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THE EQUIDAE FROM GLADYSVALE, A HOMININ LOCALITY IN THE CRADLE OF HUMANKIND, SOUTH AFRICA

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Abstract

The later Pleistocene compared to modern census data indicated that Equidae are represented lower than comparably sized bovids (BOV III & IV). The reason for this may be due to numerous factors that have been previously investigated such as, landscape usage, carnivore and prey relationships and accumulation factors. However, a largely unexplored factor that may also have played a vital role in their lower representation may have been the difference and effectiveness of predator avoidance behaviours utilized by Equidae. The Equidae remains from the external and internal deposits of Gladysvale (730 to 580 Kya and 257 to 195 Kya) in the Cradle of Humankind, may provide insight into the predatory avoidance behaviours of two different Equidae species, *Equus capensis* and *Equus quagga*. This study aimed to create and renew an understanding of the role of these animals within larger faunal communities in the Cradle of Humankind. Equidae fossil material mostly from Gladysvale along with supporting material from Sterkfontein, Kromdraai and Coopers were examined, measured and photographed, in an attempt to broaden the understanding of Equidae relations within the Cradle of Humankind. Furthermore, to also elaborate on the potential differences between *Equus capensis* and *Equus quagga*. Past research has usually assigned *Equus capensis* to the larger version of *Equus quagga* during the later Pleistocene, with other studies based on DNA analysis suggesting the two species have very little intraspecific diversity. However as seen in this study it would appear that there is a notable difference in size between the two Equidae species, but also a difference in overall representation within the Cradle of Humankind. This could imply that not only are the two species different in size but that they also employed different predatory avoidance behaviours.

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Introduction

Fossil localities dating from the Plio-Pleistocene in the Cradle of Humankind, situated northwest of Johannesburg, South Africa, are world-renowned for the important discoveries of hominins. Some of the most significant sites and finds include the Sterkfontein Caves which yielded Mrs Ples (*Australopithecus africanus*) and Little Foot (*Australopithecus prometheus*); Kromdraai which has produced multiple specimens of *Paranthropus robustus*; as well as Swartkrans with more than 200 hominin specimens, mostly attributable to *Paranthropus robustus* and *Homo ergaster* (Hilton-Barber & Berger, 2002). Some other important and well-known sites in the area include Cooper's Cave, Gondolin, Haasgat, Motsetse, Plovers Lake, Rising Star Cave, Wonder Cave, Drimolen, Gladysvale and Malapa (e.g., Val *et al.*, 2015; Schubert, 2004; Forrest, 2017; Avery, 2019; Berger, 1993; Badenhorst & Steininger, 2019; Brink, 1987; Lacruz, 2003).

Despite the Cradle of Humankind region being best known for the recovery of an extensive list of hominin specimens, the faunal remains from these localities are equally significant (Dirks & Berger, 2013, Hilton-Barber & Berger, 2002). Most notably, faunal remains are used extensively in the region to provide relative dates for the localities (e.g., McKee *et al.*, 1995, Adams *et al.*, 2016; Berger *et al.*, 2003). Faunal remains additionally offer contextual information for hominin evolution and ecology (McKee, 1995). In the Cradle of Humankind, the large mammalian fauna from Plio-Pleistocene localities usually consists of a variety of primates, carnivores, suids, bovids and equids (e.g., Adams *et al.*, 2016; Berger *et al.*, 2003; Brain, 1981; Susman & de Ruiter, 2004; Watson, 2004). Different taxa of Equidae are commonly reported from the region, although not in large numbers (e.g., Churcher & Watson, 2004). While a great deal of research has been done on the evolution of Equidae in southern Africa up until the 1980s (summary in Churcher, 1970; Maglio & Cooke, 1978), not much has been done since (cf. Bernor *et al.*, 2010, but see Orlando *et al.*, 2009). My study aims to contribute a renewed investigation into the evolution of Equidae in southern Africa through the analysis of the Equidae specimens from Gladysvale, a Plio–Pleistocene fossil locality in the Cradle of Humankind, South Africa.

Previous Research of Plio-Pleistocene Sites in the Cradle of Humankind

The Cradle of Humankind, dating from the late Pliocene to Pleistocene (3 to 0.16 Mya), has cave deposits of the world's most important hominin fossils including associated faunal and archaeological remains. Species from early *Australopithecus* to early *Homo* can be found in

numerous sites in the area such as Swartkrans, Sterkfontein, Malapa, Drimolen, Haasgat, Cooper's, Kromdraai and Gladysvale (Dirks & Berger, 2013). Hominin fossils and the associated fauna can often occur either in a monotaxic situation or as complex multitaxic vertebrate faunal assemblages. These assemblages are usually preserved in highly lithified, clastic cave sediments generally referred to as cave breccias (Wiersma, 2021).

The geology of the Cradle of Humankind, as illustrated in Figure 1, is complex as it lies on parts of formations of interacting structures that form the Johannesburg Dome (Dirks *et al.*, 2015). The Johannesburg Dome consists of a near-circular, antiformal structure comprised of basement gneiss from the Mesoarchean. The Dome is surrounded by a sequence of sedimentary and volcanic rocks from the Neoarchean to Paleoproterozoic, which forms outward-dipping platforms (Dirks *et al.*, 2015). These outward platforms occur to the east, west and north of the Dome include stromatolite-rich dolomite formations from the late-Archaeon. It is within these dolomites, referred to as the Malmani Subgroup, that most of the cave deposits are found (Dirks & Berger, 2013; Makhubela, 2018, Dirks *et al.*, 2015).

The Malmani Subgroup is subdivided into five formations based on the morphology of the stromatolites including the chert content, shales, and breccia horizons. The five formations are as follows: Oaktree, Monte Christo, Lyttelton, Eccles and Frisco, in order of precipitation/sedimentation (Dirks *et al.*, 2015). These layers vary in thickness and the presence of shale horizons and tuff layers, amongst other things. For example, the Oaktree Formation, which is the bottom-most formation, consists of 150–200 m thick chert-poor dolomite with basal quartzite; the Black Reef conglomerate further separates it from the basement gneiss (Dirks *et al.*, 2015). Within the Oaktree Formation are relatively thin and locally carbonaceous shale horizons (<2 m) with two thin layers of tuff. The most prominent layer of tuff which can be best seen in Sterkfontein has been dated to about 2580 Ma. The next overlying formation is the Monte Christo which is 600–700 m thick chert-rich dolomite with a basal oolite bed (Dirks & Berger, 2013; Makhubela, 2018, Dirks *et al.*, 2015). The Monte Christo Formation, like the Oaktree, has shale horizons, however, these are much thinner. The remaining formations of Lyttelton, Eccles and Frisco for the most part are relatively thick, well-bedded successions with chert breccia layers which tend to contain some deformed chert layers and erosional features. All these layers of dolomite are capped by an irregular karstic layer with an irregular mix of chert-rich breccia and sandstone matrix, known as the Rooihoogte Formation (Dirks & Berger, 2013; Makhubela, 2018).

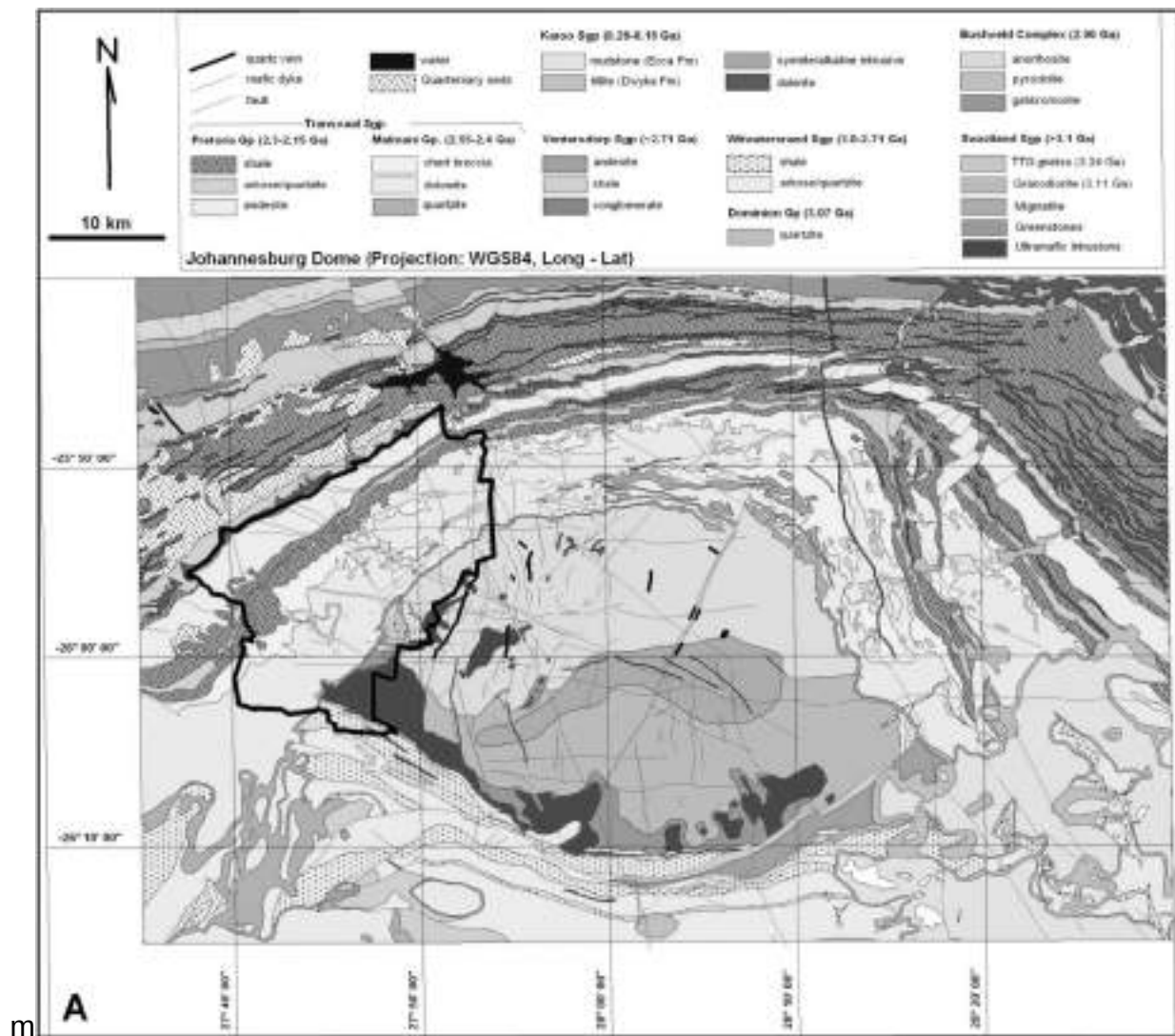


Figure 1: Detailed geology of the Grootvleispruit catchment with the five formations of the Malmani Subgroup (Dirks *et al*, 2015)

Caves and cave systems in the Cradle of Humankind (about 750) occur mostly within the dolomite formations of the Malmani Subgroup. A total of 81 of these caves have been archaeologically productive with macrofossils, some having hominin or archaeological remains. These caves offer a glimpse into the past 3 Ma, so it would be advantageous to understand the formation processes of these caves (Dirks & Berger, 2013; Makhubela, 2018).

The caves in the Cradle of Humankind are mostly developed in a phreatic environment, where slightly acidic underground water would dissolve solution cavities beneath the paleo-water table. Spatial distributions of the caves are all suggested to form along the contact boundary of the different dolomites of the Malmani Subgroup (Dirks & Berger, 2013). This can be seen in the main caves of the well-known sites of Swartkrans, Sterkfontein and

Kromdraai, all of which are found along the contact zone of the Oaktree Formation with the Monte Christo Formation. Similarly, there are also other caves, such as Gladysvale, which lie on the contact zone immediately below the Rooihooft and the Frisco Formations. Haasgat and Malapa follow the same trend as they are laying on the contact of the Lyttelton and Eccles Formations (Dirks & Berger, 2013). These dolomites hosted caves which would eventually be exposed due to the erosion of the African land surface, and sediment would eventually start accumulating in these exposed caves (Dirks & Berger, 2013; Makhubela, 2018).

The general trend in cave formation in the Cradle of Humankind follows numerous stages as illustrated in Figure 2 below, starting with the formation of underground voids, which form along fault lines in the dolomitic layers within the Malmani Subgroup. These voids would at the time coincide with the paleo-water table level. Figure 2 is specifically referring to the formation processes at Bolts Farm however with the understanding that the general process can be applied to most cave formations with the Cradle of Humankind. When, through numerous erosion factors and the general trend to a more arid environment, the paleo-water table dropped and resulted in the creation of underground caves as well as the formation of speleothems (Dirks & Berger, 2013). Speleothems, such as flowstones, stalactites, or stalagmites, only dissolve/precipitate from calcareous dolomite after the water table has lowered to the same level as that of the cave system. In most cases, erosion of the surface of the landscape leads to an eventual opening of the cave. Where the cave entrance remained relatively closed there would be increased precipitation of speleothems which is likely to result in flowstone bounded units (Brain, 1983, Edwards *et al.*, 2020).

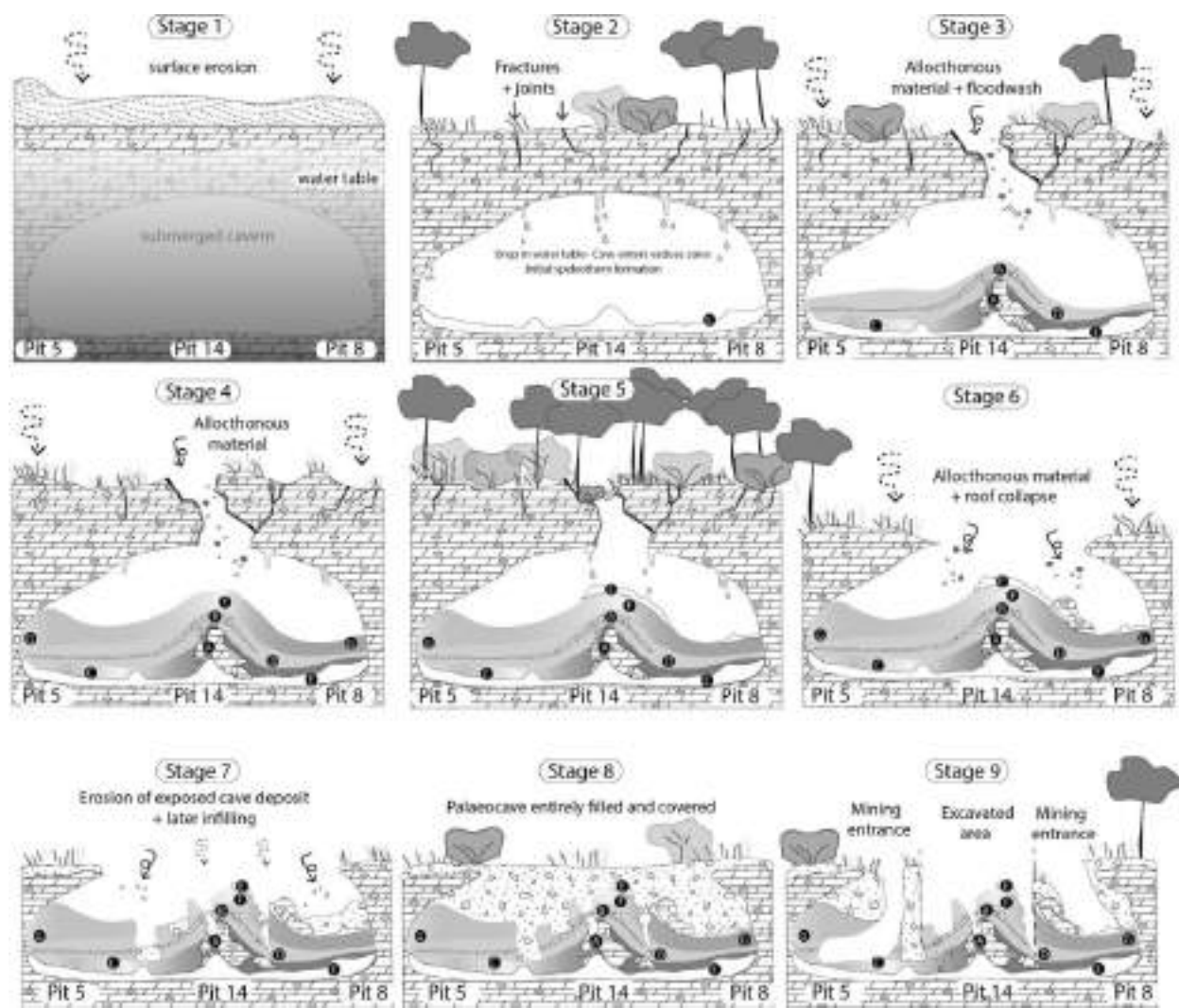


Figure 2: Simple nine stage model of development for the Aves Cave Complex at Bolts Farm (Edwards *et al.*, 2020)

If a cave were to open to the surface, flood-washed or other allochthonous materials from the surface would be deposited inside the cave. Allochthonous material, i.e., imported materials, both inorganic and organic, usually end up in a matrix of either mud or sand, cemented together by calcium carbonate (CaCO_3), forming a breccia (Edwards *et al.*, 2020). The calcium carbonate may remain in the deposits or sometimes, due to the presence of water, return to a decalcified state. However, floods are not the only means by which material can be deposited in the cave. Depending on the cave entrance animals may aid in the import of organic material. The accumulation of bones in the deposits also occurs by means of different agents such as but not limited to: hominins, leopards, hyaenas, other carnivores, raptors, or porcupines. All the agents of accumulation affect the deposits in different ways and have been studied on the basis of the taphonomic processes and modification of fossils (Brain, 1983, Edwards *et al.*, 2020).

Absolute dating of the cave deposits within the Cradle of Humankind in a precise and accurate manner has proven difficult for some time (e.g., Pickering *et al.*, 2011; Granger *et al.*, 2015; Dirks *et al.*, 2017; Dirks & Berger, 2013; Makhubela, 2018). The past approaches of applying geochronology (radiometry and dosimetry) have proved ineffective for most of the cave deposits in the Cradle of Humankind, as the Cradle of Humankind has little suitable material formed during deposition that can be dated or has deposits that are outside the dating range of these techniques. However, before the advent and use of absolute dating techniques, there was a typical form of relative dating based on biostratigraphy. This was based on the principle of sequential ordering of stratigraphy based on the many fossils usually or expected to be found in a stratigraphic layer (Lister, 1992).

Dating through radiometric techniques apply the concept of radioactive isotope decay in a material. This decay rate, in which an isotope breaks down into other products, is at a known and constant statistical rate. Various isotopes are used in radiometric techniques such as carbon 14 (^{14}C), potassium-argon (K-Ar) and the various forms of uranium (U-Th and U-Pb) (Dirks & Berger, 2013; Makhubela, 2018). Carbon 14, which is the most widely applied technique, is based on the decay rate of carbon (^{14}C) to nitrogen (^{14}N), which has a half-life of $5,730 \pm 40$ years. The amount of carbon in a living organism remains relatively constant and only starts to decay after the organism has died. The absolute date of the organism can be made by measuring the amount of its residual radiocarbon. As such there are two main limitations of this technique which relies on analysing carbon-bearing materials such as bone and has complications dating materials younger than 50 k years (Wright, 2017).

Potassium-argon (K-Ar) dating, now superseded by argon/argon dating ($^{40}\text{Ar}/^{39}\text{Ar}$), follows the same principle of radiocarbon dating, however, it is based on the relative quantities of the potassium and argon in a rock or mineral. Potassium is a common element found in a variety of materials, however, it is most common in volcanic ash layers and associated fluvial deposits. As the Cradle of Humankind is not associated with any volcanism, there are unfortunately no suitable potassium-bearing minerals that formed in the deposits (Berger *et al.*, 2003; Pickering *et al.*, 2011; Dirks & Berger, 2013; Makhubela, 2018).

Uranium-based dating follows the same concept of isotope decay, and it is with uranium series disequilibrium (U-Th) that some dating has been possible in the Cradle of Humankind. This technique is based on different series of production and decay for thorium (Th) and uranium (U). By its nature, thorium is not soluble in water under most conditions, and as a result, materials are grown in or from natural water usually do not contain this element. By

contrast, uranium is highly soluble in water and as a result, it is often found in trace amounts in precipitates. (Berger *et al.*, 2003; Dirks & Berger, 2013; Makhubela, 2018). Eventually, the rate of thorium (^{230}Th) build-up due to uranium (^{234}U) decay will match the rate of decay of thorium (^{230}Th); this is known as secular equilibrium. This leads to one drawback which is that the upper limit of this technique is about 500 Kya. This technique has been widely and successfully used when dating CaCO_3 speleothems in the Cradle of Humankind. Another uranium-based technique, uranium-lead (U-Pb), has also been successfully applied to CaCO_3 speleothems dating (Walker *et al.*, 2006; de Ruiter *et al.*, 2009; Pickering *et al.*, 2011) and it has been most successful when combined with palaeomagnetic work (Herries *et al.*, 2019; Herries & Shaw, 2011; Dirks & Berger, 2013; Makhubela, 2018). The main complication comes from finding suitable speleothems which should be devoid of as much common Pb contamination and U content greater than 1 ppm. Paleomagnetic dating, based on the sequence of geomagnetic polarity and reversal characteristics, when used in isolation, requires a long-time scale in order to provide dated age points (Pickering *et al.*, 2018).

A radiometric technique that has been interesting and mostly successful in the Cradle of Humankind, for dates between 0.1 to 5 Ma, is cosmogenic nuclides burial dating. This technique is based on rare isotopes, produced in the atmosphere by cosmic radiation. The premise behind the technique denotes that when sediments that were exposed to cosmic rays at the surface and were subsequently buried, result in the production of cosmogenic nuclides being halted. These cosmogenic nuclides are often paired with radionuclides, the ratio of which is fixed and known, and can be measured. The principle follows much the same process as the previously mentioned techniques and follows the decay constants of the nuclides. This method has been used in sites such as Swartkrans with varying degrees of success as the sediments that were exposed to complex histories of cosmic rays in the shallower areas of the cave offered some complications (e.g., Partridge *et al.*, 2003; Granger *et al.*, 2015; Kramers & Dirks, 2017; Dirks & Berger, 2013; Makhubela, 2018).

Dosimetry dating techniques that have been used in the Cradle of Humankind in the past are the Optically Stimulated Luminescence (OSL) and the Electron Spin Resonance (ESR) methods. These two methods evaluate the rate and time period of damage acquired due to radiation of a sample in a sedimentary environment (Deino, 2013). The Electron Spin Resonance (ESR) method gives an age that is quantified by the radiation damage applied to mineral lattices of a sample, basically accounting for trapped electrons as a local radioactive dose (Dirks & Berger, 2013; Makhubela, 2018). This local radioactive dose is the

sum of the concentration of radioactive elements and the immediate surroundings. This makes ESR extremely handy when directly dating fossils with tooth enamel or where quartz is present. The accurate age which this produces can range from 1 Ma to 5 Ma, however, it seems that the best application of this method is in conjunction with the previously mentioned uranium-series disequilibrium technique. Together, these techniques have been used for directly dating hominin and bovid tooth enamel, as in recent cases such as the dating of *Homo naledi* in 2017 (Dirks *et al.*, 2017). The drawbacks of this method are based on the differential nature of radiation from uranium, thorium and potassium decay series and their concentrations in the sample which can be troublesome to constrain. Optically Stimulated Luminescence (OSL), an indirect way to date fossils, is in theory very similar to ESR and cosmogenic nuclides burial dating. This method is predominantly done on quartz and estimates the time elapsed since the now buried sample had any sunlight exposure, making it ideal for cave sites where the samples were quickly buried by a sand wash and deposited into the darker depths. The only drawback of this method is the precision of the upper range that can be dated only at about 0.5 Ma (Dirks *et al.*, 2017).

The below Table 1 summarises some of the sites in the Cradle of Humankind with the estimated ages for each sites according to member/layer. Along with reference made there are two other methods previously not mentioned: biochronology and lithostratigraphy. Biochronology is very similar to biostratigraphy and is predominantly used to date deposits/sediments through analysis of their fossil content. Lithostratigraphy, the study of strata rock layers, focuses on aspects of geochronology and petrology in a chronological order often correlated to known strata of a known age. This would prove the most applicable in areas where the deposits are extensive horizontally interbedded layers of CaCO₃ (flowstones) (Edwards *et al.*, 2020). These layers would form a unit of bound clastic sediment with over- and underlying flowstones known as a flowstone bounded unit (FBU). Each of these units would account for well-defined, discrete periods (timelines) in time and avoid any drawbacks of lithostratigraphy.

Table 1: List of site ages & techniques used.

Site	Relative Age (Ma)	Dating Method
Gondolin (GD A)	2.17 – 1.82 (Adams, 2018)	U-Pb & Faunal association
Haasgat (HDG)	2.83 – 1.63 (Adams, 2012)	Biochronology
Malapa	2.00 – 1.82 (Val <i>et al.</i> , 2015)	U-Pb & Faunal association

(D)		
Coopers D Cave	1.5 - 1.4 (de Ruiter <i>et al.</i> , 2009) & 1.6 - 1.9 (Berger <i>et al.</i> , 2003)	U-Pb & Faunal
Swartkrans	0.01 - 1.6 (de Ruiter, 2003)	¹⁴ C & ESR
Gladysvale	0.58 – 0.83 (Lacruz <i>et al.</i> , 2003) & 0.57 – 0.007 (Pickering <i>et al.</i> , 2007)	ESR & U-series
Hoogland	3.19 – 2.28 (Adams <i>et al.</i> , 2010)	Paleomagnetic, isotopic & faunal association
Drimolen (Main Quarry)	2.83 – 1.63 (Adams <i>et al.</i> , 2016)	Biochronology
Sterkfontein	2.83 – 1.63 (Ogola, 2009)	U-Pb & Faunal association

Previous Research on agents of accumulation in the Cradle of Humankind

Hyaenidae have been well recorded in the Cradle of Humankind and especially in Gladysvale, and have a unique set of taphonomic indicators, suggesting they were an agent of accumulation. In an attempt to characterise accumulation by hyaena, Cruz-Uribe (1991) and to a lesser degree Stiner (1991), initially suggested a total of 7 characteristics indicative of accumulation by hyaena namely: carnivore-ungulate ratio, damage to bone surfaces, bone breakage patterns, cranial and postcranial ratio, representation of small dense bones, age profiles, and increased proportions of the horn. However, most of these would later be rejected and or questioned by Pickering (2002), Kuhn (2005) and Kuhn *et al.* (2010). Cruz-Uribe (1991) suggested that cranial and postcranial ratios would differ with larger ungulate size as hyaena did not transport skulls, however, this was later rejected as studies showed that this is common behaviour for both brown and striped hyaena (*Parahyaena brunnea* and *Hyaena hyaena* respectively) (Pickering, 2002). Conversely one of the other characteristics put forth by Stiner (1991), was also rejected as it suggested that in an assemblage accumulated by hyaena there would be “excessive” occurrences of horn or antler absent. This was rejected by Pickering (2002), in part, on the basis that keratinous and osseous horn pieces tend to exaggerate both the NISP and MNE values. Another characteristic suggested was the low occurrence or total absence of small dense bones, as the results of consumption and digestion by hyaena, however this too has been rejected by Pickering (2002), Kuhn (2005) and Kuhn *et al.* (2010). This was unfounded as studies showed that, although hyaena do consume, these small dense elements are often found in the faeces or regurgitated close to areas of activity (Pickering, 2002; Kuhn, 2005; Kuhn *et al.*, 2010).

However, there were some characteristics that have been retained as set out by Cruz-Urbe (1991) such as the distinctive damage evident on faunal remains prior to deposition, such as striations, pitting, grooves, scooping and acid etching (Cruz-Urbe, 1991). Hyaena damage through gnawing may occur on various bones but is particularly well-recorded on large bovid femora and tibiae, leaving behind tooth scoring on the bone surface (Cruz-Urbe, 1991). These score marks usually have a “U” shaped depression, which measures 3-5 mm at the widest point and 3-5 mm in depth, if made by an adult hyaena. Further damage is done as the hyaena gnaws further on the diaphysis of the bone, which will be crushed eventually, with epiphyses being removed. Eventually, the diaphysis will be broken down into fragments usually smaller than 15 cm. Breakage patterns along the fractured edge of the bone may often be rounded, due to repeated licking and rubbing of the fractured edges against other hard surfaces (Cruz-Urbe, 1991). There is also a high likelihood that medial distal condyles and other dense bones might remain behind and uneaten. Typical hyaena damage also occurs near or at articular surfaces of larger long bones. The cancellous tissue is exposed, gouged out and eaten, often with the evidence of tooth furrows in the remaining cancellous bone or scoring of the compact bone (Haynes, 1983). The more obvious indicators of hyaena being present in a site would be the presence of both juvenile hyaena remains (Kuhn *et al.*, 2010), and hyaena coprolites (Berger *et al.*, 2009), as is the case at Gladysvale (Backwell *et al.*, 2009).

Leopards (*Panthera pardus*) by contrast accumulate bones in a different manner than hyaena (de Ruiter & Berger, 2000). It is common practice for leopards to store a kill in a tree, upon which it would occasionally feed until either consumed or no longer of interest. During this process, the carcass would degrade, leading to elements falling to the ground. Hypothetically, if this happens in close proximity to a cave roof opening, this could result in bone material being brought into the cave, for instance through water action or by porcupines. This would result in the episodic deposition of bones within the cave deposits, representing a variety of individuals in a random spatial distribution. Another consideration is that leopards might on occasion have utilised deep recesses of some caves to store a kill. This is often considered with corroboration from numerous articulated skeletons and a relative lack of abundance of either gnawing or chew marks, say for the midshaft of limb elements (de Ruiter & Berger, 2000; Selvaggio, 1994; Cavallo, 1997). A study by Pickering *et al.* (2004) considered that the majority of smaller animal fossils accumulated in an assemblage were a result of leopard activity. Whereas the larger animal fossils, would most likely have been contributed by an extinct larger carnivore.

Accumulation by most raptors and raptor-related roosts is usually identified by mostly nocturnal mammal species such as rodents, shrews, bats, and hares. Reptile remains from species such as skinks, snakes, and monitor lizards are also accumulated (Stewart *et al.*, 1999), as well as known cases of small-bodied primates (> 13 kg) that have also been taken by raptors. These often contain a high proportion of humeral and other axial elements, with a large portion of these elements showing signs of corrosion, especially on long bones. There are cases of damage from raptors to bone, predominantly on the head, shoulders, and pelvic girdle. The most characteristic damage patterns, linked to beak and talon activity, are often reported as being single puncture holes or “V” shaped breaks on the cranial elements. These cranial elements are often damaged along the pterion region or at the cranial base, and sometimes in the frontal bone and orbital cavity (Mcgraw & Berger, 2013). This is well documented in the case of Taung by Berger and Clarke (1995). Long bones are often more complete, depending on the smaller size categories of chosen prey. Other forms of raptors, including fish-eating raptors, naturally have assemblages with a high proportion of aquatic elements such as fish and frogs (Stewart *et al.*, 1999).

As the Cradle of Humankind is rich in hominin fossils, it has been important to understand the interaction of hominins with the environment and by extension the means of accumulation by hominins. Numerous studies have tried to associate hominin collection with taphonomic marks, e.g., cutmarks and handedness, localised damage, and localised burning. However, the best approach is usually a combined effort of different taphonomic features attributed to hominin activity. A general trend is that hominin accumulations are more likely to represent a high proportion of diaphysis broken in the middle often with hammerstone percussion damage and more complete epiphyses, associated with bone marrow extraction (Cruz-Urbe, 1991; de Ruiter & Berger, 2000; Pickering, 2002). Other taphonomic factors include cutmarks on fossils as evidence of hominin activity (Shipman & Rose, 1983). These cutmarks have been shown under scanning electron microscope (SEM) inspection to have directionality and are often localised in areas of muscle or ligament attachment (e.g., Lozano *et al.*, 2009). The burning of bones has also been loosely attributed to hominid activity. Further consideration was given to other anthropogenic taphonomy such as skinning marks, bone tools and damage associated with bone marrow extraction. Elements of both the upper and lower limb usually display anthropic butchery marks, especially on the diaphysis near the articular ends. Bone marrow extraction commonly

results in percussion marks on the cranial surfaces of upper limb elements, or as tubular bony elements (Hanon *et al.*, 2022).

Porcupines, not a carnivorous animal unlike any of the above-mentioned species, have also been reported to be an agent of accumulation within the Cradle of Humankind. The species such as the African porcupine (*Hystrix africaeaustralis*), like many rodents, have open-rooted front incisors, which grow continuously. As a consequence, porcupines regularly wear down these incisors, usually on something hard and most often on bones (Behrensmeyer, 1978). This habit which seems to be driven out of compulsion means that porcupines regularly accumulate more bones than what they gnawed upon. In comparison to hominins, porcupine accumulations usually consist of an abundance of larger-sized bones than smaller-sized bones, especially bone that has been bleached and is more weathered (Behrensmeyer, 1978). Usually, the bones associated with the horn, horncore, pelvis and atlas and axis vertebrae are the most taken bones, with the highest survival rate in a porcupine accumulation (Behrensmeyer, 1978).

Lastly, death traps or pitfalls are other forms of accumulation in the Cradle of Humankind, and typically these consist of individuals who fell to their death or who died naturally within the confines of the cave. Subsequently, the most defining factor of a death trap is the presence of complete or semi-complete elements, usually in articulation. The elements also show no prepositional taphonomy (Kibii, 2007).

Plio-Pleistocene environment of the Cradle of Humankind

The Cradle of Humankind covers roughly an area of 470 km², with numerous caves and cave sites as previously mentioned. Fossil material and assemblages associated with hominin evolution have always been of great importance to researchers, with equal importance assigned to the context of the fossil material. The contextual importance in many studies focuses on the environmental conditions and changes over time (i.e., Scott *et al.*, 1997; Leichliter, 2011; Avery, 2001; Pickering *et al.*, 2019). Paleoenvironments are often reconstructed through various studies such as faunal, floral, and isotopic, often in conjunction with each other. The Cradle of Humankind Plio-Pleistocene paleoenvironment is often referred to as a mosaic of habitats and has had varied climatic conditions over the past 2.6 Mya (Pickering *et al.*, 2019).

A general trend of change in the paleoenvironment of the Cradle of Humankind is largely based on general trends seen in Southern Africa. Most of the studies within the Cradle of Humankind are, however, based on a local scale. The paleoenvironment of South Africa has been characterised by aridification, varying climate and less than 5% annual rainfall (800mm) over the landscape (Scott *et al.*, 1997). Within South Africa, there are seven unique biomes, i.e., fynbos, forest, desert, succulent karoo, Nama-karoo, savanna and grasslands. It is within the grassland biome that most of the Cradle of Humankind can be found, however, biomes are often subdivided, and the grasslands form part of the Highveld region. Within the Cradle of Humankind, there also lies a grassland-savanna border, the Sterkfontein valley, with a localised mosaic of moist and arid savanna types (Leichliter, 2011). Both the grassland and savanna biomes have expanded and contracted in correlation to regional and global climate change, especially during the Plio-Pleistocene (Avery, 2001). The trends during the Plio-Pleistocene would have been changes towards a drier hydroclimate, with less vegetation. This would have resulted in more open environments, and as previously mentioned, an increase in surface erosion (Pickering *et al.*, 2019). Studies on the cave sites within the Cradle of Humankind, at a local scale, seem to indicate that speleothem formations occur most often during times of increased moisture with temperature fluctuations, whereas clastic sedimentation occurred during interglacial and more arid phases. This as pointed out by Pickering *et al.* (2019) creates an issue in discerning the exact paleoenvironment of the entirety of the Cradle of Humankind, as there is a preference for accumulated sediments to occur most often during more arid time periods, which is likely to overrepresent arid-adapted species.

Background

Origins of Equidae

The evolution of Equidae over 55 million years involves the progressive change from a small-sized mammal into the species which exists today. Some of these changes include an increase in the complexity of the enamel patterns, a reduction in the number of distal autopod digits and an increased length of the limbs. All of these changes point towards a faster and more efficient grazing animal (Bernor *et al.*, 2010).

Hyracotherium (= *Eohippus*) is the first known Equid found in the Eocene (56 to 33.9 Mya) (Hunt, 1995) in North America, Europe, and Western Asia (Bernor *et al.*, 2010, Bernor *et al.*, 2019). It is derived from a phenacodont conylarth, with a slightly different dental

morphology of six cusped, low-crowned, square upper molars. These short-faced animals were seemingly intelligent, with a more advanced, convoluted cerebral cortex, and complex cerebellum (Bernor *et al.*, 2019). Additionally, *Hyracotherium* retains four hoofed toes on the forelimb and three on the hind limb, with a cushioning pad on each foot. The likely environment occupied by these animals ranges from a savanna-woodland to dense forest habitat (Hunt, 1995). The Equids from the Oligocene (33.9 to 23.03 Mya) (Hunt, 1995) which consisted of *Meshippus* and *Miohippus*, were about the same size as modern-day sheep and are considered to be the first true, three-toed horses, with the middle digit being much larger than the lateral toes (Hunt, 1995). Furthermore, the snout was more elongated, and the premolars showed significant molarisation with increased lophs and lophids (Hunt, 1995).

By the Miocene (23.03 to 5.333 Mya), the first signs of *Merychippus* appeared in the fossil record, predominantly in temperate North America (Bravo-Cuevas & Ferrusquía-Villafranca, 2006). *Merychippus* marked a major leap in the first of the grazing equids as this species had true hypsodont cheek teeth with very high crowns and teeth with elaborate lophs and cementum. The longer limbs of *Merychippus* consisted of a fused radius and ulna as well as a fused tibia and fibula, unlike the previous species, but still retained three toes. By the late Miocene (around 15 Mya), *Merychippus* would undergo rapid speciation that would lead to numerous lineages with at least 19 new species of grazers (Hunt, 1995). This explosive burst of equid evolution is often called the "merychippine radiation" (Hunt, 1995). During the "merychippine" radiation the lineage of Hipparions known for their distinctive three toes and unique protocone dentition would arise. Hipparions appear to have originated about 15 Mya in Northern America with several waves emigrating outwards, where they survived up until the late Pleistocene, and finally with the last African species going extinct between 0.6 and 0.4 Ma (van der Made *et al.*, 2022). The last of the Hipparion equids would have very reduced lateral toes (Savage & Long, 1986). This taxon would split into 4 genera and at least 16 species and was rather successful at inhabiting a wide assortment of niches (Hunt, 1995). Unlike *Equus*, Hipparions had large and elaborate facial fossae. The second lineage is known as "Protohippines" consisting of smaller-bodied equid species of *Protohippus* and *Calippus*. The third lineage that arose is often referred to as "true equines". These Equidae would begin to decrease in body size, typically seen in *Merychippus* primus compared to later merychippines such as *Merychippus sejunctus* and *Merychippus isonesus* (Bernor *et al.*, 2019). These species, however, still retained "primitive", Hipparion features mixed with later equine features such as the three-

toed to one-toed limb morphology exhibited by extant Equidae. *Merychippus cf.* is still considered a monophyletic group within the Hipparionines (Bravo-Cuevas & Ferrusquía-Villafranca, 2006).

"True equines" appear after the late Miocene (after 15 Mya) through to the Pleistocene (2,58 Ma to 11,7 Kya) (Bernor *et al.*, 2019). This time period would see the evolution of *Pliohippus*, *Astrohippus*, *Dinohippus* and finally *Equus*. *Pliohippus*, a three-toed species, is similar to *Equus*, however, differs in the presence of facial fossae, which are absent in *Equus*, and dentition morphology (Hunt, 1995). Even if related, *Pliohippus* is probably not the ancestor to *Equus*, but it is said to be the ancestor to *Astrohippus*. *Astrohippus* is another one-toed equid from about 10 Mya, with similar facial fossae to *Pliohippus*. *Dinohippus* from the upper Miocene to Pliocene (10 Mya to 3.6 Mya) are also one-toed equids, with the earliest known species being *Dinohippus spectans*, *Dinohippus interpolatus*, and *Dinohippus leidyanus*, and have a widespread fossil record throughout temperate regions in North America (Hunt, 1995). The facial and dental morphology for this genus tends to be more similar to that of *Equus*, with *Dinohippus mexicanus* being suggested as a transitional group closer to *Equus* (Carranza-Castañeda, 2019). The last lineage to arise would be that of *Equus*, seen as numerous extant *Equus* species and some extinct species such as *Equus capensis* (Hunt, 1995).

Extinct Equidae in Africa

The basal species of *Equus* is considered to be *Equus simplicidentis* which is best represented in the Hagerman Horse Quarry in North America, dated to about 3.19 Mya (Bernor *et al.*, 2010, 2019). This species would have shown a mosaic of features of *Dinohippus* and *Equus*. Later during the first glaciation periods in the Pliocene certain *Equus* species diversified and entered Africa, proliferating into the extant species of modern-day Equidae. These extant species are commonly broken into two subdivisions, either caballine or non-caballine. Caballine equids are typically linked to *Equus caballus* (horses), whereas non-caballine equids are usually zebras and donkeys: *Equus burchelli* (Burchell's zebra) *Equus zebra* (mountain zebra), *Equus grevyi* (Grevy's zebra) and *Equus asinus/africanus* (true asses and donkeys) (Bernor *et al.*, 2019). *Equus capensis*, *Equus oldowayensis*, *Equus koobiforensis*, *Equus numidicus* and *Equus tabeti* are the majority of the known extinct Equidae in Africa, with varying temporal and geographical ranges, as seen in Figure 3 below.

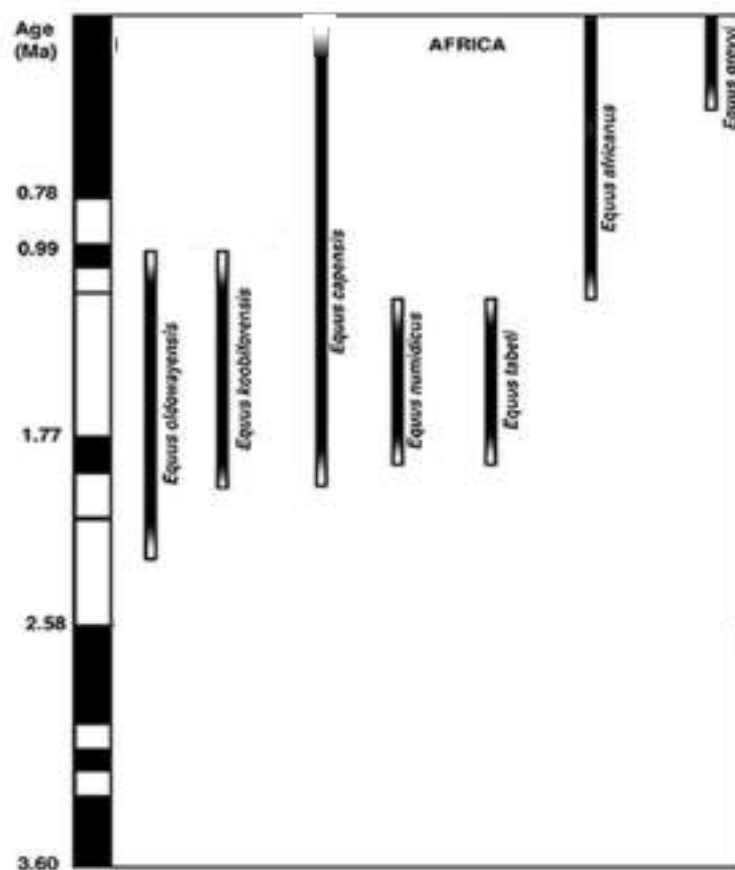


Figure 3: Chronology of taxa in Africa modified from Bernor et al. (2019)

Equus oldowayensis (Hopwood, 1937) was first recorded in Bed I in Olduvai Gorge, Tanzania, at about 1.8 Mya and has the oldest date recorded from the Shungura Formation, in the Omo River basin, Ethiopia, at 1.9 Mya. This species has always been recorded in isolated occurrences in South Africa, and only in small samples of isolated teeth (Churcher, 2006). *Equus oldowayensis* is known as a very robust zebra and has been suggested to be ancestral to *Equus capensis*. The species of *Equus numidicus* (Arambourg, 1947) is the oldest known North African *Equus*, occurring from the early Pleistocene (2.5 Mya) in sites of Algeria and possibly in some East African sites. However, to date very little further information is available as to the dates of the last appearance of *Equus numidicus*. *Equus koobiforensis* is another species from East Africa and is dated to a similar age as *Equus oldowayensis* at about 1.8 Mya, originating from the Koobi Fora region in Kenya. The closest relatives to *Equus koobiforensis* are *Equus livenzovensis*, *Equus stenonis* and extant *Equus grevyi*, as shown through phylogenetic analysis by Cirilli et al. (2021). In their study various morphological changes were taken into account, e.g., reduction and

elongation of post vomerine and vomerine length, reduction in the preorbital fossa, derived morphology of the lingual margin of the protocone and others.

Equus capensis (Broom, 1909) otherwise known as the extinct Cape horse (also Giant Cape zebra), is a well-represented fossil equid species, especially as part of the South African Quaternary period (2.6 Mya to present). *Equus capensis* is purported to have been a large-bodied zebra that existed throughout most of Africa during the Pleistocene, and probably into the Early Holocene (roughly 1.8 Mya to 0.01 Mya) (Churcher, 2006). *Equus capensis* was first described by Broom (1909) based on fossil material that was found washed up on a beach in Table Bay. The fossil material was a left mandible embedded in a limestone slab of which parts of the dental row were obscured or had missing enamel. Broom noted the larger size of the dentition and initially suggested that the material had a great affinity to that of extant horses (*Equus caballus*). At the time there were no maxillary dentitions present, however, in later years Broom (1909, 1913) would describe upper dentition from a few isolated teeth found at both Darling in the Western Cape and Middleburg in Mpumalanga. Later, after Broom, others such as Cooke (1950) and Churcher (2000) would interpret and expand on *Equus capensis*, remarking and expanding on the dental morphology of *Equus capensis*. This, unfortunately, led to uncertainties as various forms of dental morphology and specificities of enamel features were imposed on *Equus capensis*. Thus, the classification of *Equus capensis* has been disputed, as with Churcher (2000, 2006) who suggested that, based on the larger size of the dentition, *Equus capensis* is conspecific with the extant *Equus grevyi*. Later Churcher (2014) would go on to refer to the species as morphologically identical.

Recent phylogenetic analyses based on mitochondrial DNA sequences suggest that the *Equus capensis* along with the extinct quagga (*Equus quagga quagga*) forms a separate clade within the phenotypically plastic modern plains zebra species (Orlando *et al.*, 2009). Orlando *et al.* (2009) noted that the genetic distance between *Equus capensis* and the extant plains zebra is within the range of intraspecific diversity present in other zebra species. This suggests that the status of separate species or subspecies is not warranted until further information becomes available from nuclear loci. However, the larger size of *Equus capensis* and their disappearance by the Late Pleistocene suggest that the extinct Cape horse and extant plains zebra had different evolutionary trajectories (Badenhorst & Steininger, 2019). Furthermore, other studies by Eisenmann (2000) comparing skull proportions, concluded *Equus capensis* is more similar to *Equus quagga* than to *Equus*

grevyi, and a study by Faith (2012) shows that there are similarities between *Equus capensis* and *Equus mauritanicus* in terms of the size of the teeth.

Equus capensis is a fellow grazer and has an estimated height similar to that of the extant *Equus grevyi* (Brain, 1981; Eisenmann, 2000; Churcher, 2006). This estimation of the height at the withers can be determined by multiplying the length of a limb bone by index numbers, giving an estimated height for *Equus capensis* that ranges between 144 and 156 cm (Eisenmann, 2000). The estimated weight of *Equus capensis*, determined through the exploitation of the relationship between the occlusal surface of an upper cheek tooth, body weight and regression analysis, averages about 450 kg. An alternative weight estimation, using the product of the antero-posterior diameter and transverse diameter of the distal end of the third metacarpal, yields an estimated average weight of 400 kg with a maximum weight of 500 kg (Eisenmann, 2000; Broom, 1909; Churcher, 2006).

The geographic distribution of *Equus capensis* is vast as it has been recorded in fossil sites across South Africa, the African east coast and all the way up to Egypt (Churcher 2006). These sites are also known to have a wide variety of ecological contexts (arid to coastal) suggesting *Equus capensis* had a wide tolerance of habitats and dietary flexibility (Badenhorst & Plug, 2012). In South Africa, *Equus capensis* appears in the Western Cape with its strandveld coastal areas, the Karoo with its succulent-dominated interior plains, the Northern Cape, and Free State with its grass plains, and in the former Transvaal with its more arid grasslands. Further studies which investigated mesowear analysis (Lee-Thorp et al., 1994; Faith, 2012) suggest that despite having morphological adaptations, and extreme hypsodonty, *Equus capensis* was more of a mixed feeder than a grazer. These studies, however, do consider that this flexible diet was in part due to the unique fynbos vegetation. This contrasts with another line of thinking that suggested *Equus capensis* was typically a grazer as supported by isotope data on the tooth enamel (Lee-Thorp & Beaumont, 1995). Excavations on the Holocene deposits at Wonderwerk Cave and further studies by Thackeray (1984) provided evidence for the disappearance of *Equus capensis* from the fossil record of southern Africa around 10 to 5 Kya. Furthermore, sites such as Apollo 11 and Elands Bay Cave corroborate this. The transition from the Late Pleistocene to the Holocene is often associated with a decline of large-bodied grazers as well as a reduction of open grassland. Furthermore, evidence supports this reduction of grassland efficiency after the Last Glacial Maximum (20 Kya), and the general trend of aridification on a global

scale and that the extinction of *Equus capensis* is likely due to the limitation imposed on range and numbers within the species (Klein 1977; Thackeray 1984).

Hipparion, the three-toed horse, is believed to have originated in Northern America some 11 Mya, eventually spreading to Africa and Europe. The nomenclature of the species has, similar to most equids, been complicated and *Eurygnathohippus* is often used in conjunction with “Hipparion” for the Plio-Pleistocene African Hipparions genus, which is closely related to the Indian *Sivalhippus*. The first appearance of *Eurygnathohippus* is from the end of the Miocene (about 6 Mya) and is based on fossil recordings in sites such as Lothagam in Kenya, Middle Awash in Ethiopia, and Shabi in Libya (van der Made, 2014). This African species is characterised by its retention of the unique protocone island dentition for both the molars and molarised premolars, which other Hipparionine lineages would lose (van der Made, 2014). In general, the African species of Hipparion were built rather lightly and resembled a pony in size, comparable with the plains zebra at about 120 cm in height (Brain, 1981). Hipparions have been found at sites such as Swartkrans Member 1 and Kromdraai A (Brain, 1981). The unique upper cheek teeth of Hipparions have a protocone that forms a distinct island (Brain, 1981).

Studies of mesowear of *Eurygnathohippus* from Langebaanweg, Western Cape, South Africa, suggest that these species were grazers, initially relying on green grasses and that they were highly water dependant. However, *Eurygnathohippus* did at some point during the last 5 Ma adapted its feeding behaviours and strategies to eating (drier) grasses containing less moisture and drinking more frequently (Franz-Odendaal, 2002). Further analyses by Franz-Odendaal (2002) based on stable isotopes and dental pathologies suggested that most accumulations of *Eurygnathohippus* at Langebaanweg were accompanied by droughts. The disappearance of Hipparion in the Cradle of Humankind is yet to be absolutely defined. However, fossils found in Cornelia (Bed B of Member 1) have been roughly correlated to the Upper Acheulean of Broken Hill in Zambia, dating to the Mid/Late Pleistocene (Brain, 1981). Studies by Brink *et al.* (2016) on the 1 Mya site Cornelia-Uitzoek, in the Free State, suggest this to be the last appearance of *Eurygnathohippus* in Southern Africa.

Extant Equidae in Africa

Extant equids across the world are represented by a total of eight species of horses, asses, and zebras, of the genus *Equus*. However, in Africa there exist only three species of zebra

and one species of donkey/ass, i.e., Mountain zebra (*Equus zebra*), Burchell's zebra (*Equus burchelli*), and Grevy's zebra (*Equus grevyi*) and the African wild ass (*Equus asinus*). The distribution of these equids, across Africa, is illustrated in Figures 4, 5 and 6 below.

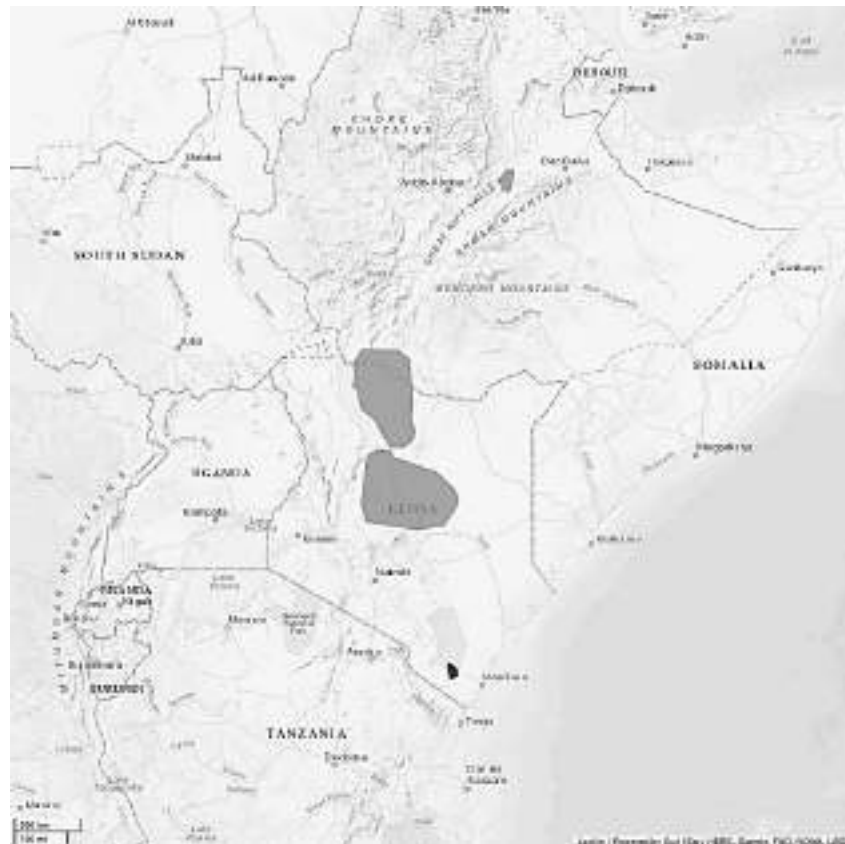


Figure 4: Distribution of *Equus grevyi* (Rubenstein *et al.*, 2016)

The mountain zebra (*Equus zebra*) can be broken down further into two subspecies, known as the Cape mountain zebra (*Equus zebra zebra*) and Hartmann's mountain zebra (*Equus zebra hartmannae*). *Equus zebra* have a distribution limited to southwest Africa and are commonly inhabiting slopes and plateaus in mountainous areas of South Africa and Namibia, illustrated in Figure 5 (Penzhorn, 1982; Gosling *et al.*, 2019). Grevy's zebra (*Equus grevyi*) have a larger distribution than *Equus zebra* and currently are commonly found in areas of Northern Kenya and small isolated areas of southern Ethiopia. However, historically *Equus grevyi* used to have a much larger distribution which included Somalia, Ethiopia, Eritrea, Djibouti, and Kenya in East Africa. The estimated world population of *Equus zebra* is around 2,571 with only about 126 individuals in Ethiopia (Churcher & Watson, 1993).



Figure 5: Distribution of *Equus zebra* (Gosling et al., 2019)

The plains zebra (*Equus quagga*) has the largest distribution of zebra (Figure 6), only in Africa and it is common throughout south-eastern Africa, Kenya, and Tanzania, extending northwards into southern Ethiopia and Sudan. *Equus quagga* is also found westward in Namibia and Botswana, and south in Zimbabwe and South Africa (Skinner & Chimimba, 2005; Bronner et al., 2003; Rubenstein et al., 2016). The taxonomy of the plains zebra has been complicated throughout the years as originally the species was formally classified by Gray (1824) as *Equus burchellii*. However, prior to this, in 1785, Boddaert and Gmelin classified the now-extinct quagga as *Equus quagga*. Subsequent studies based on DNA sequencing by Higucho et al. (1984) showed very little difference between the DNA of quaggas and plains zebras. As a result, a trinomial designation is given to the extant subspecies of plains zebra of (*Equus quagga*). The five subspecies of the plains zebra are: *Equus quagga boehmi* (Boehm's zebra or Grant's zebra), *Equus quagga borensis* (half-maned zebra), *Equus quagga chapmani* (Chapman's zebra), *Equus quagga crawshayi* (Crawshay's zebra) and *Equus quagga burchelli* (Burchell's zebra).



Figure 6 Distribution of *Equus quagga* (King, 2016)

As *Equus quagga* is so widely distributed throughout Africa and recognised by its numerous sub-species, the exact first appearance in the fossil record is difficult to pinpoint. Fossil remains of this genus have been found in areas ranging from North Africa (Morocco, Algeria, and Libya), and also in East Africa (Koobi Fora to South Africa). The consensus is that the estimated first appearance is somewhere between the latest Pliocene and early Pleistocene, i.e., 3 to 2.6 Mya (Bernor *et al.*, 2019).

Fossil remains of *Equus quagga* were first described by Malan & Cooke (1941) from Wonderwerk Cave. This was based on numerous isolated maxillary teeth and part of a mandible. During the excavation it was suggested that the age of the deposits might be from the Middle Stone Age at about 0.28 Mya as in the Koobi Fora area in East Africa where Eisenmann (1983) (Potts & Deino, 1995) described two phalanges and a few isolated teeth, assigning them "*Equus cf. Equus burchelli*". However, it is likely that these specimens belong to *Equus grevyi*. These specimens were given an estimated age of younger than 0.5 Mya, based on biostratigraphy from the *Metridiochoerus compactus* zone in Koobi Fora. Other fossils recorded were by Mendrez (1966) in the Sterkfontein Extension site in South Africa, namely two fragmentary premolar, molar and one complete maxillary molar. The

Sterkfontein Extension sites have been dated to about between 684 and 251 Kya, via electron spin resonance (Reynolds & Kibii, 2011).

The plains zebra (*Equus quagga*), which is the most common of the five sub-species, has a mean shoulder height of 128 cm in males and 123 cm in females. The mean weight of males is 248 kg and of females, it is 219 kg. The base of the skull morphology shows that the forehead is distally convex, the zygomatic arches are more robust, and the paraoccipital process is well-developed with more pronounced postorbital constriction. The mandible is rather large, and the premaxilla has a downturned curvature below the level of the alveolar cheek teeth line. The upper incisors have infundibula that change their shape or even disappear after advanced wear. Infundibula on the lower incisors are mostly absent in southern populations and simply reduced in northern populations. The tooth eruption sequence is similar to that of the horse (*Equus caballus*), with the first molar being the first cheek tooth to erupt. Plains zebra often co-exist alongside other animals such as blue wildebeest (*Connochaetes taurinus*), blesbok (*Damaliscus pygargus phillipsi*) or common ostriches (*Struthio camelus*), sometimes resulting in the formation of mutually beneficial relationships (Skinner & Chimimba, 2005).

Habitat & Diet

Equus grevyi almost exclusively inhabits semi-arid grasslands or acacia savannas, generally found at higher elevations. This is unique among members of the genus *Equus*, such as *Equus quagga*, as this species is generally not as dependent on water (Schoenecker *et al.*, 2016). However, *Equus grevyi* still prefer areas with a permanent water source, especially for the dry season during which time they tend to concentrate territories around water sources and later, in the rainy season, they disperse territories more (Schoenecker *et al.*, 2016). *Equus grevyi* will often prefer areas with a water source with surrounding grassland within daily reach. Grevy's zebras are by nature grazers, however, have on occasion had browsing tendencies. Generally, they feed on tough grasses and forbs when available, however, in the dry season they supplement their diet by browsing on leaves, which can make up 30% of their diet (Schoenecker *et al.*, 2016).

Equus quagga have a wide and varied range of habitats which they occupy, both temperate and tropical. Generally, the most common habitats that *Equus quagga* is found in are areas of open grasslands, open woodlands, and open scrub environments (Grubb, 1981). *Equus quagga* generally prefer mid-productive grasslands, with the highest quantity of green,

highest standing crop and highest grass biomass regardless of quality (Schoenecker *et al.*, 2016). *Equus quagga* is a water-dependent species, meaning that they need to drink more often throughout the day (Skinner & Chimimba, 2005). This, however, had been disputed by both Brooks (2005) and Cain *et al.* (2012) who observed that the drinking frequency in various parks in South Africa and Botswana was not daily but rather in intervals of 1 to 4 days. However, *Equus quagga* tends to prioritise water sources with a surrounding feeding opportunity less than 12km away (Grubb, 1981). There are habitats that *Equus quagga* tend to avoid such as dense forests, deserts, and wetland areas. This avoidance is for numerous reasons; one being the limitation that these habitats place on their ability to detect predators. *Equus quagga* has a highly variable diet based on the availability of local plants and has been recorded to eat over 65 different species of plants. Of the 65 species of plants, 50 species are grasses and about 9 taxa are trees or bushes. The availability of grass will determine the species of grass eaten, however, it appears that *Equus quagga* prefer some species of grass more than others. The most preferred grass, year-round and which accounts for up to 40% of their diet, is *Panicum maximum*. Some of the other species of grass preferred are *Themeda triandra*, *Cynodon dactylon*, and *Eragrostis superba*. (Arsenault & Owen-Smith 2008; Bernor *et al.*, 2010). If, however, faced with extremely dry times *Equus quagga* may take up browsing, as pointed out by studies of mesowear of zebra in drier habitats versus those in moister habitats (Bernor *et al.*, 2010).

Equidae Ecology

Equid ecology is based on biological science that studies how living organisms interact with one another within their environment. Every organism is a member of a certain species; a group that has a unique set of characteristics and behaviours that distinguish them from all other species (Miller, 2004). Ecology plays a vital role in understanding evolutionary processes as it is both the inter- and intra-species interactions of organisms that are causative in the development of new evolutionary processes. A common feature of the ecology of *Equus quagga* is the migration and subsequent tracking of abundant resources year-round (Young *et al.*, 2005). On a larger scale, *Equus quagga* populations have a delayed migration in order to find long grasses after rainfall. However, at a smaller scale, they utilise home ranges to maximise the quality and quantity of the food as well as minimise predator risk (Hopcraft *et al.*, 2010). Family groups all have their own unique home ranges but is always constrained by resource availability. In areas such as the Kruger National Park, these home ranges can stretch anywhere from 49 to 566 km² (Smuts, 1974). In areas where

there is limited resource availability, there is a great amount of daily movement recorded, as opposed to moving 12 km daily they may move up to 30 km (Brooks *et al.*, 2008).

Population dynamics of all modern extant equids is a complex interaction of abiotic factors, in terms of habitat use, but also biotic as their role in the ecosystem is often in coexistence with other medium-sized herbivores and predators. Currently, and as shown, medium-sized herbivore (grazing) communities tend to be more dominant on the current landscapes. The resulting overlap in these animals' distributions contributes to differences in adaptations which have led to fundamental changes in the groups. Equidae not only adapted a different form of the digestive system but also differences in morphological, reproductive, and social systems (Gosling, 2006). As recent taxonomic analyses studies show there have been a few subspecies of the modern plains zebra, each characterised by a variation of stripe patterns. Plains zebra being exclusively grazers are able to successfully niche partition the ecosystem, typically grasslands and savanna woodlands, with grazing bovids (blue wildebeest and African buffalo). Furthermore, in terms of social systems, plains zebra tend to have a harem-based structure that also accounts for more differences when compared to their bovid counterpart. The evolution of Equidae population dynamics, therefore, is vital in the understanding of ecosystem interactions as they pertain to predatory avoidance behaviours. Recent studies in the Serengeti suggest that plains zebra is capable of outcompeting other species for similar resources such as ruminates. This results in plains zebra having a much greater spatial dispersion (Gosling, 2006). Other adaptation includes having a lower reproductive potential and being less sensitive to resource limitation and droughts; all of which should make them more susceptible to predation, which in many cases tend to be the primary limiting factor (Gosling, 2006). It is known that there is a low first-year survival of zebra foals that limits population dynamics, however, lion and hyaena prey mostly on adult zebras (Hayward, 2006; Hayward, 2005; Gosling, 2006).

Predator Avoidance Behaviour in Extant Equidae

Studies show that lions (*Panthera leo*) are the predominant predators of modern *Equus quagga* followed by spotted hyaenas (*Crocuta crocuta*), black-back jackals (*Canis mesomelas*) and leopards (*Panthera pardus*). The lion rate of predation of *Equus quagga* tends to be lowest with young prime zebra individuals, staying relatively steady until the highest rate of predation at the relatively old age of zebra individuals (Hirst, 1969). Hyenas and jackals only constitute a small amount of the predation rate of zebra, often pulling down young zebra foals. Leopards, cheetahs, and wild dogs may also be regarded

as potential predators pulling down young zebra foal, however, the rate of predation is sporadic. Interestingly, the predation rate of female zebra stays relatively steady overall age classes whereas with male zebra there tends to be an increase in the relatively older age classes (Hirst, 1969).

Some common *Equus* anti-predator behaviour includes having an individual act as a spotter, whilst others in the group are feeding. These spotters will give loud barks to alert the rest when a predator is spotted. Vigilance in *Equus quagga* is often a group effort and the amount of vigilance remains the same regardless of predation risk. But it does appear that male *Equus quagga* have higher vigilance rates than females (Fourie, 2012). Also, in the same line of anti-predator behaviour, they will often associate themselves with other animals such as wildebeest which reduces predation risk (Gochfeld & Burger, 1994).

Equus quagga tend to avoid grassland patches where and when lions are present, thus reducing their chances of encounters. Lions indeed tend to be more active during night-time, often moving to the grassland-type terrain during the night. Although preferring grassland areas, *Equus quagga* will in response to lion night-time activity tend to move into a more woodland type of terrain during the night (Fischhoff *et al.*, 2007). This change in preferred terrain types will reduce the encounter of predators, however, the transition is not always complete. Sometimes *Equus quagga* may choose to stay in the grassland at night. This behaviour seems counterproductive, however, a new avoidance behaviour is adopted by *Equus quagga* through their change in movement and speed, enabling them to remain in the grassland (Fischhoff *et al.*, 2007). The overall movement at night when in the grassland area involves a greater speed and sharper turns. There is a more rapid and erratic night-time movement associated with grassland, most likely as a response to heightened danger from lions and a lower likelihood of being stalked (Fischhoff *et al.*, 2007). Furthermore, the spatial awareness of *Equus quagga* is particularly useful to them as it allows for efficient movement across large distances (Brooks *et al.*, 2008). As previously mentioned, *Equus quagga* also try to avoid any dense habitats as often their spatial awareness and ability to detect predators become limited.

It is likely that all the above factors were mutually inclusive and Equidae used them in an integrated manner. These behaviours of Equidae are considered part of an evolutionary ecological approach which predicts the types of behaviour organisms use to avoid predation. These include a combination of sound, smell, colour, pattern, form, posture and/or

movement devices (Pianka, 2011). In the case of *Equus quagga*, they tend to associate with other antelope and are more likely to react to alarm signals of blue wildebeest (*Connocahetes taurinus*) and impala (*Aepyceros melampus*) (Schaller, 2009). Moreover, Equidae are able to defend themselves effectively against attacks by predators by kicking, bucking, and biting (Schaller, 2009), however, there is almost no recorded evidence of *Equus grevyi* displaying these active defence measures. The Hartmann's zebra, a sub-species of *Equus quagga*, has been recorded to not only kick an adult spotted hyaena (*Crocuta crocuta*) to death but to counter and chase hyaena well over 100 m away. Furthermore, the Hartmann's zebra has been documented in continued kicking of an hyaena even after death. Further accounts of plains zebra kicking other predators such as lions have resulted in broken jaws and broken forelimbs (Schaller, 2009).

A group structure is common to all extant Equidae and often when in a family group, the head stallion will keep to the flanks or the rear when a predator is spotted. Often following the encounter, the head stallion will defend members of the group, while mares tend to defend foals. At times, a cohesive group effort is made in order to defend themselves. The defence is often shown as biting and kicking (illustrated in Figure 8), together with loud vocalisation. If this does not ward off the potential predator, the Equidae flee and are able to outpace predators such as lions and hyaenas (Skinner & Chimimba, 2005).



Figure 7: Adult zebra kicking lion (*Panthera leo*). Taken from Daily Mail Online, 2011. Available at: <https://www.dailymail.co.uk/news/article-1371251/Lion-regrets-making-zebra-cross--lashes-kick-face.html>.

Further research on predatory avoidance behaviours of modern *Equus quagga* show an interesting change in behaviour at night *versus* in the day. Research done by Fischhoff *et al.* (2007) show that zebra make different use of the terrain in which they are found. *Equus quagga* employs different avoidance techniques against their primary predator, the lion, depending on the number of sightings of the predator, the time of day and the terrain which they choose to occupy. A study by Williams (1998) observed the habitat usage of *Equus grevyi* in response to predators and concluded that *Equus grevyi* tend to aggregate at water sources to lower predation risk through dilution. Also, *Equus grevyi* would utilise water sources during the hottest parts of the day, when predator activity is at its lowest. This behaviour seems to be shared with *Equus quagga*, who also tend to not travel to local water sources during the night, as commonly predator risk is much higher at night and water sources (Schaller, 1972). When confronted by a predator, *Equus quagga* tend to flee more than a kilometre from the initial site of encounter, as well as relocate up to 3 km away after following encounters. After the encounter, *Equus quagga* are also more likely to abandon the area, they were previously foraging in (Martin and Owen-Smith, 2016).

Gladysvale

Gladysvale is reported to be one of the earlier caves examined by Broom around 1930, which was further investigated by Tobias, in 1946, leading to the discovery of fossilised primate remains (Berger *et al.*, 1993). Later in 1991 Berger, Keyser and Tobias would continue excavations in earnest, and in the process discovered new australopithecine remains, some of the first since 1948. The Gladysvale cave is located 13 km northeast of the hominin-bearing sites Sterkfontein and Swartkrans, 45 km north-northwest of Johannesburg (Figure 9) and is a National Heritage Site. Gladysvale itself consists of both *in situ* fossiliferous cave fill, found in three large sections of the cave system, and mining dumps which are the remains of early limestone mining of the Eccles Formation (Berger *et al.*, 2009).

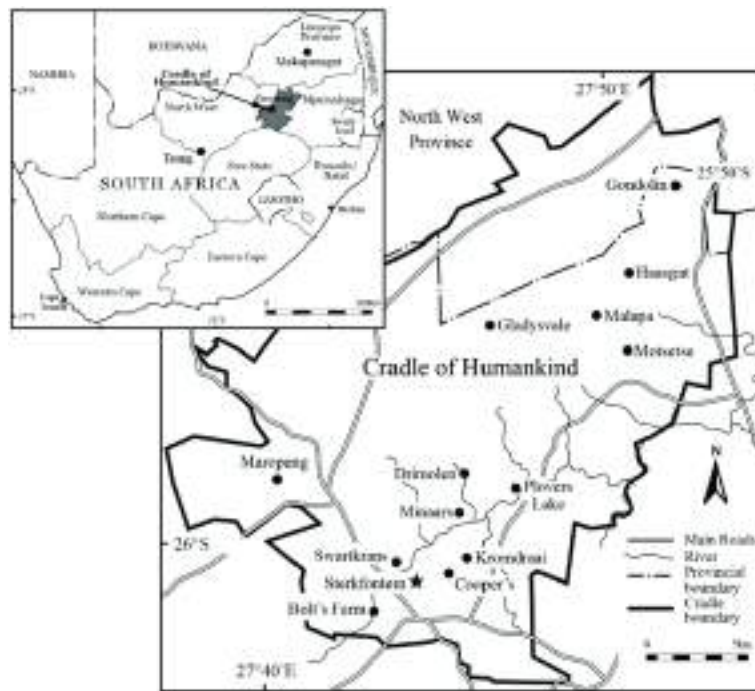


Figure 8: Location of the Gladysvale Cave in relation to other Plio-Pleistocene sites in the Cradle of Humankind, South Africa (Delmas & de la Pena, 2019)

The geology of Gladysvale comprises numerous underground chambers in dolomitic terrane, some of which extend down to 65 m below the modern ground surface. In addition, the cave system contains open-air deposits which have been exposed through the collapse and erosion of dolomitic roof blocks. A total of three chambers comprises the total size of the site, with the larger fossil deposits referred to as the Gladysvale External Deposits (GVED), an 80 m² area which forms part of the upper chamber. The GVED is specifically the outer de-roofed section of the upper chamber. The chambers that have been studied show the existence of sections of well-cemented breccias with interspersed pockets of decalcified sediments (Lacruz *et al.*, 2003). Flowstone layers across the calcified and decalcified sediments have been recognised as geological layers that can be correlated with other geologically correlatable marker units. These marker units delimit and separate clastic sedimentary sequences and allow for correlation with similar units at other hominin-bearing cave deposits in the Cradle of Humankind (Lacruz *et al.*, 2003).

Gladysvale preserves some of the most extensive and continuous-time sequences of the hominin-bearing sites in the Cradle of Humankind. The fossils found at Gladysvale suggest dates ranging between the Late Pliocene (2.6 Mya) and the Late–Middle Pleistocene (1.25 to 0.7 Mya) (Lacruz *et al.*, 2003). Different remains from parts of Gladysvale, and in particular, *Australopithecus cf. africanus* teeth that were recovered from the breccia dumps, have been dated to as early as 2.4 to 2 Mya. This was based on the electron spin resonance

(ESR) dating technique (Berger *et al.*, 1993; Pickering *et al.*, 2007). There are, however, also younger deposits that have been dated to 780 to 530 Kya by Lacruz *et al.* (2003). These deposits (GVED) have sediments with strata of calcified and decalcified breccias which in turn gives a total of nine recognised flowstone bounded units (FBUs). Thus, the usage of both ESR, as well as palaeomagnetic age estimation, could be applied to the dating of Gladysvale and these techniques were performed on three bovid teeth and their stereographic position in relation to breccia layers found within the GVED in the pursuit of dating Gladysvale Cave. Further studies by Berger *et al.* (2009) investigated the deposits of the roofed and upper section of the main chamber, as well as the other two chambers collectively referred to as the Gladysvale Internal Deposits (GVID). In the GVID, again there were FBUs, which lay both basal and overhead a fossil hyaena latrine. These FBU's were dated according to the ESR methods. Additionally, an overlying stalagmite was present, but poorly preserved, which was dated to an upper limit of 250 ka using uranium-series decay techniques (U–Th) (Lacruz *et al.*, 2003). The estimated age of 257 to 195 Kya was assigned to the collective internal Gladysvale deposit (Berger *et al.*, 2009).

A wide taxonomic range of fauna has been identified from Gladysvale, most of which dates from the younger deposits (Table 2). In 2002, a study by Lacruz *et al.*, went on to expand the faunal assemblage of the GVED, which contained 29 mammal species, including some that are considered rare in the Witwatersrand fossil accumulations: taxa such as *Kobus leche* and *Pelorovis*. The apparent main agents of accumulation found during this study were reported to be both carnivores and porcupines, however, no evidence related to hominin activity was found. Taphonomic features such as punctate depression, tooth scratches, gnawing of epiphyses and other elements corroborate these findings (Lacruz *et al.*, 2002).

As for the faunal assemblage (Table 2), a total of seven primate species were identified, including two hominin specimens and numerous non-human specimens. The two hominin specimens are a manual phalanx identified as belonging to the genus *Homo* and a third molar belonging to *Homo sapiens*. The non-human primate specimens consist mostly of dental elements (12 isolated teeth), however, post-cranial elements were also identified such as phalanges, metacarpals, metatarsals, distal humerus fragments and tarsal bones. The majority of the non-human primate specimens were attributed to *Papionini*, a tribe of old-world baboons.

Bovidae species were also found by Lacruz *et al.* (2002) and constitute the majority (78%) of the GVED identified specimens. Those of the Bovidae species found most common were of the tribe *Alcelaphini*, known by extant taxa such as common tsessebe (*Damaliscus lunatus*), bontebok (*Damaliscus pygargus*), hartebeest (*Alcelaphus buselaphus*), black wildebeest (*Connochaetes gnou*) and the blue wildebeest (*Connochaetes taurinus*). The wildebeest (*Connochaetes sp.*) is the most common identified taxa and have a minimum number of individuals (MNI) of 9, and a number of identified specimens (NISP) of 41. Also, a substantial number of specimens were identified to be medium-sized Alcelaphines. A few specimens of the larger-sized Bovidae were also found and these include the species roan (*Hippotragus equinus*), sable (*Hippotragus niger*), gemsbok (*Oryx gazella*), extinct buffalo (*Pelorovis*), buffalo (*Syncerus*), kudu (*Tragelaphus strepsiceros*) and the eland (*Taurotragus oryx*).

Numerous Carnivora species were identified and account for about 4% of the total sample size in the study by Lacruz *et al.* (2002). These include the extant species of lion (*Panthera leo*), leopard (*Panthera cf. pardus*) and spotted hyaena (*Crocuta crocuta*). Other carnivore species were also discovered, such as *Pachycrocuta bellax*, which is an extinct species of giant striped hyaena (Reynolds, 2010). These species are thought to be similar to the modern-day striped hyaena, as it most likely would have primarily been a scavenger, and expectedly would have benefitted from having other large carnivores on the landscape at the time (Edwards *et al.*, 2019; Mills 1982; Yarnell *et al.*, 2013, Reynolds, 2010). The other extinct larger carnivores that might have been on the landscape and which is also reflected in the GVED assemblage is the species related to *Dinofelis*. *Dinofelis*, suggested to be a close relative to *Panthera pardus*, would likely have occupied the same niche of leopards and would possibly have played the same role in faunal accumulation (Reynolds, 2010).

Equidae, which according to Lacruz *et al.* (2002) and Berger (1993) only accounts for about 6% of the specimens found at Gladysvale (GVED) are represented in three different taxa. These three taxa are that of plains zebra (*Equus quagga*), the extinct Cape horse (*Equus capensis*), and the three-toed horse (Hipparion). Initially, the *Equus quagga* was tentatively identified by Berger (1993) based on two isolated teeth and then later by Lacruz *et al.* (2002) who identified a minimum of two individuals based on post-cranial material. Hipparion sp., was tentatively identified from isolated teeth found by Berger (1993), however, Lacruz *et al.* (2002) reportedly did not recover any specimens, thus only a singular MNI value was given. As such, there is a possibility to assign an upper limit to GVED, as the presence

of *Equus quagga* may limit the earliest age estimation of the assemblage as 0.7 Mya (Oakenfull *et al.*, 2000).

Other families of species that were present in the GVED included: Giraffidae, Suidae, Rhinocerotidae, and Elephantidae. Giraffidae, Rhinocerotidae, and Elephantidae were not abundant in the sample and only one MNI value could be assigned to each. Suids were slightly more abundant, with extinct suids such as *Potamochoeroides cf. shawi*, *Kolpochoerus cf. paiceae*, as well as the extant bushpig (*Potamochoerus porcus*) and possibly warthog (*cf. Phacochoerus sp.*) being present.

Lastly, another important study by Hall *et al.* (2006) elaborates that Gladysvale is the second site within the Cradle of Humankind to have an *in situ* Achuelean handaxe dated to older than 780 Kya. This single stone tool is considered of significant importance as the relative scarcity of such stone tools within the Cradle of Humankind has contributed greatly to artefact assemblages from Plio-Pleistocene. This same handaxe was found on the oldest most boundary of the external deposits from Gladysvale (GVED). Similar other handaxes have also been found at Sterkfontein which have been dated to c. 1.7–1.4 Mya.

Table 2: Fauna from Gladysvale (Berger, 1993; Lacruz *et al.*, 2003).

Gladysvale External Deposits (GVED) Species List		NISP	MNI
Order Primates			
Family Hominidae			
	<i>Homo sp.</i>	3	1
	<i>Australopithecus cf. africanus</i>		1
Family Cercopithecidae			
	<i>Cercopithecoides williamsi</i>		1
	<i>Papio cf. izodi</i>		1
	<i>Papio cf. robinsoni</i>		1
	<i>Theropithecus oswaldi</i>		2
	<i>Papionini</i> indet.	12	1
Order Carnivora			
Family Felidae			
	<i>Panthera leo</i>	1	1
	<i>Panthera cf. pardus</i>		1
	<i>Dinofelis cf. piveteaui</i>		1

Family Hyaenidae	<i>Dinofelis</i> sp.		1	
	<i>Pachycrocuta bellax</i>		3	
	<i>Crocuta</i>		1	
	<i>Hyaenid</i> indet.	3	1	
Family Canidae				
	<i>cf. Nyctereutes</i> sp.		1	
	<i>Canis mesomelas</i>	4	1	
	<i>Lycaon sekowei</i>		1	
Order Artiodactyla				
Family Bovidae				
	<i>Tragelaphus angasii</i>		1	
	<i>Tragelaphus strepsiceros</i>	5	2	
	<i>Taurotragus oryx</i>	4	2	
	<i>Pelorovis</i> sp.	1	1	
	<i>Syncerus</i> sp.	1	1	
	<i>Kobus leche</i>	17	7	
	<i>Redunca arundinum</i>	8	3	
	<i>Redunca fulvorufula</i>	3	1	
	<i>Hippotragus equinus</i>	21	5	
	<i>Hippotragus niger</i>	2	1	
	<i>cf. Oryx gazella</i>	1	1	
	<i>Megalotragus</i> sp.	3	1	
	<i>Connochaetes taurinus</i>	4	3	
	<i>Connochaetes</i> sp. indet.	41	9	
	<i>Damaliscus dorcas</i>	12	2	
	Medium sized <i>alcelaphines</i>	119	13	
	<i>cf. Aepyceros</i> sp.	1	1	
	<i>Raphicerus campestris</i>	1	1	
	<i>Oreotragus</i>	1	1	
	<i>Antidorcas bondi</i>	1	1	
	<i>Makapania</i> sp.	37	4	
	<i>Alcelaphus</i> sp.		7	
	<i>Alcelaphus buselaphus</i>		3	
	Family Suidae			

	<i>Potamochoeroides cf. shawi</i>	3	
	<i>Kolpochoerus cf. paiceae</i>	1	
	<i>Potamochoerus porcus</i>	1	
	<i>cf. Phacochoerus sp.</i>	1	1
Family Giraffidae		1	1
Order Perissodactyla			
Family Equidae			
	<i>Equus capensis</i>	9	3
	<i>Equus burchelli</i>	4	2
	<i>Hipparion sp.</i>		1
Family Rhinocerotidae			
	<i>Diceros bicornis</i>		1
Order Proboscidea			
Family Elephantidae			
	<i>Elephas sp.</i>		1
Order Hyracoidea			
	<i>Procavia capensis</i>	5	2
	<i>Procavia transvaalensis</i>	8	2
Order Rodentia			
	<i>Hystrix africaeaustralis</i>	4	1

Aims

The principal aim of this study was to investigate the different Equidae species remains from Gladysvale, in order to understand the role of these animals within the larger faunal communities in the Cradle of Humankind, the potential differences between *Equus capensis* and *Equus quagga*, and establish relative dates for the Gladysvale Equidae. The relevant representation of Equidae in Plio-Pleistocene localities within the Cradle of Humankind would also be under investigation.

A preliminary investigation showed that Equidae are poorly represented when compared to bovids in faunal assemblages from the Cradle of Humankind (Badenhorst & Steininger, 2019) (see results Tables 26 and 27). This pattern is in sharp contrast to modern census data of zebra in Africa. For example, in the Kruger National Park, *Equus quagga* is the third most common herbivore, preceded only by impala and buffalo (Plug, 1989). The reasons for

the low representation of Equidae within faunal assemblages from the Cradle of Humankind during the Plio-Pleistocene may include:

- Equidae were not present on the landscape for certain times of the year due to long-distance migration or selectively used different parts of the landscape.
- Equidae did not exist in large herds in the past and their availability as prey were low.
- Carnivores that accumulated most of the faunal specimens in assemblages from the Cradle of Humankind did not regard Equidae as preferred prey.
- Some Equidae employed effective predator avoidance behaviour.

In this study, a large focus was placed on predator avoidance behaviour of Equidae as a theoretical framework to aid in explaining the low representation of Equidae in Plio–Pleistocene sites in the Cradle of Humankind, compared to modern census data. The majority of these behaviours could not be tested as the only remains preserved are fossilised remains. However, it is possible to test some of these behaviours such as migration through isotope analyses (Hobson, 1999; Wolf *et al.*, 2010).

Hypotheses

The following hypotheses were assessed in this study:

- Equidae are represented in low occurrence compared to bovids at Gladysvale (and elsewhere in the Cradle of Humankind).
- Equidae employed effective behaviour to avoid predation, explaining, in part, why Equidae are poorly represented in faunal assemblages.

Identification

The excavations of Gladysvale Cave were initially done by Tobias and students from 1946 to 1947 in the hope of finding a “rich” piece of breccia (Berger, 1993). Thereafter, excavation was continued in 1948 by Charles Camp and Frank E. Peabody, who largely relied on blasting breccia while collecting material which is still housed at the University of California, Berkeley. Later in 1988, Keyser led a group to map the site and collected material from the surface breccia dumps. After this, in 1993, Berger would excavate greatly and report his findings. Berger reported that all fossils were identified and catalogued, following procedures defined by Brain (1974, 1993). With this in mind, the methods used to analyse faunal

remains are often not made explicit which makes comparisons between assemblages challenging (Driver, 2011). There are generally two sets of methods used to identify faunal remains from archaeological and paleontological sites in South Africa. The first method is suggested by Brain (1974) and expanded by Voigt (1983) and regards vertebrae, ribs, enamel, and cranial fragments as well as bone flakes as unidentifiable specimens. This method has been widely applied to faunal studies in South Africa ever since (e.g., Voigt, 1983; Plug & Badenhorst, 2001; Van Zyl *et al.*, 2013; Badenhorst & Plug, 2004; Badenhorst *et al.*, 2016). Intact teeth and crania were mainly used to identify species (Brain, 1981).

Later research in the decades to follow has found that post-crania, including vertebrae, can be used to separate orders, families, genera, and species (e.g., Plug, 2014). Accordingly, the method suggested by Driver (2005) was used to form the basis on the framework of the identification process, as seen in Appendix A and B. Based on this method, any specimen is identifiable if the element (e.g., humerus, femur, phalanx, etc.) can be determined. A database of the identified material can be found in Appendix A and Appendix B in which each specimen was assigned the following: taxa, element, portion, side, age, length, modification, breakage, and measurements. Taxa would refer to the potential of *Equus quagga*, *Equus capensis* or Hipparion, and if uncertain, was assigned to indeterminate Equidae. "Element" was given a code according to each specimen identified as either cranial dental or post-cranial bone or tooth, as well as determining if the tooth was deciduous or permanent. "Portion" is a code given to each element based on what is present and how much. "Modification" was done according to codes for different taphonomic processes i.e., gnawing.

By using an explicit method, it is possible to compare faunal assemblages more reliably (e.g., Reynard *et al.*, 2016; Reynard & Wurz, 2020). For this study, a detailed description of every individual specimen was not given. This is mostly because size is most often used to separate *Equus capensis* from *Equus quagga* (Malherbe, 2020). As such, general size, which has been the closest form of consensus to distinguish *Equus capensis* from *Equus quagga*, was the primary focus. Also included in this context was the theoretical work of how these species might have differed in terms of environmental interaction including predators and predatory avoidance behaviours.

However, certain morphological differences can be expected to be found between the species of *Equus* and Hipparion both cranial dentally in unique upper and lower isolated

protocones, and post cranially in metatarsals (Sriton, 1941; Bernor *et al.*, 1988; Badenhorst & Steininger, 2019). With regards to the other expected species of *Equus capensis* and *Equus quagga*, there is an expected size difference in terms of both cranial dental and post-crania specimens (Badenhorst & Steininger, 2019).

The Equidae from Gladysvale which were used in this study have already been excavated and prepared (Berger, 1993). The material has largely been sorted and is housed in the Evolutionary Studies Institute (ESI) at the University of the Witwatersrand. Comparative skeletal collections of the ESI, as well as the modern specimens housed in the Ditsong National Museum of Natural History in Pretoria, were used in identifications. Although Equidae remains which have been reported by Lacruz *et al.* (2003) were part of this sample and part of the majority used for this study (Appendix A), there were also specimens that were not previously analysed that account for part of the sample and as reflected in Appendix B, have not yet been extensively analysed. These newly identified specimens (Appendix B) were coded according to the previously mentioned Driver method and have the available relative east, north and height coordinates, and were provided with the appropriate GVID sections and layers they were initially excavated from.

Materials & Methods

This study attempted to identify plains zebra (*Equus quagga*), the extinct Cape horse (*Equus capensis*) and possibly the small Hipparion in the Gladysvale site. The presence of these taxa indicated the age of the deposits, which provided a relative date for the sample. Equidae have been prolific in the fossil record and are found in basically all other sites in the Cradle of Humankind.

A total of 280 Equidae specimens were identified as part of the Gladysvale material, this consisted of both the older GVED (780 to 530 Kya) and younger GVID (257 to 195 Kya), however, the majority (67%) of the sample was from the GVED. Some GVID specimens had already been identified to a genus level, however, all the samples in the study from the GVID were identified or re-identified from the largely unsorted material house in the ESI. Numerous specimens of both GVED and GVID were identified to add to the smaller existing collection, which prior to this study consisted of 13 previously identified specimens. Equidae from Gladysvale both GVED and GVID, Swartkrans member 2 and 3 (SK specimens), Coopers A (COA), Kromdraai (KA) and comparative specimens from the ESI (BP

specimens) and the Ditsong National Museum of Natural History (AZ and TM specimens) were measured. With regards to the comparative specimens, both male and female individuals were measured in roughly equal numbers together with two sub-adults. These specimens are mostly housed at the Ditsong National Museum of Natural History.

Most of the 13 Equidae GVED specimens for the study by Lacruz *et al.* (2002) as seen in Table 3 below, were re-identified, apart from a few specimens that could not be found in the collection (i.e., GV 7089, GV 4836, GV 4809, GV 5136). Those that were to be found were all assigned the same identification, apart from GV 7596 which was tentatively identified as indeterminate Equidae. The measurements taken by Lacruz *et al.* (2002) are comparable to those taken in this study (Appendix A and D). Within the study done by Lacruz *et al.* (2002), there was no explanation given as to why GV 7961 was potentially a third premolar nor why GV 4809 has no breadth measurement. It can only be assumed that GV4809 was broken in a manner where the measurement could not be taken nor estimated.

Table 3: Previous Equidae GVED Specimens: Measurements of identified specimens from the GVED taken from Lacruz *et al.*, 2002.

Specimen Number	Taxonomy	Element	Side	Upper / Lower	Length (mm)	Breadth (mm)
GV 5406	<i>Equus capensis</i>	Premolar 3	Left	Lower	33.48	22.40
GV 7089	<i>Equus capensis</i>	Premolar 2	Left	Lower	38.86	14.56
GV 4836	<i>Equus capensis</i>	Premolar 2	Right	Lower	35.39	19.9
GV 4789b	<i>Equus capensis</i>	Molar 3	Right	Lower	40.03	17.13
GV 8048	<i>Equus capensis</i>	Premolar 2	Right	Lower	36.68	19.82
GV 7961	<i>Equus capensis</i>	Premolar 3 (Potential)	Left	Lower	38.25	18.51
GV 7248	<i>Equus capensis</i>	Incisor 2	Right	Upper	21.86	10.75
GV 4809	<i>Equus capensis</i>	Molar 3	Right	Upper	33.98	
GV 5871	<i>Equus capensis</i>	Incisor 2	Right	Upper	20.10	11.28
GV 5136	<i>Equus capensis</i>	Incisor 3	Right	Upper	22.51	13.14
GV 7596	<i>Equus quagga</i>	Molar 2	Right	Upper	25.61	27.22
GV 8096	<i>Equus quagga</i>	Premolar 2	Right	Upper	27.62	15.50
GV 5121	<i>Equus quagga</i>	Molar 1	Right	Upper	25.09*	14.80*

*Estimated measurement.

Aging & Sexing

The individual Equidae teeth from Gladysvale were aged using the approaches of Penzhorn (1982) and Smuts (1974), which considers tooth wear, cementum layer count, tooth replacement and eruption sequences in order to determine ages. Admittedly, Penzhorn (1982) specifically studied *Equus grevyi*, however, he goes on to suggest the tooth eruption and replacement sequence is similar for plains zebras. Smuts (1974) exclusively studied plains zebra within the Kruger National Park in South Africa. This, together with the method suggested by Lesnik and Thackeray (2006), which uses crown heights of permanent premolars and molars, aided in creating age classes for the Equidae found at Gladysvale. For example, some predators such as lions and sabre-toothed cats likely preyed on young and old zebra (Lesnik & Thackeray, 2006), and by ageing teeth, provisional age of accumulation could be determined. Lastly, there exists a small degree of sexual dimorphism in equids, which is seen in a small amount of general size difference but more importantly in the presence or absence of canine teeth.

In this study, the ageing of the post-cranial specimens was done firstly according to codes given by Driver (2005) which indicate what age the individual might be. This is done through inspection of both proximal and distal articular ends of most long bones wherever possible with specific consideration of the fusion state and the growth plate (e.g., Reynard, 2015, Albarella *et al.*, 2017) be these neonates, juvenile, sub-adult, adult or aged.

Quantification

In this study, the Equidae from Gladysvale were quantified using the Number of Identified Specimens (NISP) and the Minimum Number of Individuals (MNI). These two methods have their unique strengths and weaknesses (Grayson, 1984) and are widely used in faunal studies in South Africa. The Number of Identified Specimens (NISP) is the most basic method of archaeofaunal quantification (Grayson, 1984; Plug, 2014) and is the standard measure of taxon abundance, which is simply the number of specimens assigned to a taxon (Klein & Cruz-Urbe, 1984). NISP is relatively simple to calculate and can be conducted during the identification stage (Klein & Cruz-Urbe, 1984). However, there are some criticisms of NISP, regarding the skeletal parts potentially coming from either the same or different individuals in an assemblage. Furthermore, NISP is subject to inflation over time due to taphonomic processes and fragmentation (Dominguez-Rodrigo, 2012). In addition, NISP varies between taxa, since more bones in different taxa have a greater chance of

survival and retrieval than other taxa (Perkins, 1973). Other criticisms of NISP as suggested by Dominguez-Rodrigo (2012), are that different values might be calculated based on differences in skill level, procedures used in the identifying process, and accuracy of the analyst.

The Minimum Number of Individuals (MNI) is another common quantification method, which is simply the minimum number of individual animals necessary to account for all the identified specimens (Klein & Cruz-Urbe, 1984). The best-suggested method to calculate MNI is to take age, sex, size, and different sides of the body into account (Hesse & Wapnish, 1985; Reitz & Wing, 1999). It is important to note that MNI has its criticisms, with the main critique being that MNI is not an actual number. Rather, it is a lower limit on the possible number of animals in a sample (Perkins, 1973; Plug & Plug, 1990). Another criticism of MNI is that the scale at which it is calculated will result in vastly different MNI values (Grayson, 1984). Further criticism of MNI is that it is derived from the NISP within an assemblage, and might also be subject to similar criticisms that would affect the latter (NISP) such as fragmentation and procedures taken (Lyman, 2008; Dominguez-Rodrigo, 2012). However, MNI has potentially more merit as it can still provide a reliable value based on the accurate identification of a portion of the assemblage, whereas NISP relies more on the accurate identification of all of the assemblage (Dominguez-Rodrigo, 2012). The previous excavations by Berger (1993) and studies by Lacruz *et al.* (2002) which were done according to Brain (1993) quantified specimens utilising the NISP and MNI, however, their work only displays a very small sample of the total amount of specimens excavated in the full sample.

Taphonomy

Taphonomy is the process and study of the transformation of organic remains into fossil deposits as a result of spatial, temporal, and biological factors, and is considered crucial for contextual information (Shaw & Jameson, 1999). It is equally important to understand the site formation processes to formulate any conclusions on the study of fossil remains (Brain, 1981). While following the Driver (2011) method, it was possible to record any taphonomic modifications, mostly with the naked eye or under slight magnification. Taphonomic characteristics (e.g., Reynard, 2015; Kuman, 1994; Albarella *et al.*; 2017; Brain, 1981) of the sample were used to determine the agent of accumulation and include various species of carnivores. These taphonomic features were determined by looking at differences between potential cut marks (V-shaped) and carnivore teeth marks (U shaped) under slight

magnification, as well as differences of cortical bone surface wear based on rodent teeth marks, root etching and possible hyaena digestion. As the previous work by Berger (1993) states there were indications of carnivore and porcupine marks on the material. Further taphonomic features regarding the breakage patterns of the specimens were also considered. According to Driver (2005), all breakage patterns that were investigated were the result of specimens that were eroded, splintered, gnawing by rodents, spiral fracture, transverse fracture, and irregular fractures.

Taphonomy related to eroded breaks in the results is an indication of the possible agent that caused abrasion to bone, and these may be chemical, mechanical, or biological. Often hyaenas, as an agent of accumulation, tend to gnaw on one end of the bone and while doing so they place pressure on the other end as it erodes against the ground. Gnawing by rodents often presents as fine, high-gloss abrasion in a localised area. Bones with spiral fractures and showing a rough surface tend to have been green or fresh when broken, as do flaked bones. Bones with spiral fractures and a smooth surface are generally dry or more weathered. Transverse fractures are commonly assigned to dry bones, and together with longitudinal fractures may point towards heat applications. Irregular fractures often point towards the presence of either rodent or carnivore chewing, but in most cases is linked to extreme weathering (Pokines *et al.*, 2021).

This largely explains the different states of weathering of the surface of the bone, and it should be noted that often, harsher-weathered bone breaks differently from other less-weathered bone. Furthermore, the recently deposited bone tends to have breakage patterns determined by agents of accumulation. Osteology and taphonomic studies have shown this numerous times (e.g., Reynard, 2015; Kuman, 1994; Albarella *et al.*, 2017; Brain, 1981). Lastly, as part of the taphonomy, it is important to remark on the potential for manganese to stain the fossil material, which has been accepted as a proxy for arid deposition. Manganese staining is commonly associated with the blackening of fossil surfaces (Foecke, 2016).

Measurements

The measurements were taken according to Von den Driesch (1976). Cranial-dental measurements were taken and recorded as Length (mesiodistal length) and Breadth (buccolingual breadth). Although not many of the bony elements were complete enough to take measurements, certain measurements were taken where possible on the most

common elements of metacarpals and metatarsals. The elements were represented by both taxa of *Equus quagga* and *Equus capensis*. Further measurements of fossil Equidae were taken for comparative reasons from Swartkrans, Coopers and Kromdraai, and modern equid material from both the comparative laboratory at the ESI and the Ditsong National Museum of Natural History. Measurements were taken on a new plastic vernier calliper in millimetres to an accuracy of 0.01 mm and where needed were estimated.

Lastly, the length classes and the amount of fragmentation of the sample were taken into account as often this suggests potential agents of accumulation (e.g., Reynard, 2015; Kuman, 1994; Albarella *et al.*, 2017; Brain, 1981, Edwards *et al.*, 2020). This was done simply by using a 1 cm X 10 cm graph paper and an overhead view of all specimens, aligned against a defined start point at the bottom of the graph paper. The overall length of and the constituent amount of fragmentation are important to note as it serves as a proxy to taphonomic processes involved with the specific activity of the site such as butchering, and bone accumulation in the den of both rodents and hyaena.

Results

Sample Size

A total of 280 specimens were identified from the faunal assemblage from Gladysvale (Table 4). The majority of the specimens are from the external deposit, GVED, constituting 67% of the total specimens. Fewer specimens, only accounting for 33%, were recovered from the internal GVID deposits.

Table 4: Equidae sample size from Gladysvale

Provenience	NISP	Total %
GVED	186	67%
GVID	94	33%
Total	280	100%

Taxa Present

Only two taxa were identified from the sample, namely the plains zebra (*Equus quagga*) and the extinct Cape horse (*Equus capensis*). The most common taxon is *Equus capensis* (Table 5). However, many specimens lacked distinctive morphology or size indications, and they

were identified to a family level only (indeterminate Equidae). *Equus capensis* is most common in the internal deposits (GVID) rather than the external (GVED). No Hipparion (*Eurygnathohippus*) specimens were present (refer to Figure 10).

Table 5: Equidae taxa present including NISP & MNI.

Taxa	GVED NISP	GVED MNI	GVID NISP	GVID MNI	Total NISP
<i>Equus quagga</i>	41	3 (Including 1 juvenile)	29	2	70
<i>Equus capensis</i>	75	4 (Including 1 juvenile)	49	4	124
Equidae	70	4 (Including 1 juvenile)	16	2	87
Total	186	11	94	7	280

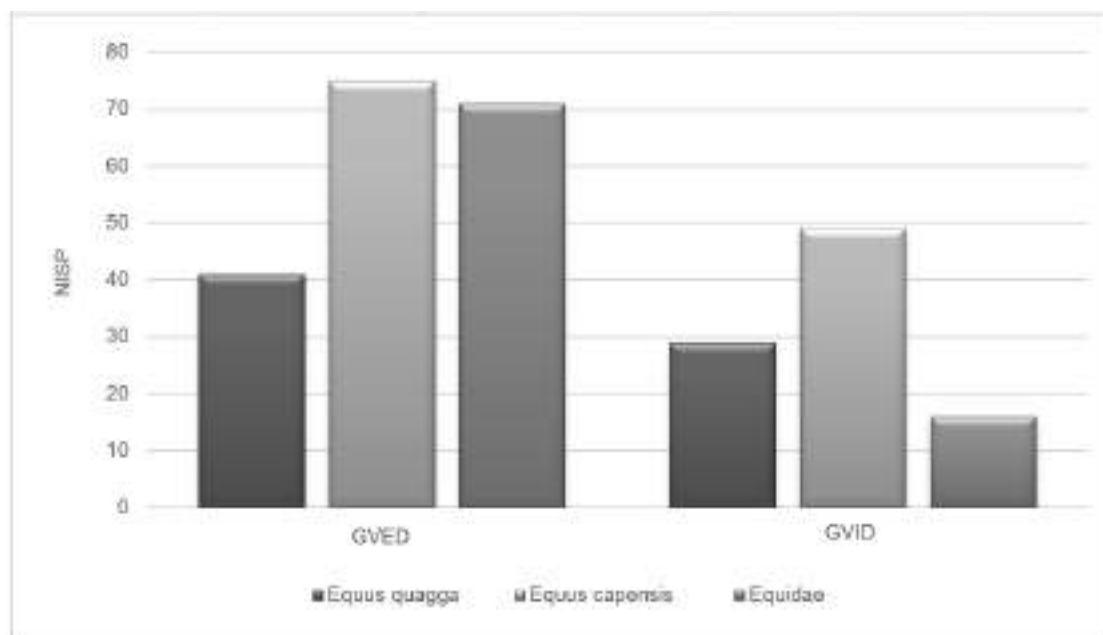


Figure 9: Provenience NISP for each taxa sample composition

Skeletal Part Representation

Teeth constitute the majority of the identified elements (72%), with other dense elements such as metacarpals, metatarsals and metapodials accounting for a further 22% (Tables 6 and 7). With regards to teeth, molars (37%) are the most common, followed by premolars (15%) and incisors (18%), with only one canine present. Apart from the teeth, no other

cranial elements were found and only a few vertebrae were identified (<2%). About 35% of the total elements belonging to the lower limbs, which include: astragali (4%), tarsals (3%), carpals (3%), phalanges (4%), and metapodials (11%). The most common taxon, *Equus capensis*, is highly represented in the elements such as tarsals, mostly cuneiform. Of the observed elements, most are of high density and thus have a higher percentage of survival.

Table 6: Skeletal part representation of all elements present.

Element	<i>Equus quagga</i> NISP	<i>Equus capensis</i> NISP	Equidae NISP	Density Category (Brain, 1981)	Total NISP	Total %
Incisor	8	30	12	High	50	18%
Canine	0	1	1	High	2	1%
Premolar	13	24	4	High	41	15%
Molar	10	41	49	High	100	37%
Tooth Fragment	0	0	7	High	7	2%
Vertebra	0	0	1	High	1	>1%
Atlas	0	0	1	High	1	>1%
Thoracic	3	0	0	Intermediate to High	3	1%
Humerus	0	0	1	Low to High	1	>1%
Carpal	5	2	0	High	7	3%
Metacarpus	4	3	0	High	7	3%
Lateral metacarpus	0	2	0	High	2	1%
Tibia	0	0	1	Low to High	1	>1%
Astragalus	3	2	5	High	10	4%
Calcaneus	0	0	1	High	1	>1%
Other tarsals	1	6	0	High	7	3%
Metatarsus	13	3	2	High	18	7%
Lateral metatarsus	0	2	0	High	2	1%
Metapodial	2	1	1	High	4	2%
Proximal phalange	4	2	0	High	6	2%
Medial phalange	2	0	0	High	2	1%
Terminal phalange	1	1	0	Intermediate	2	1%
Sesamoid	0	4	1	High	5	2%
Total	69	124	87		280	100%

The most prominent post-cranial elements are metatarsals, metacarpals and astragali, which are represented almost equally as either distal (26%) or proximal (35%) ends. Only 21% of all the post-cranial elements are complete, and most of these are either tarsals,

carpals, or sesamoids. A total of 18% of the post-cranial elements are fragmentary, with the most common elements being metatarsals at 7%, followed by metacarpals at 3%.

Table 7: Skeletal part representation of portions of post-cranial elements

Element	Complete	Proximal end	Distal end	Shaft	Fragment	Total NISP	Total %
Vertebra	0	0	0	0	1	1	1%
Atlas	0	0	0	0	1	1	1%
Thoracic	0	0	0	0	1	1	1%
Humerus	0	1	0	0	0	1	1%
Carpal	7	0	0	0	0	7	9%
Metacarpus	0	2	0	0	3	5	7%
Lateral metacarpus	0	1	1	0	0	2	3%
Tibia	0	0	1	0	0	1	1%
Astragalus	0	7	0	0	3	10	13%
Calcaneus	0	0	0	0	1	1	1%
Other tarsals	4	2	0	0	1	7	9%
Metatarsus	0	3	11	1	1	16	21%
Lateral metatarsus	0	2	0	0	0	2	3%
Metapodial	0	2	4	0	0	6	8%
Proximal phalange	0	3	2	0	1	6	8%
Medial phalange	0	1	1	0	0	2	3%
Terminal phalange	1	1	0	0	0	2	3%
Sesamoid	4	0	0	0	1	5	7%
Total	16	25	20	1	14	76	100%
Percentage	21%	33%	26%	1%	18%	100%	

The sample of teeth has a majority (80%) of the identified elements as fragmentary, with the rest being mostly complete (Table 8). Although the fragments identified account for most of the sample, the majority of these fragments were molars (43%). Incisors and premolars are equally represented in the sample and together account for 50% of the total sample. Only an exceedingly small percentage of the sample is very fragmentary and could not be identified beyond the species level.

Table 8: Skeletal part representation of proportions of teeth

Teeth Element	Complete	Fragment	Total NISP	Total %
Incisor	11	39	50	25%
Canine	1	1	2	1%

Premolar	13	40	53	27%
Molar	14	71	85	43%
Unknown	0	7	7	4%
Total	39	158	197	100%
Total %	20%	80%	100%	

As indicated, the most common elements identified in the sample are teeth at 72% (Table 6). Of the teeth (197 NISP), both the upper and the lower dentition are represented roughly equally with 91 specimens of the lower dentition and 99 from the upper dentition as shown in Tables 9 and 10. Within this context, the most common elements are molars in both the upper and lower dentition (43%) (Table 8). However, based on the overall fragmentation within the sample, elements such as premolars and molars were indistinguishable from each other (Table 8). Premolars and incisors are equally represented in the total sample size, however, the most common species to which these elements have been attributed to is *Equus capensis*. *Equus capensis* which represents the largest components of both the lower and upper dentition is also represented by one lower canine. A total of two canine elements were present in the sample, however, only one could be attributed to Equidae. *Equus quagga* only accounts for 19% (Table 9) of the lower dentition and only 11% (Table 10) of the upper dentition, such as molars and premolars. The indeterminate Equidae and *Equus capensis* specimens are mostly comprised of molar and premolar fragments, as well as a few newly erupted teeth.

Table 9: Skeletal part representation of lower dentition

Teeth Element	<i>Equus quagga</i> NISP	<i>Equus capensis</i> NISP	Equidae NISP	Total NISP	Total %
1st Incisor	2	3	2	7	8%
2nd Incisor	2	1	1	4	4%
3rd Incisor	2	1	1	4	4%
Canine	0	1	1	2	2%
2nd Premolar	0	2	1	3	3%
3rd Premolar	1	3	0	4	4%
4th Premolar	2	1	0	3	3%
1st Molar	0	3	2	5	5%
2nd Molar	0	0	1	1	1%
3rd Molar	3	4	2	9	10%
Incisor indet	1	3	4	8	9%
Premolar / Molar indet	6	17	18	41	45%
Total NISP	19	39	33	91	100%

Total %	21%	43%	36%	100%	
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Table 10: Skeletal part representation of upper dentition

Teeth Element	<i>Equus quagga</i> NISP	<i>Equus capensis</i> NISP	Equidae NISP	Total NISP	Total %
1 st Incisor	0	4	1	5	5%
2 nd Incisor	0	6	2	8	8%
3 rd Incisor	0	8	1	9	9%
2 nd Premolar	1	7	0	8	8%
3 rd Premolar	1	4	0	5	5%
4 th Premolar	2	3	0	5	5%
1 st Molar	1	6	2	9	9%
2 nd Molar	1	2	0	3	3%
3 rd Molar	1	7	1	9	9%
Incisor indet	2	4	2	8	8%
Premolar / Molar indet	2	7	17	30	30%
Total NISP	11	58	26	99	100%
Total %	11%	59%	26%	100%	

Aging

The age determination of teeth of the sample (Table 11) shows that there is a wide range present, with the youngest age class of 4 to the oldest class of 24. *Equus capensis* is determined to have the youngest age groups present with 6 individuals from groups 4 to 7 (3 months to 1 year), which account for 8% of the total. *Equus capensis* and *Equus quagga* are equally present in the oldest individuals in the sample. The majority of the teeth samples (60%) can be found between the age groups of 17 to 21 (6-7 years to 12 years), with *Equus capensis* being the most common.

Table 11: Age classes of taxa represented by teeth.

Age Class	Relative Age	<i>Equus quagga</i>	<i>Equus capensis</i>	Equidae	Total NISP	Total %
1	< 3 MTH	0	0	0	0	0%
2		0	0	0	0	0%
3		0	0	0	0	0%
4		0	1	0	1	1%
5	3 – 6 MTH	0	0	0	0	0%
6	6 – 9 MTH	0	1	0	1	1%
7	9 MTH – 1 YRS	0	4	0	4	5%
8	1 - 1½ YRS	1	1	0	2	3%

9	1½ - 2 YRS	0	1	0	1	1%
10	2 - 2½ YRS	0	2	0	2	3%
11	2½ - 3 YRS	0	1	0	1	1%
12	3¼ YRS	0	0	0	0	0%
13	3½ YRS	0	0	0	0	0%
14	4 YRS	0	0	0	0	0%
15	4½ YRS	0	1	1	2	3%
16	5 YRS	1	3	0	4	5%
17	6 - 7 YRS	5	4	2	11	14%
18	8 - 9 YRS	1	10	0	11	14%
19	10 YRS	1	4	1	6	8%
20	11 YRS	1	5	0	6	8%
21	12 YRS	2	10	2	14	18%
22	13 YRS	0	3	1	4	5%
23	14 YRS	2	0	0	2	3%
24	>15 YRS	1	2	5	8	10%

Most of the post-cranial specimens are from adult individuals and these could be identified to species level. The most common specimens that were either recently fused or fully fused are from individuals within the *Equus quagga* taxon. There was also a small number of unfused specimens that were identified all belonging to *Equus quagga* (6%) (refer to Table 12).

Table 12: Age classes of taxa represented by fusion.

Taxa	Fused	Unfused	Total NISP	Percentage
<i>Equus quagga</i>	33	4	37	54%
<i>Equus capensis</i>	27	0	27	39%
Equidae	5	0	5	7%
Total NISP	65	4	69	100%
Percentage	94%	6%	100%	

Bone Breakage

As demonstrated in Table 13, the elements, long bones, show a dominance of eroded breaks which display rounded sponge bone (63%), usually in conjunction with either complete proximal or distal ends. There are bones with either no breaks or that remained intact (20%), with a few gnawing instances of either carnivore (2%) or rodent (3%) in the sample. Most of the remaining samples have a lesser amount of transverse and irregular

breaks related to the bone that is in an older stage of weathering. No elements showed signs of spiral breakage.

Table 13: Bone Breakage

Breakage Type	Total Identified Breakage Types	Percentage
Intact	12	20%
Eroded break	38	63%
Chewed by carnivores	1	2%
Splintered	1	2%
Gnawed by rodents	2	3%
Transverse fracture	5	8%
Irregular fracture	1	2%

Element Lengths

The sample which consists of lengths of post-cranial elements and teeth elements is predominately under 6 mm (78%), and most elements fall within length classes 3 to 7, which is reflected in Table 14 and Figure 11. This is mostly due to the fragmentation of the most common elements of molars and premolars. Of the elements longer than 6 mm, only a small amount was found to be larger than 9 mm (3%). The longest element found at 16 mm was that of a relatively complete long bone. However, the total amounted fragmentation of the sample is below 15cm.

Table 14: Length of all specimens

Length Class (cm)	Total NISP	Percentage
1	2	1%
2	17	6%
3	42	15%
4	62	22%
5	44	16%
6	52	19%
7	31	11%
8	15	5%
9	7	3%
10	3	1%
11	1	>1%
12	1	>1%
13	1	>1%
14	1	>1%
15	0	0%
16	1	>1%

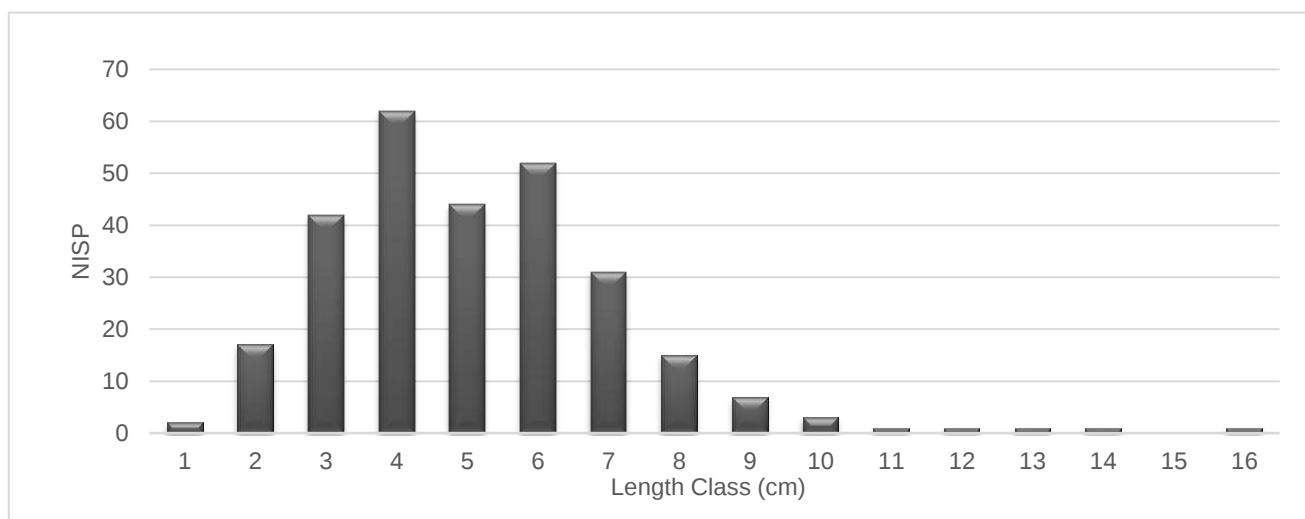


Figure 10: Length of all specimens

Modification

The overall extent of modification (Table 15) found within the sample is extremely limited as only a total of 8 specimens had any modification to record. The majority (38%) of this is included in the modification type of being burnt black and one account (13%) of being burnt white. There are also limited numbers of carnivore and rodent modification, with one record of evidence of potential saw marks as a result of hominin activity.

Table 15: Taphonomic Modification

Modification Type	Total NISP	Percentage
Burnt black	3	38%
Burnt white	1	13%
Carnivore damage	1	13%
Rodent gnawing	1	13%
Pathological	1	13%
Anthropic taphonomy	1	13%

Osteometry

The lower dentition (Table 16) of *Equus capensis* has a large mean value for both length and breadth in all forms of dentition when compared to modern *Equus quagga*. The larger teeth of the *Equus capensis*, i.e., the 1st and 2nd molars, have the largest differences to *Equus quagga*. These elements have much higher breadth and length values, as no *Equus quagga* specimen has a breadth value higher than 25 mm and length of 35 mm whereas *Equus*

capensis does (Table 16 and 17). The modern *Equus quagga* seems to have slightly smaller values for length and breadth when compared to the fossil material of *Equus quagga*. In some cases, modern *Equus quagga* and fossil material of *Equus quagga* seem remarkably similar as in the instance of the 2nd and 3rd premolars. The fossil material of *Equus quagga* appears overall more similar in value to the modern material than *Equus capensis*.

Table 16: Cranial-dental measurement statistics of lower dentition

Element	Species	No.	Mean length (mm)	Mean breadth (mm)
1 st Incisor	<i>Equus quagga</i>	1	11.48	12.88
	<i>Equus quagga</i> (modern)	12	12.86	8
	<i>Equus capensis</i>	8	17.16	10.51
2 nd Incisor	<i>Equus quagga</i>	4	18.73	9.87
	<i>Equus quagga</i> (modern)	17	14.35	7.53
	<i>Equus capensis</i>	3	19.54	12.53
3 rd Incisor	<i>Equus quagga</i>	3	15.42	8.17
	<i>Equus quagga</i> (modern)	15	15.44	6.79
	<i>Equus capensis</i>	5	20.09	9.84
2 nd Premolar	<i>Equus quagga</i>	4	30.04	14.42
	<i>Equus quagga</i> (modern)	19	29.69	15.22
	<i>Equus capensis</i>	8	31.8	17.14
3 rd Premolar	<i>Equus quagga</i>	3	26.07	15.34
	<i>Equus quagga</i> (modern)	15	25.32	16.87
	<i>Equus capensis</i>	6	30.54	15.97
4 th Premolar	<i>Equus quagga</i>	5	28.06	18.64
	<i>Equus quagga</i> (modern)	15	25.28	17.25
	<i>Equus capensis</i>	4	31.58	19.61
1 st Molar	<i>Equus quagga</i>	4	24.7	17.96
	<i>Equus quagga</i> (modern)	18	24.81	15.11
	<i>Equus capensis</i>	9	27.84	21.7
2 nd Molar	<i>Equus quagga</i>	3	25.68	15.41
	<i>Equus quagga</i> (modern)	19	24.49	14.41
	<i>Equus capensis</i>	6	30.63	20.92
3 rd Molar	<i>Equus quagga</i>	5	26.97	15.29
	<i>Equus quagga</i> (modern)	19	27.17	12.64
	<i>Equus capensis</i>	2	35.41	15.32

The upper dentition (Table 17) follows much of the same pattern as the lower dentition, where *Equus capensis* has on average a larger mean value for both length and breadth. However, it is interesting to note that with regard to the 3rd incisor, *Equus capensis* has the smallest mean length and the greatest mean breadth values of the different taxa. Again, the fossil material of *Equus quagga* appears overall much more similar in value to that of the modern taxa. *Equus capensis* does appear to have the biggest difference to the other taxa

with regards to incisors as they cluster in an area with a much higher length and breadth value than the modern *Equus quagga*. These differences are further illustrated and supported in Figures 12 and 13.

Table 17: Cranial-dental measurement statistics of upper dentition

Element	Species	No.	Mean length (mm)	Mean breadth (mm)
1st Incisor	<i>Equus quagga</i>	1	16.06	8.94
	<i>Equus quagga</i> (modern)	15	15.67	9.7
	<i>Equus capensis</i>	9	18.13	16.34
2nd Incisor	<i>Equus quagga</i>	3	16.36	12.03
	<i>Equus quagga</i> (modern)	17	16.74	9.39
	<i>Equus capensis</i>	12	18.46	12.08
3rd Incisor	<i>Equus quagga</i>	1	16.84	8.96
	<i>Equus quagga</i> (modern)	18	18.89	8.57
	<i>Equus capensis</i>	9	21.17	11.81
2nd Premolar	<i>Equus quagga</i>	3	35.21	21.12
	<i>Equus quagga</i> (modern)	23	34.81	23.97
	<i>Equus capensis</i>	6	31.38	24.92
3rd Premolar	<i>Equus quagga</i>	2	27.36	28.32
	<i>Equus quagga</i> (modern)	24	26.88	25.89
	<i>Equus capensis</i>	6	30.58	29.13
4th Premolar	<i>Equus quagga</i>	10	24.02	22.68
	<i>Equus quagga</i> (modern)	21	25.66	26.4
	<i>Equus capensis</i>	6	30.8	29.33
1st Molar	<i>Equus quagga</i>	5	25.9	24.12
	<i>Equus quagga</i> (modern)	25	23.9	24.43
	<i>Equus capensis</i>	9	30.62	27.89
2nd Molar	<i>Equus quagga</i>	2	22.71	19.23
	<i>Equus quagga</i> (modern)	24	23.79	24.12
	<i>Equus capensis</i>	6	30.82	25.1
3rd Molar	<i>Equus quagga</i>	1	24.23	17.7
	<i>Equus quagga</i> (modern)	24	23.95	21.71
	<i>Equus capensis</i>	9	31.55	26.45



Figure 11: Example of teeth assigned to *Equus capensis* (specimen GV 5876), upper molar, compared to modern *Equus quagga* (BP/4/1304) upper row of molars & premolars.



Figure 12: Example of 2nd premolar assigned to *Equus capensis* (specimen GV Indet 36, Appendix B) (Right), compared to modern *Equus quagga* (BP/4/1304) (Left)

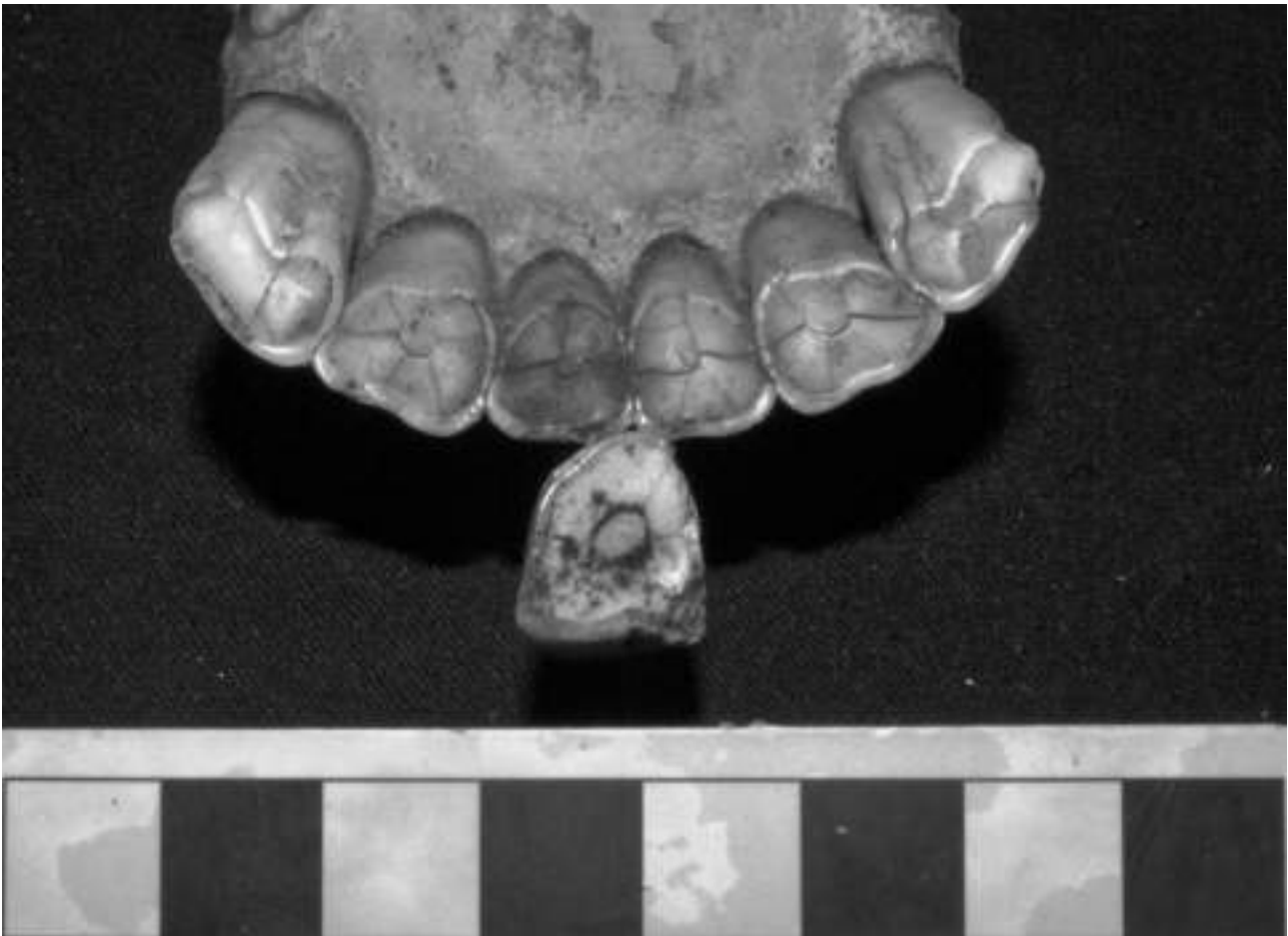


Figure 13: Example of teeth assigned to *Equus capensis* (specimen GV 5035), lower incisor, compared to modern *Equus quagga* (CR 49/4/B) lower incisors.

The measurements taken of all the available post-cranial elements from Gladysvale are listed in Appendix D. The most common elements that did provide comparative data for both species, were proximal and intermediate phalanges, metacarpals, and metatarsals (Tables 18, 19, 20 and 21). The single *Equus capensis* intermediate phalange is shown to be much larger than *Equus quagga* in all measurement codes, being larger than any of the maximum measurements. Three specimens of metacarpals from *Equus capensis* were measured, with most being the greatest in-depth of proximal end (Figure 15). This again is shown in all aspects that *Equus capensis* is much larger than *Equus quagga*. With regards to metatarsals, specifically the greatest breadth of the distal end, the trend is much the same. Lastly, two specimens of the proximal phalange of *Equus capensis* yielded appropriate useable data and the trend continues in that most of the maximum values of *Equus quagga* is roughly similar to the minimum values of *Equus capensis*.

The biggest set of measurements of any element was taken from all the *Equus quagga* (modern and extinct) and *Equus capensis* was the intermediate phalange (Table 18). The modern *Equus quagga* measurements are all smaller than the extinct *Equus quagga*, which

remain smaller in size than *Equus capensis*. However, the standard deviation within the data range of the modern *Equus quagga* does allow for some measurements of the extinct *Equus quagga* to fall within a reasonable range, especially the great depths of the proximal end (Dp) and the greatest breadth of the distal end (Bd).

Table 18: Intermediate Phalange measurements

Code	Modern <i>Equus quagga</i>					<i>Equus quagga</i>					<i>Equus capensis</i>				
	n	Mean	S.D.	Min	Max	n	Mean	S.D.	Min	Max	n	Mean	S.D.	Min	Max
GL	8	40.7	0.98	39.3	42.7	1	42.61				1	49.59			
Bp	8	43.96	1.41	42.18	45.62	1	47.15				1	56.32			
BFp	8	38.75	1.21	36.93	40.76	1	41.56				1	52.23			
Dp	8	28.56	0.93	27.39	30.1	1	29.31				1	35.5			
SD	8	36.42	1.33	34.66	39.56	1	38.45				1	48.6			
Bd	8	38.3	1.72	35.77	41.69	1	40.5				1	53.31			

Measurements taken of the proximal phalange (Table 19) indicate that there is closeness in the measurements of both between modern and extinct *Equus quagga*, and *Equus capensis*, however that there is also a high degree of deviation of the extinct species. *Equus quagga*. However, differences are indicated by the measurements of the smallest breadth of the diaphysis (SD) in which *Equus capensis* seemingly has the greatest mean values, with both the minimum and maximum values higher than the mean of *Equus quagga*. This is further illustrated in Figure 14, which is an example of the proximal end of *Equus capensis* and modern *Equus quagga*. *Equus capensis* is indicated to have values similar to extinct *Equus quagga* and with greater divergence from modern *Equus quagga*.

Table 19: Proximal Phalange measurements

Code	Modern <i>Equus quagga</i>					<i>Equus quagga</i>					<i>Equus capensis</i>				
	n	Mean	S.D.	Min	Max	n	Mean	S.D.	Min	Max	n	Mean	S.D.	Min	Max
SD	8	29.26	0.85	27.93	30.54	4	29.78	1.43	28.05	31.89	3	35.38	6.65	30.65	45.33
Bd	8	38.83	0.81	37.37	39.9	4	39.39	2.61	37.3	43.91	2	39.12	0.37	38.75	39.49
BFd	8	36.78	1.35	34.8	38.93	4	38.29	2.89	36.36	43.36	2	38.57	0.09	38.48	38.66

The measurements of both the metacarpal and metatarsal follow a similar trend as in previous paragraphs in that *Equus capensis* appears to have a greater mean value than both modern and extinct *Equus quagga* (Tables 20 and 21). The metacarpal measurements

illustrate this best as the values appear well out the standard deviations of the modern *Equus quagga*, with the largest difference in both breadth and depth of the proximal end, further illustrated in Figure 15. However, with the few measurements of metatarsal the measurement data indicated very little difference in the great depth of the proximal end between the three species, however, only a single measurement could be taken of the extinct species (Table 21). The greatest breadth of the distal end shows the same trend of *Equus capensis* being much larger than *Equus quagga*.

Table 20: Metacarpal measurements

Code	Modern <i>Equus quagga</i>					<i>Equus quagga</i>					<i>Equus capensis</i>				
	n	Mean	S.D.	Min	Max	n	Mean	S.D.	Min	Max	n	Mean	S.D.	Min	Max
Bp	8	45.77	2.55	41.9	49.28	1	50.67				2	56.62	0.03	56.59	56.66
Dp	8	28.84	4.66	21.8	36.44	1	32.61				2	38.01	2.94	35.18	41.06
Bd	8	36.37	7.74	23.5	44	4	43.99	4.06	39.4	50.31	1	50.3			

Table 21: Metatarsal measurements

Code	Modern <i>Equus quagga</i>					<i>Equus quagga</i>					<i>Equus capensis</i>				
	n	Mean	S.D.	Min	Max	n	Mean	S.D.	Min	Max	n	Mean	S.D.	Min	Max
Dp	3	39.03	0.91	37.79	39.92	1	26.05				1	30.74			
Bd	3	42.28	1.83	40.15	44.62	5	48.38	0.87	46.74	49.12	1	51.68			

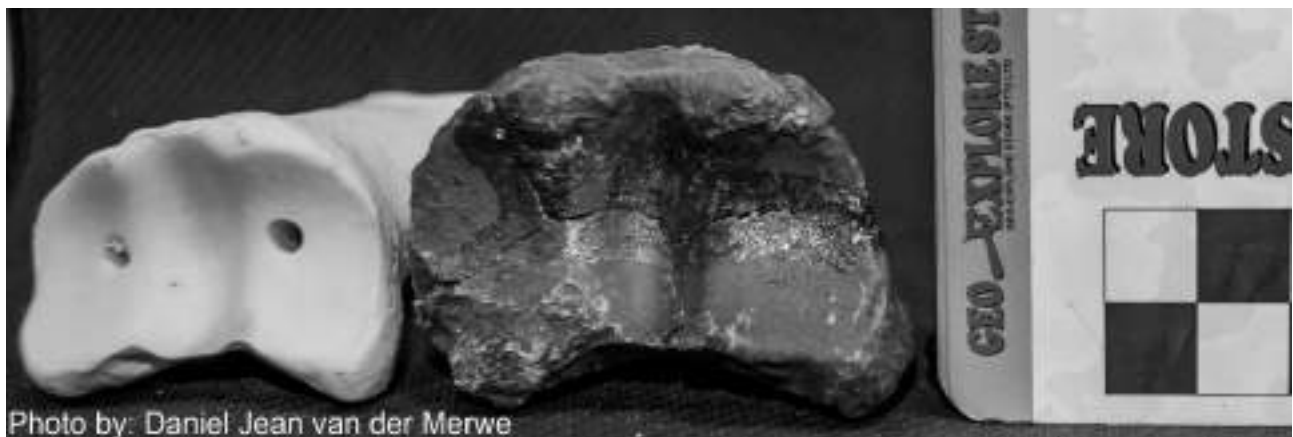


Figure 14: Example of proximal end of proximal phalange assigned to *Equus capensis* (specimen GV5223) (Right) compared to modern *Equus quagga* (BP/4/1304) (Left)



Figure 15: Example of proximal end of Metacarpal assigned to *Equus capensis* (specimen GV Indet 15, Appendix B) (Left) compared to modern *Equus quagga* (BP/4/1304) (Right)



Figure 16: Example of Navicular sesamoid assigned to *Equus capensis* (specimen GV 4682) (Left) compared to modern *Equus quagga* (BP/4/1304) (Right)



Figure 17: Example of Navicular sesamoid assigned to *Equus capensis* (specimen GV 4682) (Left) compared to modern *Equus quagga* (BP/4/1304) (Right)



Figure 18: Example of a Central tarsal assigned to *Equus capensis* (specimen GV 4966) (Right) compared to modern *Equus quagga* (BP/4/1304) (Left)



Figure 19: Example of Astragalus assigned to *Equus capensis* (specimen GV 18300) (Right) compared to modern *Equus quagga* (BP/4/1304) (Left)



Figure 20: Example of distal end of metapodial assigned to *Equus capensis* (specimen GV 18701) (Right) compared to modern *Equus quagga* (BP/4/1304) (Left)



Figure 211: Example of terminal phalange assigned to *Equus capensis* (specimen GV 18315) (Left) compared to modern *Equus quagga* (BP/4/1304) (Right)

Statistics on Osteometry

A statistical analyse of the two distinct species (*Equus quagga* and *Equus capensis*) would unfortunately be impossible to complete on the post-cranial elements as there is no sample size large ($n > 5$) for any of the *Equus capensis* fossil material (Tables 18, 19, 20 and 21). However, there are plenty of on cranial dental elements with a sample size that are large enough to accommodate a T-test. The more recognisable teeth elements of upper premolar 2 and molar 3, as well as lower premolar 2 were used in an unpaired T-test, testing for both length and breadth (Table 22). The upper teeth of molar 3 were shown to be statistically different, in terms of both length and breadth, with length being the most different. A similar trend is observed in the upper and lower premolar 2, however there was no significant difference observed in the breadth of the upper premolar 2.

Table 22: T-test results of *Equus capensis* & modern *Equus quagga*

Tested Parameters	Confidence interval:	Intermediate values	Two-tailed P value
Upper M3 length	MD = 6.74 CI = 4.4100 to 9.0700	t = 7.31 df = 55 SED = 0.92	< 0.0001

Upper M3 breath	MD = 2.83 CI = 0.6071 to 5.0613	t = 2.60 df = 30 SED = 1.09	0.0144
Upper PM2 length	MD = -2.99 CI = -5.7775 to -0.1933	t = 2.19 df = 28 SED = 1.36	0.0370
Upper PM2 breadth	MD = 1.31 CI = -1.1516 to 3.7724	t = 1.09 df = 28 SED = 1.20	0.2849
Lower PM2 length	MD = 2.45 CI = 1.2554 to 3.6481	t = 4.21 df = 26 SED = 0.58	0.0003
Lower PM2 breadth	MD = 1.85 CI = 0.6148 to 3.0887	t = 3.08 df = 26 SED = 0.60	0.0049

*MD (mean difference), CI (95% confidence intervals), SED (standard error of difference)

Extant Zebra Numbers

Through the aid of modern census data, and further supported by aerial counts, the following table (Table 23) has been constructed to show the relative abundance of equids (almost entirely Burchell's zebra) and bovids of size class three and four, namely African buffalo (*Syncerus caffer*), greater kudu (*Tragelaphus strepsiceros*), blue wildebeest (*Connochaetes taurinus*), sable (*Hippotragus niger*), roan (*Hippotragus equinus*) and the common eland (*Taurotragus oryx*). Equids only account about 30% to 45% of the total of the large prey types on the landscape, when the most common ecosystem is the preferred ecosystem of equids. The Kruger National Park, Pilanesberg National Park, Serengeti, and most of Northern Botswana are prime examples of this trend. However, there are also areas in which the total number of equids is rather low, with the lowest being 6% from the Selous Game Reserve

Table 23: Estimated number of Bovids & Equids within large conservation areas in southern Africa

Parks & Conservation	BOV (III + IV)	Equids	Equids %	Area (km ²)	Ecosystem types	References
Kruger National Park	67 420	29 500	30%	19 485	Savanna with some thicket	Kruger National Park. 2011.
Pilanesberg National Park	2453	1988	45%	572	Transition from Kalahari to Lowveld with savanna & thicket	Van Dyk, 2003.
Mapungubwe National Park	831	228	22%	280	Mopane Bushveld & savanna	Sanparks.org, 2022.
Limpopo National Park	3344	394	11%	6400	Lowland savanna	Grossmann, 2014.
Serengeti National Park	27 1445	17 1873	39%	14 763	Grasslands with Acacia & Terminalia woodlands	Talbot & Stewart, 1964.

Niassa Reserve	39 390	6229	14%	42 000	Miombo woodlands	Craig, 2009.
Namib-Naukluft National Park	4598	442	9%	49 768	Namib desert & Atlantic Ocean coast	Keding <i>et al.</i> , 2006.
Selous Game Reserve	34 3980	21 500	6%	54 600	Grassland, Acacia savanna, wetlands & Miombo woodlands	World Heritage Datasheet, 2011.
Ngorongoro Conservation Area	12 70000	20 0000	14%	8 292	Montane forest, swampy, marshy, dry forest, & grassland	Manongi, 2016.
Hwange National Park	6858	1500	18%	14 651	Kalahari Desert, seasonal wetlands, grasslands, & woodland	Thehide.com, 2018.
Northern Botswana	55 751	47 841	46%	± 8000	Wetlands, mopane, sandveld, riparian woodlands & grasslands	Library.wur.nl, 2012.

Pleistocene Equid Numbers

In the well-known Plio-Pleistocene fossil localities reflected in Table 24, there is a common trend that Equidae are underrepresented in the fossil records when compared to similar-sized Bovidae. The majority of the sites have fossil Equids represented well under 30% of the larger ungulates. The most indicative sites where the percentage of Equidae compared to Bovidae (III & IV) is less than 10% are: Coopers (D), Drimolen (Main Quarry), Malapa (D), Kromdraai (M2), Sterkfontein (Name Chamber) and Makapansgat Limeworks Cave. There are a few sites where Equidae constitute a much great percentage of the NISP within the site, namely Haasgat and (66%), which is higher than any of the extant numbers. This is largely due to the relatively small sample size within these sites, which were recorded as NISP values. Furthermore, in sites such as Goldsmith's in the region of Bolts Farm, fossil Equidae were not abundant at all in the recorded data.

Table 244: Database of fossil localities comparing NISP & MNI of Equidae to Bovid size class III & IV.

Locality	Equid NISP	Equid MNI	BOV III NISP	BOV III MNI	BOV IV NISP	BOV IV MNI	Equid vs BOV (III & IV) NISP
Makapansgat Limeworks Cave	5	1	112	33	401	42	1%
Hoogland (FBU 4 & 5)	3	2	25	12			11%

Drimolen (Main Quarry)	3	1	15	8	15	6	9%
Sterkfontein (M6)	5	3	26	20			16%
Sterkfontein (Post M6)	70	63	205	170			25%
Sterkfontein (Name Chamber)	6	3	115	56	6	3	5%
Haasgat (HGD)	21	2	6	3	5	3	66%
Gladysvale (GVED)	13	5	59	12	26	8	13%
Kromdraai	2	2	516	22	61	2	0%
Gondolin (GD A)	14	3	16	6	6	3	39%
Swartkrans (M1)	48	13	302	66	16	5	13%
Swartkrans (M5)	25	9	157	15			14%
Swartkrans (M2)	32	8	145	18	7	2	17%

Discussion

Extant Equidae as Prey

Predator-prey relationships help shape numerous factors within the ecology of both predator and prey, ranging from physical evolution over time to behavioural aspects. Predator-prey relationships also affect the accumulation of faunal assemblages, which are dependent not only on the surrounding environment but also on the predators in the area. Often, when given a choice, predators tend to choose between two or more prey types, with an affinity towards the most preferential as determined by the prey type densities and predatory avoidance behaviours (Churcher & Richardson, 1978).

Jacobs index values (as seen in Table 25) attempt to explain the prey preferences of predators, accounting for the relative abundances of the prey in the environment and the predator rate thereof. The Jacobs index values are based on the mortality rate of the prey, independent of different population abundances, and indicate the prey that is often most preferred or prey that is actively avoided (Jacobs, 1974; Hayward & Kerley, 2005). The following table (Table 25) accounts for certain of the prey preferences of a selection of African predators, i.e., lion (*Panthera leo*), leopard (*Panthera pardus*), Spotted hyaena (*Crocuta Crocuta*), African wild dog (*Lycaon pictus*) and cheetah (*Acinonyx jubatus*). Most

of these studies were conducted by Hayward (Hayward & Kerley, 2005; Hayward, 2006; Hayward *et al.*, 2006a; Hayward *et al.*, 2006b) in various regions in southern Africa which includes numerous national parks and reserves in South Africa, Namibia, Tanzania, Zimbabwe, and Zambia.

Table 255: Jacobs index values large carnivores & prey in southern Africa

	Lion (<i>P. leo</i>)	Leopard (<i>P. pardus</i>)	Spotted hyaena (<i>C. crocuta</i>)	Africa Wild Dog (<i>L. pictus</i>)	Cheetah (<i>A. jubatus</i>)
Buffalo (<i>S. caffer</i>)	0.32 ± 0.10	-0.84 ± 0.10	-0.39 ± 0.17	-0.98 ± 0.02	- 0.98 ± 0.01
Eland (<i>T. oryx</i>).	0.18 ± 0.14	-0.68 ± 0.16	-0.34 ± 0.33	-0.71 ± 0.14	-0.84 ± 0.06
Gemsbok (<i>O. gazella</i>)	0.70 ± 0.06	-0.33 ± 0.21	0.62 ± 0.25	-1 ± 0	-0.66 ± 0.19
Hartebeest (<i>A. buselaphus</i>)	0.02 ± 0.13	-0.65 ± 0.11	-0.36 ± 0.24	-0.56 ± 0.15	-0.18 ± 0.11
Kudu (<i>T. strepsiceros</i>)	0.13 ± 0.12	-0.31 ± 0.12	0.11 ± 0.19	0.35 ± 0.10	-0.04 ± 0.10
Roan (<i>H. equinus</i>)	0.15 ± 0.17	-0.78 ± 0.18	-0.56 ± 0.44	-1 ± 0	-0.79 ± 0.21
Sable (<i>H. niger</i>)	-0.05 ± 0.20	-0.80 ± 0.15	-1 ± 0	-0.63 ± 0.17	-0.61 ± 0.18
Blue wildebeest (<i>C. taurinus</i>)	0.27 ± 0.08	-0.77 ± 0.06	0.02 ± 0.13	-0.70 ± 0.08	-0.69 ± 0.07
Burchell's Zebra (<i>E. quagga</i>)	0.16 ± 0.07	-0.80 ± 0.06	-0.44 ± 0.12	-0.88 ± 0.07	-1 ± 0
Preferred prey weight range	190–550 kg	10–40 kg	56–182 kg	16–32 & 12–140 kg	23–56 kg

* Jacobs index values range from -1 to 1, the more positive the value the more preferred the prey.

In terms of the large modern-day predators found in Africa, most likely to prey on zebra are lions, leopards, spotted hyaenas, African wild dogs and cheetahs. Each of these predators specialises in the hunting/stalking of their prey in their distinctive forms, be it through endurance hunting, stalking, pack hunting or ambush. Each predator has its preferred prey. For lions it is often dependent on the area of study, however, their preferred prey is usually either buffalo, wildebeest, or gemsbok. Often these lions would be hunting in a pride with the female lions as the main hunters. There are, however, recorded cases in which male lions do the hunting alone or with a small group of other young male lions. Although not the most preferred prey, lions do have some preference towards Burchell's zebra (Hayward & Kerley, 2005).

With regards to leopards, spotted hyaena and African wild dogs, Burchell's zebra are not the preferred prey and, in most cases, the larger bovids are not preferred either. However, in the case of African wild dogs, when hunting as a pack, they are capable of running down much larger bovids and show an interesting preference towards kudu (Hayward *et al.*, 2006a; Hayward *et al.*, 2006b; Hayward, 2006). Both leopard and African wild dogs seem to mostly avoid the Burchell's zebra as a prey type but have been recorded to take neo-natal and juvenile individuals where possible. This is, however, often met with resistance from either the family group of zebra or mares that will defend their foal. Similarly, the cheetah shows little preference towards any of the bigger bovids or the Burchell's zebra; in fact, the Burchell's zebra is one of the most avoided prey types. The reason for this is not entirely clear but accounts of zebra defending themselves against smaller predators such as leopards, African wild dogs and cheetah are not uncommon. There have been accounts of African wild dogs attacking a family group of plains zebras, resulting in a cohesive family effort in fleeing and also defences by stallions through kicking and biting. Other accounts of the interactions between African wild dogs and plains zebra, recorded the plains zebra lowering their heads and approaching several African wild dogs to within 2 m, after which the African wild dogs retreated (Schaller, 2009). Ultimately, the most likely reason why plains zebras are avoided is likely due to smaller predators perceiving them as more of a threat, outweighing the reward of feeding on them.

In areas such as Etosha and the Kruger National Park, lions preferentially prey upon zebra foals as they are easier to prey upon than adults (Hayward & Kerley, 2005). Predation rates of zebra numbers tend to remain constant regardless of varying abundance through the wet and dry seasons. This is in part due to a significant proportion of the zebra numbers being migratory which renders less of a limiting factor than with more sedentary bovids (Courbin *et al.*, 2016). Generally speaking, buffalo, gemsbok, giraffe, warthog, wildebeest, and plains zebra constitute the majority of the diet of lions, however, plains zebra only account for 11% of the total (Hayward & Kerley, 2005). The study by Lacruz *et al.* (2003) also yielded specimens of lions found in Gladysvale External Deposits, indicating the presence of lions as a highly likely predator of equids in the fossil record.

Similarly, the other most likely predator of zebra, the spotted hyaena, generally prefers juvenile individuals. Studies done at Lewa Wildlife Conservancy and Borana Conservancy in central Kenya, indicate that almost 30% of the diet of the spotted hyaena is made up of both *Equus grevyi* and plains zebra (Dheer, 2016; Trinkel, 2010). In areas such as Etosha, research shows that plains zebra (mostly foals) account for a similar part of the diet,

independent of abundance. Accounts of hyaena groups occasionally hunting plains zebra have been recorded in Etosha. Often these hyaena groups are much larger in numbers, about 24 individuals, than the hyaena groups hunting wildebeest or smaller bovids, which is about 18 individuals (Trinkel, 2010). Spotted hyaenas have accordingly been recorded, in places such as Etosha, to hunt cooperatively in groups (on occasion), but they most often hunt alone, much the same as lions. The spotted hyaena is, however, generally able to satisfy its dietary requirements through scavenging (Hayward, 2006). Therefore, it is probably best to conclude that spotted hyaena should rather be viewed as an opportunist hunter of plains zebra with high scavenging tendencies aided by the presence of other larger carnivores such as lions (Hayward, 2006; Edwards *et al.*, 2019).

Based on the above-mentioned studies the most likely extant predators of plains zebra, lions, and the spotted hyaena, would also have been the greatest potential contributor to the faunal assemblage. However, studies show that the natural habitat selection of lions usually consists of grasslands (88%) followed by woodland (62%), shrubland (60%) and savanna (52%) with very little evidence found of lions living in caves (Sargent *et al.*, 2022). Research by Berger *et al.* (2009) on the in-situ fossil latrine usage investigated both the contents of the latrine and the overall shape that was deemed similar to that of modern-day brown hyaena (*Parahyaena brunnea*). This gives one of the oldest recorded occurrences of an in-situ latrine of *P. brunnea*, which occupied the cave from 257–195 ka. Further research by Taru (2016) expands upon this by examining the contents of the coprolites themselves. The fossil hair identified within the coprolites unquestionably shows that the area of Gladysvale was shared among various forms of bovids and with zebra. Whether or not the hyaenas that made use of Gladysvale cave during this time period actively hunted or scavenged from these animals is uncertain. Brown hyaena are mostly habitual scavengers, actively avoiding lions and spotted hyaena. They would actively hunt at times, such as when they rear pups, but this only accounts for less than 6% of their diet (Mills, 1990). Brown hyaena benefit greatly from the presence of larger carnivore species through which they have higher scavenging opportunities (Edwards *et al.*, 2019; Mills, 1982; Yarnell *et al.*, 2013).

Equidae in the Cradle of Humankind

Throughout southern Africa, there is an abundance of protected areas and by extension areas that are able to support and sustain a wide range of biodiversity, ecosystems, and wildlife. These areas vary in size from about 300 km² such as the Mapungubwe National Park to areas well in excess of 80 000 km² (Table 23). Within these areas, numerous

amounts of wildlife can be found existing within their closest possible natural and uninhibited forms. These areas also cover a wide range of habits, ranging from the desert of the Namib, with an average annual rainfall of 10 mm to 60 mm (Sharon, 1981), to the delta of the Okavango with a catchment of over 1000 mm annual rainfall (McCarthy & Ellery, 1998). When comparing the numbers from the modern parks and conservation areas it clearly shows that, on average, extant zebra account for most of the total number of large ungulates, except for habitats which they commonly do not occupy. Furthermore, as shown by modern census data and aerial counts (Table 23) Equidae (mostly *Equus quagga*) account for roughly 30% to 45% of the large prey animals on the landscape. This is in stark contrast to numerous fossil localities, within the Cradle of Humankind (Table 24 and 26), in which the Equidae usually account for less than 20%. The Plio-Pleistocene fossil localities as reflected in Table 24, show that Equidae are underrepresented in the fossil records when compared to similar-sized Bovidae. The sites in which this trend is most commonly seen are Coopers (D), Drimolen (Main Quarry), Malapa (D), Kromdraai (M2), Sterkfontein (Name Chamber) and Makapansgat Limeworks Cave. These sites cover the relative ages from about 3.5 Ma to 10 Ka and are some of the most well-known Plio-Pleistocene fossil localities. Previous research on sites such as Swartkrans and Sterkfontein offers some of the best comparative NISP and MNI numbers for both equids and comparable-sized bovids (BOV III & IV). There are a few sites where Equidae constitute a much great percentage of the NISP as seen at Haasgat (66%), which is higher than any of the extant numbers. This however is largely due to the relatively small sample size within the sites, recorded as an NISP value.

The most common agents of accumulation within most Plio-Pleistocene sites in the Cradle of Humankind are either carnivores or porcupines with the occasional natural death trap or evidence of hominin activity (Table 26). Sterkfontein and Swartkrans, have an interesting and complex history in both taphonomy and accumulation, whereby Hyaenidae, Felidae and Canidae are all likely to have been agents of accumulation (Ogola, 2009; Val & Stratford, 2015; Brain, 1993a & Brian, 1993b). Furthermore, these sites are also well known for Hominins involvement as part of the accumulation process. It is interesting to note that here for both of these sites we see that Equidae are also underrepresented at under 20%, with the exception of Sterkfontein Post M6 and Wonderwerk Cave, where Equidae represent about 25%. The Sterkfontein Post M6 locality has been dated to between 252 Kya ($\pm$ 35 Kya) and 116 Kya ($\pm$ 7 Kya), based on diagnostic Middle Stone Age tools, similar in age to Lincoln Cave North deposit (Ogola, 2009; Reynolds *et al.*, 2003). Outside of the Cradle of Humankind we also have sites such as Wonderwerk Cave, Holocene deposit, where it is

purported to have *Homo sapiens* as the main accumulator for the later deposits, with some contribution from leopard (*Panthera pardus*) (Thackeray, 1984). This increase in the representation of Equidae may be due to the increased involvement of *Homo* as well as the increased and more sophisticated use of stone tools.

Other sites in the Cradle of Humankind, further shown to have underrepresentation of Equidae such as Makapansgat Limeworks Cave and Kromdraai, have carnivores as the main agents of accumulation. It is interesting to note that in the case of Makapansgat Limeworks Cave, the purported agent of accumulation is most likely that of a leopard (*Panthera pardus*) or similar small-bodied felid (Churcher, 1970; Churcher, 2000). As for Kromdraai the carnivores involved in site accumulation are likely that of Felidae and Hyaenidae, with leopards (*Panthera pardus*) being largely responsible for the accumulation of the smaller-sized animal remains, and three Hyaenidae considered as important accumulators. Both brown and striped hyaenas as well as a single “crocutoid” specimen are considered to have played a role at Kromdraai (Fourvel *et al.*, 2018). Furthermore, sites such as: Gondolin, Malapa, and Coopers Cave, also have carnivore accumulators together with contributions from other agents such as porcupines, other rodents, and possible death traps. However, there are sites in the Cradle of Humankind, such as: Hoogland (FBU 4 and 5), Drimolen (Main Quarry) and Haasgat (HDG) which have assemblages formed as a result of sedimentary accumulation. This in part might also explain the greater percentage of the Equidae NISP seen at Haasgat, compared to other sites with different agents of accumulation.

It should be noted that the true representations of Equidae versus Bovidae may not be correct as this is assuming that the common species of Bovidae (size III & IV) are properly represented in the fossil records. Numerous factors such as different habitats, taphonomy and predators within the different localities can cause some bias in which species are over and/or underrepresented. In this respect, various factors would have contributed to the formation of different elements being brought into these localities, and different agents of accumulation, as well as different localised habitats, would have played a role in accumulation as each would have a preference in each unique fossil locality.

Table 266: Fossil localities containing NISP & MNI of Equidae & Bovid size class III & IV.

Locality	Accumulation Agent	References
Makapansgat Limeworks Cave	Carnivore (most likely Leopard)	Churcher, 1970, 2000.
Clyde Site	Carnivore	Churcher, 1970, 2000.
Goldsmiths	Natural death trap	Mokokwe, 2006.
Hoogland (FBU 4 & 5)	Sedimentary	Adams <i>et al.</i> , 2010.
Drimolen (Main Quarry)	Sedimentary & rodent	Adams <i>et al.</i> , 2016.
Sterkfontein (M6)	Carnivore porcupine, rodents & Hominin (<i>Australopithecus</i> , <i>Paranthropus</i> or early <i>Homo</i>)	Ogola, 2009.
Sterkfontein (Post M6)	Carnivore, porcupine, rodents & Hominin (<i>Australopithecus</i> , <i>Paranthropus</i> or early <i>Homo</i>)	Ogola, 2009.
Sterkfontein (Name Chamber)	Carnivore (mostly Hyaenidae), porcupine & rodents	Val & Stratford, 2015.
Haasgat (HDG)	Sedimentary	Adams, 2012.
Gladysvale (GVED)	Carnivore & porcupine	Lacruz <i>et al.</i> , 2002.
Kromdraai (M2)	Carnivore (Felidae & Hyaenidae)	Fourvel <i>et al.</i> , 2018.
Gondolin (GD A)	Carnivore (most Felidae), porcupine & rodent	Adams, 2018.
Malapa (D)	Natural death trap & carnivore (Felidae & Hyaenidae)	Val <i>et al.</i> , 2015.
Wonderwerk Cave	Carnivore (mostly Felidae), rodent & Hominidae	Thackeray, 1984.
Swartkrans (M1)	Carnivore, porcupine & Hominin (<i>Australopithecus</i> & <i>Homo</i>)	Brain, 1993a; Brian, 1993b
Swartkrans (M5)	Carnivore, porcupine & Hominin (<i>Australopithecus</i> & <i>Homo</i>)	Brain, 1993a; Brian, 1993b.
Cooper's Cave (D)	Carnivore (Felidae & Hyaenidae) & rodent	Badenhorst & Steininger, 2019.
Swartkrans (M2)	Carnivore & porcupine	Brain, 1993a; Brian, 1993b
Swartkrans (M3)	Carnivore, porcupine & Hominin (<i>Australopithecus</i> & <i>Homo</i>)	Brain, 1993a; Brian, 1993b

Swartkrans (M6)	Carnivore, porcupine & Hominin (<i>Homo</i>)	Brain, 1993a; Brian,1993b
Swartkrans (Post M6)	Carnivore, porcupine & Hominin (<i>Homo</i>)	Brain, 1993a; Brian,1993b

Equidae Predatory Avoidance Behaviours & Reasons for Variance

As previously stated, it does appear that equids are often underrepresented in the fossil records when compared to the numbers of extant large ungulates on the landscape (Tables 24 and 26), with the assumption that Bovidae are correctly represented and that numbers on the landscape would equate to numbers in the fossil record. This could be attributed to many aspects such as: changes in climates over time, seasonality, migration patterns, whether Equidae was scavenged or hunted, predator-prey relations in the Plio-Pleistocene, presence and abundance of large carnivores that can take down zebra, and the relative abundance of zebra itself, and predatory avoidance behaviour.

Changes in the climate over the last 3 million years have certainly been one that tends towards more aridity, varying climate, and less annual rainfall over the landscape (Scott *et al.*, 1997). As already stated, equids are more adaptable to survive on a wider array of vegetation and have greater dietary variation. Equids also have variable home ranges that are shaped by the fragmentation of the landscape. Moreover, in areas of highly fragmentary distribution of food and low availability, Equidae are more likely to move around and occupy larger home ranges (Penzhorn, 1982; Bartlam-Brooks *et al.*, 2013a). As the Cradle of Humankind has seen significant changes to the landscape in drier periods (0.9 Ma to 0.3 Ma), it is highly likely that Equidae home ranges were variable and could have occupied larger areas extending well beyond the Cradle of Humankind. The drier periods almost certainly would have affected *Equus capensis* as the species likely would have had limitations on the range of habitat and numbers within the species (Klein 1977; Thackeray 1984). Whereas, the more adaptable *Equus quagga* would have been more likely on the landscape as it has a wider array of dietary variation, as previously stated. It is true that both these species are still reliant on water, and *Equus quagga* tends to prioritise water sources within a certain range of feeding opportunities, less than 12km (Grubb, 1981). It is highly likely that *Equus capensis* would have had a very similar dependency on water, water sources would still have been available at a local level in numerous areas within the Cradle of Humankind. Considering that water-dependant species such as *Potamochoerus*

porcus, *Hippotragus niger*, *Aepyceros melampus*, *Kobus leche* and *Pelorovis* have also been found at Gladysvale (Lacruz *et al.*, 2010, Skinner & Chimimba, 2005), it is reasonable to infer the proximal existence of water sources. Whilst noting the diverse faunal fossil assemblages found within the Cradle of Humankind, and Gladysvale, water sources would have been a determining factor in the micro-environment of each site (Dirks *et al.*, 2010, Dirks and Berger, 2013). More studies done outside the scope of the Cradle of Humankind also suggest that the extinction of *Equus capensis*, along with *Syncerus antiquus* and *Megalotragus priscus*, would have been the result of the loss of suitable habitat, but also perhaps the increased presence of *Homo sapiens* (Helm *et al.*, 2023). All three of these species were adapted to consume large amounts of low-quality forage resulting in the need for larger home ranges (Faith, 2012).

Migration patterns, of *Equus* have been known to be as much as 480 km in extreme cases, with emphasis on following behind grasses and often migrating out of areas during drier periods (Hopcraft *et al.*, 2010; Bartlam-Brooks *et al.*, 2013b). Certainly, there is a trend in the Cradle of Humankind that accumulated sediments occur most often during more arid time periods, resulting in the overrepresentation of arid-adapted species (Pickering *et al.*, 2019). However, we still see the presence of *Equus* on the paleo-landscape in the Cradle of Humankind, as reflected in Tables 23, 24 and 26. Isotope analysis can indeed provide data on migration as seen in Hobson (1999) and Wolf *et al.* (2010), however very little isotope analysis has been done on Equidae migration within the Cradle of Humankind and would merit further study. Previous research by Bartlam-Brooks *et al.*, (2013b) further suggests that the migration of Equidae is largely determined by precipitation and vegetation availability. As *Equus quagga* have been known to travel up to 480 km in extremely long migration, often following the rains and ensuing fresh grazing, it seems highly likely that *Equus quagga* might have occasionally been in the Cradle of Humankind but would have migrated away during drier periods.

Another factor that might account for variance within the Cradle of Humankind is the predator-prey relations in the Plio-Pleistocene and the subsequent presence and abundance of large carnivores that can take down Equidae. A study by Reynolds (2010) assessed the occurrence and spatial patterning of the larger carnivores in the Cradle of Humankind. The occurrence of Carnivora in the fossils record of the Cradle of Humankind is best represented through studies in the southern region, such as Sterkfontein, Swartkrans, Coopers, Kromdraai and Bolts Farm. However, this record is less well

represented in the northern region, such as at Gondolin, Haasgat, Motsetse, and Gladysvale. Regardless, the record accounting from the past 2.5 Ma does indicate the presence of all the modern-day large carnivores previously mentioned but also the presence of some now extinct carnivores such as sabre-toothed cats (Reynolds, 2010).

Megantereon whitei, with only a single species in the genus, has been found in the Cradle of Humankind. This species is the smallest size of the sabre-toothed cats, and it has been suggested that this species would have had prey preferences similar to that of the leopard and hyaenids, which would have either employed an ambushing method of hunting and/or scavenged (Pamlqvist *et al.*, 2007). Thus, it could be suggested that this predator might have been able to at least contribute to the accumulation of Equidae. This species shows a relatively tight spatial distribution occurring only in the southern region of the Cradle of Humankind, with its occurrence in the fossil record only from >2.5 Ma to ca. 0.7 Ma (Reynolds, 2010).

Homotherium latidens, although best represented in Europe, was also present on the landscape in the Cradle of Humankind. It is, however, only represented in two sites, namely Swartkrans and Sterkfontein. This sabre-toothed cat would have been comparable in proportion to that of the modern-day lion or tiger. It did, however, differ in appearance as it had much longer sabre-like canines accompanied by longer front legs, shorter hind legs, and a short tail. This posture is best displayed in modern days by that of a hyaena (Serangeli *et al.*, 2015). Bone damage associated with this predator has also been compared to that of leopards and hyaena. *Homotherium* seems to have had a strong prey preference for proboscideans, particularly the juveniles (Serangeli *et al.*, 2015). Unfortunately, no group size has yet been determined for this taxon. The spatial distribution of the taxon has also only been limited to the southern region of the Cradle of Humankind, with its last appearance at about 1.1 Ma (Reynolds, 2010).

Other large cats such as *Dinofelis barlowi*, *Dinofelis piveteaui* and *Dinofelis aronoki* have been found in the Cradle of Humankind (i.e., O'Regan & Steininger, 2017). These two taxa are regarded as the false sabre-toothed cat genus and have been abundant in the area. It has been suggested that *Dinofelis* was a close relative to *Panthera* at one point. Having been compared closest to leopard, morphologically speaking this genus is usually seen as being larger and more robust (Werdelin & Lewis, 2001). Furthermore, the genus tends to have a shorter tail than modern large cats. *Dinofelis barlowi* is the first of the species to appear in the Cradle of Humankind and is spatially distributed only to a small region in the

southernmost end of the Sterkfontein Valley. *Dinofelis piveteaui*, on the other hand, seems to have a much more northern distribution and has been found in Drimolen and Motsetse (Reynolds, 2010). The last appearance of *Dinofelis*, is delayed after the extinction period of larger cats and hyaenas at c. 1.5 Ma (Turner & Anton, 1998) with last appearance date proposed c. 1.0 Ma (Ditchfield *et al.*, 1999).

Other extinct predators include the genus *Chasmaporthetes*, often referred to as hunting hyaena, which are also present in the Cradle of Humankind. Morphologically this genus would often have longer and more slender limbs than the modern-day equivalent with less robust cheek teeth. A few species within this genus appear in the Cradle of Humankind, the majority at Sterkfontein and Swartkrans, however, two species have been identified at Haasgat and Drimolen. This suggests that this genus did have a bigger spatial distribution and a more northwards range is evident in later species (Reynolds, 2010).

Pachycrocuta brevirostris, otherwise known as the short face hyaena is one of the largest of the extinct hyaenids found in the Cradle of Humankind (Reynolds, 2010). This taxon has been compared to the overall size of modern-day lions and has been suggested to occupy much the same ecological niche as the modern spotted hyaena (Reynolds, 2010). This taxon has been identified from a largely complete skull in Kromdraai and some well-persevered cranial material in Gladysvale (Reynolds, 2010). Another material representative of this taxon is a few fossil canines found in other sites in the southern region. The spatial distribution of this predator has mostly been limited to the region around Gladysvale and Bolts Farm (Reynolds, 2010). However, based on fossil evidence it does suggest that this taxon was only ever-present in low levels through time, or alternatively that this taxon could be viewed as an infrequent visitor species (Reynolds, 2010).

Studies by Lesnik & Thackeray (2006) in which they took a combined large sample of *Equus capensis* from Swartkrans and *Equus quagga* from Sterkfontein, Kromdraai and Minnaar's Cave concluded that *Dinofelis* preferred taking juveniles and old adult zebras. This practice is much the same as modern extant predators of *Equus quagga*. Owen-Smith and Mills (2008) suggest that modern carnivores have a preference for prey half to twice the carnivore's body weight. In cases of group hunting, as seen in African wild dogs and lions, a carnivore is able to take down prey much larger than itself. It, therefore, seems highly likely that, similar to the lion, the *Dinofelis* species and *Homotherium latidens* would have had a prey preference for the larger bovids and Equidae. Conversely, the smaller-sized sabre-toothed cats such as *Megantereon whitei*, would have had prey preferences similar to that

of leopards, African wild dogs and hyaenas. So, it is possible that for Gladysvale, lions and *Dinofelis* could have hunted zebras, and that scavenging hyaena and hunting and/or scavenging *Dinofelis* brought them back to the caves. However, although *Dinofelis* has been found in Gladysvale, the specimens were found as part of the older GVED assemblage (1.25 to 0.72 Mya) and thus not associated with younger GVID (780 to 530 Kya), as they would have been extinct by then (Werdelin & Lewis, 2001).

The last possible factor for variance in equid numbers within the Cradle of Humankind could be the antipredator avoidance behaviours of Equidae. Unfortunately, behaviours do not fossilise, but certain inferences can be made. Some of the antipredator behaviours could potentially be investigated, for example the kicking forces of modern-day horses have been studied and relatively well documented with even some cases resulting in fatalities of handlers (i.e., Ebert *et al.*, 2012; Gorman, 2012; Von Wachenfelt *et al.*, 2013). Further research on the kicking force of *Equus quagga* and *Equus capensis* is needed, but the behaviour itself has been documented (i.e., Penzhorn, 1984; Grubb, 1981; and Eisenmann, 2000).

Differences in predatory avoidance behaviours might be due to the size of *Equus quagga* as compared to *Equus capensis*. Previous research on the evolution of Equidae alluded to one adaptation that can be tested in terms of predatory avoidance. This adaptation of having more gracile metapodials than any extant living equids, is seen in the case of *Equus numidicus* and *Equus tabeti*. This implies that they relied on speed to protect them from predators, whereas the more robust equids such as *Equus oldowayensis*, *Equus mauritanicus* and *Equus capensis* may have actively defended themselves (Hunt, 1995). This may imply differences in success in predatory avoidance behaviours. Certainly, both *Equus numidicus* and *Equus tabeti* are different in build and both went extinct before the arrival of *Equus quagga*, but they did exist in the same temporal range of *Equus capensis* (Bernor *et al.*, 2019). Accounts of the predatory avoidance behaviours of extant *Equus quagga* can be viewed as containing the natures of both the gracile and the robust, i.e., they often flee from predators but have also been known to actively defend themselves.

Studies on modern interactions regularly show that zebra can outpace lions, and unless a lion can catch a zebra within the first 6 seconds of the chase the zebra will escape as it can

reach its top speed of between 60 and 70 km/h after about 10 seconds. As a result, 28.6% of the time a zebra hunt will end in failure for lions; a failure which is further compounded by the lion having spent time and energy stalking zebra beforehand (Hayward & Kerley, 2005). The previously mentioned anti-predatory behaviours such as habitat preferences and usages after an encounter, together with a cohesive family group and vigilance, provide equids with an effective reactive defence against predators. These are all considered common behaviours with extant equids but in the case of *Equus capensis*, this is still uncertain and mostly speculative.

***Equus quagga* compared to *Equus capensis*.**

Regarding the taxonomy related to *Equus quagga* and *Equus capensis*, phylogenetic research by Orlando *et al.* (2009) has shown these two species to be conspecific, implying that they are within range of each other based on interspecific variation and diversity. Measurements taken on both cranial and post-cranial elements seem to indicate that in the fossil record, *Equus quagga* is slightly larger than extant plains zebra, which is still much smaller than *Equus capensis*, both in upper and lower dentition and post-crania. The most apparent difference between the species is the overall size as all the incisors have a mean mesiodistal length and mean buccolingual breadth greater in *Equus capensis* than in *Equus quagga* with the mean buccolingual breadth being the most deciding factor between the species (Tables 16 and 17). The statistical analyses of modern-day *Equus quagga* and *Equus capensis* upper premolar 2 and molar 3, as well as lower premolar 2, yielded similar results for the most part (Table 22). Both the upper molar 3 and lower premolar 2 elements were shown to be statistically different, in terms of both mesiodistal length and buccolingual breadth. However, the upper premolar 2 had mixed results, as there was no significant difference observed in the buccolingual breadth. The post-crania measurement, however, is relatively limited in this study. But by all accounts, the *Equus capensis* measurements as laid out by Von den Dreich (1976) are outside of the standard deviations of the extant *Equus quagga* measurement, while the fossil *Equus quagga* measurements are only slightly larger. The same trend is seen in the proximal phalanges, metacarpals, and metatarsals (Tables 18 through 21). Furthermore, this is also observed in other sites within the Cradle of Humankind such as in Coopers (Badenhorst & Steininger, 2019).

It is highly likely that being a larger and more robust animal, *Equus capensis* did employ more active defences such as kicking and biting. It certainly had a large body mass and consequently greater muscle mass (Eisenmann, 2000; Broom, 1909; Churcher, 2006). However, active defence is not always the greatest deterrent as in the case of buffalo and lions. Buffalo are the most preferred prey of lions in the Kruger National Park, where lions are the apex predator. Accordingly, given their heavy build, buffalo only have a slight speed advantage over lions. Buffalo are also a water dependant species and are more susceptible to falling prey to lions, especially during times of drought. This seems noteworthy as buffalo remains would most likely have accumulated under very similar conditions in the Cradle of Humankind and by extension also at Gladysvale (Eisenmann, 2000; Broom, 1909; Churcher, 2006, Lacruz *et al.*, 2002, Pickering *et al.*, 2007).

Furthermore, even with extant equids species, there does seem to be differences in anti-predator behaviours as previously mentioned. This could further imply that the *Equus capensis* and Hipparions might have had different forms of anti-predator behaviours, which might have been less successful, and which contributed to their eventual extinction over and above other pressures such as environmental and climatic changes. Trends of *Equus capensis* within the fossils record versus *Equus quagga* may provide some insight into this possibility. In Table 27, most of the previously mentioned localities provide NISP and/or MNI values, however, not all sites are mentioned as some studies only identified fossil remains to family level or only had indeterminate Equidae material. Most of the localities in Table 27 have a higher representation of *Equus capensis*, often with a few Hipparion specimens present. Localities such as Haasgat (HDG) and Gladysvale (GVED) have a roughly equal representation of the two *Equus* species in terms of MNI values, but, usually with a higher NISP value. Drimolen (Main Quarry) and Sterkfontein (M6) are localities where *Equus capensis* and Hipparion are not represented at all, with the only *Equus quagga* present.

Table 27: NISP & MNI of *Equus capensis*, *Equus quagga* & Hipparion in the Cradle of Humankind

Locality	<i>Equus capensis</i> NISP/MNI	<i>Equus quagga</i> NISP/MNI	Hipparion NISP/MNI
Drimolen (Main Quarry)	-/-	3/1	-/-
Sterkfontein (M6)	-/-	6/2	-/-
Haasgat (HDG)	19/1	3/1	-/-

Gladysvale (GVED)	9/3	4/2	-/-
Sterkfontein (M4)	18/7	-/-	-/-
Kromdraai (A)	59/23	5/5	1/1
Gondolin (GD A)	3/3	-/-	-/-
Swartkrans (M1 lower bank)	8/3	-/-	8/1
Swartkrans (M1) *Brain, 1993a	9/6	-/-	1/1
Swartkrans (M1) *Brain, 1993b	-/8	-/-	-/1
Swartkrans (M5) *Brain, 1993b	7/2	19/6	-/-
Cooper's Cave (D)	16/2	-/-	1/1
Swartkrans (M2) *Brain, 1993a	12/4	21/9	-/-
Swartkrans (M2) *Brain, 1993b	10/3	-/-	9/1
Swartkrans (M3) *Brain, 1993b	36/5	4/1	13/1

Gladysvale Equidae & assemblage

The modern-day ecosystems found within the Cradle of Humankind are mostly grassland and woodlands with variable vegetation patterns at localised scales. This is not too dissimilar to the area's ecosystems of the past, albeit with a more open savanna environment and light grassland. Some of the more humid microhabitats, such as rivers and valleys would have had denser vegetation much like the current woodlands found close to Gladysvale today (Schmid, 2002). Gladysvale itself currently present grasslands with a scattering of woodland and bushes and it is situated on the edge of a mixed savanna. Isotope studies on the Gladysvale deposits show that during the early Pleistocene there would have been a large C4 vegetation component that appeared outside the cave, and which was associated with cooler and drier conditions. However, towards the mid-Pleistocene, there was a shift towards higher proportions of C3 vegetation (Pickering, *et al.*, 2007). This infers that the past ecosystems in the Cradle of Humankind would have been very similar to that of the modern-day Cradle of Humankind, however over time there was a loss of the open savanna, which was slowly replaced by open grasslands. This is to suggest that the past habitat close to and around Gladysvale would not have been antipathetic to Equidae, although as previously mentioned these Equidae would have most likely been migratory during the drier periods.

Within Gladysvale, based on solely the Equidae, age classes according to teeth showed that the mortality profiles belonged in part to a few very young individuals present, but the majority of the sample consisted of older individuals (60%) (Table 11). Furthermore, the age classes as defined by post-cranial elements are mostly adults (Table 12). Also, it appears that most of the post-cranial elements in the Gladysvale sample do have either the proximal or distal end present (Table 7). This according to Pickering (2002), Kuhn (2005) and Kuhn *et al.* (2010) is not uncommon for a hyaena assemblage as one would generally expect more bone cylinders, as the hyaena often gnaw epiphyses. Furthermore, the majority of the post-cranial elements of the Gladysvale assemblage are dense limb bones, metatarsals, metacarpals, astragali and phalanges which again is not uncommon for hyaena accumulation (Pickering, 2002; Kuhn, 2005; Kuhn *et al.*, 2010). Moreover, the taphonomic modifications (Table 15) indicate the presence of chew marks, rodent gnawing, transverse fractures, and large components of eroded breaks, suggesting hyaena involvement. As previously stated the definitive indicators of hyaena presence, are the remains of juvenile hyaena within a site (Kuhn *et al.*, 2010), and the presence of coprolites within the site (Berger *et al.*, 2009). As per Lacruz *et al.* (2010) no juvenile hyaena remains were observed at Gladysvale, however the presence of in situ coprolites is well documented (Berger *et al.*, 2009). The diversity of the predators on the landscape may also suggest hyaena activity (Badenhorst *et al.*, 2021) but additional factors seem to suggest that other agents of accumulation are also present. Factors such as presence of a few complete long bones, many hard compact bones and taphonomic features such as rodent gnaw marks (Table 15) also suggest that another likely agent of accumulation is the porcupine.

Lastly, hominids, are the third potential agent of accumulation that was present on the landscape. Hominids have been suggested to scavenge from kills by other large predators (Bunn & Pickering 2010). Often, as a result of scavenging hominids, an abundance of large-bovid limb bone specimens may be present in an assemblage, sometimes with cut marks. The post-cranial skeletal elements most common in the Gladysvale assemblage are limb bones such as metatarsals, metacarpals, astragali and phalanges (Table 7). As previously stated, a single Achuelean handaxe has also been found at Gladysvale and is dated to about 780 Kya (Hall *et al.*, 2006). This temporal range is just outside the age range of the older part of the Gladysvale assemblage (GVED) however, it could still be of importance as it may indicate that hominids may have hunted zebra or scavenged. This may concern the impact and implications of Hominin subsistence strategies as it is evident that some form of anthropogenic modification has been involved in this sample (Table 15), one tentative case

was observed with localised and repeated cutmarks in the entirety of the Gladysvale sample. A supporting factor may be the bone marrow amount from *Equus quagga*, which is generally lower than a comparable bovid of similar size, with the exception of the tibia (Blumenschinea & Madrigala, 1993). However, in a contradicting manner, this bone marrow is perceived to be of better quality and greatly preferred by modern hunter-gatherer people, such as the Hadza (Lam *et al.*, 1999).

There is also a third equid, Hipparion, that appears in the Cradle of Humankind, which was initially tentatively assigned to a specimen from Gladysvale. Further research is needed on Hipparion in order to elaborate on the species' dietary variation, however, according to both Striton (1941) and Bernor *et al* (1980), it is evident that Hipparion did adapt to eating drier grasses. Whether this extended to the same degree of dietary variation of *Equus* is unclear. What is known is that similar to Gladysvale, the accumulation of Hipparion has been linked to times of drought, as in Langebaanweg (Franz-Odendaal, 2002). The Hipparion previously recorded at Gladysvale by Berger (1993) was only given a tentative identification based on an isolated tooth and no further record of the tooth was given.

Ultimately there are three potential agents of accumulation as stated above, i.e., porcupine, hyaena, and hominids. The main issue in the identification of the agent of accumulation comes from the deposits found at Gladysvale as stated by Berger (1993), i.e., the depositional process within Gladysvale is problematic as the site was essentially closed to external deposits of about 150 Kyra. The deposition most likely occurred in short periods of accumulation, often during dry periods. Furthermore, faunal fossil preservation overrepresents arid-adapted species.

Conclusion

In this study, the principal aim was to investigate Equidae remains from Gladysvale, the role that Equidae played in the larger faunal communities in the Cradle of Humankind and establish relative dates for the Gladysvale Equidae. Of the three possible Equidae in the cradle of humankind, only *Equus quagga* and *Equus capensis* were found at Gladysvale, the genus Hipparion was not positively identified. Although Hipparion was tentatively assigned one specimen by Berger *et al.* (1993), however, this specimen was not later found by Lacruz *et al.* (2003) nor in this study. The absences of Hipparion which had a temporal range roughly between 2.5 and 1 Mya in Southern Africa (Brink *et al.*, 2016), would imply an upper range to the relative date at Gladysvale under 2.5 Mya. The temporal ranges for

Equus capensis, roughly 2.5 Mya to 10 Kya (Avery, 2019, Klein 1983, Badenhorst & Steininger, 2019), and *Equus quagga*, roughly 1 Mya to present (Bernor *et al.*, 2010, Badenhorst & Steininger, 2019) would suggest an upper limit at roughly 1 Mya to present. This is in full support the temporal range of 730 to 580 Kya for the external deposits and 257 to 195 Kya for the internal deposits of Gladysvale (Berger *et al.*, 1993; Pickering *et al.*, 2007; Lacruz *et al.*, 2003)

It is evident that Equidae is poorly represented when compared to bovids of similar sizes, within the Plio-Pleistocene localities in the Cradle of Humankind (Table 27). This is in sharp contrast to modern census data for large parts of Southern Africa (Tables 23 & 24). The reasons for the low representation of Equidae within faunal assemblages from the Cradle of Humankind during the Plio-Pleistocene may include various factors such as: climates over time, seasonality, migration patterns, whether Equidae were scavenged or hunted, predator-prey relations in the Plio-Pleistocene, presence and abundance of large carnivores that can take down zebra, and the relative abundance of zebra itself, and predatory avoidance behaviour. Further to this, the notion that Equidae were not present on the landscape for certain times of the year due to long-distance migration or selectively used different parts of the landscape is a possible reason for the lower representation. However, there are numerous sites within the Cradle of Humankind, previously mentioned, that contain Equidae fossils in which most accumulation would have happened during drier periods. This has further been supported by previous research on stable isotopes and dental pathologies (i.e., Franz-Odenaal, 2002). This is counterintuitive as Equidae are a water-dependant species and likely would have made greater use of the localised water sources within the cradle of Humankind during the drier periods as well as employed migration behaviours. There is certainly further capacity for research at Gladysvale, and other sites within the Cradle of Humankind, in which isotope analysis could provide insight into the migration patterns of the faunal assemblages. Whether Equidae existed in large herds in the past and was readily available as prey is unfortunately largely untested, as there is little usable evidence and procedures available to determine the population size of the past.

Most of the carnivores that accumulated faunal specimens in assemblages from the Cradle of Humankind would likely not have regarded Equidae as preferred prey. Of the possible carnivora found, throughout the Cradle of Humankind, such as: *Panthera*, Hyaenidae, *Dinofelis* and *Megantereon whitei*, which may have had a slight penchant for Equidae, it is certain that Hyaenidae and possibly lion (*P. leo*) have contributed to the Gladysvale assemblage. A larger emphasis was placed on the contribution from Hyaenidae, as there

has not been any documented evidence of cave usage by lion (*P. leo*) and the taphonomic signatures found at Gladysvale that suggest hyaena activity. This is also possibility supported by documented evidence that extant hyaena benefit in scavenging success with the presence of other larger carnivora on the landscape (Edwards *et al.*, 2019; Mills, 1982; Yarnell *et al.*, 2013). However, although *Dinofelis* has been found in Gladysvale, the specimens were found as part of the older GVED assemblage (1.25 to 0.72 Mya) and thus not associated with younger GVID (780 to 530 Kya), as they would have been extinct by then (Werdelin & Lewis, 2001). This may in part allude to the notion that some Equidae employed effective predator avoidance behaviour, as Equidae are still found throughout sites within the Cradle of Humankind. All the above-mentioned factors are mutually inclusive concerning Equidae and should be considered in an integrated manner. Such behaviours of Equidae are considered part of an evolutionary ecological approach which predicts the types of behaviour organisms use to avoid predation. Unfortunately, behaviours do not fossilise, and ultimately this limits the extent to which the horizons can be broadened with regards to the role of Equidae within the Cradle of Humankind.

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Appendix

Appendix A: Database of GVED Equidae fossil material previously examined & catalogued.

GV NUMBER	Species	Element	Part	Side	Upper/ Lower	Fusion	Breakage	Mod.	Length	Age Class	Length (mm)	Break (mm)
4938	Equidae	Calcaneus	Fragment with less than 50%	Left		Fused, no gap between epiphysis & diaphysis.	Transverse fracture		7	Adult		
18699	Capensis	Lateral Metacarpus	Proximal end complete, <50% of shaft	Right		N.A.	Transverse fracture		11	Adult		
4673	Capensis	Lateral Metacarpus	Proximal end incomplete, <50% of shaft	Left		Fused, no gap between epiphysis & diaphysis.	Broken during excavation					
5172	Quagga	Proximal Phalanx	Fragment with more than 50%	N.A.		Fused, no gap between epiphysis & diaphysis.	Broken during excavation	Anthropological	8		SD = 31,89 BD = 43,91 BFD = 43,3	
2092	Quagga	Thoracic Vertebrae	Spinous process present, fragment		Upper	Fused, no gap between epiphysis & diaphysis.	Carnivore damage & irregular fractures		7			
5131	Quagga	Medial Phalanx	Proximal end incomplete, >50% of shaft	N.A.		Fused, no gap between epiphysis & diaphysis.	Intact	Burnt black	4			
5247	Quagga	Terminal Phalanx	Proximal end incomplete, >50% of shaft	N.A.		Fused, no gap between epiphysis & diaphysis.	Intact		5		LF = 23,92 LD = 40,86 HP = 40,86	

7635	Quagga	Metapodial	Distal end incomplete, <50% of shaft			Fused, no gap between epiphysis & diaphysis.	Intact		4			
8901	Quagga	Metapodial	Distal end incomplete, <50% of shaft			Fused, no gap between epiphysis & diaphysis.	Intact		3			
8956	Quagga	Astragalus	Proximal end complete, >50% of shaft	N.A.		Fused, no gap between epiphysis & diaphysis.	Intact		6			
7585	Quagga	Proximal Phalanx	Proximal end incomplete, >50% of shaft	N.A.		Unfused	Intact		6		SD = 30,23 BD = 37,30 BFD = 36,3	
7823	Quagga	Metapodial	Distal end incomplete, <50% of shaft	Left		Unfused	Intact	Carnivore damage	4		BD = 44,99	
7995	Quagga	Proximal Phalanx	Proximal end incomplete, >50% of shaft	N.A.		Unfused	Intact		6		SD = 29,07 BD = 38,73 BFD = 36,5	
2624	Capensis	Lateral Metacarpus	Proximal end incomplete, <50% of shaft	N.A.		Fused, no gap between epiphysis & diaphysis.	Intact & eroded		7			
4682	Capensis	Sesamoid	Complete	Left		Fused, no gap between epiphysis & diaphysis.	Intact & eroded		6	Adult	GB = 51,48	
4853	Capensis	Metatarsus	Proximal end incomplete, <50% of shaft	Right		Fused, no gap between epiphysis & diaphysis.	Intact & eroded		7			

18248	Quagga	Metapodial	Distal end incomplete, >50% of shaft	Right		N.A.	Intact & eroded		6			
5223	Capensis	Proximal Phalanx	Proximal end incomplete, <50% of shaft	Right		Fused, no gap between epiphysis & diaphysis.	Intact & spiral fracture		5			
7067	Quagga	Proximal Phalanx	Fragment with more than 50%	N.A.		Unfused.	Intact & spiral fracture		6			
4676	Capensis	Carpal	Complete	Right		Fused, no gap between epiphysis & diaphysis.	Intact		4	Adult		
4966	Capensis	Other Tarsals	Complete	Left		Fused, no gap between epiphysis & diaphysis.	Intact		6	A	GB = 51,48	
5244	Quagga	Carpal	Complete	Right		Fused, no gap between epiphysis & diaphysis.	Intact		5	Adult	GB = 42,70	
7576	Quagga	Carpal	Complete	Left		Fused, no gap between epiphysis & diaphysis.	Intact		5	Adult	GB = 38,38	
7706	Quagga	Carpal	Complete	Right		Fused, no gap between epiphysis & diaphysis.	Intact		3	Adult		
7784	Quagga	Carpal	Complete	Right		Fused, no gap between epiphysis & diaphysis.	Intact		6	Adult	GB = 39,46	

7815	Quagga	Carpal	Complete	Right		Fused, no gap between epiphysis & diaphysis.	Intact		4	Adult		
7910	Capensis	Carpal	Complete	Left		Fused, no gap between epiphysis & diaphysis.	Intact		4	Adult		
8038	Capensis	Sesamoid	Complete	Left		Fused, no gap between epiphysis & diaphysis.	Intact		4	A		
8223	Capensis	Sesamoid	Complete	Left		Fused, no gap between epiphysis & diaphysis.	Intact		4	A		
18244	Equidae	Astragalus	Proximal end incomplete, <50% of shaft	Right		N.A.	Intact		6	Adult		
18318	Capensis	Metacarpus	Proximal end incomplete, <50% of shaft	Right		N.A.	Intact	Carnivore damage	6	Adult	DP = 41,06	
2110	Quagga	Thoracic Vertebrae	Neural arch fragment		Upper	Fused, no gap between epiphysis & diaphysis.	Splintered		5			
2057	Quagga	Metatarsus	Distal end incomplete, <50% of shaft	Left	Lower	Fused, no gap between epiphysis & diaphysis.	Eroded		5	Adult		
2059	Quagga	Metatarsus	Proximal end complete, <50% of shaft	Right	Upper	Fused, no gap between epiphysis & diaphysis.	Eroded		6	Adult		

2109	Quagga	Thoracic Vertebrae	Spinous process, complete or fragment			Fused, no gap between epiphysis & diaphysis.	Eroded		6			
5443	Quagga	Incisor	Fragment	Left		Fused, no gap between epiphysis & diaphysis.	Eroded		9	Adult		
7858	Quagga	Other Tarsals	Complete	Right		Fused, no gap between epiphysis & diaphysis.	Eroded		4	Adult		
8218	Equidae	Metapodial	Proximal end incomplete, <50% of shaft	Left		Fused, no gap between epiphysis & diaphysis.	Eroded		4	Adult		
8619	Quagga	Medial Phalanx	Distal end incomplete, <50% of shaft	Right		Fused, no gap between epiphysis & diaphysis.	Eroded		5		BFd = 42,42	
2638	Capensis	Metapodial	Proximal end complete, <50% of shaft	N.A.		N.A.	Eroded		3			
5871	Capensis	Incisor Permanent	Complete	Left	Upper	N.A.	Eroded		4	2 to 2,5	20,83	10,89
18233	Equidae	Humerus	Proximal end present, <50% of shaft	Unk.		N.A.	Eroded		5	?		
18236	Capensis	Proximal Phalanx	Distal end incomplete, <50% of shaft	Unk.		N.A.	Eroded		6	Adult		
18256	Equidae	Astragalus	Fragment with more than 50%	Right		N.A.	Eroded		8	Adult	BFd = 60,33	

18260	Equidae	Astragalus	Proximal end incomplete, <50% of shaft	Right		N.A.	Eroded		9	Adult	BFd = 59,01	
18282	Capensis	Other Tarsals	Proximal end complete, <50% of shaft	Right		N.A.	Eroded		4	Adult		
18288	Capensis	Other Tarsals	Fragment with less than 50%	Right		N.A.	Eroded		4	Adult		
18294	Equidae	Atlas	Vertebra split along anterior/posterior axis	N.A.		N.A.	Eroded		9	Adult		
18299	Equidae	Astragalus	Proximal end incomplete, <50% of shaft	Left		N.A.	Eroded	Pathological	8	Adult		
18302	Quagga	Metatarsus	Proximal end incomplete, <50% of shaft	N.A.		N.A.	Eroded		6	Adult		
18331	Quagga	Astragalus	Fragment with less than 50%	Right		N.A.	Eroded		7			
18336	Quagga	Metatarsus	Distal end incomplete, <50% of shaft	Left		N.A.	Eroded		5	Adult		
18585	Capensis	Astragalus	Proximal end incomplete, <50% of shaft	Right		N.A.	Eroded		8	Adult		
18607	Capensis	Astragalus	Proximal end incomplete, <50% of shaft	Right		N.A.	Eroded		6	Adult		
18642	Quagga	Metatarsus	Distal end incomplete, <50% of shaft	Unk.		N.A.	Eroded		4			
18659	Capensis	Other Tarsals	Proximal end complete, <50% of shaft	Left		N.A.	Eroded		5	Adult		
18751	Equidae	Metatarsus	Distal end incomplete, <50% of shaft	Unk.		N.A.	Eroded		4			

D1-073-B15	Equidae	Incisor Permanent	Fragment	Unk.	Upper	N.A.	Eroded		4			
18614	Quagga	Tibia	Distal end incomplete, <50% of shaft	Left		N.A.	Eroded		8	Adult		
402	Equidae	Molar Permanent	Fragment	Right	Upper	N.A.	Eroded		5	Adult	29,38	23,12
5053	Capensis	Premolar Permanent	Fragment	Left	Lower	N.A.	Eroded		6	Adult	31,26	14,42
6191	Equidae	Molar Permanent	Fragment	Right	Lower	N.A.	Eroded		3			
8474	Equidae	Incisor Permanent	Fragment	Unk.		N.A.	Eroded		5		11,74	15
8506	Equidae	Molar Permanent	Fragment	Right	Lower	N.A.	Eroded		5			14,84
18180	Equidae	Incisor Permanent	Fragment	Right	Upper	N.A.	Eroded		7	CA 5YRS		
18184	Equidae	Molar Permanent	Fragment	Unk.	Upper	N.A.	Eroded		7			
18185	Equidae	Molar Permanent	Fragment	Left	Lower	N.A.	Eroded		7	Adult		
18199	Equidae	Molar Permanent	Fragment	Left	Upper	N.A.	Eroded		4			
18207	Quagga	Incisor Permanent	Fragment	Right	Lower	N.A.	Eroded		3			
18386	Equidae	Molar Permanent	Fragment	Unk.		N.A.	Eroded		7			
18387	Equidae	Molar Permanent	Fragment	Unk.	Upper	N.A.	Eroded		7			
18588	Equidae	Molar Permanent	Fragment	Left	Lower	N.A.	Eroded		5	Old Adult		
18589	Equidae	Molar Permanent	Fragment	Left	Lower	N.A.	Eroded		3	Old Adult		
18629	Quagga	Incisor Deciduous	Complete	Left	Lower	N.A.	Eroded		2	CA 4YRS	13,33	7,12
18651	Quagga	Incisor Deciduous	Complete	Left	Upper	N.A.	Eroded		3	CA 2YRS	16,06	8,94

18693	Equidae	Molar Permanent	Fragment	Right	Upper	N.A.	Eroded		7			
18787	Equidae	Molar Permanent	Fragment	Unk.		N.A.	Eroded		3	Old Adult		
18788	Equidae	Molar Permanent	Fragment	Left		N.A.	Eroded		4	Old Adult		
18789	Equidae	Molar Permanent	Fragment	Unk.		N.A.	Eroded		3	Old Adult		
D1-186-B46	Quagga	Premolar Permanent	Fragment	Left	Lower	N.A.	Eroded		4	Sub Adult	32,42	13,2
217	Equidae	Premolar Permanent	Fragment	Right	Lower	N.A.			3			
403	Capensis	Incisor Permanent	Fragment	Left	Upper	N.A.			3	8 to 9	20,21	11,03
1589	Capensis	Molar Permanent	Fragment	Left	Lower	N.A.			6	Adult		
1637	Equidae	Molar Permanent	Fragment	Right	Upper	N.A.			8			
3891	Capensis	Premolar Permanent	Fragment	Left	Upper	N.A.			4		39,25	25,23
3891	Capensis	Premolar Permanent	Fragment	Left	Upper	N.A.			4	Adult	39,28	27,35
4082	Equidae	Incisor Permanent	Fragment	Left	Upper	N.A.			6	15	19,99	13,33
4083	Capensis	Molar Permanent	Fragment	Left	Upper	N.A.			7		24,78	23,27
4523	Capensis	Molar Permanent	Fragment	Right	Lower	N.A.		Burnt white, grey, or blue/grey.	7	Adult		
4642	Capensis	Incisor Permanent	Complete	Right	Lower	N.A.			5	Very Old Adult	11,68	15,98
4667	Equidae	Molar	Fragment	Left	Upper	N.A.			5			
4670	Equidae	Premolar	Fragment	Unk.		N.A.			4			
4761	Equidae	Unk. Tooth Fragment	Fragment	Unk.		N.A.			5			

4789	Capensis	Molar Permanent	Fragment	Right	Lower	N.A.			5		36,41	13,91
4807	Equidae	Incisor	Fragment	Unk.		N.A.			4			
4834	Equidae	Incisor	Fragment	Right	Lower	N.A.			2			
4913	Equidae	Unk. Tooth Fragment	Fragment	Unk.		N.A.			2			
5035	Capensis	Incisor Permanent	Complete	Left	Lower	N.A.			5	Old Adult	12,2	13
5044	Equidae	Molar	Fragment	Right	Upper	N.A.			4			
5046	Equidae	Molar	Fragment	Unk.		N.A.			6			
5049	Equidae	Incisor	Fragment	Unk.		N.A.			5			
5067	Capensis	Incisor Permanent	Fragment	Left	Lower	N.A.			5	14		
5091	Equidae	Sesamoid	Fragment	Unk.		N.A.			3			
5102	Capensis	Canine Permanent	Fragment	Left	Lower	N.A.			4	Adult	17,16	17,54
5104	Capensis	Incisor Permanent	Fragment	Right	Upper	N.A.			6	Very Old Adult	17,56	12,88
5121	Quagga	Molar Permanent	Fragment	Right	Lower	N.A.			4	12-14 YRS		
5252	Capensis	Molar	Fragment	Right	Lower	N.A.			6			
5253	Equidae	Molar	Fragment	Left	Lower	N.A.			8			
5278	Equidae	Molar	Fragment	Right	Lower	N.A.			7			
5332	Equidae	Molar	Fragment	Left	Lower	N.A.			3			
5350	Capensis	Premolar Permanent	Fragment	Left	Lower	N.A.			7	Adult	29,86	18,84
5374	Equidae	Premolar	Fragment	Left	Lower	N.A.			6			
5402	Equidae	Molar	Fragment	Right	Lower	N.A.			3			
5406	Capensis	Premolar Deciduous	Fragment	Left	Lower	N.A.			4		33,87	22,15
5676	Capensis	Premolar Permanent	Fragment	Left	Lower	N.A.			4			
5876	Capensis	Premolar Permanent	Fragment	Right	Upper	N.A.			4			

5904	Capensis	Molar	Fragment	Right	Lower	N.A.			5			
5905	Equidae	Unk. Tooth Fragment	Fragment	Unk.		N.A.			3			
6172	Equidae	Unk. Tooth Fragment	Fragment	Unk.		N.A.			2			
6185	Capensis	Molar	Fragment	Unk.	Lower	N.A.			7			
6186	Equidae	Unk. Tooth Fragment	Fragment	Unk.		N.A.			6			
6187	Equidae	Unk. Tooth Fragment	Fragment	Unk.		N.A.			3			
6198	Capensis	Molar Permanent	Fragment	Left	Upper	N.A.			4			
6273	Equidae	Incisor	Fragment	Unk.		N.A.			2			
6848	Equidae	Premolar Permanent	Fragment	Right	Upper	N.A.			5			
6872	Quagga	Incisor Permanent	Fragment	Left	Lower	N.A.			3	Adult	11,48	12,88
7242	Capensis	Incisor Deciduous	Fragment	Left	Upper	N.A.			2	Juvenile	15,58	8,24
7248	Capensis	Incisor Deciduous	Fragment	Left	Upper	N.A.			2	4	20,53	10,11
7548	Capensis	Incisor Deciduous	Fragment	Right	Lower	N.A.			4	Juvenile		
7563	Capensis	Incisor Deciduous	Fragment	Right	Lower	N.A.			2	Juvenile	19,72	0,78
7596	Equidae	Molar Permanent	Fragment	Left	Upper	N.A.			6		25.01	26.98
7643	Capensis	Incisor Deciduous	Fragment	Right	Upper	N.A.			2	0,8 to 1 YRS	17,92	9,23
7688	Capensis	Molar Permanent	Fragment	Right	Upper	N.A.			3	Adult		
7688	Equidae	Molar Permanent	Fragment	Right	Upper	N.A.			4			
7742	Equidae	Molar	Fragment	Right	Lower	N.A.			4			
7762	Equidae	Molar	Fragment	Unk.		N.A.			4			
7763	Capensis	Molar	Fragment	Unk.	Upper	N.A.			3			

7766	Capensis	Molar	Fragment	Left	Lower	N.A.			4			
7790	Equidae	Molar	Fragment	Right	Upper	N.A.			3			
7870	Equidae	Unk. Tooth Fragment	Fragment	Unk.	Upper	N.A.			6			
7961	Capensis	Molar Permanent	Fragment	Left	Lower	N.A.			4	Adult	37,2	18,45
8096	Quagga	Premolar Permanent	Fragment	Left	Lower	N.A.			5	Adult	26,32	14,84
8279	Equidae	Molar	Fragment	Right	Lower	N.A.			3			
8281	Equidae	Molar	Fragment	Left	Lower	N.A.			6			
8334	Equidae	Molar	Fragment	Left	Lower	N.A.			2			
8505	Quagga	Molar Permanent	Fragment	Right	Lower	N.A.			3			
8922	Capensis	Incisor Permanent	Fragment	Left	Upper	N.A.			4	Adult	18,54	13,08
8930	Capensis	Incisor Permanent	Fragment	Right	Upper	N.A.			6	Old Adult	13,48	13,98
8958	Capensis	Incisor Permanent	Fragment	Left	Lower	N.A.			5	Sub Adult	17,8	13,88
18170	Equidae	Molar Permanent	Fragment	Right	Lower	N.A.			4			
18172	Capensis	Molar Permanent	Complete	Left	Lower	N.A.			6		34,43	16,88
18182	Capensis	Molar Permanent	Complete	Left	Upper	N.A.			5	1 YRS	34,32	29,8
18193	Quagga	Molar Permanent	Complete	Left	Lower	N.A.			7		27,28	11,46
18200	Equidae	Incisor Permanent	Complete	Left	Lower	N.A.			4	Adult	14,78	14,22
18205	Equidae	Canine Permanent	Complete	Right	Lower	N.A.			8			
18206	Capensis	Incisor Deciduous	Complete	Left	Upper	N.A.			2	1-2 YRS	18,91	10,46
18211	Capensis	Incisor Permanent	Complete	Right	Lower	N.A.			6	Under 5	17,86	11,29

18219	Equidae	Molar Permanent	Fragment	N.A.		N.A.			3			
18243	Capensis	Other Tarsals	Complete	Left		N.A.			6	Adult		
18291	Capensis	Sesamoid	Complete	N.A.		N.A.			4	Adult		
18300	Capensis	Astragalus	Proximal end complete, <50% of shaft	Left		N.A.			8	Adult	GB = 62,35, GH = 58,66	
18315	Capensis	Terminal Phalanx	Complete	N.A.		N.A.			6	Adult	HP = 39,25, GB = 60,34, BF = 43,9, = 55,20	
18586	Quagga	Molar Permanent	Complete	Right	Upper	N.A.			4	CA 5YRS	23,31	14,08
18596	Quagga	Incisor Permanent	Complete	Left	Lower	N.A.			3	Old Adult	16,63	10,22
18612	Equidae	Incisor Permanent	Fragment	Left	Lower	N.A.			5	CA 5YRS	16,74	13,18
18614	Equidae	Molar Permanent	Fragment	Right	Upper	N.A.			4			
18630	Capensis	Premolar Permanent	Complete	Left	Lower	N.A.			6		30,6	18,68
18652	Equidae	Vertebrae	Neural arch fragment	N.A.		N.A.			4			
18657	Equidae	Molar Permanent	Fragment	Left	Lower	N.A.			4			
18679	Capensis	Premolar Permanent	Complete	Right	Upper	N.A.			7	CA 5YRS	40,33	30,04
18684	Capensis	Incisor Deciduous	Fragment	Right	Lower	N.A.			3	Juvenile	21,78	8
18692	Capensis	Molar Permanent	Complete	Left	Upper	N.A.			7	CA 10YRS	31,4	25,04
327-B124	Capensis	Molar Permanent	Fragment	Right	Upper	N.A.			6		31,68	27,99
391-B133	Capensis	Molar Permanent	Complete	Right	Upper	N.A.			8		30,67	25,92
4769 B	Equidae	Molar	Fragment	Right	Lower	N.A.			7			
540-B16	Capensis	Incisor Permanent	Fragment	Right	Upper	N.A.			5			

548-B1470	Capensis	Molar	Fragment	Right	Upper	N.A.			6			
8595 A, B, C	Equidae	Molar	Fragment	Right	Lower	N.A.			4			
D1- 058-B13	Equidae	Molar	Fragment	Right	Upper	N.A.			4			
D1-034-B10	Quagga	Premolar Permanent	Fragment	Right	Lower	N.A.			3		27,23	11,57
D1-035-B10	Capensis	Premolar Permanent	Fragment	Right	Lower	N.A.			3			
D1-104-B24	Capensis	Molar Permanent	Fragment	Left	Lower	N.A.		Burnt white, grey, or blue/grey.	5	Adult		
D1-164-B50	Capensis	Premolar Permanent	Complete	Left	Lower	N.A.			5	Adult	33,1	15,5
D1-220	Capensis	Molar Permanent	Fragment	Right	Upper	N.A.			6	Adult		
D1-223	Capensis	Incisor Permanent	Fragment	Left	Upper	N.A.			4	10 to 11	21,02	13,34
D1-231	Capensis	Incisor Permanent	Fragment	Right	Upper	N.A.			2	10	19,02	13,63
L1-115-B1	Capensis	Molar Permanent	Fragment	Left	Lower	N.A.			6		27,44	18,73

Appendix B: Database of GVID Equidae fossil material personally examined & not catalogued.

Assigned Number	Section / Layer	East	North	Height	Species	Element	Part	Side	Upper/Lower	Fusion	Break	Length	Age Class	Length (mm)	Breadth (mm)
GV Indet. 80		17,683	2,826	-6,222	Capensis	Incisor	Fragment	Right	Upper			3	8-9 YRS		
GV Indet. 22		4,6	-0,953	-6,443	Capensis	Incisor Deciduous	Fragment	Left	Upper			4	>3 YRS	18,05	8,3
GV Indet. 27		18,417	2,525	-5,669	Capensis	Incisor Deciduous	Fragment	Left	Upper			3	1 YRS	21,91	10,22
GV Indet. 30		17,965	2,542	-6,514	Capensis	Incisor Permanent	Fragment	Left	Upper		Eroded	4		16,52	16,88
GV Indet. 28		16,831	3,91	-5,961	Capensis	Incisor Permanent	Fragment	Right	Upper		Eroded	3	>15 YRS	13,5	14,52
GV Indet. 29	Station 4	16,677	2,757	-6,145	Quagga	Incisor Permanent	Fragment	Left	Lower			3	>15 YRS	11,7	7,16
GV Indet. 24		18,397	2,554	-6,526	Quagga	Incisor Permanent	Fragment	Right	Lower			2	Old Adult	11,52	6,71
GV Indet. 21		17,602	2,924	-5,65	Equidae	Incisor Permanent	Fragment	Left	Upper			6			
GV Indet. 26	IB	17,148	3,004	-6,45	Capensis	Incisor Permanent	Fragment	Left	Upper			6	9 YRS	16,68	11,51
GV Indet. 19		19,55	2,195	-6,782	Capensis	Incisor Permanent	Complete	Right	Upper			7	>6 YRS	21,87	12,88
GV Indet. 20		4,578	-1,015	-6,429	Capensis	Incisor Permanent	Complete	Right	Upper			6	>6 YRS	23,37	12,27
GV Indet. 25	IB-L1	19,283	0,646	-7,266	Capensis	Incisor Permanent	Fragment	Right	Upper			6	6YRS	21,31	11,66
GV Indet. 31		19,026	2,496	-6,371	Capensis	Incisor Permanent	Fragment	Right	Upper			6		22,62	13,94
GV Indet. 23		18,941	2,08	-6,922	Equidae	Incisor Permanent	Fragment	Unk.	Upper			2			
GV Indet. 15		15,551	2,734	-6,017	Capensis	Metacarpus	Distal end complete, <50% of shaft	Right		Fused, no gap between epiphysis & diaphysis.	Transverse & irregular fractures	13			
GV Indet. 6		19,85	2,232	-6,772	Quagga	Metacarpus	Distal end incomplete,	Right		Fused, no gap between	Irregular fractures	8			

							<50% of shaft			epiphysis & diaphysis.					
GV Indet. 10		17	2,845	-6,237	Capensis	Metacarpus	Proximal end complete, >50% of shaft	Left		Fused, no gap between epiphysis & diaphysis.	Transverse fracture	14			
GV Indet. 74		20,19	2,689	-6,378	Equidae	Molar Permanent	Fragment	Right	Upper			5			
GV Indet. 13	SB	17,075	2,862	-6,286	Quagga	Metatarsus	Distal end complete, plus >50% of shaft	Left		Fused, no gap between epiphysis & diaphysis.	Transverse fracture	12			
GV Indet. 11	SB	17,729	2,366	-6,408	Capensis	Metatarsus	Diaphysis (Shaft)	Unk.		Fused, no gap between epiphysis & diaphysis.	Transverse fracture	9			
GV Indet. 2	S4-L7	19,352	0,65	-7,526	Quagga	Metatarsus	Distal end complete, plus <50% of shaft	Left		Fused, no gap between epiphysis & diaphysis.	Transverse fracture & eroded	9			
GV Indet. 17		17,729	2,955	-5,663	Capensis	Other tarsals	Complete	Right		Fused, no gap between epiphysis & diaphysis.		5			
GV Indet. 67		18,789	2,528	-6,578	Equidae	Unk.	Fragment	N.A.	Upper			3			
GV Indet. 39	SB-L5-6	19,628	1,999	-7,329	Capensis	Premolar Permanent	Complete	Left	Lower			6	CA 9YRS	34,89	26,27
GV Indet. 59		4,564	-2,642	-6,34	Capensis	Premolar Permanent	Complete	Left	Lower			9	Long Root	31,26	21,42
GV Indet. 34	F2	18,026	2,543	-6,489	Capensis	Premolar Permanent	Fragment	Left	Lower			5	CA 5YRS	27,26	15,47
GV Indet. 60		17,086	2,841	-6,29	Capensis	Premolar Permanent	Fragment	Left	Lower			5		27,24	18,57
GV Indet. 64		16,871	2,78	-6,221	Capensis	Premolar Permanent	Fragment	Left	Lower			7			

GV Indet. 72		20,34	3,061	-4,018	Quagga	Premolar Permanent	Fragment	Left	Lower			2	Old Adult		
GV Indet. 40		17,161	2,761	-6,426	Capensis	Premolar Permanent	Fragment	Right	Lower			6	CA 5YRS		
GV Indet. 66		18,199	2,777	-6,18	Capensis	Premolar Permanent	Fragment	Right	Lower			4	CA 12 YRS		
GV Indet. 68		19,324	2,264	-6,756	Quagga	Premolar Permanent	Fragment	Right	Lower			3			
GV Indet. 51		17,022	2,797	-6,247	Capensis	Premolar Permanent	Complete	Left	Upper			8	CA 9YRS	29,4	30,18
GV Indet. 63		17,904	2,656	-6,468	Quagga	Premolar Permanent	Complete	Left	Upper			6	CA 7YRS	27,02	27,35
GV Indet. 35	IB	17,164	3,109	-6,532	Quagga	Premolar Permanent	Complete	Right	Upper			4	CA 5YRS	25,16	25,53
GV Indet. 36	IB-LD	17,102	3,034	-6,34	Capensis	Premolar Permanent	Complete	Right	Upper			5	CA 7YRS	35,46	26,17
GV Indet. 38	SA-L4-5	17,024	2,588	-6,284	Quagga	Premolar Permanent	Complete	Right	Upper			9	CA 9YRS	27,61	27,9
GV Indet. 44		18,245	2,504	-6,503	Capensis	Premolar Permanent	Complete	Right	Upper			4	Old Adult		
GV Indet. 54		16,997	2,892	-6,21	Capensis	Premolar Permanent	Complete	Right	Upper			10		31,47	26,19
GV Indet. 56	1B	18,645	2,355	-6,938	Capensis	Premolar Permanent	Complete	Right	Upper			6	CA 10 YRS	29,51	33,9
GV Indet. 53		18,535	2,526	-6,482	Capensis	Premolar Permanent	Fragment	Right	Upper			6			
GV Indet. 62		18,373	2,632	-6,232	Capensis	Premolar Permanent	Fragment	Right	Upper			6	CA 7YRS	30,71	29,34
GV Indet. 82		18,469	2,567	-6,423	Capensis	Premolar Permanent	Fragment	Right	Upper			7		33,21	29,69
GV Indet. 83		19,219	1,687	-6,107	Quagga	Premolar Permanent	Fragment	Right	Upper			4	Old Adult	24,53	29,1
GV Indet. 88		18,934	2,806	-6,186	Quagga	Premolar Permanent	Fragment	Right	Upper			5		28,1	24,36
GV Indet. 90		19,623	2,515	-6,776	Capensis	Premolar Permanent	Fragment	Right	Upper			8	CA 7YRS		
GV Indet. 92		16,383	2,655	-6,182	Equidae	Premolar Permanent	Fragment	Right	Upper			4		31,79	

GV Indet. 81		18,258	2,377	-6,943	Quagga	Molar	Fragment	N.A.	Unk.			1			
GV Indet. 77		18,029	2,515	-6,446	Equidae	Premolar Permanent	Fragment	N.A.	Unk.			3			
GV Indet. 78		19,911	2,502	-6,727	Equidae	Premolar Permanent	Fragment	N.A.	Unk.			1			
GV Indet. 79		18,799	2,6108	-6,471	Quagga	Premolar Permanent	Fragment	N.A.	Lower			3			
GV Indet. 89		16,99	2,839	-6,183	Capensis	Premolar Permanent	Fragment	N.A.	Lower			5			
GV Indet. 61		16,919	3,337	-6,143	Capensis	Premolar Permanent	Fragment	Left	Lower			4		30,92	20,2
GV Indet. 93		17,489	2,142	-6,173	Equidae	Premolar Permanent	Fragment	Left	Lower			3			
GV Indet. 75		19,539	2,204	-6,698	Equidae	Premolar Permanent	Fragment	N.A.	Upper			3			
GV Indet. 76		17,933	2,631	-4,821	Equidae	Premolar Permanent	Fragment	N.A.	Upper			3			
GV Indet. 84		17,048	2,717	-6,724	Equidae	Premolar Permanent	Fragment	N.A.	Upper			4			
GV Indet. 65		18,223	2,446	-6,634	Equidae	Premolar Permanent	Fragment	Left	Upper			7		34	28,48
GV Indet. 71	GV3	6,076	-3,255	-5,758	Equidae	Premolar Permanent	Fragment	Right	Upper			4			
GV Indet. 94		18,569	2,523	-6,48	Equidae	Premolar Permanent	Fragment	Right	Upper			4			
GV Indet. 57		16,962	2,786	-6,234	Capensis	Molar Deciduous	Complete	Right	Upper			4		29,36	28,07
GV Indet. 42		17,521	2,918	-6,21	Capensis	Molar Permanent	Fragment	Left	Lower			4	CA 12 YRS		
GV Indet. 47		20,663	3,318	-3,388	Capensis	Molar Permanent	Fragment	Left	Lower				Old Adult	26,45	20,85
GV Indet. 69		16,981	2,712	-6,248	Quagga	Molar Permanent	Fragment	Left	Lower			3			
GV Indet. 33		17,208	2,912	-6,358	Capensis	Molar Permanent	Complete	Right	Lower			10	CA 10 YRS	31,38	19,16
GV Indet. 41		19,633	2,192	-6,738	Capensis	Molar Permanent	Fragment	Right	Lower			6			

GV Indet. 70		16,979	2,843	-6,2	Quagga	Molar Permanent	Fragment	Right	Lower			3			
GV Indet. 85		18,886	2,534	-6,592	Quagga	Molar Permanent	Fragment	Right	Lower			5			
GV Indet. 43	GV3	18,731	2,45	-6,828	Quagga	Molar Permanent	Complete	Left	Upper			6	CA 5YRS	25,77	27,51
GV Indet. 49		18,501	2,487	-6,601	Capensis	Molar Permanent	Complete	Left	Upper			5	CA 9YRS	33,16	33,68
GV Indet. 50		19,301	0,503	-6,677	Capensis	Molar Permanent	Complete	Left	Upper			7	CA 5YRS	30,48	31,27
GV Indet. 55		17,059	2,775	-6,243	Capensis	Molar Permanent	Complete	Left	Upper			5		40,63	27,05
GV Indet. 37		18,775	2,918	-6,204	Equidae	Molar Permanent	Fragment	Left	Upper			7	CA 9YRS	29,69	28,15
GV Indet. 58	IB-L1	17,029	3,06	-6,298	Capensis	Molar Permanent	Fragment	Left	Upper			4			
GV Indet. 45		16,967	2,821	-6,165	Quagga	Molar Permanent	Complete	Right	Upper			3	Old Adult	27,68	31,19
GV Indet. 48		17,053	2,826	-6,165	Capensis	Molar Permanent	Complete	Right	Upper			5	CA 7YRS	27,19	28,92
GV Indet. 32		17,168	2,899	-6,268	Capensis	Molar Permanent	Fragment	Right	Upper			7	Sub Adult	32,56	27,52
GV Indet. 46		17,334	3,004	-6,211	Capensis	Molar Permanent	Fragment	Right	Upper						
GV Indet. 52		17,706	2,971	-6,101	Capensis	Molar Permanent	Fragment	Right	Upper			7	CA 5YRS		
GV Indet. 73		19,031	2,432	-6,441	Quagga	Molar Permanent	Fragment	Right	Upper			3	Short Root		
GV Indet. 86		17,739	2,774	-6,226	Capensis	Molar Permanent	Fragment	Right	Upper			5			
GV Indet. 87	**	17,98	2,585	-6,457	Capensis	Molar Permanent	Fragment	Right	Upper			8		37,42	25,32
GV Indet. 91		18,482	2,527	-6,522	Capensis	Molar Permanent	Fragment	Right	Upper			4	CA 7YRS		

Appendix C: All Cranial dental measurements of Equidae material.

Specimen Number	Species	Element	Upper/Lower	Length (mm)	Breadth (mm)
COA 3066	<i>Equus capensis</i>	I2	U	22,12	13,54
COB 181	<i>Equus capensis</i>	M	U	35,1	26,8
GV 18172	<i>Equus capensis</i>	M	L	34,43	16,88
GV 18182	<i>Equus capensis</i>	M	U	34,32	29,80
GV 18193	<i>Equus quagga</i>	M3	L	27,28	11,46
GV 18200	Equidae Indet.	I1	L	14,78	14,22
GV 18206	<i>Equus capensis</i>	I	U	18,91	10,46
GV 18211	<i>Equus capensis</i>	I1	L	17,86	11,29
GV 18586	<i>Equus quagga</i>	M2	U	23,31	14,08
GV 18596	<i>Equus quagga</i>	I3	L	16,63	10,22
GV 18612	Equidae Indet.	I2	L	16,74	13,18
GV 18629	<i>Equus quagga</i>	I3	L	13,33	7,12
GV 18630	<i>Equus capensis</i>	PM4	L	30,60	18,68
GV 18651	<i>Equus quagga</i>	I	U	16,06	8,94
GV 18679	<i>Equus capensis</i>	M	U	40,33	30,04
GV 18684	<i>Equus capensis</i>	I3	L	21,78	8,00
GV 327-B124	<i>Equus capensis</i>	M	U	31,68	27,99

GV 3891 A	<i>Equus capensis</i>	PM2	U	39,25	25,23
GV 3891 B	<i>Equus capensis</i>	PM3	U	39,28	27,35
GV 391-B133	<i>Equus capensis</i>	M1	U	30,67	25,92
GV 402	Equidae Indet.	M	U	29,38	23,12
GV 403	<i>Equus capensis</i>	I	U	20,21	11,03
GV 4082	Equidae Indet.	I2	U	19,99	13,33
GV 4083	<i>Equus capensis</i>	M3	U	24,78	23,27
GV 4642	<i>Equus capensis</i>	I1	L	11,68	15,98
GV 4789	<i>Equus capensis</i>	M3	L	36,41	13,91
GV 5035	<i>Equus capensis</i>	I1	L	12,20	13,00
GV 5053	<i>Equus capensis</i>	PM2	L	31,26	14,42
GV 5104	<i>Equus capensis</i>	I2	U	17,56	12,88
GV 5350	<i>Equus capensis</i>	PM	L	29,86	18,84
GV 5406	<i>Equus capensis</i>	PM3	L	33,87	22,15
GV 5871	<i>Equus capensis</i>	I	U	20,83	10,89
GV 6872	<i>Equus quagga</i>	I	L	11,48	12,88
GV 7242	<i>Equus capensis</i>	I	U	15,58	8,24
GV 7248	<i>Equus capensis</i>	I	U	20,53	10,11
GV 7563	<i>Equus capensis</i>	YD	L	19,72	7,82

GV 7643	<i>Equus capensis</i>	I3	U	17,92	9,23
GV 7961	<i>Equus capensis</i>	M	L	37,20	18,45
GV 8096	<i>Equus quagga</i>	M3	L	26,32	14,84
GV 8474	Equidae Indet.	I	U	11,74	15,00
GV 8922	<i>Equus capensis</i>	I2	U	18,54	13,08
GV 8930	<i>Equus capensis</i>	I	U	13,48	13,98
GV 8958	<i>Equus capensis</i>	I2	L	17,80	13,88
GV D1-034-B10	<i>Equus quagga</i>	PM3	L	27,23	11,57
GV D1-164-B50	<i>Equus capensis</i>	PM	L	33,10	15,50
GV D1-186-B46	<i>Equus quagga</i>	PM	L	32,42	13,2
GV D1-223	<i>Equus capensis</i>	I2	U	21,02	13,34
GV D1-231	<i>Equus capensis</i>	I2	U	19,02	13,63
GV Indet. 20	<i>Equus capensis</i>	I2	U	23,37	12,27
GV Indet 38	<i>Equus capensis</i>	PM2	U	27,61	27,90
GV Indet 47	<i>Equus quagga</i>	PM4	U	26,45	20,85
GV Indet 63	<i>Equus capensis</i>	M	L	27,02	27,35
GV Indet 22	<i>Equus capensis</i>	I2	U	18,05	8,30
GV Indet 24	<i>Equus capensis</i>	I2	U	11,52	6,71
GV Indet 25	Equidae Indet.	I	U	21,31	11,66

GV Indet 26	<i>Equus quagga</i>	I2	L	16,68	11,51
GV Indet 27	<i>Equus capensis</i>	I3	U	21,91	10,22
GV Indet 28	<i>Equus capensis</i>	I1	U	13,50	14,52
GV Indet 29	<i>Equus capensis</i>	I3	U	11,70	7,16
GV Indet 30	<i>Equus capensis</i>	I1	U	16,52	16,88
GV Indet 31	<i>Equus quagga</i>	I	L	22,62	13,94
GV Indet 32	<i>Equus capensis</i>	I1	U	32,56	27,52
GV Indet 33	<i>Equus capensis</i>	I3	U	31,38	19,16
GV Indet 34	<i>Equus capensis</i>	M	U	27,26	15,47
GV Indet 35	<i>Equus capensis</i>	M1	L	25,16	25,53
GV Indet 36	<i>Equus quagga</i>	PM4	L	35,46	26,17
GV Indet 37	<i>Equus quagga</i>	PM3	U	29,69	28,15
GV Indet 39	Equidae Indet.	M1	U	34,89	26,27
GV Indet 43	<i>Equus capensis</i>	M	L	25,77	27,51
GV Indet 45	<i>Equus quagga</i>	PM4	U	27,68	31,19
GV Indet 48	<i>Equus capensis</i>	PM2	U	27,19	28,92
GV Indet 49	<i>Equus capensis</i>	M	L	33,16	33,68
GV Indet 50	<i>Equus capensis</i>	PM4	U	30,48	31,27
GV Indet 51	<i>Equus capensis</i>	PM3	U	29,40	30,18

GV Indet 54	<i>Equus capensis</i>	PM4	U	31,47	26,19
GV Indet 55	<i>Equus capensis</i>	M3	U	40,63	27,05
GV Indet 56	<i>Equus capensis</i>	M1	U	29,51	33,90
GV Indet 57	<i>Equus capensis</i>	PM2	U	29,36	28,07
GV Indet 59	<i>Equus capensis</i>	M	U	31,26	21,42
GV Indet 60	<i>Equus capensis</i>	PM2	U	27,24	18,57
GV Indet 61	<i>Equus capensis</i>	M2	L	30,92	20,20
GV Indet 62	<i>Equus capensis</i>	M1	L	30,71	29,34
GV Indet 65	<i>Equus quagga</i>	M1	U	34,00	28,48
GV Indet 82	<i>Equus capensis</i>	I3	U	33,21	29,69
GV Indet 83	<i>Equus quagga</i>	M1	U	24,53	29,10
GV Indet 87	<i>Equus quagga</i>	M	L	37,42	25,32
GV Indet 88	<i>Equus capensis</i>	PM3	U	28,10	24,36
GV Indet 92	<i>Equus capensis</i>	M3	U	31,79	
GV L1-115-B1	<i>Equus capensis</i>	m1/2	L	27,44	18,73
GV18692	<i>Equus capensis</i>	M3	U	31,40	25,04
KA 107	<i>Equus capensis</i>	I2	L	18,55	
KA 1086 A	Equidae Indet.	M1	L	31,2	18,98
KA 1086 B	Equidae Indet.	M2	L		17,09

KA 1086 C	Equidae Indet.	PM	L	31,24	19,59
KA 1086 D	Equidae Indet.	M2	L		16,78
KA 1086 E	Equidae Indet.	M3	L	29,86	15,6
KA 109	<i>Equus capensis</i>	I2	U	21,19	12,7
KA 115	Equidae Indet.	M3	U	25,01	21,21
KA 117	<i>Equus quagga</i>	M1	L	23,22	19,82
KA 1179 B	<i>Equus capensis</i>	PM3	U	26,18	29,97
KA 1648	<i>Equus capensis</i>	M1	L	29,8	19,52
KA 1896 A	<i>Equus capensis</i>	p1	U	40,49	22,58
KA 1896 B	<i>Equus capensis</i>	I1	U	33,77	24,92
KA 1897 A	Equidae Indet.	PM4	U	33,88	25,74
KA 1897 B	Equidae Indet.	M1	U	39,49	23,38
KA 1901 B	Equidae Indet.	M1	L	28,91	19,76
KA 1902 A	Equidae Indet.	M1	L	28,58	17,92
KA 1902 B	Equidae Indet.	PM2	L	36,16	19,84
KA 1903	<i>Equus capensis</i>	PM4	L	30,24	20,98
KA 1904 A	Equidae Indet.	PM4	L	31,44	21,91
KA 1905 A	Equidae Indet.	PM2	L	36,75	17,15
KA 1906	<i>Equus quagga</i>	M3	U	24,23	17,7

KA 1906 A	<i>Equus quagga</i>	PM2	U	37,99	16,88
KA 1906 B	<i>Equus quagga</i>	PM4	L	33,29	17,71
KA 1906 C	<i>Equus quagga</i>	M1	L	32,04	18,84
KA 1906 D	<i>Equus quagga</i>	M2	L	28,41	17,08
KA 1909	Equidae Indet.	I3	L	18,07	8,04
KA 1910	<i>Equus capensis</i>	PM2	L	33,64	16,71
KA 1911 A	Equidae Indet.	PM4	L	30,93	20,52
KA 1985 A	<i>Equus capensis</i>	PM3	U	33,31	31,02
KA 1985 B	<i>Equus capensis</i>	PM4	U	28,71	28,63
KA 1985 C	<i>Equus capensis</i>	M1	U	28,92	27,91
KA 1985 D	<i>Equus capensis</i>	M2	U	29,87	27,6
KA 1985 E	<i>Equus capensis</i>	M3	U	28,82	24,82
KA 1985 F	<i>Equus capensis</i>	PM3	U	33,14	31,12
KA 1985 G	<i>Equus capensis</i>	PM4	U	28,48	28,81
KA 1985 H	<i>Equus capensis</i>	M1	U	30,3	29,17
KA 1985 I	<i>Equus capensis</i>	M2	U	29,55	27,27
KA 1985 J	<i>Equus capensis</i>	M3	U	25,72	23,94
KA 2151 B	<i>Equus capensis</i>	PM3	L	30,14	15,06
KA 2515 C	<i>Equus capensis</i>	PM3	L	33,03	14,98

KA 534 B	<i>Equus capensis</i>	M2	L	29,92	20,04
KA 534 C	<i>Equus capensis</i>	PM4	L	32,28	22,48
KA 575	<i>Equus capensis</i>	i3	L	18,89	9,99
KA 624 A	Equidae Indet.	PM4	U	30,31	32,61
KA 624 B	Equidae Indet.	M3	U	28,31	25,72
KA 624 C	Equidae Indet.	PM3	U	31,54	31,85
KA 624 D	Equidae Indet.	PM3	U	31,02	30,68
KA 655 B	<i>Equus capensis</i>	PM3	L	32,31	16,83
KA 655 C	<i>Equus capensis</i>	PM4	L	33,31	16,77
KA 655 D	<i>Equus capensis</i>	M1	L	33,1	13,8
KA 682 A	<i>Equus capensis</i>	M1	U	38,2	30,44
KA 682 B	<i>Equus capensis</i>	M2	U	31,22	28,79
KA 682 C	<i>Equus capensis</i>	M3	U	30,08	28,55
KA 817 A	<i>Equus capensis</i>	I2	L	22,6	11,31
KA 817 B	<i>Equus capensis</i>	I2	U	17,72	12,3
KA 817 C	<i>Equus capensis</i>	I1	L	19,1	11,3
KA 817 D	<i>Equus capensis</i>	I1	L	17,77	9,25
KA 817 E	<i>Equus capensis</i>	I1	U	14,48	14,82
KA 817 F	<i>Equus capensis</i>	I2	U	16,69	13,29

KA 817 G	<i>Equus capensis</i>	I1	U	12,91	13,95
KA 860 A	<i>Equus capensis</i>	I3	L	16,81	10,86
KA 869	<i>Equus capensis</i>	PM4	U	32,81	31,01
KA 892 A	Equidae Indet.	M2	U	32,5	26,55
KA 899 D	Equidae Indet.	M1	U	29,68	23,86
KA 910 A	<i>Equus capensis</i>	M1	U	30,81	29,03
KA 910 A	<i>Equus capensis</i>	PM4	U	33,16	30,41
KA 910 B	<i>Equus capensis</i>	M2	U	32,5	27,81
KA 927 A	<i>Equus capensis</i>	M1	L	26,2	19,5
KA 927 B	<i>Equus capensis</i>	M2	L	26,37	17,8
KA 939 B	Equidae Indet.	M1	U	26,88	29,66
KA 939 C	Equidae Indet.	M3	U	28,82	24,77
KA 939 D	Equidae Indet.	PM4	U	33,56	31,73
KA 939 E	Equidae Indet.	PM3	U	31,01	28,31
KA 939 F	Equidae Indet.	M3	U	30,9	27,17
KA 939 G	Equidae Indet.	M1	U	33,68	28,3
KA 972 A	<i>Equus capensis</i>	I1	L	20,4	8,95
KA 972 B	<i>Equus capensis</i>	I1	L	21,6	8,7
KA 972 D	<i>Equus capensis</i>	I3	L	21,31	9,89

KA 972 E	<i>Equus capensis</i>	I3	L	22,23	10,73
SK 10735	<i>Equus quagga</i>	i2	L	18,08	7,7
SK 12445	<i>Equus quagga</i>	M3	L	21,87	14,53
SK 14222	<i>Equus quagga</i>	M3	U	22,07	18,85
SK 1626 B	<i>Equus capensis</i>	PM2	L	33,31	18,35
SK 2243 B	<i>Equus quagga</i>	M1	L	22,84	15,54
SK 2243 B	<i>Equus quagga</i>	PM4	L	24	16,07
SK 24624	<i>Equus capensis</i>	M1	U	25,74	28,08
SK 2584	<i>Equus capensis</i>	M1	L	33,22	17,89
SK 2736	<i>Equus quagga</i>	I3	L	16,54	7,5
SK 3166	<i>Equus quagga</i>	PM4	U	23,36	24
SK 3989 A	<i>Equus capensis</i>	PM2	L	31,47	17,3
SK 3989 B	<i>Equus capensis</i>	PM3	L	27,86	18,37
SK 3989 C	<i>Equus capensis</i>	PM3	L	25,25	18,09
SK 3989 D	<i>Equus capensis</i>	M1	L	23,29	18,15
SK 3989 E	<i>Equus capensis</i>	PM2	L	31,34	17,31
SK 3993	<i>Equus capensis</i>	PM2	L	30,65	19,3
SK 3994	<i>Equus quagga</i>	PM2	L	31,57	12,8
SK 3996	<i>Equus capensis</i>	I2	U	17,86	16,43

SK 3997 A	<i>Equus quagga</i>	PM2	U	32,83	24,12
SK 3997 B	<i>Equus quagga</i>	PM4	U	25,69	26,4
SK 3997 C	<i>Equus quagga</i>	PM4	U	22,81	25,41
SK 3997 E	<i>Equus quagga</i>	PM4	U	21,96	25,8
SK 3997 E	<i>Equus quagga</i>	PM3	U	25,46	26,57
SK 3997 M	<i>Equus quagga</i>	PM2	L	28,1	15,46
SK 3997 N	<i>Equus quagga</i>	PM3	L	25,7	17,06
SK 3997 O	<i>Equus quagga</i>	PM4	L	24,56	16,95
SK 3997 P	<i>Equus quagga</i>	M1	L	22,61	18,8
SK 3997 Q	<i>Equus quagga</i>	M2	L	24,22	16,35
SK 3997 R	<i>Equus quagga</i>	M3	L	28,1	14,25
SK 3997 SERIES	<i>Equus quagga</i>	M1	L	22,49	18,89
SK 3997 SERIES	<i>Equus quagga</i>	M3	L	23,31	16,31
SK 3997 SERIES	<i>Equus quagga</i>	PM4	L	24,98	17,82
SK 3997 SERIES	<i>Equus quagga</i>	PM3	L	25,33	18,3
SK 3997 SERIES	<i>Equus quagga</i>	PM2	L	28,3	16,57
SK 3997 U	Equidae Indet.	I2	U	15,2	12,82
SK 3997 V	Equidae Indet.	I3	U	16,84	8,96
SK 3997 W	Equidae Indet.	I2	L	13,92	10,2

SK 3997 X	Equidae Indet.	I1	L	11,82	10,09
SK 3997 Y	Equidae Indet.	I1	U	12,02	10,22
SK 3997 Z	Equidae Indet.	I2	U	14,4	10,2
SK 3998 A	<i>Equus quagga</i>	PM4	U	22,72	15,11
SK 3998 B	<i>Equus quagga</i>	M1	U	24,49	16,59
SK 3998 E	<i>Equus quagga</i>	PM4	U	23,17	14,44
SK 5119 A	<i>Equus quagga</i>	M1	U	22,81	25,04
SK 5119 B	<i>Equus quagga</i>	M2	U	22,12	26,27
SK 5167	<i>Equus quagga</i>	M1	U	25,01	23,73
SK 5275	<i>Equus quagga</i>	M2	L	24,62	13,1
SK 5375	<i>Equus capensis</i>	I3	U	20,64	11,74
SK 8014	<i>Equus quagga</i>	i2	L	18,03	7,68
TM 10061	<i>Equus quagga</i>	M2	L	22,63	15,19
TM 10061	<i>Equus quagga</i>	M1	U	22,79	23,99
TM 10061	<i>Equus quagga</i>	M1	U	22,95	23,87
TM 10061	<i>Equus quagga</i>	M2	U	23,01	24,35
TM 10061	<i>Equus quagga</i>	M1	L	23,2	15,31
TM 10061	<i>Equus quagga</i>	M1	L	23,32	15,49
TM 10061	<i>Equus quagga</i>	M2	L	23,47	14,91

TM 10061	<i>Equus quagga</i>	M2	U	24,09	24,41
TM 10061	<i>Equus quagga</i>	PM4	L	24,64	16,62
TM 10061	<i>Equus quagga</i>	PM4	L	25,1	16,87
TM 10061	<i>Equus quagga</i>	PM3	L	25,34	16,71
TM 10061	<i>Equus quagga</i>	M3	U	25,86	21,02
TM 10061	<i>Equus quagga</i>	PM3	L	26	17,73
TM 10061	<i>Equus quagga</i>	M3	U	26,29	21,15
TM 10061	<i>Equus quagga</i>	PM4	U	26,48	25,89
TM 10061	<i>Equus quagga</i>	PM4	U	26,51	25,79
TM 10061	<i>Equus quagga</i>	PM3	U	27,53	25,4
TM 10061	<i>Equus quagga</i>	M3	L	27,79	12,98
TM 10061	<i>Equus quagga</i>	M3	L	28,05	13,12
TM 10061	<i>Equus quagga</i>	PM3	U	28,07	25,93
TM 10061	<i>Equus quagga</i>	PM2	L	29,8	15,61
TM 10061	<i>Equus quagga</i>	PM2	U	33,34	23,83
TM 10061	<i>Equus quagga</i>	PM2	U	33,61	22,78
TM 10063	<i>Equus quagga</i>	M1	U	20,55	24,75
TM 10063	<i>Equus quagga</i>	M1	U	20,88	24,18
TM 10063	<i>Equus quagga</i>	M2	U	21,07	23,96

TM 10063	<i>Equus quagga</i>	M2	U	21,58	24,01
TM 10063	<i>Equus quagga</i>	M3	U	23	21,91
TM 10063	<i>Equus quagga</i>	M3	U	23,34	22,3
TM 10063	<i>Equus quagga</i>	PM4	U	23,76	25,31
TM 10063	<i>Equus quagga</i>	PM4	U	23,82	25,34
TM 10063	<i>Equus quagga</i>	PM3	U	24,53	25,9
TM 10063	<i>Equus quagga</i>	PM3	U	24,71	25,95
TM 10063	<i>Equus quagga</i>	PM2	L	28,1	15,29
TM 10063	<i>Equus quagga</i>	M3	L	28,11	13,64
TM 10063	<i>Equus quagga</i>	PM2	L	28,2	15,36
TM 10063	<i>Equus quagga</i>	M3	L	28,33	13,71
TM 10063	<i>Equus quagga</i>	PM2	U	33,56	22,55
TM 10063	<i>Equus quagga</i>	PM2	U	34,26	22,9
TM 10071	<i>Equus quagga</i>	I1	L	13,99	8,32
TM 10071	<i>Equus quagga</i>	I1	L	14,12	8,54
TM 10071	<i>Equus quagga</i>	I1	U	14,98	9,88
TM 10071	<i>Equus quagga</i>	I1	U	15,05	9,91
TM 10071	<i>Equus quagga</i>	I3	L	15,29	6,51
TM 10071	<i>Equus quagga</i>	I3	L	15,32	5,92

TM 10071	<i>Equus quagga</i>	I2	L	15,39	7,2
TM 10071	<i>Equus quagga</i>	I2	L	15,61	7
TM 10071	<i>Equus quagga</i>	I2	U	17,37	8,963
TM 10071	<i>Equus quagga</i>	I2	U	17,65	9,01
TM 10071	<i>Equus quagga</i>	I3	U	18,69	8,14
TM 10071	<i>Equus quagga</i>	I3	U	18,99	7,9
TM 10071	<i>Equus quagga</i>	M2	L	21,44	15,72
TM 10071	<i>Equus quagga</i>	M2	U	21,46	24,46
TM 10071	<i>Equus quagga</i>	M2	L	21,61	15,59
TM 10071	<i>Equus quagga</i>	M3	U	22,71	20,9
TM 10071	<i>Equus quagga</i>	M1	L	23,6	16,51
TM 10071	<i>Equus quagga</i>	M1	L	23,63	16,67
TM 10071	<i>Equus quagga</i>	PM4	U	23,86	26,69
TM 10071	<i>Equus quagga</i>	PM3	L	24,36	17,27
TM 10071	<i>Equus quagga</i>	PM3	L	24,82	17,44
TM 10071	<i>Equus quagga</i>	PM4	L	25,15	17,81
TM 10071	<i>Equus quagga</i>	PM4	L	25,19	17,59
TM 10071	<i>Equus quagga</i>	PM3	U	26,15	25,62
TM 10071	<i>Equus quagga</i>	M3	L	26,61	13,3

TM 10071	<i>Equus quagga</i>	PM2	L	26,73	16,31
TM 10071	<i>Equus quagga</i>	PM3	U	26,73	25,73
TM 10071	<i>Equus quagga</i>	M3	L	26,75	12,92
TM 10071	<i>Equus quagga</i>	PM2	U	32,33	24,48
TM 10071	<i>Equus quagga</i>	PM2	U	33,31	24,86
TM 10074	<i>Equus quagga</i>	I1	L	11,44	8,75
TM 10074	<i>Equus quagga</i>	I1	L	12,09	9,15
TM 10074	<i>Equus quagga</i>	I2	L	13,59	8,51
TM 10074	<i>Equus quagga</i>	I2	L	14,51	8,6
TM 10074	<i>Equus quagga</i>	I3	L	15	8,2
TM 10074	<i>Equus quagga</i>	I3	L	15,27	8,3
TM 10074	<i>Equus quagga</i>	I1	U	15,81	11,26
TM 10074	<i>Equus quagga</i>	I1	U	16,16	11,24
TM 10074	<i>Equus quagga</i>	I2	U	17,1	10,66
TM 10074	<i>Equus quagga</i>	I2	U	17,53	10,63
TM 10074	<i>Equus quagga</i>	I3	U	19,38	10,09
TM 10074	<i>Equus quagga</i>	I3	U	20,08	10,15
TM 10074	<i>Equus quagga</i>	M1	U	23,19	26,44
TM 10074	<i>Equus quagga</i>	M2	U	23,45	26,51

TM 10074	<i>Equus quagga</i>	M2	L	23,52	16,55
TM 10074	<i>Equus quagga</i>	M2	U	23,54	26,27
TM 10074	<i>Equus quagga</i>	M1	U	23,6	26,66
TM 10074	<i>Equus quagga</i>	M1	L	23,9	17,58
TM 10074	<i>Equus quagga</i>	M3	U	24,18	23,14
TM 10074	<i>Equus quagga</i>	M1	L	24,31	17,89
TM 10074	<i>Equus quagga</i>	M3	U	24,52	23,26
TM 10074	<i>Equus quagga</i>	M2	L	25,2	17,34
TM 10074	<i>Equus quagga</i>	PM4	L	25,77	19,99
TM 10074	<i>Equus quagga</i>	PM4	U	26,01	28,27
TM 10074	<i>Equus quagga</i>	PM4	U	26,09	27,89
TM 10074	<i>Equus quagga</i>	PM4	L	26,26	19,82
TM 10074	<i>Equus quagga</i>	PM3	U	26,45	27,31
TM 10074	<i>Equus quagga</i>	PM3	U	26,81	27,37
TM 10074	<i>Equus quagga</i>	M3	L	28,3	15,27
TM 10074	<i>Equus quagga</i>	PM2	L	29,46	17,4
TM 10074	<i>Equus quagga</i>	M3	L	29,73	14,66
TM 10074	<i>Equus quagga</i>	PM2	L	30,66	17,32
TM 10074	<i>Equus quagga</i>	PM2	U	35,62	26,53

TM 10074	<i>Equus quagga</i>	PM2	U	35,8	26,36
TM 10075	<i>Equus quagga</i>	I2	U	18,5	9,57
TM 10075	<i>Equus quagga</i>	I3	U	19,52	9,29
TM 10075	<i>Equus quagga</i>	M3	U	21,55	21,01
TM 10075	<i>Equus quagga</i>	M1	U	22,98	25,47
TM 10075	<i>Equus quagga</i>	M1	U	23,2	25,44
TM 10075	<i>Equus quagga</i>	M3	U	23,28	21,52
TM 10075	<i>Equus quagga</i>	M2	U	24,31	23,95
TM 10075	<i>Equus quagga</i>	PM4	U	26,94	27,04
TM 10075	<i>Equus quagga</i>	PM4	U	27,05	26,97
TM 10075	<i>Equus quagga</i>	PM3	U	27,27	26,1
TM 10075	<i>Equus quagga</i>	PM3	U	27,76	26,42
TM 10075	<i>Equus quagga</i>	PM2	U	33,54	23,67
TM 10076	<i>Equus quagga</i>	I1	U	16,08	9,97
TM 10076	<i>Equus quagga</i>	I2	U	17,78	9,43
TM 10076	<i>Equus quagga</i>	I2	U	17,87	9,4
TM 10076	<i>Equus quagga</i>	I3	U	18,92	8,84
TM 10076	<i>Equus quagga</i>	I3	U	19,07	8,72
TM 10076	<i>Equus quagga</i>	M2	U	23,15	26,16

TM 10076	<i>Equus quagga</i>	M1	U	23,52	26,93
TM 10076	<i>Equus quagga</i>	M2	U	23,62	26,4
TM 10076	<i>Equus quagga</i>	M1	U	23,9	26,89
TM 10076	<i>Equus quagga</i>	M3	U	23,95	23,74
TM 10076	<i>Equus quagga</i>	M3	U	24,27	23,6
TM 10076	<i>Equus quagga</i>	PM4	U	25,94	28,76
TM 10076	<i>Equus quagga</i>	PM4	U	26,25	28,81
TM 10076	<i>Equus quagga</i>	PM3	U	28,61	28,54
TM 10076	<i>Equus quagga</i>	PM3	U	28,79	28,97
TM 10076	<i>Equus quagga</i>	PM2	U	37,53	26,93
TM 10076	<i>Equus quagga</i>	PM2	U	37,7	27,01
TM 10080	<i>Equus quagga</i>	I2	L	12,25	8,37
TM 10080	<i>Equus quagga</i>	I2	L	12,46	8,29
TM 10080	<i>Equus quagga</i>	I3	L	13,51	7,49
TM 10080	<i>Equus quagga</i>	I3	L	13,77	7,01
TM 10080	<i>Equus quagga</i>	M1	U	20,95	23,9
TM 10080	<i>Equus quagga</i>	M1	U	21,01	24,54
TM 10080	<i>Equus quagga</i>	M2	U	22,44	24,17
TM 10080	<i>Equus quagga</i>	M2	U	22,48	24,85

TM 10080	<i>Equus quagga</i>	M2	L	23,62	14,83
TM 10080	<i>Equus quagga</i>	M3	U	23,94	21,61
TM 10080	<i>Equus quagga</i>	PM4	U	24,01	25,12
TM 10080	<i>Equus quagga</i>	M2	L	24,07	15,08
TM 10080	<i>Equus quagga</i>	PM3	L	24,1	16,47
TM 10080	<i>Equus quagga</i>	PM4	U	24,28	24,42
TM 10080	<i>Equus quagga</i>	M3	U	24,33	21,48
TM 10080	<i>Equus quagga</i>	PM3	L	24,76	15,99
TM 10080	<i>Equus quagga</i>	PM3	U	25,46	23,93
TM 10080	<i>Equus quagga</i>	PM3	U	25,82	24,52
TM 10080	<i>Equus quagga</i>	PM2	L	28,14	14,25
TM 10080	<i>Equus quagga</i>	M3	L	28,99	12,94
TM 10080	<i>Equus quagga</i>	PM2	L	29	14,61
TM 10080	<i>Equus quagga</i>	M3	L	29,47	13,59
TM 10080	<i>Equus quagga</i>	PM2	U	34,22	22,42
TM 10080	<i>Equus quagga</i>	PM2	U	34,22	21,56
TM 13197	<i>Equus quagga (Juvenile)</i>	I3	L	14,18	6,94
TM 13197	<i>Equus quagga (Juvenile)</i>	I2	U	15,06	7,75
TM 13197	<i>Equus quagga (Juvenile)</i>	I1	U	15,27	7,9

TM 13197	<i>Equus quagga (Juvenile)</i>	I2	U	15,3	7,6
TM 13197	<i>Equus quagga (Juvenile)</i>	I1	U	15,38	7,74
TM 13197	<i>Equus quagga (Juvenile)</i>	i2	L	15,5	7,5
TM 13197	<i>Equus quagga (Juvenile)</i>	I3	U	15,5	7,85
TM 13197	<i>Equus quagga (Juvenile)</i>	I3	U	15,71	7,76
TM 13197	<i>Equus quagga (Juvenile)</i>	PM3	U	26,62	23,68
TM 13197	<i>Equus quagga (Juvenile)</i>	PM3	U	26,93	24,222
TM 13197	<i>Equus quagga (Juvenile)</i>	M1	U	26,99	24,13
TM 13197	<i>Equus quagga (Juvenile)</i>	M1	U	27,05	23,29
TM 13197	<i>Equus quagga (Juvenile)</i>	M1	L	27,58	15,05
TM 13197	<i>Equus quagga (Juvenile)</i>	M2	U	27,63	21,31
TM 13197	<i>Equus quagga (Juvenile)</i>	M1	L	28,13	15,08
TM 13197	<i>Equus quagga (Juvenile)</i>	M2	L	28,15	14,9
TM 13197	<i>Equus quagga (Juvenile)</i>	M2	L	28,97	14,79
TM 13197	<i>Equus quagga (Juvenile)</i>	PM2	L	32,44	13,88
TM 13197	<i>Equus quagga (Juvenile)</i>	PM2	L	32,94	13,85
TM 13197	<i>Equus quagga (Juvenile)</i>	PM2	U	35,27	21,8
TM 13197	<i>Equus quagga (Juvenile)</i>	PM2	U	35,49	21,56
TM 13204	<i>Equus quagga</i>	I2	L	14,78	5,62

TM 13204	<i>Equus quagga</i>	I2	L	14,87	5,42
TM 13204	<i>Equus quagga</i>	I3	L	14,89	4,62
TM 13204	<i>Equus quagga</i>	M3	U	19,85	19,81
TM 13204	<i>Equus quagga</i>	M3	U	19,96	19,19
TM 13204	<i>Equus quagga</i>	M1	L	20,89	14,62
TM 13204	<i>Equus quagga</i>	M2	L	21,08	13,33
TM 13204	<i>Equus quagga</i>	M2	L	21,16	13,5
TM 13204	<i>Equus quagga</i>	M1	U	21,41	24
TM 13204	<i>Equus quagga</i>	M2	U	21,52	23,33
TM 13204	<i>Equus quagga</i>	M1	U	21,54	23,87
TM 13204	<i>Equus quagga</i>	M2	U	21,93	23,14
TM 13204	<i>Equus quagga</i>	M1	L	22,15	14,64
TM 13204	<i>Equus quagga</i>	PM4	L	22,84	15,56
TM 13204	<i>Equus quagga</i>	PM4	L	22,91	15,38
TM 13204	<i>Equus quagga</i>	M3	L	23,04	11,66
TM 13204	<i>Equus quagga</i>	M3	L	23,33	11,79
TM 13204	<i>Equus quagga</i>	PM3	L	23,59	15,43
TM 13204	<i>Equus quagga</i>	PM3	L	23,82	15,62
TM 13204	<i>Equus quagga</i>	PM4	U	24,1	24,77

TM 13204	<i>Equus quagga</i>	PM4	U	24,58	24,53
TM 13204	<i>Equus quagga</i>	PM3	U	24,85	24,95
TM 13204	<i>Equus quagga</i>	PM3	U	25,4	24,58
TM 13204	<i>Equus quagga</i>	PM2	L	29,26	14,69
TM 13204	<i>Equus quagga</i>	PM2	L	29,98	14,47
TM 13204	<i>Equus quagga</i>	PM2	U	34,28	22,73
TM 13204	<i>Equus quagga</i>	PM2	U	34,59	23,87
TM 14153	<i>Equus quagga (Juvenile)</i>	I1	L	15,6	3,22
TM 14153	<i>Equus quagga (Juvenile)</i>	I3	U	15,94	6,48
TM 14153	<i>Equus quagga (Juvenile)</i>	I1	U	16,24	6,99
TM 14153	<i>Equus quagga (Juvenile)</i>	I2	L	16,72	5,47
TM 14153	<i>Equus quagga (Juvenile)</i>	I2	U	18,3	6,92
TM 14153	<i>Equus quagga (Juvenile)</i>	I3	U	18,43	6,98
TM 14153	<i>Equus quagga (Juvenile)</i>	M2	U	28,6	21,48
TM 14153	<i>Equus quagga (Juvenile)</i>	M2	U	29,63	20,17
TM 14153	<i>Equus quagga (Juvenile)</i>	M3	U	30	19,48
TM 14153	<i>Equus quagga (Juvenile)</i>	M3	U	30,58	19,42
TM 14153	<i>Equus quagga (Juvenile)</i>	M2	L	31,36	11,63
TM 14153	<i>Equus quagga (Juvenile)</i>	M2	L	31,48	11,02

TM 14153	<i>Equus quagga (Juvenile)</i>	M3	L	31,81	10,48
TM 14153	<i>Equus quagga (Juvenile)</i>	M3	L	31,86	10,3
TM 14153	<i>Equus quagga (Juvenile)</i>	M1	L	33,8	11,41
TM 14153	<i>Equus quagga (Juvenile)</i>	M1	L	34,23	11,21
TM 14153	<i>Equus quagga (Juvenile)</i>	M1	U	35,7	19,09
TM 14153	<i>Equus quagga (Juvenile)</i>	M1	U	36,52	19,82
TM 14170	<i>Equus quagga</i>	I1	L	11,58	9,98
TM 14170	<i>Equus quagga</i>	I1	L	11,62	10,05
TM 14170	<i>Equus quagga</i>	I2	L	12,73	9,91
TM 14170	<i>Equus quagga</i>	I2	L	13	9,93
TM 14170	<i>Equus quagga</i>	I2	U	14,8	11,62
TM 14170	<i>Equus quagga</i>	I3	L	14,96	9,54
TM 14170	<i>Equus quagga</i>	I2	U	15,02	11,6
TM 14170	<i>Equus quagga</i>	I1	U	15,4	11,38
TM 14170	<i>Equus quagga</i>	I3	L	15,77	8,73
TM 14170	<i>Equus quagga</i>	I1	U	18,82	11,9
TM 14170	<i>Equus quagga</i>	I3	U	20,16	10,59
TM 14170	<i>Equus quagga</i>	I3	U	20,32	10,62
TM 14170	<i>Equus quagga</i>	M2	U	24,16	26,42

TM 14170	<i>Equus quagga</i>	M1	U	24,18	27
TM 14170	<i>Equus quagga</i>	M2	U	24,37	25,82
TM 14170	<i>Equus quagga</i>	M1	U	24,79	26,45
TM 14170	<i>Equus quagga</i>	PM4	L	26,58	19,08
TM 14170	<i>Equus quagga</i>	PM3	L	26,62	18,5
TM 14170	<i>Equus quagga</i>	PM4	L	26,64	19,93
TM 14170	<i>Equus quagga</i>	PM4	U	26,9	27,84
TM 14170	<i>Equus quagga</i>	PM4	U	26,95	28,58
TM 14170	<i>Equus quagga</i>	M3	U	27,07	27,79
TM 14170	<i>Equus quagga</i>	PM3	L	27,14	18,74
TM 14170	<i>Equus quagga</i>	M3	U	27,35	23,71
TM 14170	<i>Equus quagga</i>	PM3	U	28,35	27,94
TM 14170	<i>Equus quagga</i>	PM3	U	29	27,71
TM 14170	<i>Equus quagga</i>	PM2	L	31,83	17,61
TM 14170	<i>Equus quagga</i>	PM2	L	31,93	17,41
TM 14170	<i>Equus quagga</i>	PM2	U	36,22	26,06
TM 14170	<i>Equus quagga</i>	PM2	U	36,37	25,99
TM 16690	<i>Equus quagga</i>	I1	L	13,45	8,03
TM 16690	<i>Equus quagga</i>	I1	L	13,85	8,35

TM 16690	<i>Equus quagga</i>	I1	U	15,33	10,09
TM 16690	<i>Equus quagga</i>	I1	U	15,6	10,05
TM 16690	<i>Equus quagga</i>	I2	L	16,22	7,92
TM 16690	<i>Equus quagga</i>	I2	L	16,4	7,53
TM 16690	<i>Equus quagga</i>	I2	U	17,56	9,78
TM 16690	<i>Equus quagga</i>	I2	U	18,3	9,78
TM 16690	<i>Equus quagga</i>	I3	L	19,14	4,58
TM 16690	<i>Equus quagga</i>	I3	L	19,31	4,63
TM 16690	<i>Equus quagga</i>	I3	U	21,9	9,08
TM 16690	<i>Equus quagga</i>	I3	U	22,41	9,27
TM 16690	<i>Equus quagga</i>	M3	U	23,41	20,46
TM 16690	<i>Equus quagga</i>	M3	U	23,61	20,92
TM 16690	<i>Equus quagga</i>	M2	U	23,9	23,98
TM 16690	<i>Equus quagga</i>	M1	U	23,91	25,47
TM 16690	<i>Equus quagga</i>	M2	U	23,99	24,12
TM 16690	<i>Equus quagga</i>	M1	U	24,01	25,81
TM 16690	<i>Equus quagga</i>	M1	L	24,31	16,01
TM 16690	<i>Equus quagga</i>	M2	L	24,82	15,65
TM 16690	<i>Equus quagga</i>	M2	L	25,02	15,45

TM 16690	<i>Equus quagga</i>	M1	L	25,43	16,01
TM 16690	<i>Equus quagga</i>	PM3	L	26,16	17,08
TM 16690	<i>Equus quagga</i>	PM3	L	26,69	17,25
TM 16690	<i>Equus quagga</i>	PM4	U	26,97	26,41
TM 16690	<i>Equus quagga</i>	PM4	U	26,97	26,79
TM 16690	<i>Equus quagga</i>	PM4	L	27,29	17,44
TM 16690	<i>Equus quagga</i>	PM4	L	27,29	16,9
TM 16690	<i>Equus quagga</i>	M3	L	27,51	13,12
TM 16690	<i>Equus quagga</i>	PM3	U	27,76	26,18
TM 16690	<i>Equus quagga</i>	PM3	U	27,9	25,71
TM 16690	<i>Equus quagga</i>	M3	L	28,02	13,04
TM 16690	<i>Equus quagga</i>	PM2	L	30,19	14,75
TM 16690	<i>Equus quagga</i>	PM2	L	30,22	15,07
TM 16690	<i>Equus quagga</i>	PM2	U	35,35	24,4
TM 16690	<i>Equus quagga</i>	PM2	U	35,4	25,84
TM 3086	<i>Equus quagga</i>	I1	L	12,99	8,43
TM 3086	<i>Equus quagga</i>	I1	L	13,18	8,23
TM 3086	<i>Equus quagga</i>	I2	L	14,36	7,12
TM 3086	<i>Equus quagga</i>	I2	L	14,52	7,31

TM 3086	<i>Equus quagga</i>	I1	U	16	9,53
TM 3086	<i>Equus quagga</i>	I1	U	16,01	9,6
TM 3086	<i>Equus quagga</i>	I3	L	16,34	7,01
TM 3086	<i>Equus quagga</i>	I2	U	16,91	9,05
TM 3086	<i>Equus quagga</i>	I3	L	16,92	6,95
TM 3086	<i>Equus quagga</i>	I2	U	16,95	9,05
TM 3086	<i>Equus quagga</i>	I3	U	19,7	8,4
TM 3086	<i>Equus quagga</i>	I3	U	20,01	8,55
TM 3086	<i>Equus quagga</i>	M3	U	20,62	21,53
TM 3086	<i>Equus quagga</i>	M3	U	21,46	20,62
TM 3086	<i>Equus quagga</i>	M3	L	22,62	10,95
TM 3086	<i>Equus quagga</i>	M3	L	22,82	10,82
TM 3086	<i>Equus quagga</i>	M1	U	23,32	23,91
TM 3086	<i>Equus quagga</i>	M1	U	23,69	23,87
TM 3086	<i>Equus quagga</i>	M1	L	24,12	14
TM 3086	<i>Equus quagga</i>	M1	L	24,44	13,52
TM 3086	<i>Equus quagga</i>	PM4	L	25	15,99
TM 3086	<i>Equus quagga</i>	M2	L	25,08	13,4
TM 3086	<i>Equus quagga</i>	M2	L	25,22	13

TM 3086	<i>Equus quagga</i>	PM3	L	25,5	18,98
TM 3086	<i>Equus quagga</i>	PM4	L	25,53	15,41
TM 3086	<i>Equus quagga</i>	PM4	U	25,71	25
TM 3086	<i>Equus quagga</i>	M2	U	25,88	23,61
TM 3086	<i>Equus quagga</i>	PM3	L	26,13	16,1
TM 3086	<i>Equus quagga</i>	PM4	U	26,21	24,92
TM 3086	<i>Equus quagga</i>	M2	U	26,35	23,85
TM 3086	<i>Equus quagga</i>	PM3	U	26,55	24,71
TM 3086	<i>Equus quagga</i>	PM3	U	27,74	24,86
TM 3086	<i>Equus quagga</i>	PM2	L	28,96	14,16
TM 3086	<i>Equus quagga</i>	PM2	L	28,97	14,05
TM 3086	<i>Equus quagga</i>	PM2	U	34,45	22,39
TM 3086	<i>Equus quagga</i>	PM2	U	34,68	22,32
ZA 630	<i>Equus quagga</i>	I1	L	11,19	8,02
ZA 630	<i>Equus quagga</i>	I2	L	12,32	8,32
ZA 630	<i>Equus quagga</i>	I3	L	13,3	7,85
ZA 630	<i>Equus quagga</i>	I1	U	13,4	9,49
ZA 630	<i>Equus quagga</i>	I2	U	13,7	10,22
ZA 630	<i>Equus quagga</i>	I3	U	16,99	9,29

ZA 630	<i>Equus quagga</i>	M1	L	20,6	13,8
ZA 630	<i>Equus quagga</i>	M2	L	21,04	13,5
ZA 630	<i>Equus quagga</i>	M2	U	21,27	23,49
ZA 630	<i>Equus quagga</i>	M1	U	21,32	22,94
ZA 630	<i>Equus quagga</i>	M3	U	23,15	23,15
ZA 630	<i>Equus quagga</i>	PM4	U	23,22	24,99
ZA 630	<i>Equus quagga</i>	PM4	L	23,56	15,44
ZA 630	<i>Equus quagga</i>	PM4	U	23,8	24,5
ZA 630	<i>Equus quagga</i>	PM3	L	25,05	14,4
ZA 630	<i>Equus quagga</i>	M3	L	25,65	13,31
ZA 630	<i>Equus quagga</i>	PM2	L	28,14	14,1
ZA 630	<i>Equus quagga</i>	PM2	U	35,01	23,15

Appendix D: All Post Cranial measurements of Equidae material.

Specimen number	Species	Element	Measurement Code/Type	Measurements (mm)
AZ 1132	<i>Equus quagga</i>	Metacarpal	Greatest length	210,5
			Greatest breadth of proximal end	47,22
			Greatest depth of proximal end	32,12
			Smallest breadth of diaphysis	30,97
			Smallest depth of diaphysis	23,39
			Greatest breadth of distal end	41,87
		Metatarsal	Greatest length	241,5
			Greatest breadth of proximal end	48,46
			Greatest depth of proximal end	39,92
			Smallest breadth of diaphysis	30,18
			Smallest depth of diaphysis	25,2
			Greatest breadth of distal end	40,15
		Proximal Phalange	Greatest length	74,23
			Greatest breadth of proximal end	45,35
			Greatest breadth of articular facies	43,31
			Greatest depth of proximal end	33,61
			Smallest breadth of diaphysis	29,54

			Greatest breadth of distal end	39,9
			Greatest breadth of articular facies of distal end	36,39
		Proximal Phalange	Greatest length	74,74
			Greatest breadth of proximal end	45,15
			Greatest breadth of articular facies	43,25
			Greatest depth of proximal end	33,65
			Smallest breadth of diaphysis	29,33
			Greatest breadth of distal end	39,89
			Greatest breadth of articular facies of distal end	36,24
		Intermediate Phalange	Greatest length	40,97
			Greatest breadth of proximal end	42,3
			Greatest breadth of articular facies	39,09
			Greatest depth of proximal end	29,3
			Smallest breadth of diaphysis	36,21
			Greatest breadth of distal end	37,96
		Intermediate Phalange	Greatest length	41,08
			Greatest breadth of proximal end	42,32
			Greatest breadth of articular facies	38,51
			Greatest depth of proximal end	29,59

			Smallest breadth of diaphysis	36,05
			Greatest breadth of distal end	37,98
		Distal Phalange	Greatest length	53,54
			Greatest Breadth	57,92
			Length of articular facies	23,56
			Breadth of articular facies	39,78
			Length of dorsal surface	47,82
			Height in region of extensor process	38,6
		Tarsal (Central)	Greatest length	46,08
		Tarsal (3rd)	Greatest length	37,91
		Tarsal (Central)	Greatest length	45,6
		Tarsal (3rd)	Greatest length	36
		Astragals	Greatest length	55,98
AZ 1283	<i>Equus quagga</i>	Metacarpal	Greatest length	212
			Greatest breadth of proximal end	46,11
			Greatest depth of proximal end	30,82
			Smallest breadth of diaphysis	28,83
			Smallest depth of diaphysis	23,82
			Greatest breadth of distal end	42,94

		Tarsal (Central)	Greatest length	47,21
		Metatarsal	Greatest length	240,5
			Greatest breadth of proximal end	47,73
			Greatest depth of proximal end	37,79
			Smallest breadth of diaphysis	28,91
			Smallest depth of diaphysis	24,12
			Greatest breadth of distal end	42,18
		Proximal Phalange	Greatest length	80,74
			Greatest breadth of proximal end	47,19
			Greatest breadth of articular facies	44,01
			Greatest depth of proximal end	31,64
			Smallest breadth of diaphysis	27,93
			Greatest breadth of distal end	39,25
			Greatest breadth of articular facies of distal end	38,93
		Proximal Phalange	Greatest length	76,62
			Greatest breadth of proximal end	48,67
			Greatest breadth of articular facies	42,81
			Greatest depth of proximal end	32,92
			Smallest breadth of diaphysis	27,94

			Greatest breadth of distal end	39,12
			Greatest breadth of articular facies of distal end	38,48
		Intermediate Phalange	Greatest length	40,77
			Greatest breadth of proximal end	45,62
			Greatest breadth of articular facies	40,76
			Greatest depth of proximal end	28,19
			Smallest breadth of diaphysis	39,56
			Greatest breadth of distal end	41,69
		Intermediate Phalange	Greatest length	42,7
			Greatest breadth of proximal end	45,28
			Greatest breadth of articular facies	40,12
			Greatest depth of proximal end	30,1
			Smallest breadth of diaphysis	36,91
			Greatest breadth of distal end	38,77
		SE (Navicular)	Greatest length	37,84
		SE (Navicular)	Greatest length	39,41
		Distal Phalange	Greatest length	54,86
			Greatest Breadth	54,76
			Length of articular facies	23,34

			Breadth of articular facies	41,32
			Length of dorsal surface	41,76
			Height in region of extensor process	35,55
		Distal Phalange	Greatest length	51,74
			Greatest Breadth	55,21
			Length of reticular facies	24,36
			Breadth of articular facies	39,7
			Length of dorsal surface	45,22
			Height in region of extensor process	37,15
AZ 1424	<i>Equus quagga</i>	Metacarpal	Greatest length	192
			Greatest breadth of proximal end	43,61
			Greatest depth of proximal end	30,32
			Smallest breadth of diaphysis	30,46
			Smallest depth of diaphysis	19,96
			Greatest breadth of distal end	41,15
		Metacarpal	Greatest length	226,4
			Greatest breadth of proximal end	47,32
			Greatest depth of proximal end	36,44
			Smallest breadth of diaphysis	29,11

			Smallest depth of diaphysis	22,79
			Greatest breadth of distal end	40,45
		Proximal Phalange	Greatest length	71,12
			Greatest breadth of proximal end	46,33
			Greatest breadth of articular facies	42,77
			Greatest depth of proximal end	31,6
			Smallest breadth of diaphysis	30,54
			Greatest breadth of distal end	37,37
			Greatest breadth of articular facies of distal end	35,28
			Greatest length	67,17
			Greatest breadth of proximal end	47,57
			Greatest breadth of articular facies	41,5
			Greatest depth of proximal end	33,88
			Smallest breadth of diaphysis	29,9
			Greatest breadth of distal end	38,43
			Greatest breadth of articular facies of distal end	34,8
		Intermediate Phalange	Greatest length	40,43
			Greatest breadth of proximal end	45,12
			Greatest breadth of articular facies	36,93

			Greatest depth of proximal end	27,39
			Smallest breadth of diaphysis	36,51
			Greatest breadth of distal end	39,92
		Intermediate Phalange	Greatest length	39,53
			Greatest breadth of proximal end	45,15
			Greatest breadth of articular facies	37,31
			Greatest depth of proximal end	27,46
			Smallest breadth of diaphysis	34,66
			Greatest breadth of distal end	36,72
		SE (Navicular)	Greatest Breadth	39,5
AZ 3252	<i>Equus quagga</i>	Metacarpal	Greatest length	212,2
			Greatest breadth of proximal end	49,28
			Greatest depth of proximal end	30,46
			Smallest breadth of diaphysis	29,41
			Smallest depth of diaphysis	22,3
			Greatest breadth of distal end	44
		Metacarpal	Greatest length	213,5
			Greatest breadth of proximal end	48,43
			Greatest depth of proximal end	29,94

			Smallest breadth of diaphysis	29,48
			Smallest depth of diaphysis	22,38
			Greatest breadth of distal end	40,07
		Metatarsal	Greatest length	243,6
			Greatest breadth of proximal end	47,14
			Greatest depth of proximal end	39,42
			Smallest breadth of diaphysis	28,88
			Smallest depth of diaphysis	25,72
			Greatest breadth of distal end	44,62
		Carpal	Greatest length	41,11
		Tarsal (Central)	Greatest length	48,15
		Astragals	Greatest length	57,25
BP 1/C/154	<i>Equus quagga</i>	Metacarpal	Greatest breadth of proximal end	46,86
			Greatest breadth of distal end	41,9
			Smallest depth of diaphysis	21,99
			Greatest breadth of proximal end	44,6
			Greatest breadth of distal end	40,6
			Smallest depth of diaphysis	23,5
		Proximal Phalange	Greatest length	69,14

			Greatest breadth of proximal end	46,33
			Greatest breadth of articular facies on proximal end	43,1
			Greatest depth of proximal end	32,97
			Smallest breadth of diaphysis	29,4
			Greatest breadth of distal end	38,5
			Greatest breadth of articular facies on distal end	36,9
		Intermediate Phalange	Greatest length	40,941
			Greatest breadth of proximal end	42,18
			Greatest breadth of articular facies on proximal end	39
			Greatest depth of proximal end	28,04
			Smallest breadth of diaphysis	36,04
			Greatest breadth of distal end	35,77
		Distal Phalange	Greatest length	48,24
			Greatest breadth	50,44
			Length of articular facies	21,93
			Breadth of articular facies	34,97
			Length of dorsal surface	36,6
			Height in region of extensor process	32,09
		Metacarpal	Greatest breadth of proximal end	46,26

BP 4/1304

Equus quagga

Metacarpal

Greatest breadth of proximal end

46,26

			Greatest breadth of distal end	42,9
			Smallest depth of diaphysis	21,8
			Greatest breadth of proximal end	48,68
			Greatest breadth of distal end	43,78
			Smallest depth of diaphysis	24,7
		Proximal Phalange	Greatest length	75,33
			Greatest breadth of proximal end	47,02
			Greatest breadth of articular facies on proximal end	23,27
			Greatest depth of proximal end	35,04
			Smallest breadth of diaphysis	29,6
			Greatest breadth of distal end	38,24
			Greatest breadth of articular facies on distal end	37,38
		Intermediate Phalange	Greatest length	39,3
			Greatest breadth of proximal end	43,93
			Greatest breadth of articular facies on proximal end	38,4
			Greatest depth of proximal end	28,57
			Smallest breadth of diaphysis	35,6
			Greatest breadth of distal end	37,9
		Distal Phalange	Greatest length	47,63

			Greatest breadth	54,27
			Length of articular facies	23,98
			Breadth of articular facies	38,03
			Length of dorsal surface	42,54
			Height in region of extensor process	34,1
COA 1178	<i>Equus quagga</i>	Proximal Phalange	Smallest breadth of diaphysis	28,05
			Greatest breadth of distal end	37,95
			Greatest breadth of articular facies of distal end	37,28
COA 623	<i>Equus capensis</i>	Proximal Phalange	Greatest length	84,12
			Greatest breadth of proximal end	56
			Greatest depth of proximal end	39,35
			Smallest breadth of diaphysis	36,81
			Greatest breadth of distal end	45,33
COB 114	<i>Equus capensis</i>	Metacarpal	Greatest breadth of proximal end	56,66
			Greatest depth of proximal end	35,18
COB 149	Equidae Indet.	Metapodial	Greatest breadth of distal end	46,16
GV 18256	Equidae Indet	Astragals	Greatest breadth of articular facies on distal end	60,33
GV 18260	Equidae Indet	Astragals	Greatest breadth of articular facies on distal end	59,01
GV 18300	<i>Equus capensis</i>	Astragals	Greatest breadth	62,35

			Greatest height	58,66
GV 18318	<i>Equus capensis</i>	Metacarpal	Greatest depth of proximal end	41,06
GV 4682	<i>Equus capensis</i>	Sesamoid	Greatest breadth	51,48
GV 4966	<i>Equus capensis</i>	Tarsal	Greatest breadth	51,48
GV 5172	<i>Equus quagga</i>	Proximal Phalange	Smallest breadth of diaphysis	31,89
			Greatest breadth of distal end	43,91
			Greatest breadth of articular facies on distal end	43,36
GV 5244	<i>Equus quagga</i>	Carpal	Greatest breadth	42,70
GV 5247	<i>Equus quagga</i>	Distal Phalange	Length of articular facies	23,92
			Length of dorsal surface	46,18
			Height in region of extensor process	40,86
GV 7576	<i>Equus quagga</i>	Carpal	Greatest breadth	38,38
GV 7585	<i>Equus quagga</i>	Proximal Phalange	Smallest breadth of diaphysis	30,23
			Greatest breadth of distal end	37,30
			Greatest breadth of articular facies on distal end	36,36
GV 7784	<i>Equus quagga</i>	Carpal	Greatest breadth	39,46
GV 7823	<i>Equus quagga</i>	Metapodial	Greatest breadth of distal end	44,99
GV 7995	<i>Equus quagga</i>	Proximal Phalange	Smallest breadth of diaphysis	29,07
			Greatest breadth of distal end	38,73

			Greatest breadth of articular facies on distal end	36,56
GV Indet 10	<i>Equus capensis</i>	Metacarpal	Greatest breadth of proximal end	56,59
GV Indet 11	<i>Equus capensis</i>	Metatarsal	Smallest depth of diaphysis	30,47
GV Indet 12	<i>Equus quagga</i>	Metatarsal	Greatest breadth of distal end	49,12
GV Indet 13	<i>Equus quagga</i>	Metatarsal	Greatest breadth of distal end	48,5
GV Indet 14	<i>Equus capensis</i>	Metatarsal	Greatest breadth of distal end	51,68
GV Indet 15	<i>Equus capensis</i>	Metacarpal	Greatest breadth of distal end	50,3
GV Indet 19	<i>Equus capensis</i>	Tarsal	Greatest length	21,87
GV Indet 19	<i>Equus capensis</i>	Tarsal	Greatest breadth	12,88
GV Indet 2	<i>Equus quagga</i>	Metatarsal	Greatest breadth of distal end	49,07
GV Indet 2	<i>Equus quagga</i>	Metatarsal	Smallest depth of diaphysis	26,05
GV Indet 3	<i>Equus quagga</i>	Metatarsal	Greatest breadth of distal end	46,74
GV Indet 5	<i>Equus quagga</i>	Metacarpal	Greatest breadth of distal end	50,31
GV Indet 7	<i>Equus quagga</i>	Metatarsal	Greatest breadth of distal end	48,5
KA 1505	<i>Equus capensis</i>	Distal Phalange	Length of articular facies	24,94
KA 796	<i>Equus capensis</i>	Proximal Phalange	Greatest length	76,25
			Greatest breadth of proximal end	48,82
			Greatest breadth of articular facies	44,11
			Greatest depth of proximal end	34,06

			Smallest breadth of diaphysis	31,88
			Greatest breadth of distal end	39,49
			Greatest breadth of articular facies of distal end	38,48
SK 4000 A	<i>Equus quagga</i>	Metacarpal	Greatest length	214,7
			Greatest breadth of proximal end	50,67
			Greatest depth of proximal end	32,61
			Smallest breadth of diaphysis	32,2
			Smallest depth of diaphysis	24,88
			Greatest breadth of distal end	42
SK 4000 C	<i>Equus quagga</i>	Proximal Phalange	Greatest length	76,84
			Greatest breadth of proximal end	46,19
			Greatest breadth of articular facies	40,43
			Greatest depth of proximal end	33,59
			Smallest breadth of diaphysis	30,65
			Greatest breadth of distal end	38,75
			Greatest breadth of articular facies of distal end	38,66
SK 4000 D	<i>Equus quagga</i>	Intermediate Phalange	Greatest length	42,61
			Greatest breadth of proximal end	47,15
			Greatest breadth of articular facies	41,56

			Greatest depth of proximal end	29,31
			Smallest breadth of diaphysis	38,45
			Greatest breadth of distal end	40,5
SK 4002 A	<i>Equus capensis</i>	Metapodial	Greatest breadth of articular facies of distal end	48,87
SK 4002 B	<i>Equus capensis</i>	Intermediate Phalange	Greatest length	49,59
			Greatest breadth of proximal end	56,32
			Greatest breadth of articular facies	52,23
			Greatest depth of proximal end	35,5
			Smallest breadth of diaphysis	48,6
			Greatest breadth of distal end	53,31
SK 4002 C	<i>Equus capensis</i>	Tarsal (Central)	Greatest length	47,85
SKX 19806, 19808	<i>Equus capensis</i>	Metapodial	Greatest breadth of proximal end	52,31
SKX 22086	<i>Equus quagga</i>	Metapodial	Greatest breadth of distal end	48,32
SKX 24952	<i>Equus quagga</i>	Metapodial	Greatest breadth of distal end	47,34
SKX 25704	Equidae Indet	Metapodial	Greatest breadth of distal end	51,18
SKX 28495	<i>Equus quagga</i>	Metapodial	Greatest breadth of distal end	48,84
SKX 28976	<i>Equus quagga</i>	Metapodial	Greatest depth of proximal end	37,37
SKX 29027	<i>Equus quagga</i>	Metatarsal	Breadth of articular facies	39,4
SKX 30256	<i>Equus capensis</i>	Tibia	Greatest breadth of distal end	63,63

			Greatest breadth of proximal end	40,32
SKX 3206	Equidae Indet	Metapodial	Greatest breadth of distal end	50,37
SKX 3466,3467,15650	Equidae Indet	Sesamoid	Greatest depth of proximal end	38,98
SKX 39181	Equidae Indet	Metatarsal	Greatest depth of proximal end	34,28
SKX 39617	<i>Equus quagga</i>	Distal Phalange	Breadth of articular facies	42,82