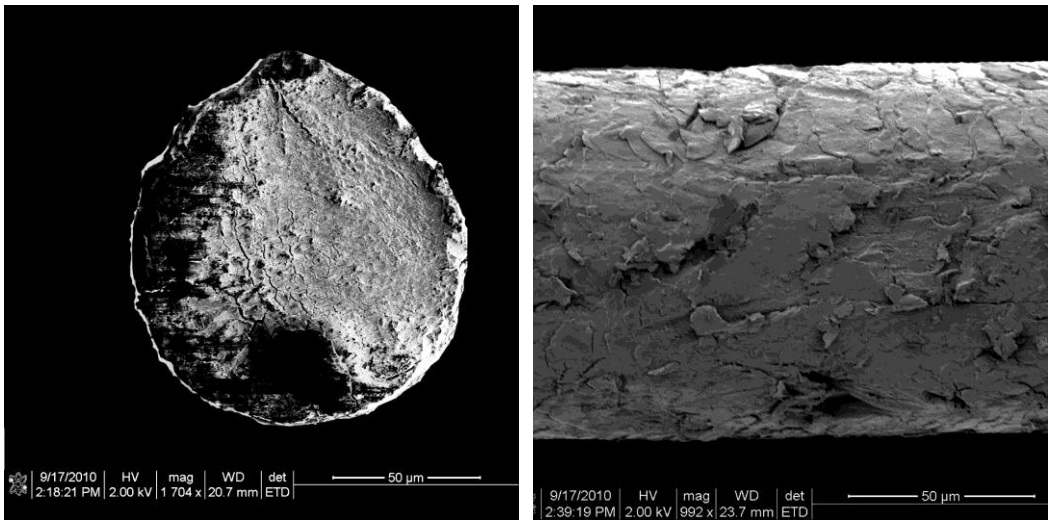


Fig 3.18: Fossil hair specimen 2 cross section (left, scale = 50 µm) and scale pattern (right, scale = 50 µm). The cross section is approximately circular. The scale pattern is poorly preserved, but in places is irregular waved, with scale margins being smooth to rippled. The distance between scales is near.

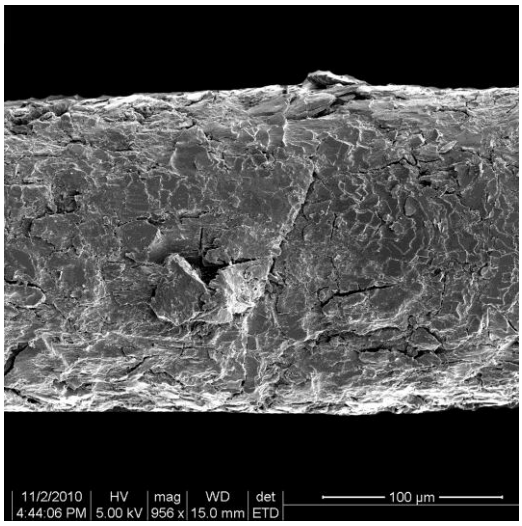


Fig 3.19: Fossil hair specimen 3 scale pattern (scale = 100 µm). The cross section is not available. The scale pattern is poorly preserved, although it shows an irregular waved pattern in places. The distance between scales is near to close.

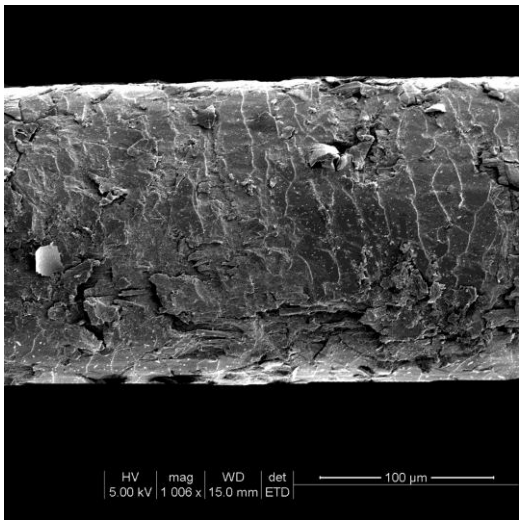


Fig 3.20: Fossil hair specimen 4 scale pattern (scale = 100 µm). The scale pattern is irregular waved mosaic and the scale margins are smooth. The distance between scales is near to distant. The cross section of this fossil hair specimen is not available.

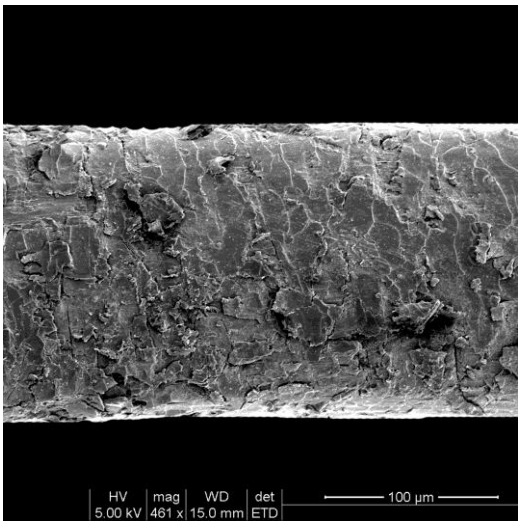


Fig 3.21: Fossil hair specimen 5 scale pattern (scale =100 µm).The scale pattern is poorly preserved, although it shows an irregular waved mosaic pattern and smooth scale margins which are near to distant. The cross section is not available.

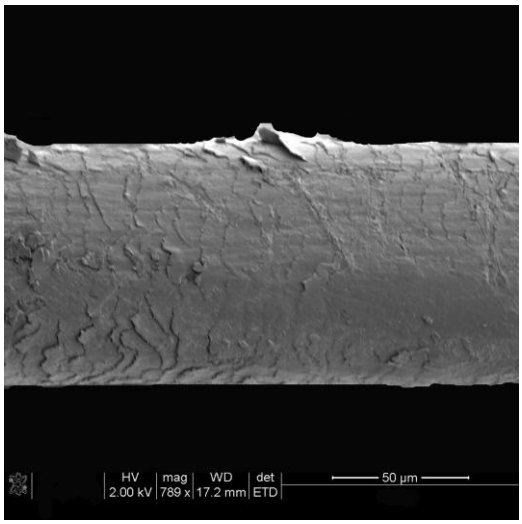


Fig 3.22: Fossil hair specimen 6 scale pattern (scale = 50 µm). The scale pattern is irregular waved mosaic and the scale margins are moderately rippled. The distance between scale margins is near to close. The cross section is not available.

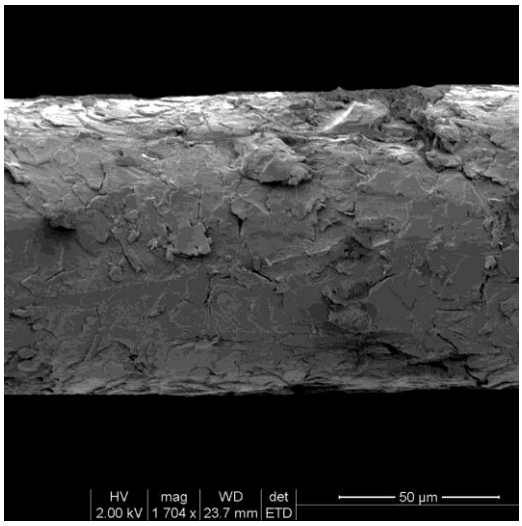


Fig 3.23: Fossil hair specimen 7 scale pattern (scale = 50 µm). The scale pattern is poorly preserved, but there is some evidence of an irregular waved pattern in places. Scale margins are smooth to rippled (on the top part of the hair). The cross section is not available.

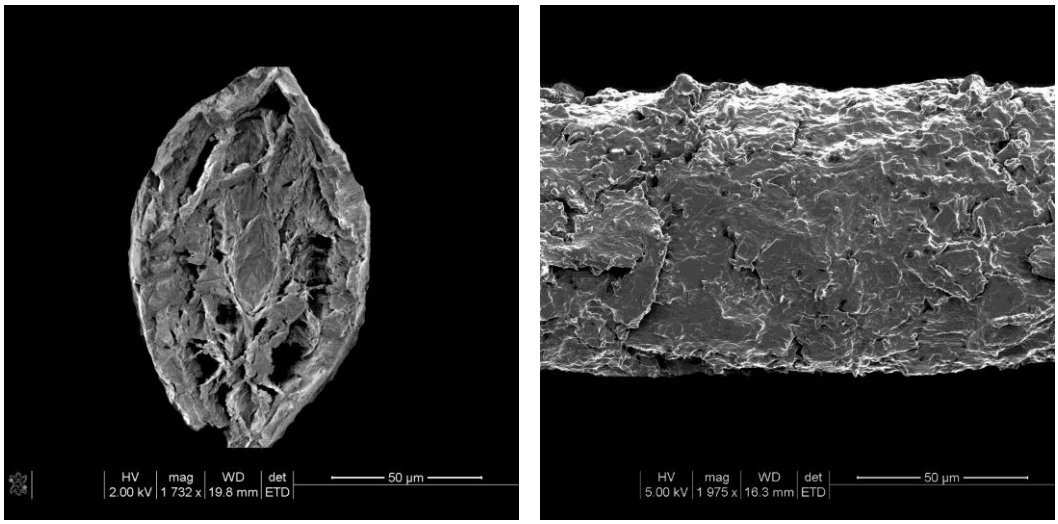


Fig 3.24: Fossil hair specimen 8 cross section (left, scale = 50 µm) and scale pattern (right, scale = 50 µm). The cross section is biconvex. Although not well defined, there is a medium to large medulla with lumen. The cortex appears to be small to medium in size. The cuticular surface is highly degraded and there are no visible scales.

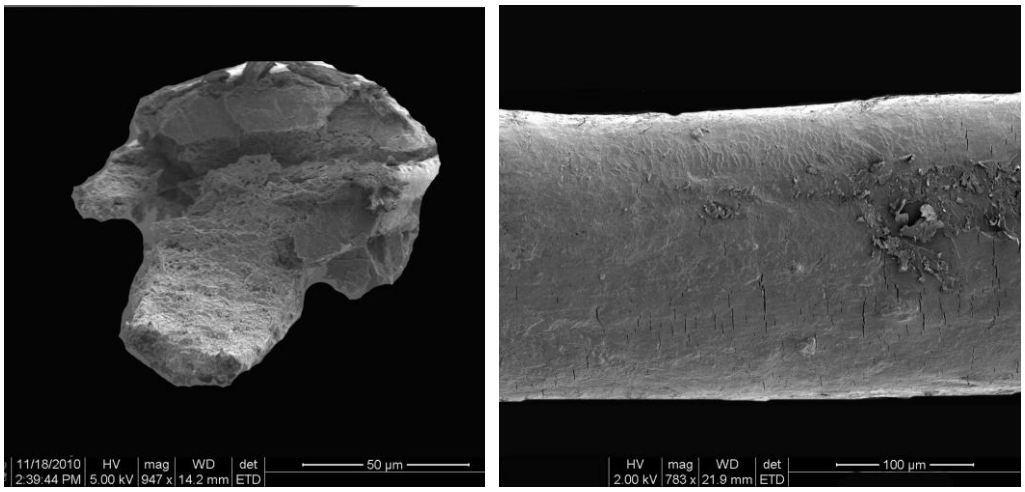


Fig 3.25: Fossil hair specimen 9 cross section (left, scale = 50 µm) and scale pattern (right, scale = 100 µm). Although the cross section is severely distorted, it may have been circular judging from the one side. It has a thin cortex. The scale pattern is highly irregular waved and the distance between scales is close.

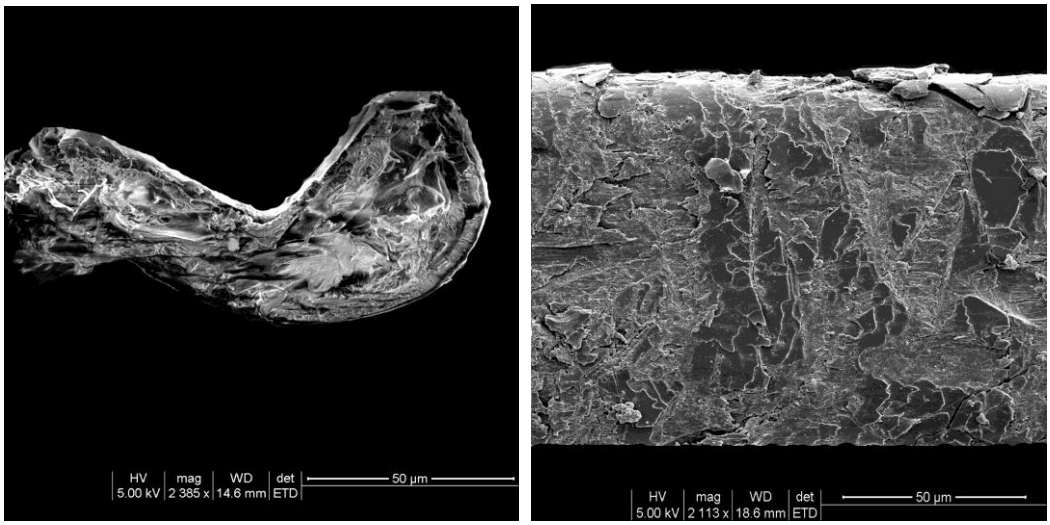


Fig 3.26: Fossil hair specimen 10 cross section (left, scale = 50 µm) and scale pattern (right, scale = 50 µm). The scale pattern is poorly preserved but shows an irregular waved pattern. The scale margins are smooth to rippled and the distance between scales is near. The cross section is distorted but appears to be concavo-convex or reniform. The cortex is thin and the medulla appears to have small cavities.

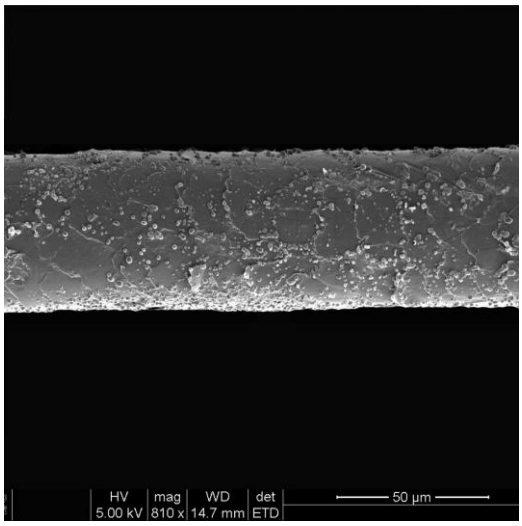


Fig 3.27: Fossil hair specimen 11 scale pattern (scale = 50 µm). The scale pattern is slightly waved and the scale margins are smooth. The distance between scales is distant. The cross section is not available.

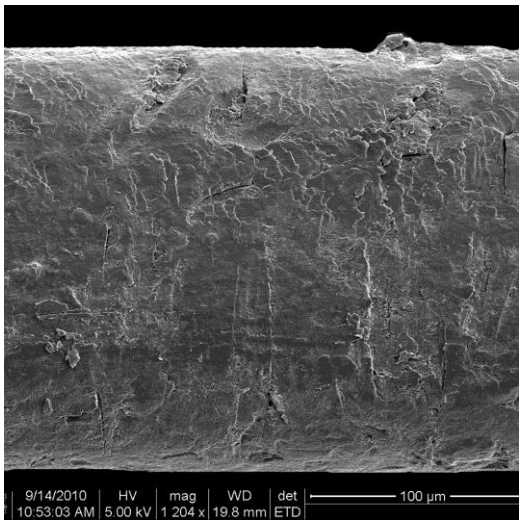


Fig 3.28: Fossil hair specimen 12 scale pattern (scale = 100 µm). The scale pattern is irregular waved mosaic. The distance between scale margins is close. The scale margins are rippled. The cross section is not available.

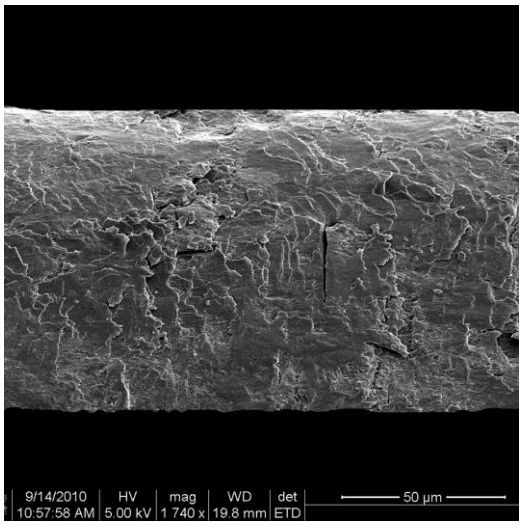


Fig 3.29: Fossil hair specimen 13 scale pattern (scale = 100 µm). The scale pattern is irregular waved mosaic. The distance between scale margins is close. Scale margins are rippled. The cross section is not available.

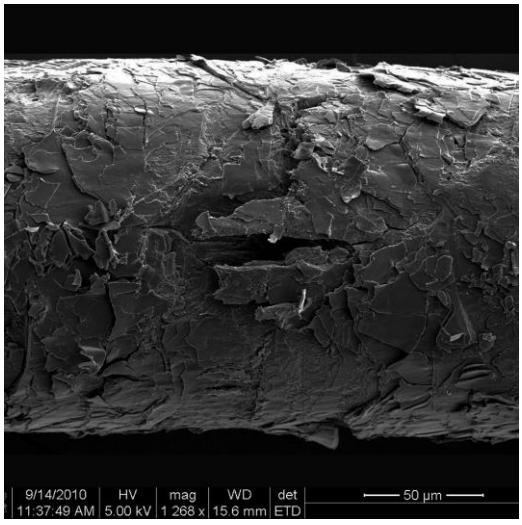


Fig 3.30: Fossil hair specimen 14 scale pattern (scale = 50 µm). The scale morphology is highly degraded and obscured. Nonetheless, the scale pattern appears to be irregular waved on the top left part of the hair. The cross section is not available.

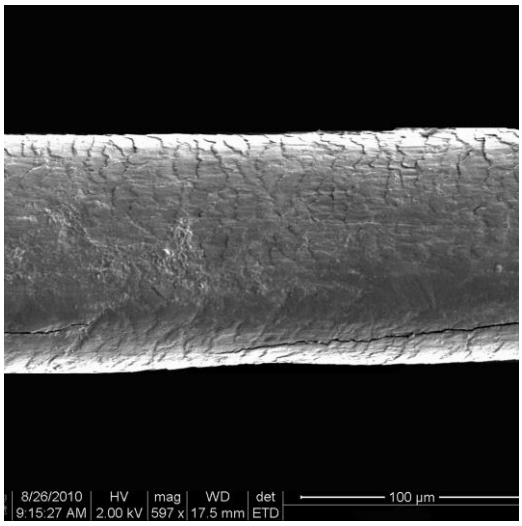


Fig 3.31: Fossil hair specimen 15 scale pattern (scale = 100 µm). Scale pattern is irregular waved mosaic and the scale margins are moderately rippled. The distance between scale margins is near to close. The cross section is not available.

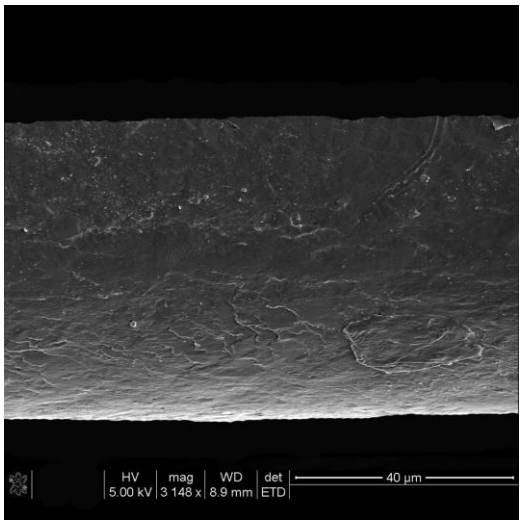


Fig 3.32: Fossil hair specimen 16 scale pattern (scale = 40 µm). Although the scale pattern is not well defined, it appears to be wavy and the scale margins are near to close. The cross section is not available.

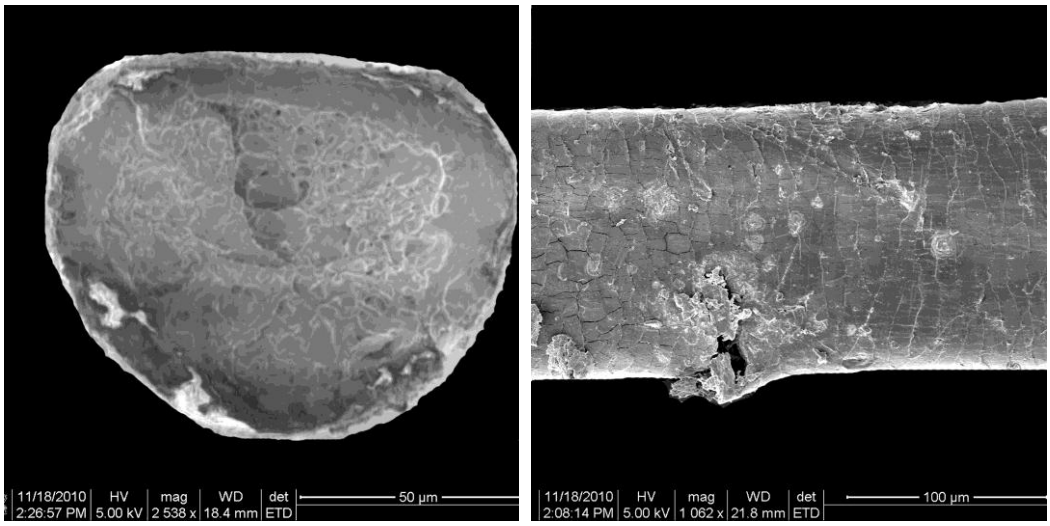


Fig 3.33: Fossil hair specimen 17 cross section (left, scale = 50 µm) and scale pattern (right, scale = 100 µm). The cross section is a triangle with blunted corners, and even though ill-defined, it appears to have a large medulla and no lumen. The scale pattern is irregular waved mosaic and the scale margins are smooth. The distance between scales is near to distant.

3.2 Possible fossil hair identifications

Fossil hair specimen 1 (Fig 3.17)

In cross section, fossil hair specimen 1 (Fig 3.17) is generally oval and shows no lumen. The medulla is amorphous (lacks a definite shape) in appearance and this is characteristic of human hair. 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. This combination of features closely resembles those observed on modern African and European hair, and fossil human hairs reported by Backwell *et al.*, 2009. Furthermore, the cross section of primates is generally oval (Backwell *et al.*, 2009) which is the case in fossil hair specimen number 1 (Fig 3.17). Because of this, fossil hair specimen 1 is considered as most probably human in origin. This human fossil hair specimen

(Fig 3.17) is terminal in nature (long and stiff) and not vellus (fine body) hair that does not usually contain medulla.

Fossil hair specimen 2 (Fig 3.18)

Fossil hair specimen 2 (Fig 3.18) shows a distinctly circular cross section which resembles that of modern black wildebeest (Fig 3.3) and modern buffalo (Fig 3.4). Although the scale pattern of this fossil hair specimen (Fig 3.18) is not very visible, a closer examination reveals an irregular waved pattern with rippled scale margins, just like in modern black wildebeest (Fig 3.3). However, the distance between scales in modern buffalo (Fig 3.4) is close and for modern black wildebeest (Fig 3.3), it is near. Because of this, fossil hair specimen 2 (Fig 3.18) most likely originated from black wildebeest rather than buffalo.

Fossil hair specimen 3 (Fig. 3.19)

Fossil hair specimen 3 (Fig. 3.19) is a highly degraded and extremely fragile piece. Nonetheless, scales show an irregular waved pattern and the distance between scales is near to close. Because the cross section of fossil hair specimen 3 is not available, the degraded scale pattern is not good enough to make a tentative identification of the mammal species represented by the fossil hair specimen.

Fossil hair specimen 4 (Fig. 3.20)

Scale morphology of fossil hair specimen 4 (Fig 3.20) is slightly obscured, but a closer examination shows an irregular waved mosaic pattern and smooth scale margins which are near to distant. A combination of these features resembles

those found in modern impala (Fig 3.1). Even though the cross section of fossil hair specimen 4 could not be obtained, the fossil hair specimen can be tentatively attributed to modern impala because the scale morphologies resemble each other closely.

Fossil hair specimen 5 (Fig 3.21)

The scale pattern of fossil hair specimen 5 (Fig 3.21) is poorly preserved, although it shows an irregular waved mosaic pattern. Scale margins are smooth and the distance between scales is near to distant. A combination of features in fossil hair specimen 5 matches those of modern impala (Fig 3.1). Hence it likely originated from an impala. The cross section is not available.

Fossil hair specimen 6 (Fig 3.22)

The cross section of fossil hair specimen 6 (Fig 3.22) is not available. However, scale morphology of this specimen is irregular waved mosaic and the scale margins are moderately rippled. The distance between fossil hair scale margins is near to close. Scale morphology of fossil hair specimen 6 (Fig 3.22) is comparable to that of modern Burchell's zebra (Fig 3.12).

Fossil hair specimen 7 (Fig 3.23)

The cross section of fossil hair specimen 7 is not available. Scale patterns are poorly preserved, but nonetheless show an irregular waved pattern. Scale margins are smooth to rippled (on the top part of the hair). However, this detail is

insufficient to identify the mammal species represented by fossil hair specimen 7 (Fig 3.23).

Fossil hair specimen 8 (Fig 3.24)

In cross section, fossil hair specimen 8 (Fig 3.24) is generally biconvex to oval, a feature shared with modern kudu (Fig 3.8). However, fossil hair scale morphology of this specimen (Fig 3.24) is not preserved at all and therefore cannot be used as a distinguishing feature. Based on cross section only, fossil hair specimen 8 (Fig 3.24) closely matches that of modern kudu (Fig 3.8).

Fossil hair specimen 9 (Fig 3.25)

The cross section of fossil hair specimen 9 (Fig 3.25) is severely distorted. Nonetheless, it appears to be circular and the cortex looks thin. The scale pattern is highly irregular waved at the top part of the fossil hair and the distance between scales is close. The scale margins are generally smooth. This detail is however insufficient to make an identification of the mammal species represented by fossil hair specimen 9 (Fig 3.25).

Fossil hair specimen 10 (Fig 3.26)

Although the cross section of fossil hair specimen 10 (Fig 3.26) is distorted, it is reniform or concavo-convex. Cross sectional shape of fossil hair specimen 10 (Fig 3.26) is very similar to that of modern steenbok (Fig 3.6) and modern springbok (Fig 3.7). The scale pattern of fossil hair specimen 10 is poorly preserved but shows an irregular waved pattern. The fossil hair scale margins are moderately

rippled, which is not the case in modern steenbok (Fig 3.6) and modern springbok (Fig 3.7) where the scale margins are very smooth. Scale morphology of fossil hair specimen 10 (Fig 3.26) could not be conclusively matched in the comparative collections hence an identification could not be made.

Fossil hair specimen 11 (Fig 3.27)

The scale pattern of fossil hair specimen 11 (Fig 3.27) is not well preserved, although it shows a regular waved pattern. Scale margins are smooth and the distance between scales is distant. Although scale morphology of fossil hair specimen 11 (Fig 3.27) is well defined, it cannot be conclusively matched in the comparative collections. The cross section of this fossil hair specimen is not available to facilitate taxonomic identification hence an identification could not be made.

Fossil hair specimen 12 (Fig 3.28)

Scale morphology of fossil hair specimen 12 (Fig 3.28) is irregular waved mosaic and the distance between scale margins is close. Scale margins are rippled. Although the cross section of this fossil hair specimen is not available, its scale morphology closely resembles that of modern warthog (Fig 3.9).

Fossil hair specimen 13 (Fig 3.29)

The scale morphology of fossil hair specimen 13 (Fig 3.29) is irregular waved mosaic. The distance between scale margins is close. Scale margins are rippled. Although the cross section is not available, scale morphology of fossil hair specimen 13 (Fig 3.29) closely matches that of modern warthog (Fig 3.9). Fossil hair specimen 13 (Fig 3.29) is also similar to fossil hair specimen 12 (Fig 3.28) which closely resemble that of modern warthog in Fig 3.9.

Fossil hair specimen 14 (Fig 3.30)

The scale morphology of fossil hair specimen 14 (Fig 3.30) is not well preserved even though the scale pattern appears to be irregular waved on the top left part of the hair. The cross section is not available and the available detail is insufficient to make an identification.

Fossil hair specimen 15 (Fig 3.31)

The cross section of fossil hair specimen 15 (Fig 3.31) is not available. The scale morphology of this specimen is irregular waved mosaic. Scale margins are moderately rippled and the distance between fossil hair scale margins is near to close. The scale morphology of fossil hair specimen 15 is comparable to that of modern Burchell's zebra (Fig 3.12). Hence fossil hair specimen 15 most probably originated from Burchell's zebra.

Fossil hair specimen 16 (Fig 3.32)

Although the scale pattern of fossil hair specimen 16 (Fig 3.32) is ill- defined, it appears to be wavy, and the distance between scale margins is close to near. The cross section of fossil hair specimen 16 (Fig 3.32) is not available and an identification of the mammal species represented by the fossil hair specimen is impossible.

Fossil hair specimen 17 (Fig 3.33)

In cross section, fossil hair specimen 17 (Fig 3.33) is a triangle with blunted corners, a feature shared with modern impala (Fig 3.1). However, there are no clear small perforations on the fossil medulla, probably due to degradation. Although ill-defined, scale pattern of fossil hair specimen 17 (Fig 3.33) is irregular waved mosaic and the scale margins are smooth, just like in modern impala (Fig 3.1). The distance between scales of fossil hair specimen 17 is distant. Fossil hair specimen 17 most likely originated from an impala as the fossil (Fig 3.33) and modern impala (Fig 3.1) hair scale morphologies closely resemble each other.

3.3 Summary of results

Of the 48 fossil hairs extracted from 12 coprolites, 31 were extremely degraded and the scale patterns were faintly perceptible and not clearly seen (e.g. Fig 3.16),

whilst 10 could be identified to species level, and 7 could not be identified (see Table 3.2) using the available comparative hair collection.

Table 3.2: Possible fossil hair identifications

Fossil hair specimen number	**State of preservation**	**Scale pattern**	**Cross section**	**Possible fossil hair identity**
1	Good	Imbricate	Oval	Human
2	Average	Irregular waved	Circular	Black wildebeest
3	Good	Irregular waved	Not available	Unknown
4	Good	Irregular waved mosaic	Not available	Impala
5	Average	Irregular waved mosaic	Not available	Impala
6	Good	Irregular waved	Not available	Burchell's zebra
7	Very poor	Not very clear although irregular waved	Not available	Unknown
8	Poor	Not visible	Biconvex	Kudu
9	Average	Highly irregular waved	Not clear but appears circular	Unknown
10	Average	Irregular waved	Concavo-convex or reniform	Unknown
11	Poor	regular waved	Not available	Unknown
12	Average	Irregular waved	Not available	Warthog
13	Poor	Irregular waved	Not available	Warthog
14	Poor	Irregular waved	Not available	Unknown
15	Average	Irregular waved mosaic	Not available	Burchell's zebra
16	Very poor	Not visible enough but somehow irregular waved	Not available	Unknown
17	Good	Irregular waved mosaic	Triangle with blunted corners	Impala

Mammals identified include black wildebeest, impala, Burchell's zebra, kudu, warthog and human. Those that could not be identified had severely degraded and obscured scale patterns. In some cases, cross sections could not be obtained to facilitate taxonomic identification of hairs because the fossil hair fragments were extremely small and preserved as high resolution casts of external and not internal morphology. Interestingly, some fossil hairs showed reasonably clear scale morphologies but could not be conclusively matched in the comparative collections (e.g. specimen number 11, Fig 3.27).

Scanning electron micrographs of fossil hairs obtained revealed that the extent of fossil hair degradation significantly varied amongst the fossil hairs. This is most likely due to microbial activity and variable diagenetic processes, but could be attributed to the position from which the fossil hairs originated on the animal. This is because some hairs e.g. those from the animal's back and tail are generally more robust than those from the neck and stomach which are usually very fine, and possibly not strong enough to resist severe degradation. Alternatively, the hair was degraded before consumption, having been exposed to the elements for some days or weeks. Soft tissues preservation occurs in several localities (Martill, 1987a, b, c, 1988, 1991, 1993, 1995), and the exceptional preservation may be a result of *in situ* preservation of degraded organic matter (Martill, 1995). Taphonomic and diagenetic alterations give few clues on soft tissue preservation styles (Martill *et al.*, 2000). According to Schweitzer (2011), the molecular composition of hair gives it relatively high preservation potential. Nevertheless, variable degradation between the hairs warrants further investigation. The

importance of understanding hair sample condition in archaeological and forensic investigation shows the need for a detailed knowledge of the sequence of degradation in samples that have been buried (Wilson *et al*., 1999, 2003, 2007; Wilson, 2008). A comprehensive knowledge of the selective progress of degradation in hair derived from archaeological or forensic contexts enables us to establish a means of quantifying the extent of change through the development of a histological index for assessing sample condition that will have widespread application to archaeology and forensic investigation (Wilson *et al*., 2004).

CHAPTER FOUR

DISCUSSION

4.1 Hair identification difficulties

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 (≤ 1mm), meaning that only a few features were present and available for use in identification. Furthermore, extracting fossil hairs using fine tweezers and a low magnification binocular microscope is a very challenging procedure.

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 (Adorjan and Kolenosky, 1969; Riggot and Wyatt, 1980, 1981). Seasonality, age and sex differences (De Boom and Dreyer, 1953; Randall and Ebling, 1991; 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.

All the modern hair samples used in this study were obtained from the Johannesburg Zoo and the Ditsong National Museum of Natural History. The effects of taxidermy, preparation and storage on cuticular scale pattern are not known and the extent to which these factors have influenced my research findings is not known. This warrants further investigation, given that rock dassie hair shows no scale pattern at all (Fig 3.14a and b).

Many other 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 study, many of which had abraded scales and obscured medullary features (e.g. Fig 3.16, Fig 3.23 and Fig 3.25). DNA analysis could have easily resolved the taxonomic identity of the fossil hairs, but unfortunately, as casts, they did not preserve any protein (Backwell *et al*., 2009). Despite this, some fossil hairs showed remarkably well preserved casts of the original hair scales, even though with some loss of surface form, and there was sufficient detail to make tentative identifications of the mammal taxa represented.

4.2 Hair comparison and identification

Some fossil hairs had well preserved cuticular surface and cross sectional morphology which is rarely observed in ancient hair (e.g. Fig 3.17). The well preserved cuticular surfaces allowed for visual comparison with modern hair

samples. Scanning electron microscope analysis was used for all the hair samples and resulted in relatively clear micrographs. In addition, it was able to elucidate any characteristic features of cuticular surface pattern or cross sectional morphology, elements on which this study was based.

Visual comparison of hair can be subjective and is open to interpretation by individual scientists (Steck-Flynn, 2009), but despite this, hair comparison was done as objectively as possible, drawing on my extensive personal experience and a wide reference collection. 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). In a study conducted by the Federal Bureau of Investigation (FBI), 11% of hairs deemed to be matches upon visual inspection were subsequently found to be non- matches after DNA testing (Saferstein, 2004). Nonetheless, I was able to identify 10 fossil hairs to species level in six cases.

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 a tentative identification has been made. Based on my collection of modern large mammals from southern Africa, this study has established that impala, Burchell's zebra and warthog hair predominated in the coprolites from Gladysvale cave (see Table 3.2). The fact that these animals represent three of the 15 new mammal hair taxa documented as part of this project, demonstrates the importance of expanding the taxonomic representation of modern southern African mammal hair samples. 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 showed different animals (impala and Burchells's zebra) represented in the same coprolite.

Skinner and van Aarde (1981) analysed hairs from scats from hyaena latrines from Wolfsbaai 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 the available evidence of brown hyaenas consuming locally available animals, which evidences hyaenas as 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 to 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).

On the evidence of scale morphology, rodents and other carnivores in general, and cats in particular, can reasonably be excluded. 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; Backwell *et al*., 2009), 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.

My results indicate that previously undocumented scub-hare (*Lepus saxatilis)* scale pattern (Fig 3.10) closely resembles that of vlei rat (*Otomys irroratus)* studied by Keogh (1975). Similarities in scale pattern were also observed between red rock hare (Fig 3.11a) 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 3.11a) 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.

Rock dassie hair shows no scales at all, with some cracks (Fig 3.14). 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 sample. In the case of the rock dassie, a lack of scales could possibly be due to abrasion of the scales as the animal predominantly inhabits rocky places, or more likely due to taxidermy preparation of the pelt. Interestingly, Perrin and Campbell (1980) report that rock dassie is a species that bears little phylogenetic affinity to most similarly sized mammals and has a hair cuticular scale pattern unlike the majority of small mammals in that it is flattened mosaic in the proximal region and changes to a waved pattern distally.

Scanning electron microscope analysis revealed that modern black wildebeest hair cross section is entirely circular. My finding is not in agreement with De Boom and Dreyer (1953), who found concavo-convex cross sections for black wildebeest. This could be due to differences in area of sampling or variability within species (age, diet, disease or season). Furthermore, my comparative collection shows that kudu hair scale pattern is irregular waved mosaic, and the scale margins are smooth to rippled-crenate. However, Dreyer (1966) observed coronal scale patterns in kudu hair and this difference in scale morphology remains unexplained, even when one considers that hair morphology can be extremely variable in a species. Marked variability within a species is evident in the differences between the number of perforations on the cross sections of red rock hare in Fig 3.11a and b. While Backwell *et al*. (2009) note the similarities

between modern African and European human hair in scale pattern and cross-sectional shape and dimensions, they also point out differences.

What is quite evident on one fossil hair is an imbricate cuticular scale pattern, with a regular waved morphology (Fig 3.17), with scales lying transversely in a more or less banded manner. These features are typical of modern primates (Backwell *et al*., 2009), and human hair is the closest match. Another clearly identified pattern observed on two fossil hairs (Fig 3.22, Fig 3.31) is one that matches Burchell's zebra. This pattern is characterised by scales that are irregular waved mosaic, and the scale margins are generally rippled to moderately crenate. Two fossil hairs (Fig 3.28, Fig 3.29) showed a highly irregular waved scale pattern whose scale margins are closely spaced relative to hair width, features that characterise suids. These fossil hair specimens have scale margins that are rippled crenate, and these features are common to modern warthog. Three fossil hairs (Fig 3.20, Fig 3.21, Fig 3.33) exhibit an irregular waved mosaic pattern and triangular cross sections with blunted corners, features typical of modern impala. These characteristics form the basis of some criteria that future researchers may look for when analysing hair samples using scanning electron microscopy.

4.3 Implications for Middle Pleistocene hyaena ecology and palaeoenvironment

Based on the fossil hairs identified here, this research has established that between 257 and 195 ka, brown hyaenas shared the Sterkfontein Valley with

warthog, impala, zebra, kudu, black wildebeest and humans. These animals are associated with savanna grasslands, much like the Highveld environment of today.

These findings provide a new source of information on the local Middle Pleistocene fossil mammal community, and insight into the environment in which archaic and modern humans in the interior of the African subcontinent lived. The fact that Middle Pleistocene hyaena fed on the above-mentioned mammals is consistent with previous researchers who reported that hyaenas accumulate a wide range of faunal remains to varying degrees and that their foraging behaviour is variable (Henschel *et al.*, 1979; Scott and Klein, 1981; Leaky *et al.*, 1999; Skinner, 2006; Faith, 2007; Kuhn *et al.*, 2010). 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 *Homo sapiens* and complex technology.

Climate records for sub-Saharan Africa are limited. In addition to this, there are difficulties in correlating southern hemisphere climate data with those from northern latitudes, which experience significantly different temperature regimes (Gasse *et al.*, 2008; Chase *et al.*, 2010). Only a few Middle Stone Age (MSA) sites are documented for the interior of southern Africa. This is largely attributed to sampling bias (Mitchell, 2008), poor preservation conditions (Schiegl and Conard, 2006), and a lack of human habitation at this climatically unfavourable period (Deacon and Deacon, 1999; Wadley, 2006). Arid climates are widely

believed to have pushed people to the coast, where they exploited an array of resources (Deacon and Deacon, 1999; Marean *et al*., 2007; Clark and Plug, 2008; Marean, 2010a, 2010b). At the same time they produced engraved artefacts (Henshilwood *et al*., 2009; Texier *et al*., 2010), ornamental shell beads (d'Errico *et al*., 2005) and evidence of complex hafting and hunting activities (Lombard, 2007; Pargeter, 2007; Backwell *et al*., 2008; Wadley and Mohapi, 2008; Lombard and Phillipson, 2010; Wadley, 2010). Attributes characteristic of modern human behaviour including symbolic and abstract thought, planning and technological innovation, undoubtedly developed in Africa in MSA contexts (McBrearty and Brooks, 2000), but the timing and geographic distribution of the emergence of modern human cognition, the mode and tempo of its evolution, and whether it is specific to modern humans is the subject of ongoing debate (Mellars, 1991; Klein, 1995, 1998, 1999, 2000, 2001; McBrearty and Brooks, 2000; Wadley, 2001; Stringer, 2002; d'Errico and Henshilwood, 2007; d'Errico and Stringer, 2011). This is partly because knowledge of African Middle and Late Pleistocene fossil hominins is limited by a small sample size, rendering the extent of their diversity, distribution and associations with lithic industries and each other, unknown (Mitchell, 2008).

It is therefore difficult to assess the impact of climate change on modern human evolution and dispersal when it is not clear if there was an accretional emergence of modern humans from an archaic ancestor with a pan-African distribution (Brauer, 2008; Pearson, 2008), or a more punctuated speciation event from a geographically-restricted population of archaic humans (Stringer, 2002). Further

complicating the situation is the fact that the fossil record is biased in favour of sampling a disproportionate number of sites near water, for example lake margins, springs, streams and deltas (Shipman and Harris, 1988). In South Africa, most fossils are preserved in cave contexts. It is widely thought that by 60 ka, people in southern Africa were anatomically modern (Marean and Assefa, 2005; McBrearty and Brooks, 2000; Wadley, 2006; Brooks *et al*., 2006; Lombard, 2007). This is, however, largely based on a small fossil record of human remains from a few sites, namely Klasies River (Rightmire, 1984; Rightmire and Deacon, 1991; Brauer *et al*., 1992), Border Cave (Beaumont *et al*., 1978; Rightmire, 1984; Beaumont, 1980), and Die Kelders Cave 1 in South Africa (Grine, 2000), and to some extent on the identification of modern features in human remains from Ethiopia, such as Herto (White *et al*., 2003) and Omo Kibish I (McDougall *et al*., 2005). The fossil hairs from Gladysvale cave thus contribute to the scant early human fossil record.

Even though we cannot attribute to which hominin species the hairs belong, we know that they lived in a grassland environment. Modern African savannas pose many challenges for humans. Besides natural hazards like drought and fire, the grasslands are home to many predators. Africa is home to the highest percentage of poisonous snakes and life-threatening animals in the world. Furthermore, birds of prey are known to have killed the Taung child, and led to Lee Berger's bird of prey hypothesis (Berger and Clarke, 1995, 1996; Berger, 2006). These factors would have played a major role in the behavioural evolution of early humans.

Predator avoidance would have stimulated complex social behaviour of early humans living in the African interior.

The existence of fossil hairs in Middle Pleistocene hyaena coprolites from Gladysvale cave can be explained in three ways. First, according to Berger *et al*. (2009), the coprolites are from a brown hyaena, based on the contents and position of the latrine in the cave, which suggests that it was used as a den for rearing pups. The coprolites are most likely from a brown hyaena because spotted hyaenas do not defacate in one place while striped hyaenas mark a large territory around the entrance (Watts and Holekamp, 2007). In accordance with 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 hunted the large mammals as part of their pup-rearing behaviour.

Second, the *Parahyaena brunnea* responsible for the coprolites scavenged the identified mammals, in accordance with the most common foraging behaviour reported for modern brown hyaena (Skinner, 1976; Skinner and Ilani, 1979; Skinner *et al.*, 1980; Owens and Owens, 1978; Mills, 1990; Skinner and Smithers, 1990; Yom-Tov and Medelssohn, 2002; Maude, 2005; Maude and Mills, 2005; Kuhn, 2001, 2005, 2006; Kuhn *et al*., 2009, 2010; Kuhn, 2011). 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 (1978, 1990), and brown hyaenas killing small livestock (Skinner, 1976, Kuhn, 2011). They are said to be poorly equipped for running and hunting, especially of large mammals, such as the zebra, kudu and black wildebeest represented in the coprolites. If this behaviour is true of extant *Parahyaena brunnea*, 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.

Third, it may be possible that Middle Pleistocene *Parahyaena brunnea* had a different foraging behaviour from their modern counterparts, namely the habitual hunting of large mammals, as practiced by the extinct long legged hunting hyaena (*Chasmaporthetes nitidula*), which is recorded at Sterkfontein, and which ran down its prey (Berger *et al.*, 2002; Clark, 2002; Berger, 2005). This scenario is, however, unlikely given the anatomical differences between the taxa, but we cannot rule out the chance that they employed a different hunting strategy.

In accordance with their regional distribution, brown hyaenas have a wide-ranging and variable diet (Owens and Owens, 1978; Maude, 2005). Nonetheless, apart from the six animals identified in this study, my research findings show that

brown hyaenas fed on mammals that could not be matched in the comparative collections, suggesting either that some extinct mammal species that also shared the landscape are represented in the hair samples, or more likely, that the modern comparative collection is insufficient.

CHAPTER FIVE

CONCLUSION

Of the 48 fossil hairs extracted from 12 coprolites, 31 were extremely abraded in scale and cross-sectional morphology, whilst 10 were identifiable to six possible species. Seven could not be identified. 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 fossil research. Based on scale pattern and cross section shape and features, when available, small mammals and other carnivores, specifically cats, are not represented by any of the fossil hairs analyzed in this research.

The identified fossil hairs show that between 257 and 195 ka, *Parahyaena brunnea* shared the Sterkfontein Valley with warthog, impala, zebra, kudu, black wildebeest and humans. These animals are associated with savanna biomes much like the Highveld region of today, where grasslands are broken by woodlands, especially in valleys near water. Whether the hyaena(s) responsible for the coprolites hunted or scavenged from these animals is unclear. Brown hyaenas are reported to hunt when rearing pups, but most evidence shows them to be habitual scavengers. Based on the principle of uniformitarianism, and the large body of research conducted on the various hyaena taxa foraging behaviours, it is likely that the fossil hairs represent scavenging by hyaenas of animals hunted by large cats in the area.

The identified hairs show that coprolites provide significant data on a range of Middle Pleistocene fauna in the Sterkfontein Valley as well as information on Middle Pleistocene *Parahyaena brunnea* palaeoenvironment and ecology. Based on an expanded modern comparative collection of hairs of known mammalian taxa, these findings provide 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 lived. 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 *Homo sapiens sapiens*, and show that predator avoidance and defence were no doubt important factors in the social and cultural adaptations of early humans living in the African interior.

This study highlights the importance of researching all aspects of the fossil record and the contribution of microscopy to palaeontology. Future research should focus on expanding the taxonomic representation of modern southern African mammal hair samples, documenting the effects of preparation and storage of hair on cuticular scale pattern preservation, and attempting to provide examples of different types of hairs from different sites on the body, as well as from young and old individuals.

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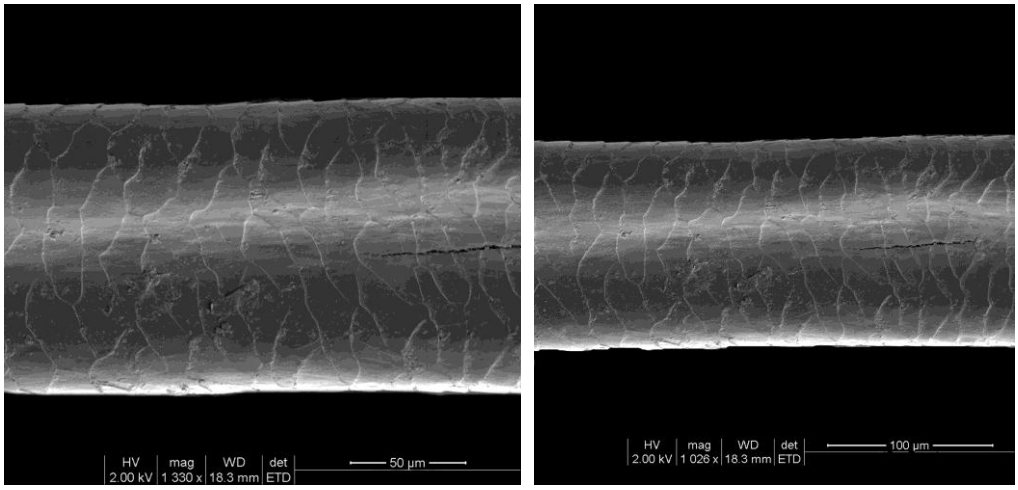
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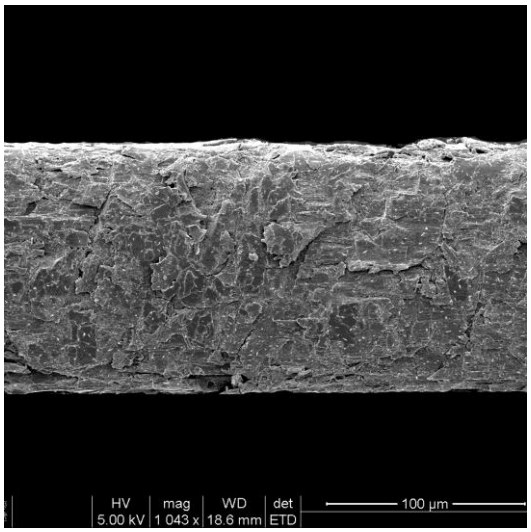
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APPENDICES

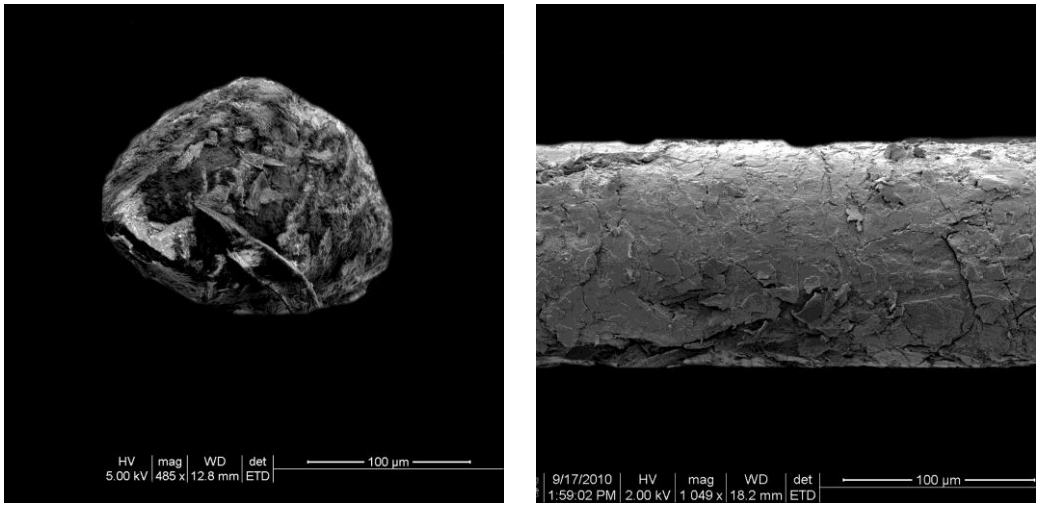
Appendix A: Modern steenbok hair scale pattern at different scales (left, scale = 50 µm) and right (scale =100 µm). There is no significant difference on the scale patterns at different scales.



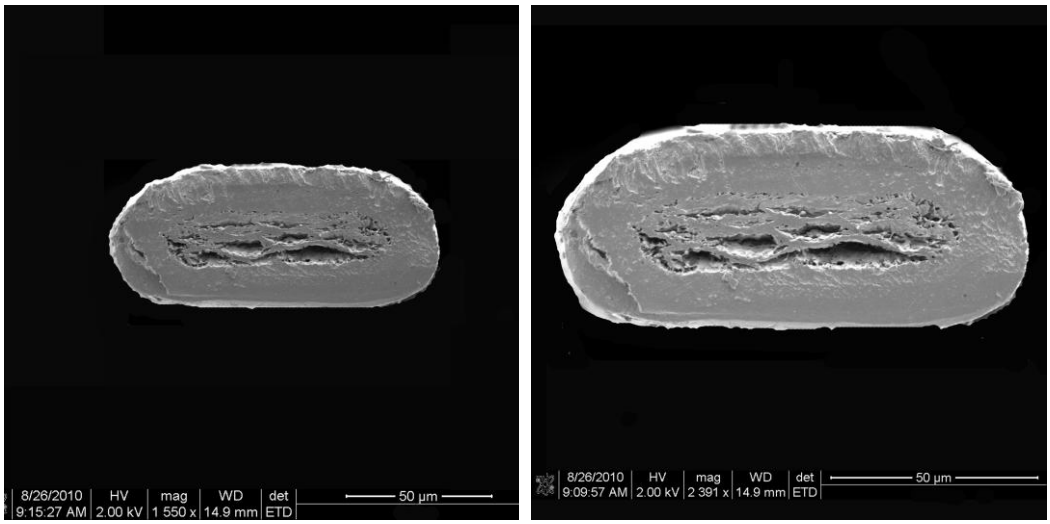
Appendix B: Unidentified fossil hair scale pattern at different scales (left, scale = 50 µm) and (right, scale = 100 µm). Although not clearly visible, the scale pattern shows a waved morphology.



Appendix C: Unidentified fossil hair cross section (left, scale = 100 µm) and scale pattern (right, scale =100 µm). Cross section appears like a distorted triangle. The cuticular scale is however abraded but nonethelesss shows an irregular waved morphology with moderately rippled margins.



Appendix D: Modern Burchell's zebra hair cross section at different magnifications (left, scale = 50 µm, magnification = 1550x) and right (scale = 50 µm, magnification = 2391x).



Appendix E: Unidentified fossil hair scale pattern at different magnifications (left, scale =40 µm and magnification = 2940x) and (right, scale =50 µm and magnification = 810x). There is no significant difference in scale morphology.

