A BACKGROUND INVESTIGATION INTO THE FEASIBILITY OF HEAVY STABLE ISOTOPES ($^{87}Sr/^{86}Sr$) AS SOURCE TRACERS OF EARLY HOMINIDS

By

GRANT HALL

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Supervisors:
Dr. A. Sillen
Dr. R. Armstrong

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ABSTRACT

Heavy stable strontium isotope ratios ($^{87}Sr/^{86}Sr$) may be used to characterize the habitat choices of early hominids. The basis for this approach is that different geological substrata may have a characteristic range of $^{87}Sr/^{86}Sr$ ratios in the **available** soil strontium pool. This range may be represented in the plants growing on these various geologies and thus into the bones of animals feeding in these areas. Through an examination of strontium isotope ratios for plants and soils from 10 different geologies in the Sterkfontein Valley and immediate vicinity, it was possible to obtain some tentative indication of the possible range in $^{87}Sr/^{86}Sr$ ratios in an area most likely to cover favoured foraging habitats of early hominids, such as *Australopithecus robustus*. On the basis of isotopic data from extensive dolomite sampling, it is clear that there is a wide range of variation in strontium isotope ratios for dolomite substrata around Swartkrans. This may be as a result of topography, water action and atmospheric pollution. However, in spite of such variation, it is possible to distinguish isotopically different habitats, such as riparian from slopes. Such variation will complicate the interpretation of early hominid home ranges, but does provide alternative avenues for behavioral interpretations and also emphasises the necessity for the collection of background isotopic data.

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1. INTRODUCTION

Recent studies of strontium isotope ratios ($^{87}Sr/^{86}Sr$) have demonstrated the potential of this technique as a possible means of source tracing individuals or specific items (Ericson 1985, 1989). $^{87}Sr/^{86}Sr$ ratios have been used to examine the movement patterns of prehistoric human populations in the American southwest (Price *et al* 1994), and in the southwestern Cape (Sealy *et al* 1991; Sealy and Sillen 1988). Strontium isotopes, used in conjunction with other isotopic and trace elemental analyses, have been used in an attempt to source elephant ivory and rhino horn from a number of locations in Africa (Hall-Martin *et al* 1993; Lee-Thorp *et al* 1992; van der Merwe *et al* 1990; Vogel *et al* 1990). In addition strontium isotopes have been used for measuring the palaeosalinity of fossil fish habitats (Koch *et al* 1992; Schmitz *et al* 1991), sourcing Neolithic shell artefacts (Shackleton and Elderfield 1990) and measuring atmospheric inputs into various ecosystems (Gosz *et al* 1983; Graustein and Armstrong 1983; Graustein 1989; Hurst and Davies 1981; Straughan *et al* 1981). These attempts have met with varying degrees of success, and serve to illustrate the range of potential applications of strontium isotope ratios, from modern ecological studies to the analysis of Miocene fossils.

The rationale behind the use of strontium isotope ratios is that $^{87}Sr/^{86}Sr$ ratios do not undergo biological fractionation, as does elemental strontium. This means that the $^{87}Sr/^{86}Sr$ ratio is a direct indication of the sources of strontium in an ecosystem. Through extensive geochemical research, it is also known that differing geologies will have a characteristic range of $^{87}Sr/^{86}Sr$ ratios, such as for granites (0.700 to 0.737) and dolomites (0.7068 to 0.7092) (Faure and Powell 1972; Graustein 1989). If the background $^{87}Sr/^{86}Sr$ ratios for a study area can be determined, it may be possible to trace the origin of strontium in individuals or artefacts, by comparing their isotopic ratios with those obtained for the environment.

The fossil hominids from Swartkrans have been the subject of numerous trace element and stable isotope analyses, particularly in terms of determining dietary distinction between robust Australopithecines and early *Homo* (Sillen 1988, 1992; Sillen *et al* In press). There have also been extensive analysis of associated fossil fauna (eg. Lee-Thorp and van der Merwe 1993; Sillen and Lee-Thorp 1994) and the modern flora (Hall 1992). $^{87}Sr/^{86}Sr$ ratios have been obtained for a number of hominids from Swartkrans Member 1, and on the basis of these data, there is some indication of isotopic differences amongst the robust Australopithecines (Sillen *et al* In press). These studies have suffered from the lack of background $^{87}Sr/^{86}Sr$ ratios for the Sterkfontein Valley and immediate vicinity, such data is necessary for allowing one to predict the foraging habits of early hominids at Swartkrans.

The Sterkfontein Valley and surrounding areas are geologically variable. Approximately 10 different substrata occur within 15 kilometers of Swartkrans (Figure 1), including a variety of shales, quartzites, volcanic rocks and granites. The formation of the Sterkfontein Valley has been well established and documented (Brain 1981, 1993; Butzer 1976). Such geological variation may provide a suitable range of $^{87}Sr/^{86}Sr$ ratios, allowing one to isotopically characterize a number of habitats in the area. The modern environment is considered to be very similar to that of 1.6 to 1.8 mya, the time period when robust Australopithecines occurred in the area. Thus by isotopically analysing modern plant and soil samples from the variety of geologies, it may be possible to reconstruct the background strontium isotopic ratios. If individuals were obtaining all their food from the dolomites in the immediate areas around Swartkrans, they would be expected to have $^{87}Sr/^{86}Sr$ ratios in the range of the plants growing on such soils. A widely different strontium isotope ratio for an individual, would be indicative of that one foraging on a different geology, further afield from Swartkrans.

In addition to examining the background strontium isotope data from the Sterkfontein Valley and surroundings, studies of primate foraging behavior and ranging patterns will also be addressed. Through the examination of a number of extant primate species such as savanna baboons and chimpanzees, as well as the use of ethnographic studies of modern Kalahari hunter-gatherers, it is possible to isolate general ecological and social factors that would have also influenced early hominid foraging and ranging patterns. If the minimum and maximum home ranges for these primates, as well as predicted home ranges for robust australopithecines. are projected onto a geological map of the Sterkfontein area, it may be possible to get an indication of expected minimum and maximum ranges for background strontium isotope ratios. These background isotopic predictions may then be compared with actual $^{87}Sr/^{86}Sr$ data for hominids from Swartkrans.

2. BACKGROUND

2.1 Geochemistry of heavy isotopes in soils and the biosphere

In order to understand how the heavy isotopes of strontium (Sr) may provide information characteristic of differing geological areas, it is necessary to examine how strontium is distributed in the lithosphere and the biosphere. The abundance of strontium isotopes have undergone a gradual evolution since the formation of the planet, resulting in a change in the relative proportions of their isotopes.

a) Strontium

The isotopic composition of strontium has been changing continuously since the formation of the planet. This is due to the ongoing radioactive decay of ^{87}Rb (rubidium) to ^{87}Sr. The amount of strontium present in a rock type will depend on the amount of rubidium in the rock and the age of the rock, as a consequence, the Rb/Sr ratio is of importance for geochronology (Kruger 1986). In very old rocks, ^{87}Rb (half-life of 49 Gyr) has through ß decay contributed significantly to the ^{87}Sr content. Thus, the isotopic composition of strontium has become increasingly heterogeneous through geological time and will continue to do so (Faure 1977; DePaolo and Ingram 1985). A corollary of the observation that strontium is becoming more heterogeneous is that it was more homogeneous at the beginning of geological time.

Additional changes in the isotopic composition of strontium have resulted due to the geochemical differentiation of the earth. This geochemical differentiation has led to the formation of rocks and minerals with differing Rb/Sr ratios. Strontium isotopic evolution is further complicated by geological forces, such as erosion and sedimentation, which serve to continuously breakdown and recombine older rocks into newer ones. In this way older strontium gets incorporated into newer rock systems (Faure 1977).

The isotopic evolution of strontium in the earth began about 4.6 x 10^9 years ago. The $^{87}Sr/^{86}Sr$ ratio of that time has been estimated to have been 0.699. This figure has been derived from the analysis of stony meteorites because no primordial rocks have been preserved (Faure 1977). The actual formation of the earth's crust is thought to have begun approximately four billion years ago, based on ancient granitic gneiss (+- 3.7 x 10^9 years old) having an $^{87}Sr/^{86}Sr$ ratio of 0.700 to 0.702.

Strontium is a member of the alkali earth group of metals, such as calcium and barium, forming part of Group IIA of the Periodic Table (Faure and Powell 1972). There are four naturally occurring isotopes; ^{84}Sr (0.56%), ^{86}Sr (9.86%), ^{87}Sr (7.02%) and ^{88}Sr (82.56%) (Rankama 1956), as well as 14 artificial ones which are all short-lived (Faure and Powell 1972). As previously mentioned the isotopic composition is not constant and depends on the Rb/Sr of the sample and the length of time the sample has been associated with rubidium. The ^{87}Sr isotope is the ß-decay product of naturally radioactive ^{87}Rb and will thus accumulate in all rubidium bearing minerals, initially having a maximum concentration in rubidium rich samples. However because of their differing geochemical properties, the two metals will become separated (Rankama 1956).

Strontium has a tendency to follow calcium. This is due to the similarity in their ionic radii (Turekian and Kulp 1956). In this way calcium bearing minerals will have a certain amount of strontium present within. Strontium is, however, capable of forming its own minerals, which are frequently dispersed in sedimentary rocks and soils (Vinogradov 1959). Although strontium resembles calcium chemically, their ionization constants, solubility products and other properties are different. Natural processes, such as weathering and leaching, will therefore act on these elements in different ways. An example of this can be illustrated by the fact that strontium tends to be excluded from ultrabasic and basic rocks during fractional crystallization and tends to work upwards in the lithosphere. This is due to its slightly larger ionic radius (Odum 1951), as well as the above mentioned properties.

A major study carried out by Turekian and Kulp (1956) attempted to evaluate the abundance and distribution of strontium in the earth (Table 1). Over 1000 samples were analysed so as to obtain a representative measure of the earth's crust. The following relationships were observed:

1. The strontium content of basaltic rocks is independent of the calcium content of these rocks. Strontium appears not to substitute for calcium in basaltic rocks. The strontium content is rather a factor of the strontium content of the source magma and local crystallization and differentiation There is however a definite relationship in granitic rocks, where strontium will substitute for calcium and the abundance of strontium is strongly affected by the calcium content of the granitic rock. The strontium content of granites increase as the calcium content increases.
2. Basaltic rocks of a particular region appear to have, within narrow limits, the same strontium concentration. This is due to the factors mentioned above.
3. Shales and limestones all indicate that strontium is not as strongly linked with calcium as it may be in other rock types. Shale strontium content appears to be influenced by the clay content. Adsorption sites on clay particles have a preference for strontium, rather than calcium. The strontium content of limestones is affected by a number of factors, including temperature, salinity, diagenesis (geological) and the action of ground-water.
4. Taking both basaltic and granitic crustal composition, the average strontium content of the crust is 440 ppm.

The process of mineral formation fractionates rubidium with respect to strontium, but not ^{87}Sr from ^{86}Sr (Graustein 1989).

The oceans are the largest strontium reservoirs on the planet, deriving strontium from numerous sources, including continental runoff, atmospheric and marine sediment deposition and the activity of submarine volcanoes (Lavelle and Armstrong 1993). Strontium is very easily up taken by marine shellfish. The strontium is received more readily by the aragonite within the shell than is calcium and results in the build up of substantial layers of fossil marine carbonates (Kulp *et al* 1952). In this way the strontium concentration of the oceans may be reduced for a period of time, but strontium will be released in to the oceans through the exposure and erosion of these fossil marine carbonates (Lavelle and Armstrong 1993). In fact the majority of strontium entering the oceans is derived from the chemical weathering and diagenesis of marine carbonate rocks (Faure 1977; Lavelle and Armstrong 1993).

The isotopic composition of strontium in modern oceans is not the same in all areas, as was previously thought, but over time (10^3 years) there is sufficient mixing of the strontium present in the oceans, resulting in a standard marine isotopic value (MIS). Areas where variation is most likely to occur are near major rivers, waters near hydrothermal vents and in the porewaters of fossil sediments undergoing rapid diagenesis (Lavelle and Armstrong 1993). There is some variation in international MIS values, with a range of between 0.709119 to 0.709178 (Normalised to SRM 987 = 0.71020), with an average of 0.709141.

Regardless of climatic region and type, soils appear to contain substantial amounts of strontium. Temperate and boreal regions range between 40 and 800 ppm; arid and semi arid regions 90 to 3000 ppm and tropical humid regions from 3 to 2000 ppm. These results are based on extensive analyses of soil samples obtained worldwide (Aubert and Pinta 1977). Essentially the strontium content of the soil depends primarily on the concentrations of strontium within the parent rocks, from which the soils have formed (Table 2). However there are, in addition, a number of other factors affecting the strontium content. These include rainfall, temperature, leaching, pH, organic matter content, erosion, degradation and local groundwater movement (Aubert and Pinta 1977; Pate and Hutton 1988).

The $^{87}Sr/^{86}Sr$ ratio of soils and near surface continental rocks lies normally between 0.709 (modern seawater) and about 0.720 (streams draining rubidium enriched areas). In older rocks that are rubidium enriched, $^{87}Sr/^{86}Sr$ ratios will be higher than the aforementioned crustal average, while younger volcanic rocks may be depleted (Graustein and Armstrong 1983).

The isotopic composition of Sr in various ecosystems represents mixing of strontium derived both atmospheric and mineral weathering (Miller *et al* 1993). Coastal and marine ecosystems will have $^{87}Sr/^{86}Sr$ ratios very close to that of the ocean, as most of the strontium will be derived from ocean aerosols. Terrestrial ecosystems are more complicated as strontium can be derived from a number of sources. As mentioned earlier soils derive their strontium mainly from the underlying parent rock and the isotopic composition should be very similar to that of the parent rock. Additional strontium will enter the ecosystem from other sources such as groundwater, streams and atmospheric deposition. In order to understand any isotopic data derived from an ecosystem, it is thus important to understand the relative contributions of each strontium source. Two major sources of strontium appear to be from atmospheric transport and mineral weathering (Miller *et al* 1993). A number of studies have been undertaken to assess the relative contribution of each.

Strontium isotopes have been used to determine the amount of strontium deposited from the atmosphere. A study carried out in the Sangre de Cristo Mountains of New Mexico, examined the $^{87}Sr/^{86}Sr$ ratios of stream water, vegetation and soils from two watersheds in the area (Graustein and Armstrong 1983). Under suitable geographic and geological conditions it is possible to use the natural isotopic composition of strontium to distinguish atmospheric and transpirational sources. The Sangre de Cristo Mountains are particularly suitable for such as study. The watersheds exist along an elevation gradient, moving from a high $^{87}Sr/^{86}Sr$ environment at the top to lowlands with a low $^{87}Sr/^{86}Sr$ ratio (Gosz *et al* 1983). Vegetation growing on these different substrata would be expected to have $^{87}Sr/^{86}Sr$ ratios similar to those of the underlying geology. Any differences in the isotopic ratio would be indicative of an additional source of strontium. For example, if the vegetation on the upper slopes had a low $^{87}Sr/^{86}Sr$, one could hypothesize that mountain soils were being affected by sedimentary material from the lowlands. This would only occur as a result of upward wind transport of dust from the lowlands. In this semiarid environment, frequent high winds do in fact move substantial quantities of dust into the upper regions, from 50 to 120 $\mu g/m^3$ (Gosz *et al* 1983). The elevation gradient produces a gradient of temperature, humidity, wind and precipitation that will affect input processes to the area.

Vegetation complicates the measure of atmospheric deposition, as foliage acts as a trap for aerosols. Strontium is derived from two sources: that present in the atmosphere and that from the transpirational flow of the plant, from roots to leaves. If one knows the $^{87}Sr/^{86}Sr$ ratio of the atmospheric input, it is possible, using mixing equations, to determine the amount derived from the transpirational flow. The isotopic composition of a sample may be expressed as

$$\triangle^{87}Sr = [^{87}Sr/(^{87}Sr + ^{86}Sr)_{sample} \\ - ^{87}Sr/(^{87}Sr + ^{86}Sr)_{standard}] \times 10^4.$$

The results of the Sagre de Cristo study revealed that dust input to the watersheds provided 75% of the strontium in the vegetation and only 25% of the strontium was ultimately derived from the weathering of underlying parent rock (Graustein and Armstrong 1983). Gosz and others (1983) also examined a range of wood samples of different age, 300 years to recent wood, as a means of determining any changes in the amount of atmospheric material contributed to the plant communities over time. In 35 to 50 year old wood, a $^{87}Sr/^{86}Sr$ ratio of 0.7216 was obtained, while 15 year old wood had a $^{87}Sr/^{86}Sr$ of 0.7130, indicating that atmospheric strontium can quickly dominate the soil strontium pool. In the space of 20 to 30 years, the soil strontium pool had decreased as a result of an increase in atmospheric strontium.

A recent study done in a spruce-fir forest at Whiteface Mountain, New York, examined the rates of soil exchangeable-cation loss and weathering using strontium isotopes (Miller *et al* 1993). It was determined that 50 - 60% of the strontium in the organic soil horizon was of atmospheric origin. Of the remaining 40 - 50%, 70% of the strontium is as of the result of mineral weathering and 30% from soil cation-exchange reactions.

The results of these studies indicates the importance of examining the strontium isotopes of plants, soils and natural waters in order to obtain an model of the sources and pathways of strontium through an ecosystem. It is clear that the isotopic examination of only mineral substrata is insufficient to provide background data on strontium isotope variation within a chosen ecosystem. This background information is necessary to allow one to interpret $^{87}Sr/^{86}Sr$ ratios of samples from such an ecosystem.

2.2 Geology of the Sterkfontein Valley

The research area can be divided into two main geological areas. To the northwest of and including Swartkrans, is the Transvaal Sequence and to the southeast is the Witerwatersrand Supergroup. Each area is comprised of a variety of shales, dolomites, and quartzites, as well as other rock types (Figures 1 and 2).

a) The Transvaal Sequence

Swartkrans is located on the dolomites of the Malmani Subgroup of the Chuniespoort Group. The Malmani Subgroup is made up of alternating bands of chert-bearing and chert-free dolomite, with Swartkrans being located on a relatively chert-free band (Brain 1981; Geological Survey 1989). Swartkrans and the other caves developed in the dolomitic limestones through the action of karstic solution and enlargement by collapse. Sedimentation occurred via a number of processes, such as brecciation of the cave walls, carbonate precipitation, accumulation of insoluble residues and flushing of colluvial detritus into the caves (Tankard *et al* 1982). At the base of the Malmani Subgroup are carbonaceous shales and underlying the whole group is the Black Reef Quartzite Formation (SACS 1980; Geological Survey 1989).

The remaining areas all form part of the Pretoria Group, consisting predominantly of quartzite and shale, with a prominent volcanic unit, the Hekpoort Andesite Formation. The Hekpoort Andesite Formation has been radiometrically dated to 2224 +/- 21 Ma (SACS 1980; Geological Survey 1989). Andesites can be distinguished by their dark colouration and fine grain and will have either hornblende or pyroxene in their compositional make-up (Brown *et al* 1992). Beyond the Hekpoort Andesite Formation, is the Daspoort Quartzite Formation, which may be up to 190 m thick in places (Geological Survey 1989). Past the Daspoort Quartzite Formation are alternating bands of diabase and undifferentiated surface deposits. The diabase sheets can be recognised by stands of *Acacia spp.* trees and diabase is a typically fine-grained, greenish-grey rock (Geological Survey 1989).

b) The Witwatersrand Supergroup

Underlying the Witwatersrand Supergroup is very old granite, referred to as the Archaean Granite. The granite has been radiometrically dated to approximately 2800 Ma (Geological Survey 1989). The granite is located to the east of Swartkrans (Figure 1). The remaining area comprises the Witerwatersrand Supergroup, represented by the Krugersdorp Quartzite Formation, with occurrences of quartzites. shales and conglomerates. There is also an outcrop of mafic and ultramafic rock. Mafic rocks are dark coloured igneous rocks, with high concentrations of magnesium and iron. Ultramafic rocks are also igneous in origin, dominated by the mineral olivine, and form the majority of the earth's crust (Brown *et al* 1992).

2.3 The archaeology of Swartkrans

a) Introduction

The Sterkfontein Valley is the location of the hominid fossil sites Swartkrans, Sterkfontein and Kromdraai. In addition there are at least two other notable sites, Gladysvale and Plovers Lake, only a few kilometers away.

Swartkrans has been the subject of numerous investigations for many years; the history of its formation, artefacts and especially the fossil assemblage have been well documented. Excavations at Swartkrans were first initiated in 1930, when the site was still in use as a limestone quarry. Between 1948 and 1949, Broom and Robinson conducted further excavations, resulting in the discovery of some superb hominid fossils, such as the first specimen of a new species of australopithecine, *Paranthropus crassidens* (now *Australopithecus robustus*), and the jaw of an early true human, first called *Telanthropus capensis* and subsequently classified as *Homo* (Brain 1981). Unfortunately between 1950 and 1951, there was renewed limestone mining. After Broom's death, Robinson returned in 1952, but only remained until 1953. There was then a twelve year hiatus, until 1965, when an attempt was made to restore the site. The farm on which the site is situated was finally purchased in 1968 by the University of the Witwatersrand. Excavation, in conjunction with the Transvaal Museum, has continued to date under the supervision of C.K. Brain (Brain 1967, 1970, 1976, 1981, 1988, 1993; Brain and Watson 1992; Robinson 1970).

Sterkfontein has yielded numerous fossil remains of *Australopithecus africanus* and *Homo habilis*, as well as a large collection of stone tools, very similar to Early Acheulean or Developed Oldowan artefacts (Stiles and Partridge 1979; Clarke 1985, 1988). These tools are associated with *H.habilis*; to date no tools have been associated with *A.africanus*. There are some similarities between the Sterkfontein and Swartkrans Formations, but no apparent lithostratigraphic overlap between their various members.

There are perceptible differences in faunal assemblages between the two sites (Partridge 1978).

The isotopic and ranging data presented in this study are specifically orientated to the Swartkrans hominids, with emphasis on the robust australopithecines. Sterkfontein and the other fossil sites, should however, not be disregarded as a similar study may yield useful information about the behavior of other hominid species.

b) Stratigraphy and chronology of Swartkrans

Five discrete Members are recognisable at Swartkrans, each separated from one another by an erosional discontinuity. As the cave functions as a sediment trap, deposits are continually being formed and eroded over time. Due to this action and alternating climatic cycles, there have been periods of deposition and erosion, resulting in a somewhat complex mosaic (Brain 1993).

Dating the deposits has been difficult, and as yet there are no absolute dates for either the sediments or the fossils. An attempt was made to date the deposits through palaeomagnetic analysis, but the results were inconclusive (Brock, McFadden and Partridge 1977).

Through the examination of fossil bovid assemblages, a tentative chronology has been developed for the Sterkfontein Valley (Table 3). Bovid material analysed from Swartkrans, Sterkfontein and Kromdraai, seems to place the Sterkfontein Valley units at between 2,0 mya and recent times (Vrba 1975). Swartkrans Members 1, 2 and 3 are thought not to differ significantly in their faunal assemblages (Watson 1993). This similarity in faunal material seems to indicate that all three Members may have a similar date of between 1,8 and 1 million years (Brain 1993; Vrba 1975, 1985a). Member 4 has yielded some Middle Stone Age artefacts, but has not provided any bone. There is no clear indication of age, apart from the MSA material at present for Member 4.. Member 5 is rich in fossil remains of the extinct springbuck (*Antidorcas bondi*), and some bone has been ^{14}C dated to 11 000 years (Brain 1993).

c) The fossil assemblages

Australopithecine fossils have been found in Members 1, 2 and 3 only. As the ultimate aim of this research is an attempt to understand more about the ecology of the robust australopithecines, the focus here is the hominid bearing Members 1 to 3 (Table 4). There are 64 mammalian taxa represented in the fossil assemblage, as well as birds, reptiles and amphibians. The hominid fossils are numerous and have been described in detail (Brain 1967, 1970, 1976, 1981, 1993, Clarke 1977; Clarke *et al* 1970; Grine 1989, 1993; Susman, 1989, 1993; Watson 1993). The most recent fossil data indicates the presence of *Australopithecus robustus* in Members 1, 2, and 3, with a total of 39 individuals, represented by both cranial and postcranial remains (Watson 1993; Grine 1989, 1993; Susman 1989, 1993). In addition, there are 3 individuals of *Homo sp.* from Members 1 and 2.

A number of fossil primates have been recovered from the same Members as the robust australopithecines (Table 4). It is pertinent to note the occurrence of these species as they represent a potential source of competition for the hominids. The presence of these primates would have had an impact on the ranging and foraging behavior of the australopithecines. There may have been intensive competition for key food items, such as the edible bulbs of *Hypoxis spp.* (Brain 1988, 1993; Sillen *et al* In press). The species include *Papio hamadryas robinsoni*, *Papio (Dinopithecus) ingens* and *Theropithecus oswaldi danieli*, all extinct species of baboon (Watson 1993). The study of modern primates, particularly their ranging and foraging behavior, may provide some information about the possible interactions between the hominids and associated primates of Swartkrans and is discussed in detail in Section 3.

d) The stone and bone tool assemblages

A total of 877 stone artefacts have been collected from Members 1, 2 and 3, the majority originating from Members 1 and 2. The raw materials used are mainly quartzite, quartz and chert. Quartzite is readily available in the form of river cobbles from in and around the Bloubank stream.

Quartz is found as chunks, blocks and fragments, and also in occasional exposed veins in rock. Dolomite bands near Swartkrans are rich in chert, providing an easily accessible supply of raw material (Brain 1981; Brain *et al* 1988; Clark 1993). All the tools were found to be in good condition, with little weathering.

It appears that there was no actual *in situ* tool manufacture in the cave, due to the absence of flaking debris and the fact that there no refitable tools (Clark 1993). There are no significant typological differences between the three Members. The assemblage is composed of core/choppers and retouched or modified pieces. An initial analysis by Leakey (1970) placed the artefacts as Developed Oldowan, rather than Oldowan or Acheulean, on the basis of the larger dimensions of the tools. The most recent analyses have concurred with this conclusion (Brain *et al* 1988; Clark 1993).

Bone tools have also been found in Members 1 through 3. A total of 68 pieces of fossil bone appear to have been used as tools (Brain *et al* 1988; Brain and Shipman 1993). The majority (40) are from member 3, with 17 from Member 1 and 11 from Member 2. The tools appear to be mostly bone flakes from long bone shafts, such as the femur, as well as a few formed from antelope horn cores. On the basis of wearing and polish patterns, three categories of tools have been defined:

1. Digging tools,
2. Highly polished bones, similar to those used as digging tools and,
3. Awl-like tools with localised wear at the tips.

Recently, Brain *et al* (1988, 1993) conducted experiments with flaked wildebeest bones used as digging implements. They were used to dig out *Hypoxis sp.* bulbs and were found to rapidly develop similar scratch patterns to those found on the fossil bones. Through the use of Scanning Electron Microscopy (SEM), it was found that scratch marks on both modern and fossil bone resulted from repeated digging motions in rocky soil. The other implements also show wear patterns, that may have developed from burnishing or rubbing skins or leather (Brain *et al* 1988).

The use of digging tools would have provided early hominids with an advantage over other primates, such as baboons. Although baboons are able to easily dig up edible bulbs and corms in fairly soft ground, bulbs in very rocky areas would be inaccessible to them (Brain *et al* 1988; Brain and Shipman 1993). According to this argument, the use of bone digging instruments would allow hominids access to those bulbs growing in rocky areas, such as those found around Swartkrans. In the experiments using modern bone digging tools, it was found that it was relatively easy to excavate a bulb in rocky terrain, taking approximately 30 minutes to excavate a bulb.

Underground storage organs are an important source of food for baboons and very likely for early hominids, particularly during the dry season. Bulbous species such as *Hypoxis rigidula* and *H.argenta* are able to supply a large amount of carbohydrate, as they can be more than 500g in weight (Brain and Shipman 1993; Hall pers. obs.). Mogg (1975) has documented that these bulbs are highly edible without cooking and were prized food items. The occurrence of such plants tends to be patchy, since the plants have fairly specific habitat preferences. This patchy distribution of an important food source would have a significant impact on the ranging behavior of early hominids, possibly resulting in a seasonally variable ranging pattern (See Section 3).

The distribution of the bone tools, when compared with the stone tools reveals some changing distribution patterns from Member to Member. In Members 1 and 2, there are only a few bone implements and a large amount of stone artefacts. This seems to be in marked contrast with Member 3, which has considerably more bone tools and fewer stone tools than the other Members. Furthermore, there is evidence for the controlled use of fire in Member 3 (Brain and Sillen 1988; Brain 1993). This appears to indicate some marked behavioral changes are occurring in Member 3. There are to date no fossil remains of *Homo sp.* from Member 3, but at least 9 *A.robustus* individuals. Did australopithecines have the controlled use of fire, and a bone tool technology?

It is thought by Brain and others (1988, 1993) that both australopithecines and Homo were making use of the stone and bone tools and may have also been using skins as carrying bags for their tools and food items. This would have provided the hominids with a great advantage and eased the manner in which they were able to exploit available resources in the Transvaal grasslands.

An alternative scenario, based on trace element analysis (Sr/Ca ratios), suggests that only *Homo* made and utilised both bone and stone tools, and extensively exploiting underground storage organs as a key dietary component. Alternatively *Homo* may also have concentrated on food items with a very high strontium content, such as hyraxes (Sillen *et al* In press).

e) Palaeoenvironment of the Sterkfontein Valley

The reconstruction of past environments is essential for understanding and interpreting early hominid behavior. There are a number of methods that may be applied, including the analysis of the abundance of certain key fossils and the use of geomorphical techniques.

The original topography around the Swartkrans site has been reconstructed through geomorphological analysis of the Bloubank and Rietspruit drainage area (Butzer 1976). The Sterkfontein Valley is a karst landscape with numerous limestone caverns and sinkholes, subject to erosion by water action. This means that the mid-Pleistocene Sterkfontein Valley looked somewhat different to what it does today. From the geomorphological analysis, it has been established that a fair amount of material has been eroded from around Swartkrans, resulting in a lower valley floor. There was an undulating upland to the rear of the cave, which has now been reduced to a small hill with a relief of about 40m. It is highly likely that Swartkrans Hill had twice the present area, but only half its present relief at the time when the cave opened (Butzer 1976).

The depositional sequence is thought to reflect a predominantly open grassland or parkland environment, similar to that of today (Figure

3). The occurrence of trees and bush cover was likely to be quite variable, particularly in valleys, along stream margins and around sinkholes (Figure 4). The evidence points toward a very similar climate to that of the present, possibly slightly wetter than today (Butzer 1976).

Based on the fossil bovid assemblage from Swartkrans and other sites Vrba (1975, 1985a, 1985b) has reconstructed palaeoenvironmental conditions in the Sterkfontein Valley. Bovids are a useful means of reconstructing past environments for a number of reasons. They are the most common large mammals in African Miocene-Recent assemblages. They can reliably be identified to species level, based on their cranial anatomy. There has been a rapid turnover of species through time. Finally the biology of extant species has been well studied and it has been found that bovids are habitat specific. This data may be applied to the fossil data. In addition, early hominids were also large-bodied, mobile, endemic, savanna mammals, all traits shared with bovids (Vrba 1985b).

There is a close relationship between vegetation type and the particular group of bovid that will inhabit the area. The Alcelaphini (hartebeeest-wildebeest-blesbuck group) and Antilopini (gazelle-springbuck group) are associated with open grasslands with moderate rainfall (+/- 400mm/yr) not with bush-covered areas (Vrba 1975, 1985b).

The bovid evidence appears to indicate a major environmental change through time. From about 2,5 to 2,0 million years ago, the Transvaal environment changed from a wetter, bush-covered environment to a more vegetationally open, arid environment (Vrba 1985a, 1985b). Robust australopithecines would therefore have had to cope in an open, drier environment. This would have an impact on their ranging patterns. In a drier environment resources are likely to be more patchy and hominids may have had to be fairly mobile in order to forage successfully.

Heavy stable isotopes, such as $^{87}Sr/^{86}Sr$ are a potential method by which one may test predictions of hominid ranging behavior. If the isotopic variation of an area can be determined by analysing the soils and plants present, and $^{87}Sr/^{86}Sr$ ratios obtained for hominid specimens, it may be possible to detect areas of intensive food resource utilization. This method has been applied to research projects in a number of fields, including palaeodietary studies in the Southwestern Cape, the sourcing of elephant ivory and rhino horn and the tracing of mobility patterns in the American Southwest. The results, conclusions and success of these projects are discussed in the following section.

2.4 Previous studies of source tracing using heavy isotopes

a) Introduction

The heavy stable isotopes, such as strontium and neodymium originally were used as geochemical tools in the study of the development of the earth. The archaeological and palaeological application of strontium analysis, particularly in palaeodietary studies, has been applied only relatively recently. A large amount of research was carried out in the 1950's and 1960's, mostly dealing with the effects of ^{90}Sr fallout due to above ground nuclear testing. This provided much useful information and has led to increasing research into the use of strontium, barium and calcium as a means of palaeodietary investigation (Sillen and Kavanagh 1982). The application of heavy isotopes, particularly those of strontium, is more recent and they seem to have great potential in archaeological and palaeological research.

Although initially developed as a geochemical technique for sourcing, as well as dating and characterising different rocks and formations, strontium isotopes have also been used in a number of ecological studies. The vast amount of geological information available, coupled with these environmental studies, have provided a foundation for the use of heavy stable isotopes in archaeological research. Although strontium isotopes are at present the most widely used, other isotopes such as those of neodymium and lead, may also be of use. This will require some further investigation and at present research is being conducted into their suitability (Lee-Thorp *et al* 1992; van der Merwe *et al* 1990; Vogel *et al* 1990).

Strontium isotopes have the potential to become a valuable tool as biogeochemical tracers in the study of animal and human ecology and behavior. There are a wide variety of possible applications:
1. In an area of known geochemistry, strontium isotope ratios of animal tissue samples may allow the determination of spatial feeding patterns.
2. Modern patterns of migration may be modelled by the analysis of stomach content and the differential turnover rates of strontium in various

animal tissues. This may also be applied to archaeological material, based only on bone samples (Sealy and Sillen 1988; Sealy *et al* 1991).

3. It may be possible to trace the movement of individuals in a group, who may have differing ranging areas. If based on factors such as gender, age and social status, additional information on the social behavior of the group will be obtained.
4. The origin and transport of specific, nutritionally important foods, such as geophytes and other seasonally available items, may be traced. By examining the characteristic isotopic ratios of the food items and the geology of the specific study area, one may be able to locate the place of origin of key resources. Not only are food items traceable, but it is possible to source other resources, such as the movement of Neolithic *Spondylus* shell artifacts in Europe (Shackleton and Elderfield 1990).
5. Characterisation of human behavior, for example subsistence patterns, food sharing and exchange and marital residence patterns, may be examined through strontium isotope analysis of a population (Ericson 1985, 1989; Krueger 1985). This may be achieved by the analysis of different tissues, such as enamel and cortical bone, as each tissue has different turnover rates.

b) Potential problems and possible solutions

There are a number of problems inherent with the technique. An important factor is sufficient geological variation within the study area. The various proposed catchment areas must be isotopically distinct from one another to allow comparison. Preliminary deductions can be made through the consultation of geological maps, which can provide initial data on the location, age and variation in rock types. The geology of the Sterkfontein Valley is well documented and is described in detail in Section 2.2. Once the location and variety of rock types is known, it is necessary to obtain isotopic ratios of each. This will allow the estimation of possible isotopic ratios within and between catchment areas.

Pollution, either through land use, industry or chemical contamination, can result in $^{87}Sr/^{86}Sr$ ratios that are not a true reflection of the original natural strontium isotope pool. This pollution may originate from atmospheric deposition of windborne material, such as flyash or dust or from water transportation of dissolved material. If the origin of the contamination can be detected and measured, it may be possible through the use of mixing equations, to determine the degree of contamination and obtain a measure of the locally available strontium isotopes.

Complications may arise with dietary studies, as small amounts of high strontium foods may mask the contribution of low strontium foods, which may form the bulk of an individuals diet. The measurement of the strontium content (ppm) of edible foods available will provide an indication of potential high strontium foods.

When examining behavioral patterns such as territoriality, ranging behavior or migration, the definition and characterisation of a group or individuals catchment area must be carefully examined. There are no specific spatial definitions for areas of major food procurement. There is no definite boundary to which an individual or group will adhere. The actual area covered will be affected by factors like group or individual mobility, topography, feeding habits or the seasonal availability of food (Ericson 1985, 1989). This is discussed in detail in Section 3, ranging behavior and foraging patterns.

In order to take the above factors into account, a number of approaches may be pursued. The direct analysis of a large sample of individuals from a population would provide an average $^{87}Sr/^{86}Sr$ ratio for the group. Another approach is the analysis of soils and biological samples (eg. plants) from a number of locations within the study area. This would provide an indication of the variation in the strontium isotopes available and allow the comparison of various mixtures with models of catchments. In other words, if an individual or group has a catchment area of "X", it most likely that their $^{87}Sr/^{86}Sr$ ratio will be very similar to the $^{87}Sr/^{86}Sr$ ratios of food items occurring in area "X", and so on for area "Y" and "Z".

Finally, the analysis of prehistoric and fossil bone will be affected by diagenesis. Diagenesis can be defined as "all of the histological, crystalline, chemical and isotopic changes which skeletal tissues undergo from the moment of death, including both the chemical destruction of skeletons and the process of fossilization" (Sillen 1993). Diagenetic change will obscure the original biological signal and the non biological strontium must be removed. This, however is not a factor in this particular study as all the samples are of modern plants and soils. Diagenesis is, however a cause of concern and one must be aware of the complications that can arise if ignored.

The applications of strontium isotope analysis are widespread, covering ecological and behavioral studies, be they modern, archaeological or palaeological. The following case studies provide an indication of the utility and efficacy of the method.

c) Environmental and ecological applications

1.) Fly ash

Strontium isotopes have been used in environmental impact studies, particularly dealing with the atmospheric deposition of material, such as fly ash (Straughan *et al* 1981; Hurst and Davies 1981). There has been some difficulty in attempting to monitor the deposition of material produced by coal-fired power plants. A major difficulty was the ability to distinguish between natural and deposited material. Strontium isotopes were seen as a possible means of identifying both natural and foreign material.

In a study carried out in the western United States, greenhouse experiments were done to examine the efficacy of strontium isotopes as a means of detecting atmospheric flyash (Straughan *et al* 1981). It was found that coal deposits in the western U.S. have a higher strontium content that elsewhere in the U.S, average strontium content of the western coal being about 300 ppm. Strontium in flyash has been estimated to be about 1334 ppm and the content tends to increase as particle size decreases. Soils also have a strontium content of approximately 300 ppm, thus any deposition of flyash should result in an increase in the strontium content of the soil (Straughan *et al* 1981). A similar project was carried out in the same area (Hurst and Davies 1981).

In both cases the strontium isotope ratios of soils, flyash deposits and plant samples were obtained. Straughan and others (1981) examined plants and prepared soils under greenhouse conditions in an attempt to model ideal natural conditions. The results revealed that there was a significant difference between the $^{87}Sr/^{86}Sr$ ratios of the soil (0.71097) and flyash (0.70807). The same results were obtained by Hurst and Davies (1981). Sensitivity is high at low concentrations of flyash (+/- 1%). As the strontium content of leaves increased, the $^{87}Sr/^{86}Sr$ ratio decreased, suggesting that flyash strontium may contribute significantly to the soil strontium pool (Straughan *et al* 1981). It is important to note that the biological accumulation of strontium is not a simple mixing process and will be affected by local circulation and precipitation patterns. The vegetation will also selectively absorb fly ash strontium, in this way increasing the contribution of strontium from an outside source. Further greenhouse experiments to clarify exchange reactions would be a logical progression of such a study. Although the data has been derived from controlled experiments, under greenhouse conditions a study of the natural environment, now that the technique has proven suitable, will also be required. The sampling of vegetation from the vicinity of a coal-fire power station would prove useful, as it would provide a direct measure of the environment, subject to all the various environmental factors, such as precipitation and wind direction.

There have been a number of investigations dealing with the source and flow of nutrients within ecosystems (Gosz *et al* 1983; Graustein and Armstrong 1983; Graustein 1989). These deal primarily with the atmospheric transport and deposition of material in a number of ecosystems and have been discussed in more detail in Section 2.1.

2.) Elephant ivory and rhino horn

An exciting application of isotope analysis has been the source tracing of elephant ivory from a number of locations in Africa (van der Merwe *et al* 1990; Vogel *et al* 1990). In an effort to aid the conservation of the elephant, a method was developed to determine the area from which the tusk originated. The use of a single isotope, such as carbon or nitrogen could not provide the necessary distinction between areas. This was due to environmental similarities between areas.

A correlation between carbon and nitrogen isotope ratios reflect relationships between climate and vegetation. Some regions, eg. Botswana and the Kruger National Park, yielded very similar results for carbon and nitrogen. This was due to the similarity in environment. In such cases the use of $^{87}Sr/^{86}Sr$ ratios allow one to clearly distinguish between the areas, because of differing local geologies. In the case of the Sterkfontein Valley study, only heavy isotopes of strontium are being used. It would be thus pertinent to examine the isotopic data on elephant ivory sources, based only on $^{87}Sr/^{86}Sr$ ratios.

The strontium isotope data from both studies have been pooled (Table 5) as a means of examining the whole of Africa (van der Merwe *et al* 1990; Vogel *et al* 1990). All the results were averaged and compared (Table 6). Certain areas have a very distinctive isotope ratio, indicating a very different geological substrate, such as the results for Sierra Leone ($^{87}Sr/^{86}Sr = 0.73314$) and Knysna ($^{87}Sr/^{86}Sr = 0.710602$). Although the number of samples from the northern areas of Africa are small, it is still clear that there are strontium isotopic differences between the various countries.

A study of over 100 adult elephants from 10 African countries, based on their three isotopic ratios, has shown the potential of using isotopic ratios to source trace ivory over a wide geographic area (van der Merwe *et al* 1990). A similar study carried out on southern African samples from

Namibia, South Africa and Zimbabwe, has also provided evidence for the suitability of the technique (Vogel *et al* 1990). Through the use of multivariate statistical analysis, it was possible to clearly distinguish between the various sample areas. For the method to be more widely applied, a larger database is needed. In addition the use of other isotopes, such as lead or neodymium, may result in more distinctive "fingerprints". The method may also have further application in the control of other illegal wildlife products, such as rhino horn.

In a similar fashion stable isotopes may be used to source trace the origin of rhino horn. In this way it may be possible to differentiate between "legal" and poached horn and thus allow trade control of such material (Lee-Thorp *et al* 1992; Hall-Martin *et al* 1993). About 150 samples of black and white rhino horn were obtained from various locations in South Africa, Namibia and Zimbabwe. The samples were analysed for carbon, nitrogen, strontium, lead and neodymium.

Rhino horn is composed of hair and not calcified tissue. This fact resulted in new preparation techniques being developed to extract the required isotopes. When the horns were analysed for carbon and nitrogen, a lot of variation was observed. An analysis of two entire horns at 5cm intervals was carried out, as a means of picking up any seasonal variation. When one of the individuals from Addo, Pixie, was analysed for strontium isotopes, it was found that there was variation between the base and tip of the horn. The tip (3958 AD002) had an $^{87}Sr/^{86}Sr$ of 0.71719, while the base (3964 AD008) had a ratio of 0.71440 This variation was due to the individual having been translocated from one geologically distinct area to another. If this occurs, the base of the horn will represent the new environment, while the tip will be indicative of the earlier environment, as the new growth will be at the base of the horn (Hall-Martin *et al* 1993; Lee-Thorp *et al* 1992)

The use of $\delta^{15}N$ values together with $\delta^{13}C$ values do not serve to separate the sample regions, in the same way as with the ivory samples. There is too much overlap between regions. Strontium isotope ratios, along with nitrogen and carbon ratios, are able to characterise each region, although there is some overlap. Additional heavy isotope ratios, such as lead ($^{206}Pb/^{204}Pb$) and neodymium ($^{143}Nd/^{144}Nd$) provide additional data which serves to successfully differentiate sample locations. The use of neodymium appears to be particularly useful as there appears to be very little local variation.

Using only strontium and neodymium ratios (Tables 7, 8, 9), it is possible to distinguish between rhino locations, although some areas are more clearly defined than others (Figures 5 and 6). There is some clear clustering for the South African rhino data (Figure 5), particularly for samples from Pilanesberg and the Addo Elephant Park. There is an indication of two distinct populations in both the Kruger National Park and Mkuze, each population being isotopically distinct. There is a lot of overlap between the Umfolozi and Hluhluwe groups, indicating a very similar geological environment. This serves to emphasise the necessity for distinct geological differences between areas under comparison, when using strontium and neodymium isotopes. If there are distinct geological differences in an area, it is possible to clearly distinguish between groups inhabiting the area, as indicated by the data from Mkuze and the Kruger Park. The outliers are most likely to be individuals that have been relocated through conservation programs. The isotopic data from Namibia and Zimbabwe (Figure 6) shows some indication of clustering, but the sample sets are very small and thus may not reflect all possible isotopic variation effectively. A small sample set may be problematic particularly if individuals range over a wide area and the environment is geologically varied.

d) Palaeological applications

Strontium isotope and trace element analysis have also been applied to a palaeological investigation into the palaeosalinity of fossil fish habitats (Schmitz *et al* 1991). A key question in palaeoichthyology is whether the first vertebrates evolved from freshwater or marine environments. The ability to accurately distinguish between the palaeosalinity of differing fossil fish habitats would be useful in providing an answer to this problem.

Some information can be obtained from sedimentological and palaeoecological studies of the fossil fish deposits. With regard to extremely old fossil beds, there is very little geological or palaeontological information available. A further complication arises from the possibility of postmortem transport of material from one environment to another, especially with river-dwelling species. All these factors can complicate the reconstruction of palaeosalinity habitats. The actual fossil matrix does not therefore appear suitable for such reconstruction. It would be most favourable to obtain some form of measurement from the fossil fish remains themselves (Schmitz *et al* 1991).

Fish teeth, scales, spines and shields are often very well preserved and it is reasonable to assume that they may have retained some chemical information about the waters in which they developed. This assumption is based on the excellent preservation of extremely fine histological details and the conversion of the carbonate apatite to a more stable fluorapatite, during fossilization. These well-preserved remains are often the well-mineralised or hyperminerlised parts of the fish skeleton. Diagenetic change may prove an important factor when dealing with fossilised bone, as it may cause the biological signal to be obscured. This does not appear to have been taken into account in this particular study (Schmitz *et al* 1991). Although the fossil samples were mechanically and chemically cleaned of the external matrix, the investigators do not appear to account for any post-mortem chemical changes to the bone mineral.

Forty-six samples of apatite from fossil fish remains, ranging in age from Silurian to Recent, were analysed. The $^{87}Sr/^{86}Sr$ ratio and Na, F, Sr and La content were obtained for each sample (Schmitz *et al* 1991). These chemical parameters are thought to provide reliable information of palaeosalinity conditions of fossil fish habitats. Strontium isotope ratios and the chemical abundance of Sr, Na and F differ characteristically between modern seawater and freshwater. Samples of Recent fish were obtained from waters of known strontium ratio and salinity and analysed. The results indicated that the chemical makeup of the fish skeletons did represent the strontium isotope ratio and elemental abundance of the water in which they developed.

The data obtained for the fossil samples indicated that it was possible to distinguish between marine and freshwater species, even in very old (400 mya) samples. The $^{87}Sr/^{86}Sr$ ratios of marine specimens were very similar to the $^{87}Sr/^{86}Sr$ ratio of contemporary seawater. Freshwater specimens had generally much higher $^{87}Sr/^{86}Sr$ ratios than seawater of the same age and infact were similar to the $^{87}Sr/^{86}Sr$ ratios of modern river and lake water. There was a strong correlation between palaeosalinity results based on $^{87}Sr/^{86}Sr$ ratios of the fossils and palaeosalinity determined by conventional sedimentological and palaeontological methods (Schmitz *et al* 1991). This consistency between the two forms of analysis may be the result of diagenetic change, whereby the fossil material has, over time, reached chemical equilibrium with the surrounding deposits. It may prove useful to also get the $^{87}Sr/^{86}Sr$ ratios and element abundance of the matrix surrounding the fossils. Further investigation, taking diagentic change into account, may provide further clarity. A strontium isotope analysis of Miocene fossil salmon bone and their surrounding sediments showed no differences in their respective ratios, even after the fossil material was treated for diagenetic change (Koch *et al* 1992).

e) Archaeological applications

The movement of people from one location to another may be difficult to detect using conventional archaeological techniques. Although ethnographic and ethnohistoric data on movement patterns provide some information, they may be biased or incomplete. Strontium isotope analysis of prehistoric populations and their environment may allow one to trace patterns of movement geochemically. Once the variation in $^{87}Sr/^{86}Sr$ ratios of the study environment are known, it may be possible to trace individuals to their place of birth on the basis of the strontium isotope ratios of their bones and teeth.

Permanent tooth enamel is largely by during adolescence and will not be reworked over during the individuals lifetime. This because enamel does not contain any organic structures and will not recrystallise after formation (Steele and Bramblett 1988). Bone is remodelled every seven to ten years, with the inorganic component being completely replaced. This will result in the isotopic composition of the bone changing over time (Lowenstein and Weiner 1989). Differences between the isotopic ratios of enamel and bone will thus reflect the residential history of an individual (Price *et al* 1994).

The permanent teeth are almost fully developed by adolescence and the isotopic composition of the enamel will reflect the diet and environment where the individual grew up. The strontium isotope ratio of bone represents the diet and environment of the last ten years of an individual. If the person has moved to another area and remained there for more than ten years, the isotopic composition of the bone will be the same as the composition of the new environment (Price *et al* 1994). A difference between the $^{87}Sr/^{86}Sr$ ratios of enamel and bone will indicate that the individual has moved away from the place of his/her birth.

A pilot study by Ericson (1985) examined movement patterns of the prehistoric Chumash Indians. The Chumash occupied part of the Pacific coast and the interior of the Santa Monica Mountains near Los Angeles. Ethnographic information indicates that Chumash families frequently migrated between villages and had exogamous weddings (Ericson 1985). Osteological material from two sites, one coastal and one inland, were analysed for strontium isotope ratios. The second molar and metatarsal of a male and female from Malibu (coast) and an individual from Century Ranch (inland) provided the samples. In addition geological samples from each area were obtained and their $^{87}Sr/^{86}Sr$ ratios determined.

From the analysis of these teeth, it was concluded that the $^{87}Sr/^{86}Sr$ ratios of the female did not change significantly from adolescence (M_2 $^{87}Sr/^{86}Sr = 0.7086$) to adulthood (Metatarsal $^{87}Sr/^{86}Sr = 0.7088$). The inland individual ($^{87}Sr/^{86}Sr = 0.7077$) appeared to have an elevated $^{87}Sr/^{86}Sr$ ratio relative to the ratio of the local environment ($^{87}Sr/^{86}Sr = 0.7045$). The Malibu female appears to have stayed on the coast for her whole life, whereas the inland person seems to have moved around. This is supported by ethnographic evidence indicating that inland Chumash moved to the coast in spring and summer (Ericson 1985).

Residential mobility and migration patterns of prehistoric people in east-central Arizona were examined by Price and others (1994). There are numerous archaeological sites in the area and the burial populations have been well documented. Two sites were selected, Grasshopper Pueblo and Walnut Creek. Grasshopper Pueblo appears to have been an aggregation site, with the coexistence of three social groups during the development of the site. These groups are distinguished by different building styles, ceramics, morphological traits (cranial deformation, growth rate) and burial practices. They are thought to have moved into the Grasshopper area, as other regions were being depopulated. Thus the burial population is representative of local and outside inhabitants (Price *et al* 1994). In addition, the geology of the area is varied and has been well studied. Grasshopper Pueblo is located on Upper Palaeozoic Limestone with $^{87}Sr/^{86}Sr$ ratios ranging from 0.70893 to 0.71627. Walnut Creek on Precambrian intrusive rocks range from $^{87}Sr/^{86}Sr$ ratios of 0.70718 to 0.71523.

Twenty samples of bone and tooth enamel, as well as eight bone-tooth pairs were analysed. It was found that the bone isotope ratios were relatively consistent to those of tooth enamel. A number of burials from Grasshopper Pueblo and Walnut Creek were within the range expected for the local diet, based on agricultural crops and plants and animals gathered elsewhere. The human isotopic ratios from Grasshopper Pueblo (Mean $^{87}Sr/^{86}Sr$ bone = 0.71012) are similar to the ratio for the Naco Limestone ($^{87}Sr/^{86}Sr$ = 0.70893) in the area, which suggests that this was the main area from which the people obtained their food. The slightly higher ratio may be due to other foods originating on the Supai Sandstone ($^{87}Sr/^{86}Sr$ = 0.71627). This suggested that these individuals had lived there for their entire lives. Three individuals from Grasshopper Pueblo and four from Walnut Creek had significantly different enamel isotope ratios than those of the local environment. The isotopic ratios for bone from three of the above mentioned skeletons were similar to the those of the local environment, indicating that they had spent at least 7 to 10 years in the area, based on differential turnover rates of tissues. It is likely that these people were not indigenous to the area and had migrated in from elsewhere. These patterns of local and migrant settlement as indicated by the isotopic analysis are consistent with previous models based on other forms of analysis (Price *et al* 1994).

Modern and prehistoric foodwebs in the southwestern Cape of South Africa have been well studied in an attempt to understand the dietary habits of prehistoric people inhabiting the area. The use of strontium and calcium analysis has played an important part in this ongoing investigation (Sealy and Sillen 1988; Sealy *et al* 1991). In areas of contrasting geology or in coastal areas where the terrestrial $^{87}Sr/^{86}Sr$ ratios are different from seawater ratio (0.70923), it is possible to use strontium isotope ratios of bone to determine the relative importance of foods from different isotopic environments (Ericson 1985; Krueger 1985).

In the southwestern Cape it was expected that $^{87}Sr/^{86}Sr$ ratios of inland terrestrial environments would differ from those of coastal and marine environments. Marine plants and animals will have the same or very similar $^{87}Sr/^{86}Sr$ ratios as seawater (0.70923). Similarly coastal marine sands should have strontium isotope ratios close to that of seawater. Inland areas are located on Precambrian to Cambrian rocks and will have relatively higher $^{87}Sr/^{86}Sr$ ratios because of their age, resulting in ^{87}Sr enrichment. The expected isotopic patterns are summarised in Table 10.

A sample set of modern indigenous animal bones from the coastal, marine and inland environments was collected for analysis. Samples of archaeological animal bone and prehistoric human bone were obtained and their $^{87}Sr/^{86}Sr$ ratios determined. The isotopic nature of animals from the coastal/marine areas was found to be markedly different from those of inland animals. Animals with marine derived diets and coastal terrestrial animals had isotopic ratios very close to that of seawater, ranging from 0.70926 to 0.70933 for marine feeders and 0.70938 to 0.71169 for coastal terrestrial animals. In contrast the inland specimens had

$^{87}Sr/^{86}Sr$ ratios from 0.71543 to 0.71794. These isotopic differences can be used as a means of reconstructing prehistoric diet.

Five samples of whole bone from coastal skeletons and four from inland skeletons were analysed for their respective $^{87}Sr/^{86}Sr$ ratios. It was found that all the coastal skeletons had isotopic ratios close to those obtained for marine and coastal animals, ranging between 0.70920 and 0.71009. The inland skeletons had much higher $^{87}Sr/^{86}Sr$ values, due to a ^{87}Sr enriched environment. Their isotopic ratios were from 0.71382 to 0.71898. This seems to indicate that inland people spent little, if any time at the coast, while coastal dwellers seem to derive all their bone strontium from purely coastal terrestrial and marine resources (Sealy *et al* 1991).

A complication is that some of the strontium in the archaeological bone may have been of diagenetic rather than biological origin. The coastal individuals were buried in shell middens and had very high strontium contents. This strontium may have been derived from the marine shells in the middens, as shells have elevated strontium levels due to the affinity for strontium uptake during shell growth (Kulp *et al* 1952). This would explain why the coastal skeletons were so close to the $^{87}Sr/^{86}Sr$ ratio of seawater.

Four skeletal samples, two coastal and two inland, and four faunal samples were analysed by means of the solubility profile technique (Sillen 1986; Sillen and LeGros 1991; Sealy and Sillen 1988; Tuross *et al* 1989). The faunal samples, a modern sheep and three archaeological specimens yielded valuable results. The $^{87}Sr/^{86}Sr$ ratios of the modern sheep remained constant through all the washes. A sample of archaeological hartebeest (*Alcelaphus buselaphus*) from the Kasteelberg shell midden yielded $^{87}Sr/^{86}Sr$ ratios that became more enriched through the various washes, moving from a marine signal to a terrestrial one. Similarly, results of an analysis of mammoth bone from Vineu, France, indicated the removal of a diagenetic signal. By means of the solubility profile technique, it may thus be possible in certain circumstances to obtain a biological strontium signal from archaeological bone.

The analysis of the coastal skeletons washes indicated that, although there was some diagentic strontium present, the overall biological strontium was still derived from a coastal terrestrial/marine based diet. With an expanded database, it seems that the use of strontium isotopic analysis will provide a valuable means of studying palaeodietary behavior.

3. RANGING BEHAVIOR AND FORAGING PATTERNS

a) Introduction

Intensive study of primate species during the 20th century has resulted in a wealth of information regarding patterns of growth, sexual behavior, social patterning, dietary selection and ranging behavior. This information has bearing on the reconstruction of early hominid behavioral patterns.

The suitability of different primate species as models for early hominid behavior has been much debated (eg. Tooby and DeVore 1987; McGrew 1991). It would be unwise to make direct analogies between extant primate behavioral patterns and early hominid behavior, but primate studies nevertheless may be used to set constraints and to provide guidelines for interpretation. There are two central types of models that may be applied to hominid behavioral studies. The first may be called a referential model, where a real phenomenon such as a gathering economy or extant primate species is used as a referent to a less tangible phenomenon. The second type of model is a conceptual one, with sets of concepts or variables that are defined and whose relationships are analytically specified (Ghiglieri 1987). In the case of the Swartkrans hominids, it is pertinent to apply a referential model, rather than a conceptual one, as the focus is to examine their possible ranging behavioral strategies and there are a number of suitable primate referents that will aid in such a study.

An attempt will be made to relate the strontium isotope data from the Sterkfontein Valley and the surrounding areas, with reported home ranges of selected primate species, as well as contemporary hunter-gatherers. Each species or group will be discussed in terms of their habitats, social, dietary and ranging behaviors. In addition to the observed primate behavioral data, the predicted home range for each primate species and robust australopithecines will be calculated and compared to observed primate home ranges. These data will in turn be compared and related to what is currently understood about early hominid ranging behavior and foraging strategies.

A possible method by which to test these home range predictions is to examine the variation in strontium isotope ratios in the Sterkfontein Valley and compare them to the predicted home ranges of early hominids, primates and hunter-gatherers. This will provide an indication of what the possible range of strontium isotope ratios may be for an individual in the Sterkfontein Valley and surroundings. In other words if an individual had a minimum and maximum home range, one would look at the strontium isotope distribution in the area covered by both the minimum and maximum ranges to obtain the minimum and maximum range of strontium isotope variation. The minimum and maximum home range areas of the selected primates, hunter-gatherers and robust australopithecines (Table 11 and 12) were projected on to geological maps of the Sterkfontein area,(Figures 7, 8, 9, 11, 12, 13, 14, 16, 17), as if they all hypothetically occurred in the Sterkfontein Valley. The small central circles are representative of the minimum home range size, extended in four quadrants and the outside circle represents the maximum area covered.

The following primate species were selected: gorillas, orangutans, chimpanzees (including bonobos), and several species of baboon, as well as two groups of hunter-gatherers, the !Kung and G/wi. These have been considered as the mostly likely analogues for reconstructing early hominid behavioral patterns. Early hominids were thought to have adapted to open savanna environments and thus it is logical to firstly look at savanna dwelling primates, such as baboons, hunter-gatherers and savanna chimpanzees, and then at forest dwelling species such as forest chimpanzees and gorillas. No single species that may be seen as being the only analogue, but one should rather examine a suite of characteristics based on the data available on the above mentioned groups and species.

A number of features need to be defined when looking at ranging behavior and foraging strategies. The **day range** is the distance travelled by and individual or group in a day, and this will vary from individual to individual. The **home range** is a combination of all the day ranges of all the member of a group. Individual home ranges may be smaller or larger than that of the groups, and is influenced by the age and sex of the individual. A group member's **year range** is seen as all the areas visited by that individual over a period of a year and may not be the same size as the home range. There are certain areas within the home range that are intensively used throughout the year and are called **core areas.** These core areas may also shift from season to season (Fleagle 1988; Goodall 1986). A home range is not the same as a **territory**, although a territory may form part of a home range. A territory may be defined as "... an area more or less exclusively occupied by an individual or group by means of repulsion through overt defense or some form of communication" (Dyson-Hudson and Smith 1978). This will include both aggressive defense and more subtle means of communication such as scent or visual markings.

It is thought that territoriality will result when resources are limited and defendable (Mitani and Rodman 1979). The defense of such a resource will depend on the ability of the individual or group to monitor the boundaries of their home range as a means of successfully detecting any potential threats. If defending a particular resource does not provide sufficient yields to an individual or group, then that resource will no longer be defended (Mitani and Rodman 1979). It is possible for species or populations to become territorial only at particular times of the year, normally as a result of seasonal occurrences of certain resources. Certain critical resources with particular spatial and temporal distributions may provide sufficient energy or advantages to merit their defense against other competitors. There is some genetic basis to territorial behavior, but is not genetically fixed and will thus not always be expressed. The ability to exhibit territorial behavior only at certain times is a possible strategy individuals may use when it is to their adaptive advantage to do so (Dyson-Hudson and Smith 1978)

One of the key factors affecting ranging behavior and foraging strategies of primates is diet. There are a number of other factors involved, but ultimately all are linked to diet in one way or another, such as group size, environmental conditions and the presence or absence of competitors. There is a wide variety of food items available, but primates tend to be very selective in terms of what food items to consume and will only exploit a small proportion of available foods. The choice of an item may be influenced by the energetic value, protein availability, individual specific nutrient requirements, secondary compounds and toxins, spatial and temporal distributions and both intra- and interspecific competion (Chapmann 1988; Clutton-Brock 1977; Oftedal 1992). An individual's foraging strategy may be considered successful only if the diet obtained provides sufficient nutrition to satisfy the requirements of the forager. Nutrients consumed in marginal or inadequate amounts may adversely affect an individual's performance and therefore he/she must develop suitable alternatives, such dietary flexibility or altering home range size, to prevent this.

If food availability decreases non-migratory animals may either increase the time spent foraging or become less selective and concentrate on poorer quality food items (Clutton-Brock 1977). Depending on the primate species, the ranging behavior and group movements will be affected in varying degrees by the dispersal of food resources. Seasonal variation in the diet is closely correlated to changes in ranging behavior. Species will respond to specific problems in a number of ways, varying from species to species (Chapman 1988). Some species may respond to decreasing food availability by reducing day range length and the time spent feeding, while other species may actually increase them (Clutton-Brock 1977).

The size of a group will also have an effect on the ranging behavior of the group (Clutton-Brock and Harvey 1977). A larger group generally needs a larger home range to support all its members, although there are exceptions, such as the Gelada Baboon. Geladas are able to live at very high population densities within fairly small home ranges, because of their highly specialised diet. Although groups would have to travel further, the advantages of a larger group include improved predator defense and easier access to resources because of superior numbers, more of an interspecies competitive advantage (Isbell 1991).

b) Baboons

Baboons are very adaptable and have managed to inhabit a number of different habitats. Most species are savanna dwellers, but have also managed to move into and successfully populate environments as diverse as deserts, swamps, forests and montane areas (Whiten *et al* 1992).

The key to this adaptation to varying habitats may be a product of baboon dietary flexibility. They are able to extract nutrients from almost all sections of the environment. Although the foraging strategies of baboons are adaptably broad, they are very selective in what food items they consume and will only utilize a specified selection of the plant food species available. For instance, Drakensberg baboons will consume corms from only one species of *Hypoxis*, although there are three very similar species growing in the same area. This selectivity may be based on nutritional factors such as the protein content, amount of fibre and the presence or absence of secondary compounds (Whiten *et al* 1992). Baboons may be seen as ecologically flexible omnivores, but highly selective in their diet choice and home range use (Barton *et al* 1992).

The Yellow Baboon (*Papio cyanocephalus*) inhabits a semi-arid savanna environment. Altmann and Altmann (1970) spent a long period of time observing these baboons in Amboseli, Kenya. The group size is extremely variable, ranging from groups of 16 individuals up to troops of over 200 members. The group structure is flexible as males tend to move from group to group and may also range alone.

Although the size of groups varies, yellow baboons have a fairly fixed daily routine, with only slight seasonal variations. Day ranges are normally about 5km, between sleeping sites and foraging areas. The furthest distances will be covered during the wet season, but baboons will tend to remain closer to their sleeping sites in drier periods. Yellow baboons have comparatively fixed boundaries for their home ranges, with the furthermost boundaries representing the extent of travel during the wet season. The home range is heterogeneous, with certain areas only visited at particular times of the year (Altmann and Altmann 1970). After more than 159 days of observation, the home ranges of the Altmann's study group was estimated to be about 24.2km^2. Devore and Hall (1965) have estimated ranges of 7.7 to 40km^2 for other savanna baboon groups. When the average home range for savanna baboons is projected on to the Sterkfontein Valley geological map (Figure 7), it is clear that they would range over a number of geologies and thus have considerably variable strontium isotope ratios. Approximately 65 to 70% of the area covered by savanna baboons would be on a dolomitic substrate, with shales, quartzites and mafic rocks forming the remaining area.

The Hamadryas or desert baboon (*Papio hamadryas*) is found in the dry regions of eastern Sudan, Somalia and the eastern Ethiopian lowlands. There is little water available and as a result tall trees are scarce. The scarcity of tall trees forces the Hamadryas baboons to sleep on vertical cliff faces, as a means of avoiding predators (Kummer 1968).

The basic unit of a Hamadryas troop is the single male group. This made up of a single adult male with several females constantly and exclusively associated with the male. These single male units live together in large troops and as a whole can allow coordinated ground defense against any possible predators.

The daily routine remains constant throughout the year. The troop moves out from their sleeping rocks to the savanna to forage. Depending on the size of the group, individuals may spread out for up to a kilometer. Group sizes may vary from a single male unit of 6 individuals to a troop of more than 490 foraging members, while as many as 750 individuals have been recorded at a single sleeping site. Day ranges are from 4 to 19km, depending on the season. Home ranges are not possible to determine in the case of Hamadryas baboons, as troops are not constant in their membership (Kummer 1968).

Gelada baboons (*Theropithecus gelada*) are the only surviving members of a genus, which in the Pleistocene, was found throughout the grasslands of sub-Saharan Africa. Today Gelada baboons are only found on the Amhara Plateau in Ethiopia. Their sleeping areas are located in gorges and individuals do not move very far from them (Dunbar 1977).

Geladas are unique amongst baboons, as they are almost exclusive graminivores. Their dental morphology and hands have become highly specialised for subsisting on grass blades, seeds and rhizomes. They may occasionally eat flowers, small fruits or tubers, but at least 90% of their diet is grass. The proportion of blades, seeds and rhizomes consumed will change through the year, as a result of seasonal availability. Such dietary specialization allows Geladas to exist at a much higher population density than other baboons and primates. At the time of observation, it was estimated that there was 78 to 80 individuals per km^2 and that a single square kilometer of grassland may have been able to support up to 250 animals. Generally *Papio* species will occur at densities of between 5 to 15 individuals per km^2, although Hamadryas baboons only have a population density of 1.8 individuals per km^2 (Dunbar 1977; Kummer 1968).

The social structure of a Gelada community is complex, as there are various levels of stability with in a group. The smallest unit is the single male unit, which is very similar to that found amongst Hamadryas baboons. There are all male groups, composed of a stable social group of subadult males. A band is composed of all the single male units that share a common moving range, while the community is seen as a network of social relationships formed the bands that share a common area. There are also a number of temporary groupings, such as a multiherd, joint foraging group of single male units from two or more bands, or senior/junior groups of subadults and juveniles (Kawai *et al* 1983).

The home range of a band will overlap to varying extents with the home ranges of neighboring bands. The foraging herd may or may not include all the band members when moving through the home range. The size of the herd is largely affected by the amount of grasscover available. Individuals may range beyond their normal range, due to the availability of sufficient water supplies during the wet season or the local availability of a preferred food item during the dry season. On average the home range tends to be about 3 to $4km^2$ (Dunbar 1977). If their home range were to be projected on to the Sterkfontein geological map (Figure 8), Geladas would only exhibit strontium isotope ratios in the range characteristic for dolomites, their range being on 100% dolomitic substrata.

c) Kalahari hunter-gatherers

i) General hunter-gatherer characteristics

Frequent seasonal movement from habitat to habitat is one of the key features of hunter-gatherer behavior. This behavior is seen by some as a uniquely human one (Liebermann 1993). However this may not be the case and this issue is discussed in the following section on chimpanzees and bonobos. Hunter-gatherer mobility is closely related to the structure of food and water sources in a given environment, and thus foraging strategies are an important factor affecting the mobility of a group. Other factors such as social behavior and individual actions will also have an effect on the mobility of a population or group (Kelly 1983, 1992). The group will usually move to a different location when the daily cost of foraging in a certain area becomes more than the cost of moving to another region. Resource accessibility is important, the time and effort to obtain faunal and plant resources from an environment needs to be carefully balanced against the actual gains obtained from the environment (Kelly 1983; Liebermann 1993). In areas of relatively little food, hunter-gatherers will move more frequently and tend to camp in the center of their habitat. In richer environments, groups will be less mobile and tend to camp near ecotones, where a variety of habitats are accessible. Surface water sources also have an effect the behavior of a group. With the presence of adequate surface water, groups tend to be small and highly mobile, while in the absence of surface water groups will be larger and highly mobile (Hitchcock and Ebert 1989). As a general rule, hunter-gatherer groups will disperse in times of shortage and aggregate in seasons of plenty (Liebermann 1993).

There are two basic mobility strategies, namely circulating and radiating. Circulating mobility is typical of groups who depend on daily hunting and gathering to gain enough food and other resources. This form of mobility is favoured in tropical savanna or arid environments, as well as tropical forested areas. Circulating mobility has a number of advantages; avoidance of resource depletion, exploitation of a greater range of resources, flexibility of group size and the reduction of social stress or conflict. There are also a number of costs involved, such as limitations on property and untransportable resources and increased foraging time in less well-known areas (Kelly 1992; Liebermann 1993).

ii) !Kung and G/wi hunter-gatherers

The Kalahari San are one of the best understood hunter-gatherer populations and it is clear that they have managed to develop successful survival strategies to cope with living in a highly seasonal environment. However one must be aware that a number of changes have taken place in last 2000 years and that these changes will have had an effect on the lifestyles of hunter-gatherers. These include increasing contacts with outside populations, such as pastoralists. More recently groups have started spending more time at permanent waterholes, becoming more dependant on Herero or Tswana pastoralists for their livelihood. There have also been forced relocations of various groups and this would have a major effect on their lifestyle. These effects have been the subject of a longstanding debate amongst ethnographers as to how drastic changes have been for Kalahari hunter-gatherers (Solway and Lee 1990; Wilmsen and Denbow 1990).

The !Kung live along the northern fringe of the Kalahari desert, between Namibia and Botswana. They are, but one group of hunter-gatheres living in the Kalahari and are the best understood in terms of hunter-gatherer lifestyles. The area consists of longitudinal dunes and dry riverbeds, with both tree and bush savanna. The !Kung live in the Dobe-/Du/da area, about 1000 to 1200m above sea level. Summers are hot with a rainy period of 4 to 6 months, while winters are moderate to cool with no rain. The area itself forms a transitional zone between dry shrub savanna and the more lush areas near the Okavango River (Lee 1965, 1979; Yellen and Lee 1976).

!Kung subsistence is based on a systematic strategy of exploiting abundant food resources. Very little of their food gathering is left to chance. The areas inhabited by the !Kung tend to be rich, with very good supplies of water and plant resources. The !Kung have an intimate knowledge of their environment and know what and where particular food resources will be available during each season. In this way they can plan their activities to take maximum advantage of these resources, having in addition, a number of alternative strategies if complications arise.

Plant foods form the bulk of their diet, while meat is only of secondary importance. This division occurs because plant foods are abundant, locally available and fairly predictable, whereas game animals tend to be scarce and unpredictable. About 105 plant species are considered edible by the !Kung, but only 14 species comprise 75% of their vegetable diet. These species are important for a number of reasons. They are abundant and may have a long period of availability and include mongongo nuts, baobab pods, vegetable ivory palms, marula nuts, wild oranges and tsama melons (Lee 1965, 1979). Other plant species are sought out because they are easy to collect, like fruits rather than roots. Some are merely sought due to personal taste. This results in ranking of the plants. A similar ranking occurs with game animals. Although 54 species are considered edible, only 17 species are consistently hunted. There are also a number of personal, age specific and sex specific taboos that will influence the eating of animal species (Lee 1965).

A camp will be occupied for only a few weeks, with the occupants virtually eating their way out of the camp. In more recent times, the time spent at a particular camp may also be influenced by the presence of other groups, such as Herero or Tswana pastoralists (Barnard 1992). This means the longer the group remains in an area, the further they will need to travel each day to find sufficient food. !Kung are very selective in their food choice and will preferentially consume the most desirable foods in an area first. Hunting and gathering trips are kept as short as possible, minimizing travelling distances. However, the time and distance spent foraging and hunting will increase as the group stays longer in a single area, increases in size or due to varying resource availability form year to year (Lee 1965, 1979; Yellen 1976). There are two alternatives for coping with these problems. Foragers may travel further to get the most desirable foods or else they may switch to less desirable items and remain closer to camp.

!Kung groups normally comprise 10 to 30 members, although the composition of camps will change frequently. Groups are very flexible, with frequent shifts of individuals or families from camp to camp, a high incidence of visiting, including long term visitors from different territories and group members visiting other camps beyond their own range. Each group or band has a number of individuals who have a territorial claim to the land they occupy. These individuals are normally the older members of the band and tend to spend the majority of their time residing in their territory and not visiting as much as they would have in their youth. Their descendants and spouses will form the largest proportion of the band. This results in a close link between territoriality and band membership (Lee 1965).

Territories are very flexible and most will overlap with each other. The !Kung do not see a territory as an area of exclusive occupation. A !Kung territory may be defined as the area within which an independent band will move during their annual subsistence cycle. The locations and spatial configurations of territories are determined by the distribution of water and food resources. In wetter periods camps are larger and more permanent, but small, widely dispersed and short-lived in dry seasons (Yellen 1976). Some bands may even spend all year at a permanent waterhole, although most groups will move off in summer to exploit water and plant resources in other areas (Barnard 1992). Each group's territory will have a permanent waterhole, one or more mongongo nut forests, as well as a selection of both winter and summer foods. No two territories are the same and not all resources are equally available within a single territory, but each is capable of supporting some members throughout the year. If in need of a particular resource, members of an outside camp may make use of certain resources in another camps territory (Lee 1965).

In the Dobe area, the intensity of land utilization varies inversely with the distance from standing water sources. Day ranges for !Kung are about 9.6 to 11.2km away from camp with a total round trip of about 19 to 23km. The total annual range of the Dobe !Kung (population = 430) is approximately 2590km^2, with a population density of about 0.16 individuals per square kilometer (Lee 1965). On average however, the !Kung have ranges of between 300 to 1000km^2 (Barnard 1992, Yellen 1977).

G/wi bushmen live in the lower-lying central area of the Kalahari. Aggregation and dispersing units are generally larger than those of the !Kung and population densities are lower (0.07 individuals per square kilometer). Group sizes range between 21 and 85 individuals with territories of between 457 and 1036km^2, with an average size of 780km^2 (Barnard 1992, Silberbauer 1981). The G/wi have a different settlement pattern to that of the !Kung, tending to do the reverse. In wet seasons the G/wi will aggregate and disperse as family units during the dry periods. The reason for this, is that there is no available surface water during the dry season in the lower-lying Central Kalahari and the G/wi have to obtain water from plants and animals collected or caught (Barnard 1992).

Kalahari hunter-gatherers are most likely to range beyond the boundaries of the Sterkfontein Valley sample area and will probably have extremely variable isotopic ratios (Figure 9). Dolomites would form about 20% of their range, with the other geologies contributing in varying degrees. Unlike the Kalahari, the Sterkfontein Valley has very good water supplies and it is probable that the distribution of plant food resources would most likely affect the ranging patterns of hunter-gatherers.

d) Chimpanzees and Bonobos

Two species of chimpanzee are recognised, the common chimpanzee (*Pan troglodytes*) and the bonobo or pygmy chimpanzee (*Pan paniscus*) (Kano 1979). The common chimpanzee occurs from Sierra Leone to western Tanzania and Lake Tanganyika, but bonobos have a more restricted distribution, only occurring between Zaire and the Lualabo

Rivers in the Congo Basin (Duplaix and Simon 1977; Kano 1979). Both species are essentially forest dwellers, although common chimpanzees will also successfully inhabit savanna environments. The majority of research has been carried out in western Tanzania with emphasis on the areas around Lake Tanganyika. The predominant habitat is a mosaic of woodlands with intervening strips of riverine forest (Collins and McGrew 1988). A heterogeneous environment in terms of habitat type is important if one has a seasonally variable diet, as it allows the exploitation of a broader range of food items throughout the year. Chimpanzees and bonobos require access to both forest and open woodlands to forage successfully.

Bonobos live in low to medium altitude forests and secondary forest. They tend to avoid the more swampy, flooded forests also found in the Congo Basin. Much of their food is derived from the secondary forests, but they will normally nest in more mature forest at night (Kano 1979). At present there is not all that much data on bonobo behavioral patterns.

The particular habitat of a group of chimpanzees will have a considerable effect on both group and individual behavior and social relationships. A number of environmental factors, such as vegetation type, climate, topography and even soil type will have an influence on how a group or individual will behave. The abundance of foods, both plant and animal, the presence or absence of competitors, especially frugivores, predators and human activities will also all have an effect on how chimpanzees will behave (Collins and McGrew 1988).

The distribution of chimpanzees across the landscape is to a large extent affected by the following three factors. Firstly chimpanzees require access to forested area, especially as a source of wet season foods. This results in generally higher, more concentrated populations in forested areas during wet periods. Secondly, woodland areas are an important source of fruits and seeds in the dry season, as well as insects, small animals and bamboo shoots. Finally the heterogeneity of the landscape brings forest and woodland into a close mosaic with locally increased floral richness. This heterogeneity may allow chimpanzees to live at higher densities in a smaller area. Chimpanzees making use of both forest and woodland environments will have an advantage over purely forest or purely savanna dwelling populations, especially due to the productivity of woodland trees during the dry season (Collins and McGrew 1988; Suzuki 1969).

Chimpanzees, gorillas, orangutans and other primates tend to live in fairly small territories and preferentially exploit certain areas within their home ranges on a seasonal basis. According to Liebermann (1993) the only documented seasonal movement in primates are a few groups of baboons, who live at such extreme altitudes that they must move from lower to higher elevations within their territories on a seasonal basis.

One key characteristic of hunter-gatherer populations is frequent seasonal movement from habitat to habitat. This behavior is seen by some as a uniquely human one (Liebermann 1993). This may not be the case, as certain primates, like savanna dwelling chimpanzees have rather large home ranges. The chimpanzees at Mt. Asserick, Senegal have been recorded as having home ranges of 278 to 333km^2, which are comparable to the size of some San home ranges (Collins and McGrew 1988; Goodall 1986). These chimpanzees will move through their range on a seasonal basis, exploiting certain habitats at certain times of the year. Similarly gorillas will move from rainforests to bamboo forests, on a seasonal basis. These seasonal movements are similar to those of hunter-gatherer groups, only on a smaller scale. This seems to indicate that frequent seasonal movements from one habitat to another is not a uniquely human behavior.

Bonobos and chimpanzees are mainly dependant on fruit as a food source, 81 % of chimpanzee diet and up to 85% of bonobo diet consists of fruit (Figure 10) (Ghiglieri 1987). Chimpanzees in the Lope Reserve, Gabon have been observed feeding on up to 96 species of fruit through the year (Tutin *et al* 1992). It would, however, be incorrect to classify both as pure frugivores, as there is a substantial amount of non-fruit items in their diets. An analysis of savanna-dwelling chimpanzees diet, based on an examination of their fecal matter, revealed that at least 78 species of plants and 7 species of animals formed part of their diets (Suzuki 1969). On average 8 to 21 species of plants were eaten during each month of the year, with alterations based on seasonal availability.

Bonobos have three main food groups; rich, juicy, pulpy fruits, fibrous foods and hard nuts. They have also been documented to dig in the ground for insects and underground storage organs and to fish (Kano 1979). Common chimpanzees have not shown any inclination to do and have never been documented as feeding on underground storage organs (McGrew 1991). They will occasionally practise geophagy or earth eating. Approximately 10 to 20 g of clay is consumed, usually material that has been moulded by insects, such as termites. This process is thought to aid in the adsorption of harmful components in the stomach (Goodall 1971; Hladik 1977).

Although they are primarily frugivorous, chimpanzees will also feed on other plant foods, particularly when fruits are scarce. There are a number of ways in which chimpanzees will deal with such a shortage of fruits. They may move to more productive areas, reduce their energy expenditure or broaden their diet to include more low quality food items, for example fibrous piths. The exploitation of these piths have also been observed in gorillas and bonobos and depending on location, there are between 2 and 28 species available. Piths have been analysed and appear to be a good source of sugars and have a high protein value (Wrangham *et al* 1992).

Meat eating has been well documented in a number of chimpanzee populations and may be considered as a species typical occurrence. There are a number of methods by which chimpanzees obtain meat. Chimpanzees may deliberately stalk and hunt down prey, they may stumble across a prey animal and opportunistically catch it, or else they may scavenge. If they do hunt, chimpanzees will avoid solitary, quick-moving prey and will not take animals over 15 kg in weight (McGrew 1991). Goodall (1971) documents that Gombe Stream chimpanzees may catch up to 20 prey animals per year. Most common prey animals are the young of bushbucks, bushpigs, baboons and Colobus monkeys. Similarly, Brewer (1978) recorded chimpanzees hunting and catching Colobus and

Green Vervet monkeys, as well as smaller animals, like mice, birds and reptiles.

Bonobos and chimpanzees have a number of similarities and differences in their social behavior. Both are female exogamous. In both societies subadult males tend to remain in their natal groups, with females investing heavily in their offspring. Female associations in chimpanzee groups are based on the presence of kin-related males, while female bonobos develop bonds on the basis of resources, as well as due to related males. Chimpanzees have a stable closed community with day to day fission-fusion units. Food resource availability strongly affects bonobo fission-fusion groups. Each community of chimpanzees and bonobos are fairly strongly territorial and will aggressively defend their home range (Ghiglieri 1987). Bonobos, in general, spend more time feeding arboreally than chimpanzees, have smaller day ranges and have lower levels of aggression than common chimpanzees (Tooby and DeVore 1987).

Chimpanzees do not have a regular route on their daily search for food, and will rather nest near a food source than return to a well used sleeping area. Adult chimpanzees may move freely around the home range, although some individuals may be able to influence the movements of others, particularly females in estrus (Goodall 1986). Males and females will utilize the home range in different ways, with males tending to range much further and widely than females. An exception to this, are females in estrus. They can be very wide ranging and may even move beyond the community range (Goodall 1986; Wrangham 1977). Male chimpanzees may move up to 5km per day, while females only about 3km a day. Every four days or so, males will patrol the boundaries of the home range, while anestrous females tend to remain within core areas. Based on over 250 hours of observation, Goodall (1986) estimated the year range of the Gombe chimpanzees. Adult males had a range of 9 to $12km^2$, anestrous females 6 to $7km^2$ and cycling females 8 to $11km^2$. The total area covered by a male throughout his life will most likely be the equivalent of the community range. Females, although they do not have as long a day range as males, will infact move over a much wider area. This is due to females transferring between communities, particularly when they are in estrus (Goodall 1986).

The community range may be seen as the sum of all areas visited by each adult male of the community. Thus the community range is approximately the same size as the ranges of its male members and larger than the ranges of the anestrous females. The community range however must be large enough to support all the males, females and offspring in the group. There is some degree of overlap between community ranges, but different groups will tend to avoid being in the same location as another group. The males, as previously mentioned, patrol the boundaries of their ranges and will aggressively attack any intruders, particularly other males (Goodall 1986).

Home ranges will vary in size as a result of the number of males in a group. A Gombe group of 14 males had a range of more than 24km^2, while another group of 6 males only had a range of 9.6km^2 (Goodall 1986). Mahale has a similar environment to that of Gombe, and two groups observed revealed similar ranging patterns to those of the Gombe chimpanzees. A group of 6 males had a range of about 10.4km^2 and the other group of 11 males a range of about 33km^2. In dry areas with few natural boundaries, for instance rivers, home ranges will be much larger. At Mt. Asserik, Senegal, a home range of 278 to 333km^2 was recorded. This was during the wet season and the range substantially decreased in the dry season, due to poor water supplies and extreme heat. Another group has been documented as having a home range of over 122km^2 (Collins and McGrew 1988; Goodall 1986). When home ranges for forest dwelling common chimpanzees are plotted on the Sterkfontein geological map (Figure 11), they would cover the majority of the geologies, particularly to the southeast of Swartkrans, moving over granites, shales and quartzites. The strontium isotope ratios for forest dwelling chimpanzees would be variable even though 45 to 50% of their range covers dolomite areas. Savanna chimpanzees would range beyond the boundaries of the sample area, in a similar pattern to Kalahari hunter-gatherers.

e) Gorillas

There are three recognised subspecies of gorilla and are classified according to their habitat. They are as follows; the Eastern Lowland Gorilla (*Gorilla gorilla graueri*), the Western Lowland Gorilla (*G.gorilla gorilla*) and the Mountain Gorilla (*G.gorilla berengi*) (Fossey and Harcourt 1977). They inhabit three basic types of rainforest; lowland or montane rainforest, mountain or moist evergreen rainforest and bamboo forest (Dixon 1981; Schaller 1963). In addition, secondary or regenerating forests are an important habitat, particularly in lowland forests. Secondary forest develops after an area has been cleared, usually for agriculture, and then abandoned after a season or two. New natural growth will move into the open areas and is initially mostly low growing herbaceous material. Mountain rainforest tends to be a more broken, rugged environment and has more of a shrub layer than lowland rainforest. Although secondary forest is important, gorilla's prefer mountain rainforest, as it is more open and has a denser herbaceous layer. Bamboo forest occurs above the mountain rainforest, but is only seasonally favoured, during the wet season, when there is copious new shoot growth. Occasionally gorillas will venture into the lower limits of the Ericaceae forests above the bamboo forests (Dixon 1981).

Gorillas generally subsist on the most common food types with the bulk of their diet comprising leaves and other herbaceous material (Figure 10). This can be up to 88% of their dietary intake, with very small contributions in the form of fruits, bark and occasionally invertebrates (Ghiglieri 1987). Not all the plant species in their range are eaten, only a few species will form the bulk of their diet. Seasonal variation due to wet and dry periods will affect the nutritional quality of their diet and will result in changing choices of preferred food items through the year. Of particular importance are bamboo shoots, flowers and fruit. When seasonally available, gorillas will increase their intake of these high quality foods, switching to lower quality bulk foods, such as leaves, in the dryer periods (Dixon 1981; Fossey and Harcourt 1977).

A study of Mountain gorillas from the Tshibunda-Zahuzi region in Zaire, revealed that 104 food plants from 42 families were consumed (Goodall 1977). It was possible to classify these food items into five broad categories:

1) Main food items with a wide distribution, always plentiful and with very little seasonal variation.
2) Preferred food items which tended to be patchy and rare, but always consumed in large amounts when found.
3) Occasional food items which are not always consumed when located.
4) Rarely eaten food items.
5) Seasonal food items, such as fruits and bamboo shoots, which are eaten in large amounts when available.

As previously mentioned, gorillas tend to be foliovorous, but there are exceptions. Gorilla diet in the Lope Reserve, Gabon appears to be determined by the variety of alternative foods available in the area. It was found that the gorillas were consuming more fruit with an increase in plant diversity. 203 food items were identified, with 91 species of fruit contributing significantly to their diets. When fruits are scarce, the proportion of foliage eaten increases. In this case the gorillas are not true foliovores, due to the large amount of fruit in their diet. This is an indication of dietary flexibility amongst gorilla populations (Tutin *et al* 1992).

The social structure of a group of gorillas consists of a stable core of a leading male, generally a silverback and one or more females with their dependant offspring. Subadult males can stay within a group, but will normally leave become solitary for a number of years. These solitary males may be joined by young females at a later stage or else they will challenge older males (Harcourt 1979).

The number of individuals in a group will be to a large extent be affected by ecological pressures, such as food availability, climatic conditions or human activity (Dixon 1981; Fossey and Harcourt 1977). Eastern Lowland and Mountain gorillas tend to have slightly larger groups than Western Lowland gorillas. The average group is about 10 to 11 individuals, but groups of up to 20 have been observed (Dixon 1981).

Gorilla home ranges tend to be variable in size, being affected by actual group size and a number of environmental and geographical factors. The home range is a particular, familiar area of forest and is generally not defended as gorillas are non-territorial. There are core areas within the home range, but these are not constant and will vary seasonally. Factors such as the seasonal availability of key food items, like fruiting trees or bamboo shoots, will result in groups concentrating their foraging activities in different sections of their home range. Not all nutritional requirements will be met from any single area of the home range. This means that different sections will be utilised at different time with varying intensity. The group will have a well established pattern of home range utilisation, moving from area to area. In this way they prevent over-utilisation and allow the regeneration of resources (Dixon 1981; Fossey and Harcourt 1977; Goodall 1977).

The actual size of a home range is extremely variable, as are day range lengths. Estimates of six Western Lowland gorilla groups ranged between 6 and 12km^2 and six Mountain gorilla groups had home ranges of between 6.4 and 13.7km^2. There are also extremes, home ranges of 16 to 32km^2 and even 40 to 50km^2 have been recorded for gorilla groups. Some Mountain gorilla groups have ranges as small as 6 to 8km^2. Lone males are not very nomadic, tending to range over areas of about 4km^2 (Dixon 1981). Fossey and Harcourt (1977) recorded home ranges of between 4 and 25km^2. A group of Mountain gorillas in the Tshibunda-Kahuzi area of Zaire has been documented as having home ranges of about 34km^2 and day ranges of 0.7 to 3.4km (Goodall 1977). The area covered by Mountain gorillas (Figure 12) when projected on to the Sterkfontein geological map, is largely dolomitic (90 to 95%) with only slight overlap on to shales and quartzites. Western Lowland gorillas have a slightly smaller range than Mountain gorillas. Their range covering mostly dolomite (95%) and overlapping only slightly on to quartzites (Figure 13).

f) Orangutans

The orangutan (*Pongo pygmaeus*) is one of the least understood of the Great Apes, partly due to the environment in which they live and partly because of their social behavior. Orangutans inhabit the dense rainforests of Borneo and Sumatra. These forests have very high rainfalls and due to the density of tree cover, a complex internal variety of microenvironments. The forest may be divided into a number of distinct layers, with vertical gradients for light, temperature and humidity. This results in a complex 3-dimensional matrix, rather than a simple two dimensional one (MacKinnon 1974). The general habitat of orangutans is made up of lowland forests alternating with shallow peat-swamps and limited areas of tropical heath forest (Galdikas 1977).

Orangutans subsist mostly on fruits, about 60% of their diet (Figure 7) (Ghiglieri 1987). This is supplemented by leaves, young shoots, flowers, epiphytes, wood pith, bark, insects, eggs and small vertebrates. They will also consume small amounts of mineral rich soils (MacKinnon 1974). Feeding normally occurs in or near the periphery of tree crowns, with orangutans often breaking branches while eating. The seeds of the various fruits are often swallowed, rather than discarded. This practise makes orangutans effective seed dispersal agents within their home ranges (Rodman 1977). A wide variety of items are eaten throughout the year, but due to seasonal availability certain species or items will only be eaten when present. Foraging groups will move around their home ranges based on the differential availability of fruiting trees and their uneven distribution (Mackinnon 1974).

Orangutans are usually solitary animals, moving independently through the forest. The basic social units consist of the following:
1) Solitary adult males.
2) Adult females with one or two dependant young.
3) Immature individuals who alternate between staying with their mother and a solitary existence.

Larger groups have been observed, but these tend to last for a very short period of time (MacKinnon 1974).

The size of orangutan home ranges are also variable and are to large extent affected by the seasonal occurrence of food resources at different times and locations. Adult females and their dependant offspring have stable ranges and tend to stay in the same general area. The boundaries of each home range are well defined, but do overlap extensively with those of other female units. The home ranges of adult and subadult males are more complex. They are larger than those of females and there is a lot overlap, between both other male ranges and female ranges. Populations are highly dispersed and this results in relatively little social interaction, even with extensively overlapping home ranges.

A study of orangutans in Tanjung Puting Reserve revealed that females had home ranges of between 5 and 6km^2 (Galdikas 1979). Rodman (1977) observed markedly smaller ranges in the Kutai Reserve, East Kalimantan. The average home range was 0.42km^2, with day range lengths of between 300 and 800m. This size difference may be partly due to factors such as local climates, topography, population density, varying resource bases and human activity. Orangutans have the smallest home ranges of the great apes, and if they occurred at Swartkrans (Figure 14), they would only range on dolomitic areas and thus have strontium isotope ratios characteristic of dolomites.

g) Robust Austraolopithecines at Swartkrans

Inorder to interpret the behavioral pattern of early hominids, it is essential to have an indication of what their past environment was like. When attempting to reconstruct palaeoenvironments, a number of factors need to be considered. Depending on the situation, some will be of more concern than others, in terms of trying to reconstruct a past environment. Factors include the following:

1) Taphonomic factors which may disrupt or obscure the fossil record and associations between species. The taphonomy of the Swartkrans deposits

have been well documented and the processes involved in their formation clearly established (Brain 1981, 1993).

2) The behavioral flexibility of species, such as whether animals are territorial or free-ranging or differences between males and females. The behavioral flexibility of robust australopithecines is at present not clearly understood and it is hoped that the combined use of methods such as strontium isotope ratios, primate behavioral studies and modern ecosystem analogues will shed some light on the subject.

3) Depositional factors. The depositional factors at Swartkrans are well understood. The geomorphology of the area has not changed all that much, although the landscape may be considered as more geologically mature (Brain 1981, 1993; Butzer 1976).

4) There are problems associated with the classification of habitats, as often habitats tend to be mosaic in nature rather than simple. The modern environment of Swartkrans and the Sterkfontein Valley is thought to be very similar to that of the palaeoenvironment in which the robust australopithecines lived (Peters and Maguire 1981; Shipman and Harris 1988; Vrba 1975, 1985a, 1985b).

On the basis of the fossil bovids and the use of modern ecosystem analogues, *A.robustus* is thought to have been living in an open environment, comprising mostly grasslands (Peters and Maguire 1981; Shipman and Harris 1988; White 1988). In addition to the open grasslands, there were also patches of riverine woodland and fairly densely wooded valleys that would have been available for exploitation. Evidence in the form of fossil otter and hippo remains and waterworn pebbles from Member 1 indicates that the Bloubank Stream may have been much larger 1.6 to 1.8 million years ago (Brain 1988). There are still small patches of indigenous vegetation present in the area, particularly to the north of the Sterkfontein Valley (Hall 1992). The occurrence of a variety of habitats, ranging from open grassland to riverine woodland may have provide early hominids with heterogeneous environment with a wide diversity of resources to exploit.

There has not been much emphasis on plant foods in palaeodietary studies until fairly recently (Peters and O'Brien 1981). Plants infact form the major proportion of the diet of most higher primates and humans. The !Kung San derive 75% of their diet from about 14 species of plants and meat is considered as of secondary importance (Lee 1965, 1979). Chimpanzees, bonobos, gorillas and baboons all derive the majority of their food items from plant foods. In a recent study of 131 primate species' dietary composition, it was found that 90% consume fruits, 79% consume soft plant foods, such as buds and shoots, 69% feed on mature leaves, 65% consume invertebrates, 41% seeds and 37% of the species examined will eat animal foods, including eggs (Figure 15) (Oftedal 1992). From these examples it is clear that plant foods play a vital role in the diets of primates and humans, so it would not be unreasonable to assume that early hominids also had a substantial plant food diet and this would have an impact on their foraging and ranging patterns.

A study was conducted by Peters and O'Brien (1981) in which they compared the plant food diets of modern baboons, chimpanzees and humans in order to establish the possible plant food niche of early hominids. It is thought that hominids may have had more of a restricted diet than baboons or chimpanzees, but almost all primates are highly selective in their dietary choices (Oftedal 1992). They identified the plant food items eaten by baboons, chimpanzees and humans that may have also been consumed by early hominids. Over 461 plant genera are reputed to be eaten by one or more of the three primates, totalling more than 801 food items. The most common food items all three consumed, were fruits and leaves, while underground storage organs were of particular importance to humans and baboons. It has been documented that common chimpanzees do not exploit underground storage organs, but bonobos have been observed to do so (Kano 1979; McGrew 1991). At Swartkrans it is suspected that underground storage organs were an important source of food to hominids living in the area (Brain *et al* 1993; Hall 1992; Sillen *et al* In press). 45 to 55% of all the genera exploited by each primate are also used by one or both of the others. This overlap may result in intense competion for certain key items, such as fruit or other energy rich foods. It was finally estimated that there was between 140 and 333 genera that may have been exploited by early hominids (Peters and O'Brien 1981).

All the primates and hunter-gatherers examined in this section are all selective in their diets, only utilizing a fraction of the available food resources. They will all rank their foods according to quality, concentrating on those which are highly desirable, such as fruit and then moving on to less favourable ones. The seasonal availability of foods have an important impact on the foraging strategies and ranging patterns of *A.robustus*, as the Sterkfontein Valley is in a highly seasonal environment with distinct dry and wet seasons. It is probable that the australopithecines would have had a wet season strategy and a dry season one. The very thick tooth enamel of the robust australopithecines may be an adaptation for a more varied diet and a product of an increasingly seasonal environment (Andrews and Martin 1992). Foley (1987) has devised a model of such possible strategies. In the wet season, a broad based eclectic, but largely herbivorous diet with little interspecific competition would be most favourable. There would be a time lag between the first rains and the appearance of resources, but some such as termites and grasses will appear before flowers and fruits. In addition there would be eggs, fledglings and young mammals available. In the dry season, the pattern would change as there are less high quality foods available and thus both inter and intraspecific competion would increase. Items such as grass seeds and rhizomes would be important in the early part of the dry season, with underground storage organs forming the main food item later. Meat would also become important as a source of energy and may either be hunted or scavenged. Peters, O'Brien and Drummond (1992) have ranked a number of possible food items that a non-fire using hominid may have exploited (Table 11). During the dryer periods fruit and seeds and shallow underground storage organs will most likely form the bulk of the diet. Living in a variable environment, such as that around Swartkrans, would allow early hominids to forage more widely from season to season and thus cope with seasonal abundance by concentrating their foraging patterns in the most seasonally favourable areas.

It is nearly impossible to recreate the social structure of a group of early hominids, but by looking at the social structures of closely related primates, such as the great apes and present-day human societies, it may be possible to examine common elements. These common elements may also have be present in early hominid societies, an "ancestral" suite of characters.(Ghiglieri 1987; Tooby and DeVore 1987).

Basic social characteristics, common to gorillas, chimpanzees, bonobos and humans, include the following (Table 14):

1. Female exogamy.
2. Bonds between females are fairly weak.
3. Closed social groups.
4. Social groups are stable multimale and multifemale communities.
5. Males will be active in the defence of a territory, if necessary.
6. Males will seek out, attack and in the case of chimpanzees and humans kill rival males.
7. Polygynous mating systems.
8. Males sometimes travel alone and tend to move more widely than females. The exception to this may be females who are in estrus.
9. Females often travel alone or with dependant offspring.
10. Within communities, fusion-fission groups are socially common.
11. Female associations are due primarily to the attraction of females to the same male(s).
12. Males remain in their natal groups (endogamy).
13. Communal territoriality is typical amongst the males, and occasionally amongst females.
14. Mating competion between males of the same community is mild, relative to competion between communities.
15. Sexual dimorphism is moderate (excl. gorillas), with males cooperating in alliances against rivals.

Orangutans are very dissimilar to the other great apes with regard their social behavior and are thus not a very good candidate as a model for early hominid social behavior. Savanna baboons and Hamadryas baboons also have some similar social patterns to the above mentioned groups and should also be considered as potential candidates (Ghiglieri 1987; Rodseth *et al* 1991; Tooby and DeVore 1987). It is thought that robust australopithecines may have harems with males moving around much more widely than females (Ambrose pers. comm.)

The home range of a hominid will increase with four factors: body size, trophic level, group size and the openness of the habitat (Ambrose pers. comm.; Foley 1987; Wheeler 1992). A larger animal has some advantages over smaller animals. Their dietary niche is broadened as a larger organism requires less energy per unit of body weight per day and in this way can subsist on lower quality foods as well as high quality ones. This would provide an advantage in a highly seasonal environment, such as the Transvaal grasslands. A larger animal is generally more mobile and has better thermoregulation and will thus be able to travel further from a water source, expanding the home range and day range. Improved thermoregulation would allow hominids, such *A.robustus*, to forage at higher temperatures for longer periods and distances, an advantage in dryer and warmer savanna areas (Wheeler 1992).

Different trophic levels will affect the size of a home range, as the higher the trophic level of an animal the larger the home range. Carnivores and omnivores should generally have larger ranges than herbivores (Ambrose pers. comm.). The trophic level of *A.robustus* is contentious. While conventionally seen as herbivores (Robinson 1954, 1956; Pilbeam and Gould 1974; Grine 1981), trace element and stable isotope analyses of fossil material from Swartkrans, it is evident that *A.robustus* was omnivorous to a certain extent (Hall 1992; Lee-Thorp and van der Merwe 1993; Sillen and Lee-Thorp 1994; Sillen 1988, 1992). A high quality diet, such as certain fruits, require more time to locate and obtain, whereas it is easier and quicker to forage if one has a low quality diet. In a seasonal environment, the time spent foraging would change from season to season, with a larger area being covered in wet periods, as high quality food would be more readily available, but patchily distributed in space and time (Table 13).

Much of the home range data from primates has been based on observation in closed forested environments. Home ranges for primates living in more open areas, like savanna, are generally much larger. Savanna dwelling chimpanzees have been documented to have home ranges of between 122 and 333km^2, while forest dwelling chimpanzees have ranges only in the region of 9 to 30km^2 (Collins and McGrew 1988;

Goodall 1986). This indicates that early hominids may have had fairly substantial ranges.

Predictions of hominid home ranges have been calculated on the basis of body weight. Extensive studies have revealed that there is a strong positive relationship between body weight and home range area in lizards, birds and solitary mammals. A formula developed by Milton and May (1975) uses body weight to calculate the predicted home range size for hominids living in groups:

$$\log_{10} HR_t = 1.23 \log_{10} BW - 2.86$$

HR_t = the total home range in hectares.
BW = mean adult body weight in grams.
The relationship was tested using data on body weight, diet and home range size for 36 primate species and the results showed a very strong positive relationship between body weight and home range size (Milton and May 1976). On the basis of this equation, estimates of expected early hominid home ranges range from 3.71km^2 for *A.afarensis* and 7.3km^2 for *Homo erectus* (Foley 1987). These results were compared with actual distances between raw material sources and points of discard at Koobi Fora and Oldvai. It was found that the home ranges obtained from this data were much larger than the expected home ranges. Data from Lake Turkana suggest that hominid in the area had home ranges of between 12.56 and 50.2km^2, if the distance of 4km for transporting raw materials is take as a radius or diameter. In a similar way data from Olduvai Gorge indicates home ranges of between 113.1 and 452.3km^2 (Foley 1987). Ambrose (pers. comm.) predicts that the radius for a circular robust australopithecine home range would be about 5.5km, resulting in a home range of about 95km^2.

Predicted home ranges were calculated for five *A.robustus* individuals from Swartkrans, using Milton and May's equation and body weight calculations based on McHenry's (1976, 1988, 1994) and Jungers (1988) research on body size and weight (Table 11). The minimum ranges are those calculated by means of Milton and May's equation, while the maximum ranges were obtained by using the minimum ranges as the radii of circular home ranges and calculating the area of the circle using *pi**r^2. SK 3981 had an average minimum and maximum predicted range of 5.8 to 98.5km^2, SK 82, a range of 8.8 to 246.1km^2, SK97, a range of 10.32 to 334.6km^2, SK3155, had a range of 6.3 to 124.7km^2 and SKX1084 had a range of between 13.38 to 559.9km^2 with an average minimum and maximum range size of between 9.24 and 266.2km^2.

Body weight only accounts for part of the home range variability, and this is illustrated by comparing expected home range sizes, based on body weight, with observed home ranges of living primate groups in their natural environments (Table 15). The observed home ranges for common chimpanzees and orangutans are significantly different from the expected ranges. The expected home ranges for chimpanzees are much smaller than in reality, while the expected home ranges for orangutans are much larger than the observed ones. What is clear form the non-human primate studies is that the quality of diet and availability of sufficient resources has a major impact on the foraging strategies and ranging patterns of most primates. The early hominids lived in more open savanna environments with a more widely dispersed range of resources. Forest dwelling chimpanzees utilize between 141 and 330 species of plants, while savanna baboons utilize only about 14 species and Kalahari San between 45 and 85 species (Altmann and Altmann 1970; Foley 1987; Lee 1965, 1979; Silberbauer 1981). Peters and O'Brien (1981) predicted that early hominids may have had between 140 and 333 genera available to them, but it is very likely that only a few key species were extensively exploited, particularly in savanna areas. The presence of a larger Bloubank Stream at Swartkrans may have provided an additional source of food items for *A.robustus*. A further factor influencing their diet would be the presence of other primates, such as baboons, competing for the same resources, such as underground storage organs and fruits. At least three species of fossil baboon have been found in the same members as the australopithecine fossils at Swartkrans (See Section 2.3). The presence of these baboons may have resulted in intense resource competion around Swartkrans, and would have very likely affected the ranging behavior of *A.robustus*.

Based on the predicted home ranges from Ambrose (pers. comm.) of a radius of 5.5km (Figure 16), robust australopithecines would either have highly variable strontium isotope ratios derived from a number of geological areas, if they had the maximum size home range, or else their isotope ratios would be very characteristic of food items occurring on dolomitic sediments, if they had a minimum size home range. Similarly, based on the predicted ranges for *A.robustus* individuals from Swartkrans (Figure 17), the maximum range covers all of the geological areas and any strontium isotope ratios obtained would be highly varied. The minimum range would also be largely on dolomitic areas.

Robust australopithecines are thought to have had fairly small home ranges. Based on calculations using McHenry's (1976, 1988, 1994) body weight estimates and the general regression formula for carnivores developed by Harestad and Bunnel (1979), Ambrose (pers. comm.) obtained predicted home ranges of between 5 and 9km for australopithecines. The use of the carnivore regression formula provides home range data that accords well observed home range data for primates living in open environments. Since the area around Swartkrans is and was open and australopithecines are adapted to an open environment, ie. savanna, it seems logical to use the most appropriate regression formula, in this case carnivores. The minimum radius for robust australopithecine home ranges was approximately 5.5km. By comparing all the ranging data with strontium isotope ratios obtained for the Sterkfontein Valley and for individual *A.robustus* specimens one will be able to determine whether it is possible to estimate actual home range size or merely to predict areas that were favoured by particular individuals. Such comparisons will be carried out and the data presented in Section 6, which deals with the interpretation of the strontium isotope data from the Sterkfontein Valley.

4. METHODOLOGY

4.1 Sampling Strategy

The Sterkfontein Valley and surrounding areas include a wide range of environments and geological localities, including open grasslands, wooded kloofs and riverine bush. In order to sample from the majority of environments, a sample zone of about 550 km^2 (Figure 1) was established, based on the study of 1:50 000 topographical maps and 1:250 000 geological maps (Geological Survey 1989). An area of 550 km^2 is thought to most likely cover the possible ranging area of early hominids that were present in the valley and surroundings (See Section 3). Although the majority of hominid fossils have been found in the Sterkfontein Valley, it is likely that hominids also inhabited other areas around the valley. In addition the large sample zone includes a wide range of different geological substrates, allowing one to obtain a measure of isotopic variation between geologies.

The sample zone is situated between the Witwatersrand in the south and the Hekpoort Valley to the north. Swartkrans is more or less located in the center and forms the focal point for this study (Figure 18). The Witwatersrand forms the northernmost boundary of the South African tableland, between the broken country down to the Limpopo River and the Highveld. Located between the Limpopo and Vaal Rivers, the Witwatersrand forms the watershed of the Limpopo Basin (Adamson 1938).

On steep ridges and valleys, bush vegetation tends to predominate, with the more gentle slopes being covered by grasslands (Figure 4). On steeper slopes, trees will occur, although the soils tend to be poorer, as a result of leaching. Larger trees will also tend to occur along stream and river banks, although invasive aliens, such as Australian Wattles and industrial pollution may restrict growth. Small pockets of indigenous woodland are still present, although located in very sheltered areas (Adamson 1938). There are still to date the occasional leopard, antelope and baboons noted in the kloofs to the north of Swartkrans (Hall pers. comm.).

A total of 14 soil samples, 5 rock samples, 48 plant samples and one water sample were obtained from collections during the course of three field trips to the Sterkfontein Valley and surrounding areas. The first trip was made in November 1991, the second in June 1992 and the third in February 1993. This collection is housed in the Trace Element Laboratory, Archaeology Department at the University of Cape Town.

Where possible, both plant and soil samples for each different geological location were collected (Figure 1). Approximately 200 to 300 grams of surface soil was obtained, while plant samples were mostly composed of whole grass plants or in a few cases leaf and twig samples from trees. Table 16 summarizes the location and geology of each sample site. The network of roads through the sample zone facilitated the collection of material. The R560 runs to the northwest, toward the Hekpoort Valley and passes through a series of geologies. These geologies lie in bands running from the southwest to the northeast and include the chert rich dolomite on which Swartkrans occurs. To the east and southeast, the R47 (Johannesburg) and the R28 (Pretoria) pass through various rocks forming part of the Witwatersrand Complex. For more detail on the geology of the area, refer to Section 2.2.

The area around the archaeological site of Swartkrans was intensively sampled, as a means of obtaining a measure of the variance in $^{87}Sr/^{86}Sr$ ratios. Four soil samples, five rock samples, 36 plant samples and a water sample from the Bloubank stream were gathered from the immediate vicinity of the site. Plant and soil samples were obtained from the following points, SSI 1, SSI 2, SSI 3 and SSI 4, while only plant samples were taken from SSI 10, SSI 11 and SSI 12 (Figure 19). Two reference points were used and their grid positions determined by GPS (Global Positioning System). The first is the beacon on the upper slope, just below the parking area, 26°00`4727``S and 27°43`2911``E. The beacon provided the starting point for three transects:

1. A 200m transect due west, with samples taken every 50m.

2. A 500m transect due east, with samples taken every 50m.

3. A 300m transect south-east to the Bloubank stream and then due south across the streambed (Table 17).

The second reference point is designated Brain's datum point and is situated in the cave complex, forming part of the permanent grid system (Figure 19). Its GPS position is as follows, 26°00`5827``S and 27°43`2785``E. The datum provides a reference point for samples from SSI 10 to SSI 12.

The five rock samples were collected from the cave complex and surrounding area by Dr. Richard Armstrong from the Geochemistry Department, UCT. These included calcite precipitate, calcite seepage, Member 1 breccia and two samples of dolomite. The water sample from the Bloubank stream was collected by Dr. Francis Thackeray of the Transvaal Museum, shortly after a thunderstorm.

Three other samples were made on dolomite. SSI 17 and SSI 18 are both situated on streams which flow into the Bloubank, SSI 17 on a small tributary and SSI 18 on the Rietspruit (Figure 18). These should provide an indication of any additional strontium moving into or possibly out of the Sterkfontein Valley. A plant and soil sample were taken from the area close to the Sterkfontein Caves.

The remainder of the soil and plant samples were obtained the other geological locations in the sample zone. Samples from SSI 5 to SSI 8 cover the area to the northwest of Swartkrans. These range from shales to rocks of volcanic origin (Table 16). To the southeast, samples from SSI 9 and SSI 13 to SSI 16 represent some of the rocks forming the Witwatersrand Complex and include granites, quartzites and mafic rocks.

4.2 Analytical procedure

All sample preparation, apart from the ashing of plant material, was carried out in the ultraclean laboratories of the Radiogenic Isotope Facility, located in the Geochemistry Department.

a) Plant Samples:

All the plant samples were ashed in a muffle furnace for three hours at 750°C. This process removed all organic material and ensured that digestion was complete. The ashed material was then weighed out into 0,05 to 0,09g amounts, on a Mettler PM4600 top loading scale. The weighed ash samples were then digested in 2,5 N HCl in clean teflon beakers, for 24 hours at 50°C. One milliliter of solution was then drawn off, placed in small plastic centrifuge tubes and centrifuged in a Heraeus Sepatech Medifuge for ten minutes at 4000 rpm.

0,75 ml of solution was placed into equilibrated cation exchange resin columns and leached through with 2,5 N HCl. A total of 7 ml of leachate was collected in clean teflon beakers and then brought to dryness. The resulting residue was then loaded onto ultraclean 99,95% pure tantalum ribbon filaments in a solution of 0,48 N H_3PO_4 and 2% xx HNO_3, as a nitrate. Strontium isotope ratios were measured on a VG Sector thermal ionization mass spectrometer. The strontium isotope values were normalised to the value obtained for the NBS strontium carbonate standard SRM-987, which was measured during each sample run. The $^{87}Sr/^{86}Sr$ ratios were measured to precisions better than 0.001%.

b) Soil Samples:

Soil samples were prepared in two ways. The first method extracted all the strontium present in the soils, providing the total soil strontium isotope ratio for each. The second method extracted only the biologically available strontium in the soils. In this way it was possible to determine how much soil strontium was available to plants growing on the soils. In addition, neodymium was extracted from the soils, but has not been analysed as yet. The procedures were as follows:

1) Total soil strontium:

0,19 to 0,21 g of soil was weighed out on a Mettler PM4600 top loading scale and placed clean in teflon beakers. HF was added and the resulting solution was brought to dryness at 50°C over a period of 24 hours. 6,0 N HCl was then added to the residue and the solution was also brought to dryness at 50°C over 24 hours. Finally the residue was digested in 2,5 N HCl for 24 hours at 50°C. One milliliter of this solution was then placed in small plastic centrifuge tubes and centrifuged in a Heraeus Sepatech Medifuge for ten minutes at 4000 rpm.

0,75 ml of the solution was placed in equilibrated cation exchange resin columns and leached through with 2,5 N HCl. 7 ml of leachate was collected in clean teflon beakers and brought to dryness. The residues were loaded onto ultraclean 99,95% pure tantalum ribbon filaments in a solution of 0,48 N H_3PO_4 and 2% xx HNO_3, as a nitrate. Strontium isotope ratios were then measured on a VG Sector thermal ionization mass spectrometer. The strontium isotope values were normalised to the value obtained for the NBS strontium carbonate standard SRM-987, which was measured during each sample run. The $^{87}Sr/^{86}Sr$ ratios were measured to precisions better than 0.001%.

2) Biologically available soil strontium:

0,19 to 0,21 g of soil was weighed out on a Mettler PM4600 top loading balance and placed in clean teflon beakers. The soil samples were then prepared according to the same procedure as applied to the plant samples.

3) Streamwater sample:

250 ml of water from the Bloubank Stream was filtered and then dried down. This process took 48 hours at 75°C to reach dryness. The resulting residue was then dissolved in 6,0 N HCl and placed in a clean teflon beaker and dried down. 2,5 N HCl was then added and shaken well to ensure complete dissolution. One milliliter of solution was drawn off

and centrifuged in a small plastic centrifuge tube in a Heraeus Sepatech Medifuge for ten minutes at 4000 rpm.

0,75 ml of sample was then placed in an equilibrated cation exchange resin column and leached through with 2,5 N HCl. 7 ml of leachate was collected in a clean teflon beaker and brought to dryness. The resulting residue was then loaded onto a 99,95% pure tantalum ribbon filament in the same manner as the plant and soil samples and strontium isotope ratios were measured on a VG Sector thermal ionization mass spectrometer. The strontium isotope values were normalised to the value obtained for the NBS strontium carbonate standard SRM-987, which was measured during each sample run. The $^{87}Sr/^{86}Sr$ ratios were measured to precisions better than 0.001%.

5. RESULTS

Strontium isotope data for whole plant samples are indicated in Table 18. These data are representative of all the sample sites in the Sterkfontein Valley and immediate vicinity. Table 19 shows the strontium isotope results for three transects sampled around Swartkrans. All samples were whole plants. Isotopic data for soil samples are presented in Tables 20 and 21. Table 20 shows results for total soil strontium isotope ratios from 14 sites in the sample area, as well as the $^{87}Sr/^{86}Sr$ ratio for a water sample from the Bloubank Stream. The results for three available soil strontium samples are shown in Table 21. All three samples are from dolomitic substrates around Swartkrans. During the analytical period, the $^{87}Sr/^{86}Sr$ value for the NBS strontium carbonate standard SRM 987 was 0.71020 and all strontium isotope results were normalised accordingly. In addition, the $^{87}Sr/^{86}Sr$ ratios for five *A.robustus* individuals from Swartkrans Member 1 were made available (Table 22).

Figure 20 shows the $^{87}Sr/^{86}Sr$ ratios for all the whole plant samples and their corresponding total soil strontium samples for 10 different geologies examined. It should be noted that in all, but two cases, the $^{87}Sr/^{86}Sr$ values of the soils are much higher than those of the plants. The data are arranged in such a manner as to represent the distribution of the geologies as one moves from north to south, through the study area. In addition $^{87}Sr/^{86}Sr$ ratios for 5 *A.robustus* individuals (SK 1588, SK 876, SK 46, SK 54 and Sk 57) are indicated. These results are based on the pooled washes 16 to 20 of solubility profiles carried on each (Sillen *et al* In press). The results for the *A.robustus* individuals lie within the range of $^{87}Sr/^{86}Sr$ ratios obtained for the dolomitic substrata.

It should however be noted that $^{87}Sr/^{86}Sr$ ratios obtained for the other geologies, with the exception of two samples, also lie within the range for dolomites. This is a result of the sampling strategy. The majority of samples were obtained from dolomites, while only single plant and soil samples were collected from other areas. The lack of additional isotopic data from other geologies will not allow comparison as the amount of internal isotopic variation has not yet been established for each.

To establish the range of internal variation requires additional sampling of both plants and soils from each geological area.

The wide range of variation in $^{87}Sr/^{86}Sr$ ratios for the different geologies is indicated by the total soil strontium results (Figure 21). In Figure 20, it is clearly visible that there is extreme isotopic variation between plants and the soils on which they grow. Plant $^{87}Sr/^{86}Sr$ ratios are depleted with regard to the ratios for **total** soil strontium. When one uses the same sample preparation for soils, as for plants, extracting only the **available** strontium, the $^{87}Sr/^{86}Sr$ ratios are almost identical (Figure 23). It is the available soil strontium that will determine the strontium isotope ratios of the plants and australopithecines. The implications of the large difference between total and available soil strontium are important and indicate that care must be taken for actual sample collection and sample preparation.

The isotopic data for whole plants show extensive overlap and are very likely to affect predictions of foraging and ranging behavior of early hominids occurring in the study area, particularly in terms of separating different geological areas. When one looks at the isotopic data for the *A.robustus* individuals, it is clear that they fall in the lower spectrum the strontium isotopic variation for the study area (Figure 21).

When the $^{87}Sr/^{86}Sr$ ratios for plants growing on dolomitic substrates are compared (Figure 22), it is possible to distinguish between two environments. Samples taken from SSI 3, 17 and 18 are all significantly lower than those from SSI 1, 2, 4, 10, 11, 12 and the Sterkfontein Caves. SSI 3, 17 and 18 are all located close to streams; SSI 3 is close to the Bloubank Stream, SSI 17 near to tributary of the Rietspruit and SSI 18 is next to the Rietspruit (Figure 18). The other samples were taken from higher elevations around the sites of Swartkrans and Sterkfontein. This division is confirmed by the $^{87}Sr/^{86}Sr$ ratio for a water sample from the Bloubank Stream (0.721169) which is similar to that of SSI 3 (0.72318). On the basis of their $^{87}Sr/^{86}Sr$ ratios, robust australopithecines appear to be divided into two groups, one group having ratios similar to those obtained for plants near to stream margins and one with ratios similar to those obtained for plants from the upper areas of Swartkrans and Sterkfontein.

The majority of plant samples were taken from dolomite substrates and show considerable variation in their $^{87}Sr/^{86}Sr$ ratios. Data from the three transects illustrates this point effectively (Figure 24). Results for the western transect (TW) shows an increase in the $^{87}Sr/^{86}Sr$ ratios as one moves further from the point of origin. The eastern transect (TE) is extremely variable, increasing and decreasing, as the distance from the point of origin increases. The results for the southern transect (TS) are of particular interest. The southern transect runs from the beacon below the parking area at Swartkrans, down the slope to the Bloubank Stream, across the streambed and up the opposite slope (Figure 19). The $^{87}Sr/^{86}Sr$ ratios increase slightly and then dramatically decreases and then increases rapidly again. It was found that the lowest $^{87}Sr/^{86}Sr$ ratios were for plants growing in the floodplain and streambed and the highest from areas near the beacon and on the upper slopes on the opposite side of the stream. This indicates that strontium isotope ratios for the floodplain are affected by the flow of the stream. The topography of an area will also have an effect on the isotope ratios. In cross-section across the Sterkfontein Valley, it is possible to see the isotopic variation between the upper slopes and the lowest point in the streambed (Figure 25). SSI 12, the highest point sampled (>1475m), has a $^{87}Sr/^{86}Sr$ ratio of 0.748606, while on the Bloubank floodplain (1454m), a $^{87}Sr/^{86}Sr$ ratio of 0.720282 was obtained. Such variation due to topography and drainage will very likely complicate the interpretation of early hominid home ranges, but does provide alternative opportunities for behavioral interpretations based on strontium isotopes.

6. INTERPRETATION

Strontium isotope ratios from the Sterkfontein Valley and the immediate vicinity show a wide range of variation (Figure 21). Such a range of isotopic variation will complicate attempts to examine any ranging or dietary behavior. This is, in part, due to the geological formation of the study area. In general, the shales and granite have high $^{87}Sr/^{86}Sr$ ratios (Figure 20). Not suprisingly the granites (SSI 16) have the highest (0.900582), due to their extreme age, 2880 Ma (Geological Survey 1989). There is a fair amount of overlap between the various geologies, when the $^{87}Sr/^{86}Sr$ ratios for plants are considered (Figure 21). The total soil ratios do not show as much overlap. The these soil data are also very much higher than the average $^{87}Sr/^{86}Sr$ ratios reported by Faure and Powell (1972) and Graustein (1989) (Table 2).

The extreme differences (Figures 21, 23) between the $^{87}Sr/^{86}Sr$ ratios of plants and soils are due to a number of factors, particularly those affecting the elemental soil strontium pool. Isotopic data for total soil strontium is representative of the strontium isotope ratios for the actual mineral components of the soil, as well as the strontium present in the soil solution around soil particles. By virtue of soil sample preparation, all the strontium in the soil is mixed together, resulting in high $^{87}Sr/^{86}Sr$ ratios. When the soil sample are prepared in the same manner as the plant samples, only the available strontium is obtained. This is the strontium present in the soil solution surrounding soil particles and the strontium bound to the soil particles. It is this strontium that is taken up by plants and thus they should have similar ratios to that of the available soil strontium (Figure 23). Any animal then consuming these plants should then also have similar $^{87}Sr/^{86}Sr$ ratios to those of the plants and available soil strontium.

The available soil strontium may be derived from a number of sources, such as atmospheric deposition, groundwater, mineral weathering of parent rocks and the biological decay of organic matter. Annual plants, such as grasses will have $^{87}Sr/^{86}Sr$ ratios very similar to those of the available soil strontium, but this will representative of only one season of growth and hence only one period of new atmospheric deposition. If one wants to obtain a measure of atmospheric strontium contribution to the soil strontium pool, it is necessary to analyse the $^{87}Sr/^{86}Sr$ ratios of a perennial plant, such as a tree. The youngest parts of the tree, new shoots and buds, should be representative of the present soil strontium pool, while older parts are likely to have ratios somewhat different to the newer parts. This has been documented by Gosz and others (1983), who found that $^{87}Sr/^{86}Sr$ ratios changed rapidly over a short period of time. A 35 to 50 year section of wood had a $^{87}Sr/^{86}Sr$ of 0.7216, while a 15 year old section had a ratio of 0.7130. This decrease in strontium isotope ratios was due to an increase in atmospheric strontium in the soil strontium pool. Plants will preferentially take up atmospheric strontium via their roots and leaves, resulting in lower $^{87}Sr/^{86}Sr$ ratios (Hurst and Davies 1981). SSI 10 (*Euclea sp.*) has a ratio of 0.73006, which is much lower than the ratios obtained for other plant (grass) samples taken in the same area. This may be due to changes in the relative contributions from the soil strontium pool and atmospheric strontium.

In addition to the effects of atmospheric deposition, industrial effluent from industrial areas and sewage systems upstream, pumped into the streams flowing through the study area is likely to affect strontium isotopic ratios. A possible indication of such pollution, may be the $^{87}Sr/^{86}Sr$ ratio obtained for a plant sample from the streambed of the Bloubank Stream. The plant yielded a ratio of 0.76778, which is very much higher than any other ratio obtained for plants in the entire study area and has not been considered in any of the interpretations in this study.

Strontium isotope ratios appear to be very sensitive to changes in the topography of an area, varying considerably over a small distance. Factors such as groundwater movements, sandiness, rockiness and slope are likely to affect the distribution of strontium. This will result in areas of high and low strontium concentration and varied strontium isotope ratios, even on the same geological substrate. In addition to the above mentioned factors, the distribution of strontium in limestones and dolomites are also affected by temperature, salinity and geological diagenesis (Kulp and Turekian

1956). This can be clearly seen in the data from the three transects taken around Swartkrans (Figure 24). The western transect (TW) moves downslope toward the floodplain of the Bloubank Stream, but stops at the Swartkrans cliff (Figure 19). The four $^{87}Sr/^{86}Sr$ ratios obtained, show an increase as one moves toward the cliff. The cliff may be acting as a buffer to material being transported by runoff and causing the build up of strontium and hence resulting in elevated strontium isotope ratios. The variation seen in the eastern transect (TE) may be accounted for in a similar fashion.

The variation seen in the data from the southern transect (TS) has a more complex explanation. Both the topography of the area covered by the transect and the Bloubank Stream are responsible for the variation. The stream has a two fold effect, by bringing in new strontium derived from areas upstream and at the same time removing dolomitic strontium downstream. This has resulted in depleted ratios obtained from the floodplain and streambed and higher ratios as one moves further away from the stream (Figure 25).

Of particular interest to early hominid behavioral interpretation is the apparent strontium isotope distinction between riparian environments and the area beyond the streambanks at Swartkrans (Figures 22, 24, 25). The riparian areas are isotopically depleted with respect to the plains and hills. This due to the flow of the Bloubank Stream, as mentioned above. The $^{87}Sr/^{86}Sr$ ratio obtained for the Bloubank Stream water is low (0.72116), as is the ratio for SSI 3 (0.72318). It appears that the Bloubank Stream, along with the Rietspruit (flows into the Bloubank, about 1km upstream) and several smaller tributaries, are transporting isotopically depleted strontium into and through the Sterkfontein Valley (Figure 18). This strontium may be derived from mineral weathering on other geologies, atmospheric deposition via precipitation and runoff or industrial effluent (sewage). SSI 17 and 18 are located further upstream and do not have as depleted $^{87}Sr/^{86}Sr$ ratios. It is suspected that, the further upstream one moves, the less depleted the $^{87}Sr/^{86}Sr$ ratios will be.

Taken as a group, the $^{87}Sr/^{86}Sr$ ratios for the 5 *A.robustus* individuals from Swartkrans appear to indicate that they may not have ranged into areas to the north of Swartkrans. The ratios obtained for plants from the northern areas are generally higher than those for the australopithecines. The southern geologies do have $^{87}Sr/^{86}Sr$ ratios within the range of the australopithecines. However it would be unwise to draw any definite interpretations on the basis of the isotopic data at this stage, due to the fact that only single samples have been analysed from all geologies, excluding the dolomite.

One southern geology that does not appear to have been covered by the australopithecines is the Archaen granite in the southeast. This area has the highest $^{87}Sr/^{86}Sr$ ratios for plants and if the australopithecines had been foraging in this area, this high strontium isotope ratio would be reflected in their individual ratios. Although it is likely that *A.robustus* spent the majority of time foraging on dolomite, they would also probably have moved onto the quartzite/conglomerate, ferrigenous shale and quartzite/greywacke areas (Figures 16 and 17). A possible reason, apart from foraging for food, for visiting these areas may have been to obtain raw material (quartzite) for the manufacture of stone tools. The quartzites (SSI 9 and 14) are the closest and most accessible source of raw material, only about three kilometers away from Swartkrans. The nearest northern source of quartzite is approximately 8 or 9 kilometers away (Figure 1).

When the $^{87}Sr/^{86}Sr$ ratios of the 5 *A.robustus* individuals are compared with the plots of predicted minimum and maximum home ranges calculated for individuals from Swartkrans, as well as Ambrose's calculations, it seems that the australopithecines were covering areas close to the minimum predicted ranges of about 5 to 10km^2 (Figures 16 and 17). However due to the range of variation observed for the dolomites, it would be unwise to predict home ranges on the basis of strontium isotopes alone. More data regarding the internal isotopic variation for the other geological areas is required before it is possible to compare the various sample sites.

If the robust australopithecines are examined individually, it may be possible to distinguish environmental preferences. One individual SK 876 (adult male) has a depleted $^{87}Sr/^{86}Sr$ result similar to those obtained for plants at SSI 3. The other robust australopithecines have $^{87}Sr/^{86}Sr$ ratios more consistent with those obtained further away from the streams. Such a separation may be indicative of individual foraging patterns amongst the robust australopithecines occurring in the area, rather than an indication of SK 876 originating from a different region, as previously suggested by Sillen and others (In press). This separation, however, may also be due to taphonomic factors causing differing strontium isotopic ratios amongst individuals, such as was indicated in the study done on archaeological bone from Kasteelberg (Section 2.4). There is an indication that SK 876 was exposed to a considerable amount of weathering before being covered by sediment (Thackeray pers. comm.)

From the projected primate home range plots, it may seen that $^{87}Sr/^{86}Sr$ ratios are not a suitable means of tracing home ranges in this region. This is especially the case when home ranges are large and the areas covered, geologically varied. Too much geological variation results in extremely varied strontium isotope ratios and isotopic overlap between areas. Such variation would be difficult to interpret, in terms of establishing an individuals ranging behavior. However, as indicated by the data for australopithecines from Swartkrans, it may be possible to predict certain key areas of exploitation for individuals. It may be possible to use $^{87}Sr/^{86}Sr$ ratios to trace home ranges for highly territorial species or individuals with small home ranges. In addition, one can look at those factors that result in primate species having small home ranges, such as resource density, population density, degree of competion and social behavior. These factors may be applicable to early hominids, as the isotopic data indicates that they may have ranged over a small area.

7. CONCLUSION

The use of strontium isotope ratios as a means of tracing early hominid home ranges, may not be possible in the Sterkfontein Valley, owing to the extreme range in variation of the $^{87}Sr/^{86}Sr$ ratios obtained. Isotopic data obtained for plant and soil samples from the study area indicate that there may be very large differences in $^{87}Sr/^{86}Sr$ ratios within a single geological area. These differences may occur over a very short distance and are likely due to a number of factors.

As a whole, the various geologies of the Sterkfontein Valley and surrounding areas may be generally distinguished from each other by means of their respective strontium isotope ratios. That is, shales and granites will generally have higher $^{87}Sr/^{86}Sr$ ratios than quartzites and mafic rocks. These differences are due to geological factors, such as the geological age of the parent rocks of each individual area.

It has become clear that there is no single characteristic strontium isotope ratio for the geologies, and it is suspected that each will have a range of strontium isotope ratios that will overlap with other ranges. An indication of this, is the range of $^{87}Sr/^{86}Sr$ ratios obtained for samples from the dolomitic areas, particularly around Swartkrans, where $^{87}Sr/^{86}Sr$ ratios range from 0.748606 to 0.720282. This variation is most likely due to two main factors; firstly the topography and secondly the twofold deposition and removal process of the Bloubank Stream. The results from the three transects taken around Swartkrans provide clear evidence for the effects of the above mentioned factors. It is probable that if similar transects were taken on the other geological areas, a similar distribution pattern would be evident. The isotopic variation found at Swartkrans should serve as an indication that it would be unwise to base any interpretations on single background $^{87}Sr/^{86}Sr$ ratios from any one area. One would stress the need for an intensive sampling strategy to get a measure of background strontium ratios for a study area, before making any predictions, be they for behavioral interpretations or sourcing a particular item or individual.

The $^{87}Sr/^{86}Sr$ ratios of plants are not a reflection of the total strontium isotope ratio of a particular geology, but rather reflect the $^{87}Sr/^{86}Sr$ ratio of the available strontium in the soil cation pool. This available soil strontium may be derived from a number of sources, including chemical weathering of parent rocks, atmospheric strontium, decaying organic material and from groundwater. Thus, if one requires an indication of the variation in background strontium for the Sterkfontein Valley, it is necessary to analyse a variety of plants and the available soil strontium, rather than the total soil strontium, as it will the strontium in the plants that will be reflected in the diet of an individual.

A complication in this method, is the amount of mixing that has occurred and the contribution of the various above mentioned sources to the environment around Swartkrans. This may be overcome through the collection of additional samples from the Swartkrans area. These would include grass and tree samples, rainwater, atmospheric dust and streamwater samples from upstream (Rietspruit and tributaries), as well as downstream (Bloubank Stream). Through the analysis of this material one may be able to determine the relative contribution of waterborne and atmospheric strontium to the Swartkrans soil strontium pool and hence the plants. As mentioned in section 5, grasses are representative of one season of mixing, while perennials will reflect a number of years of mixing, hence the need to sample both to obtain an indication the changes to the soil strontium pool.

Although additional sampling from the Sterkfontein valley is desirable, it is still possible to derive important, albeit unexpected environmental interpretations. It is possible to distinguish between riparian areas along the Bloubank Stream and the hill slopes on either side. The riparian area has lower $^{87}Sr/^{86}Sr$ ratios, compared to the upper areas. Thus hominids foraging along the streambanks should have lower $^{87}Sr/^{86}Sr$ ratios than those foraging mainly on the hill. This seem to be the case with the robust Australopithecines from Swartkrans Member 1, one individual (SK 876) has a depleted $^{87}Sr/^{86}Sr$, compared to four other individuals (Sillen *et al* In press).

It would appear that the hominids at Swartkrans were not moving into the northern areas, but rather concentrating their foraging activities in the southern areas. Their $^{87}Sr/^{86}Sr$ are more similar to the $^{87}Sr/^{86}Sr$ ratios obtained for the southern geologies. Additional sampling of the southern geologies may help in strengthening this interpretation. Unlike strontium isotopes, neodymium isotopes have yet to be more fully applied to archaeological and palaeontological studies. It appears, based on results using neodymium in tracing ivory and rhino horn, that they may provide an additional means of characterising geological environments and serve as a further data source with which to identify and clarify hominid catchment areas, as well as having further application in palaeodietary and palaeoenvironmental studies.

The most important conclusion of this study is that it is unlikely to accurately predict hominid home ranges, based on strontium isotope ratios alone. This is largely due to the extreme variation in $^{87}Sr/^{86}Sr$ ratios obtained for a single geology, such as dolomite. This is also indicated by the projected home range data for the selected primate species. If one has a large home range in the Sterkfontein Valley, it will cover a number of geologies and as a consequence, individuals will have a very mixed isotopic signal. Unless an individual has a small home range and is very territorial, it is unlikely that it would be possible to trace the home range using strontium isotopes. A means of reducing the strontium isotopic variation in an area, may be to use a combination of heavy stable isotope ratios such as neodymium (Nd) and lead (Pb), in addition to strontium isotope ratios, in order to isotopically characterise different geologies or even habitats on a single geological substrate.

Although it may not be possible at this stage to accurately trace the home ranges of early hominids using strontium isotopes, the method may be used to explore other avenues of early hominid behavior, such as an individual's choice of foraging habitat. Further research into the method, as well as into the use of a combination of heavy stable isotopes may yet prove that the heavy stable isotopes of strontium, neodymium and lead are a powerful means of interpreting early hominid behavior.

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FIGURES AND TABLES

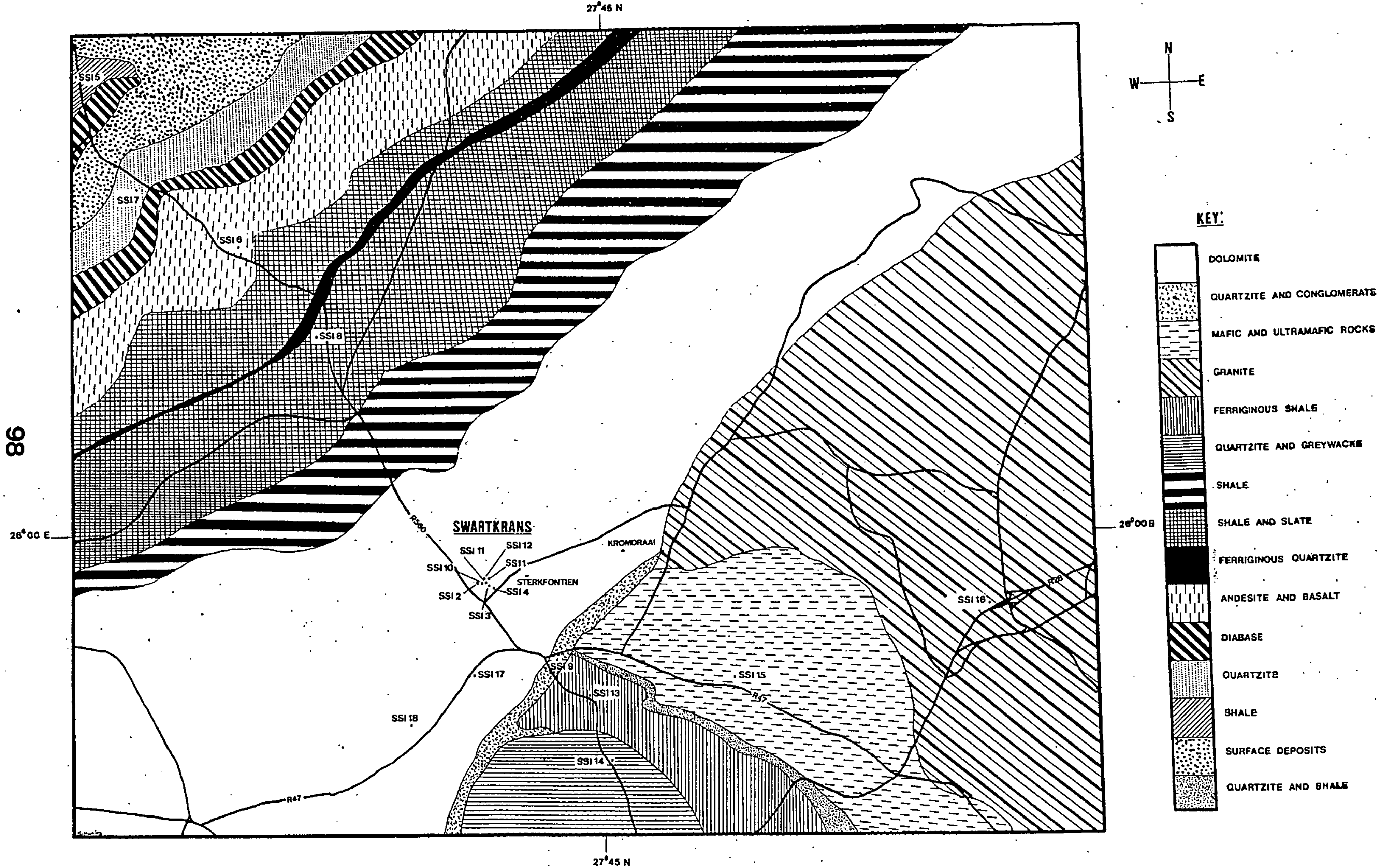

Figure 1: Geological map of the Sterkfontein Valley and surrounding areas. Scale = 0 1 2 3 4 5 KM 1:50 000.

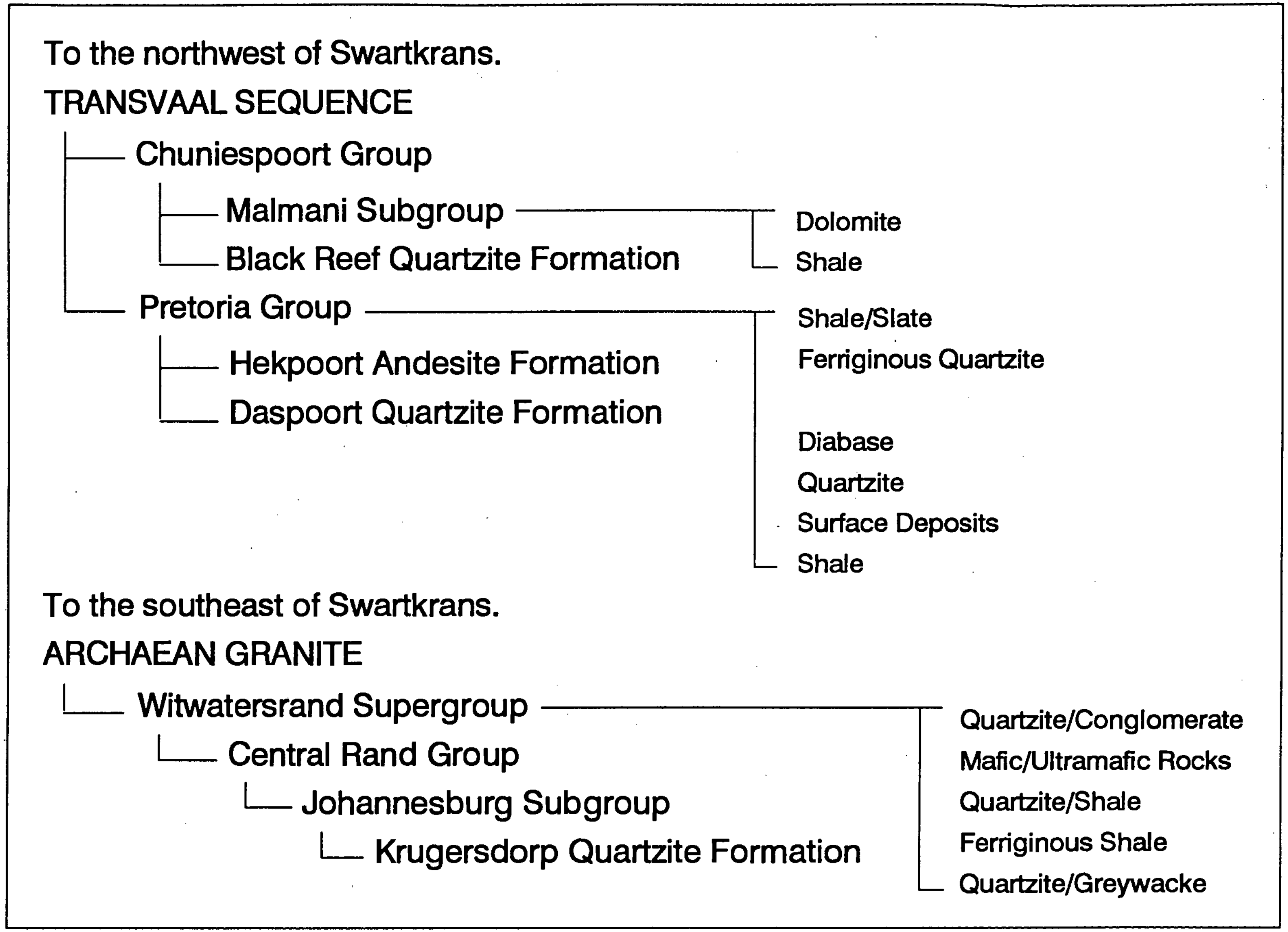

Figure 2: Simplified geological sequence for the Sterkfontein Valley and surrounding areas.

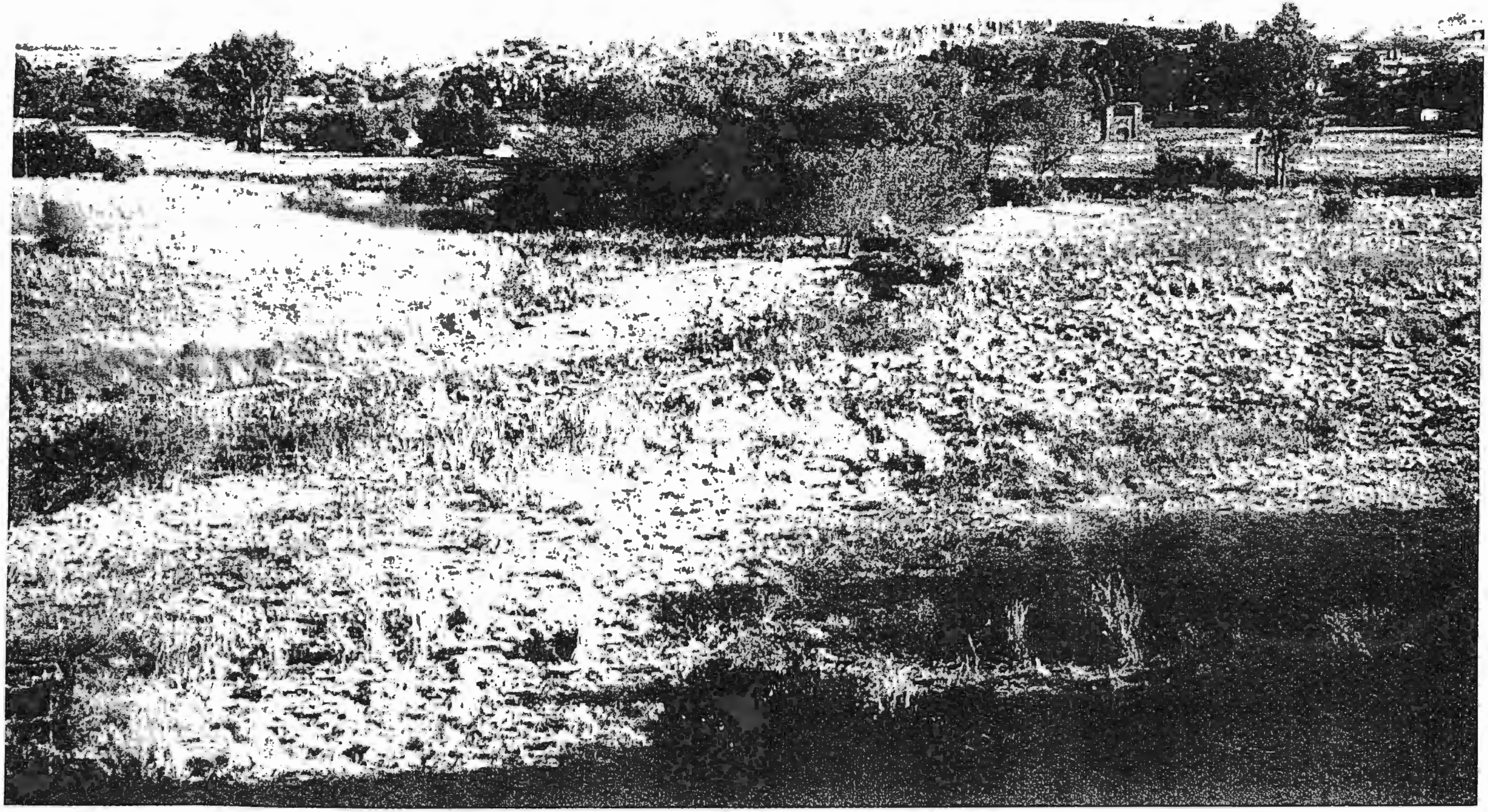

Figure 3: Western view from Swartkrans, overlooking the floodplain of the Bloubank Stream.

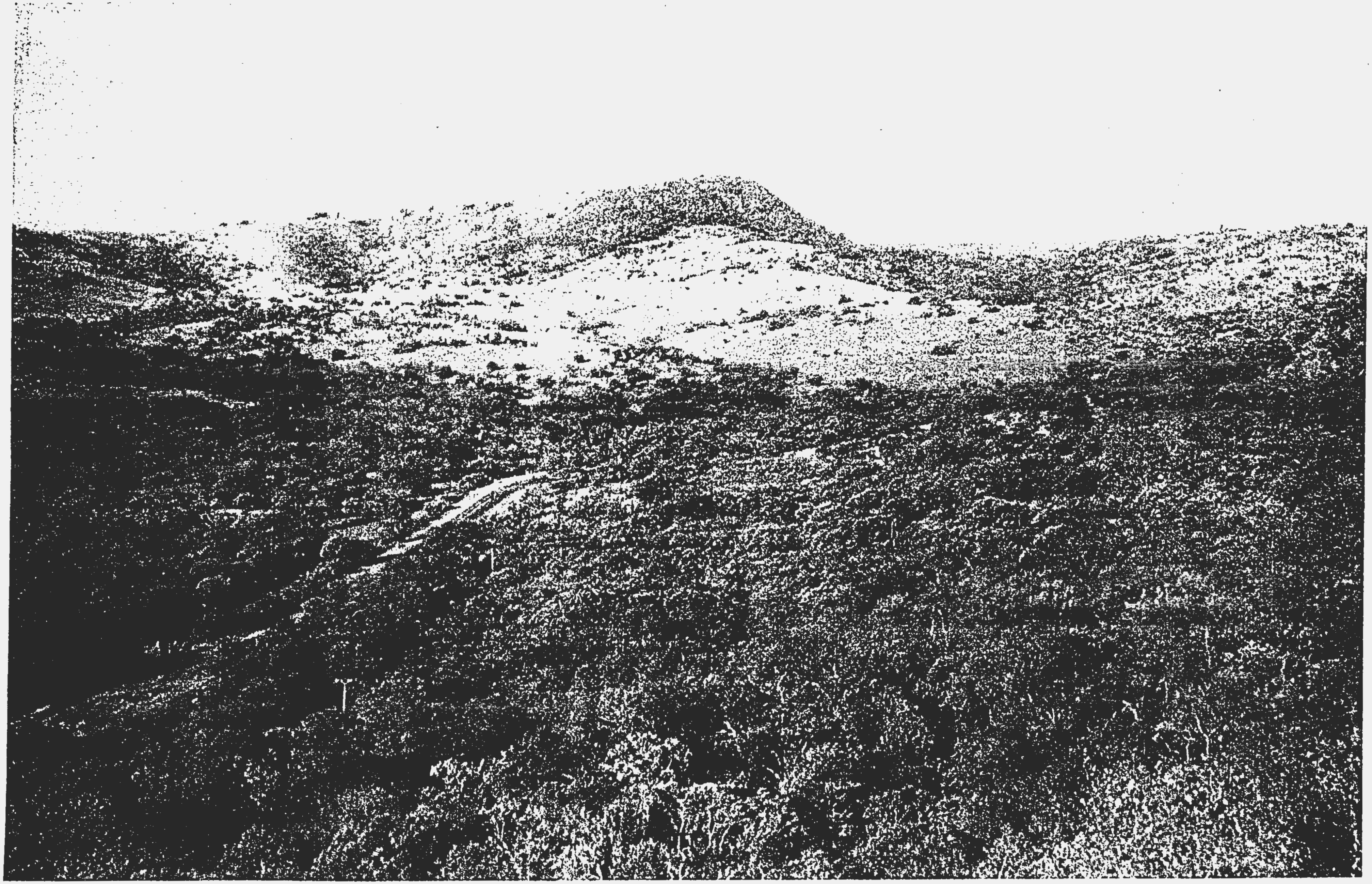

Figure 4: Southern view from SSI 7 (Quartzite) along the Hekpoort Kloof towards Swartkrans.

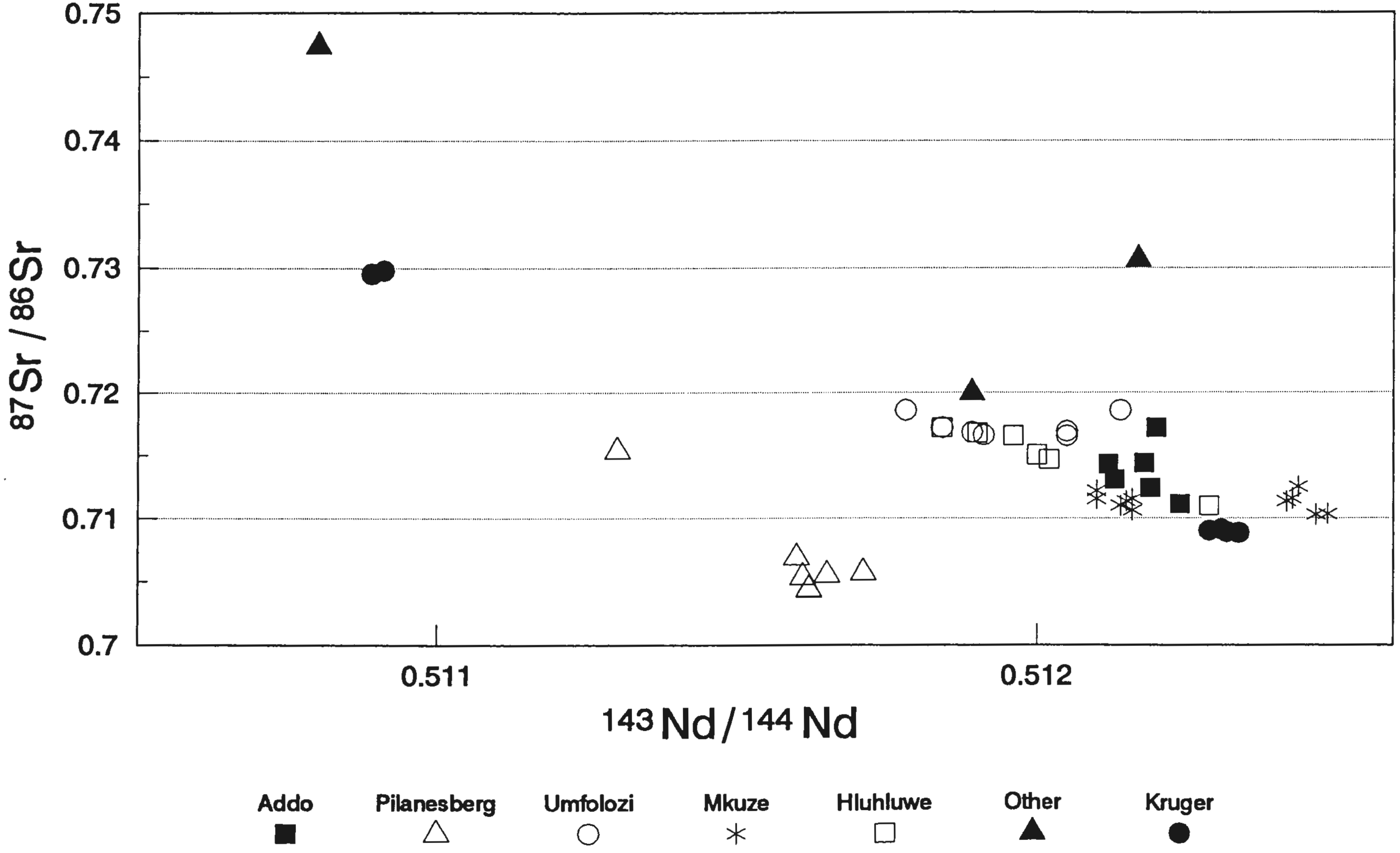

Figure 5: Plot of $^{87}Sr/^{86}Sr$ against $^{143}Nd/^{144}Nd$ for rhino horn from South Africa. Adapted from Lee-Thorp *et al* (1992).

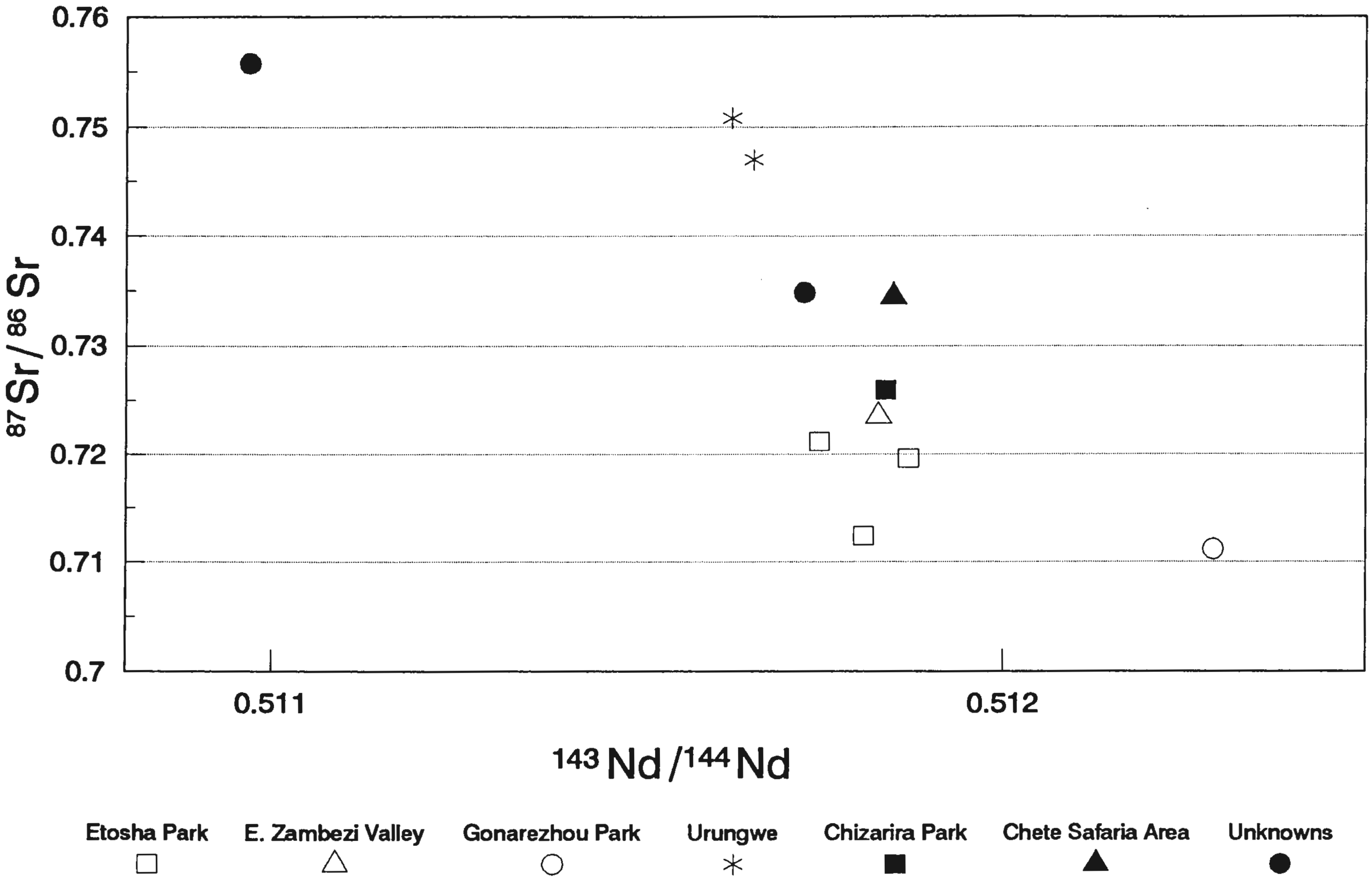

Figure 6: Plot of $^{87}Sr/^{86}Sr$ against $^{143}Nd/^{144}Nd$ for rhino horn from Africa. Adapted from Lee-Thorp *et al* (1992).

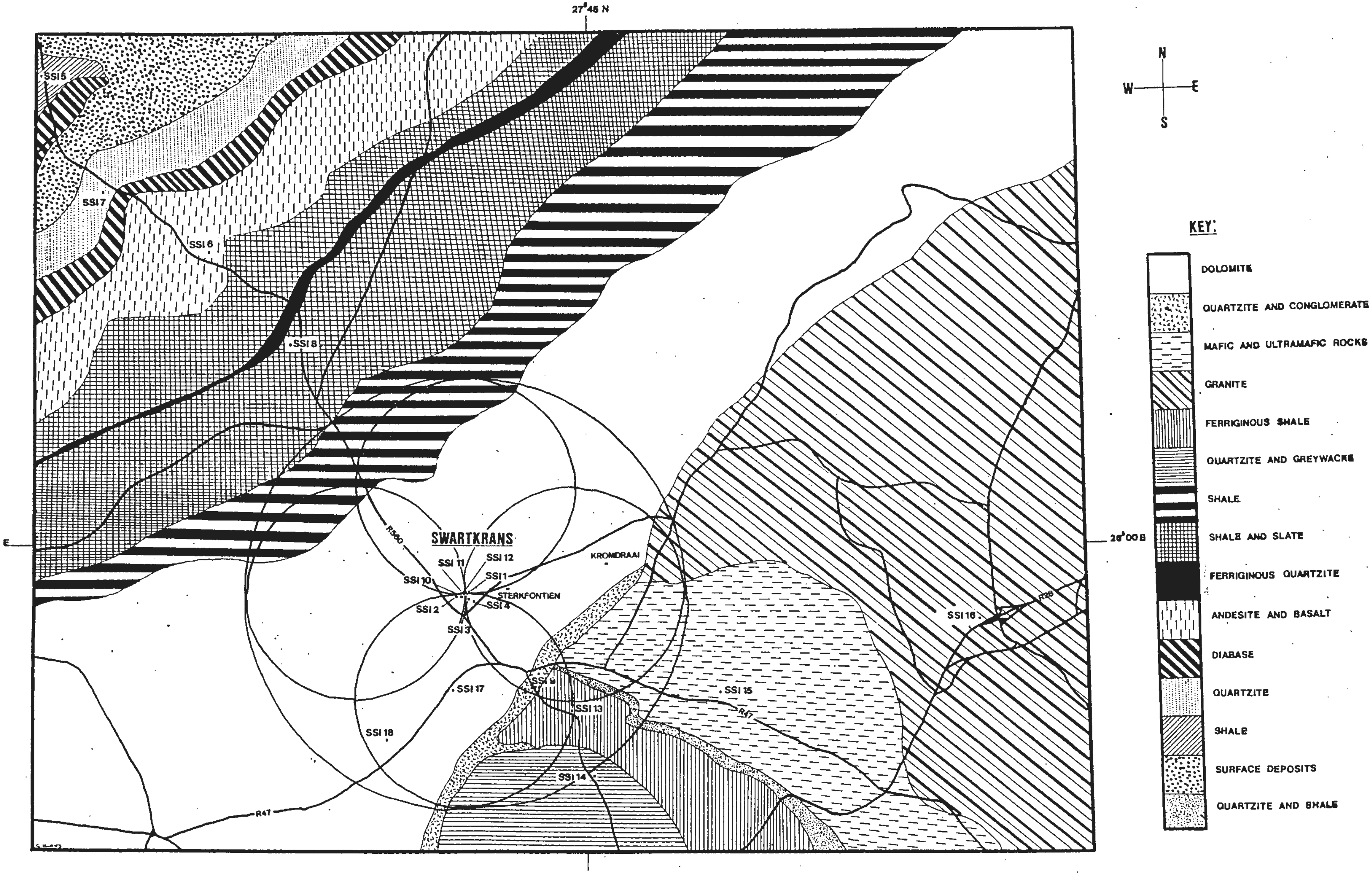

Figure 7: Average home range for Savanna Baboons, including Yellow (*Papio cyanocephalus*) and Chacma Baboons (*P.anubis*), with Swartkrans as the point of origin.

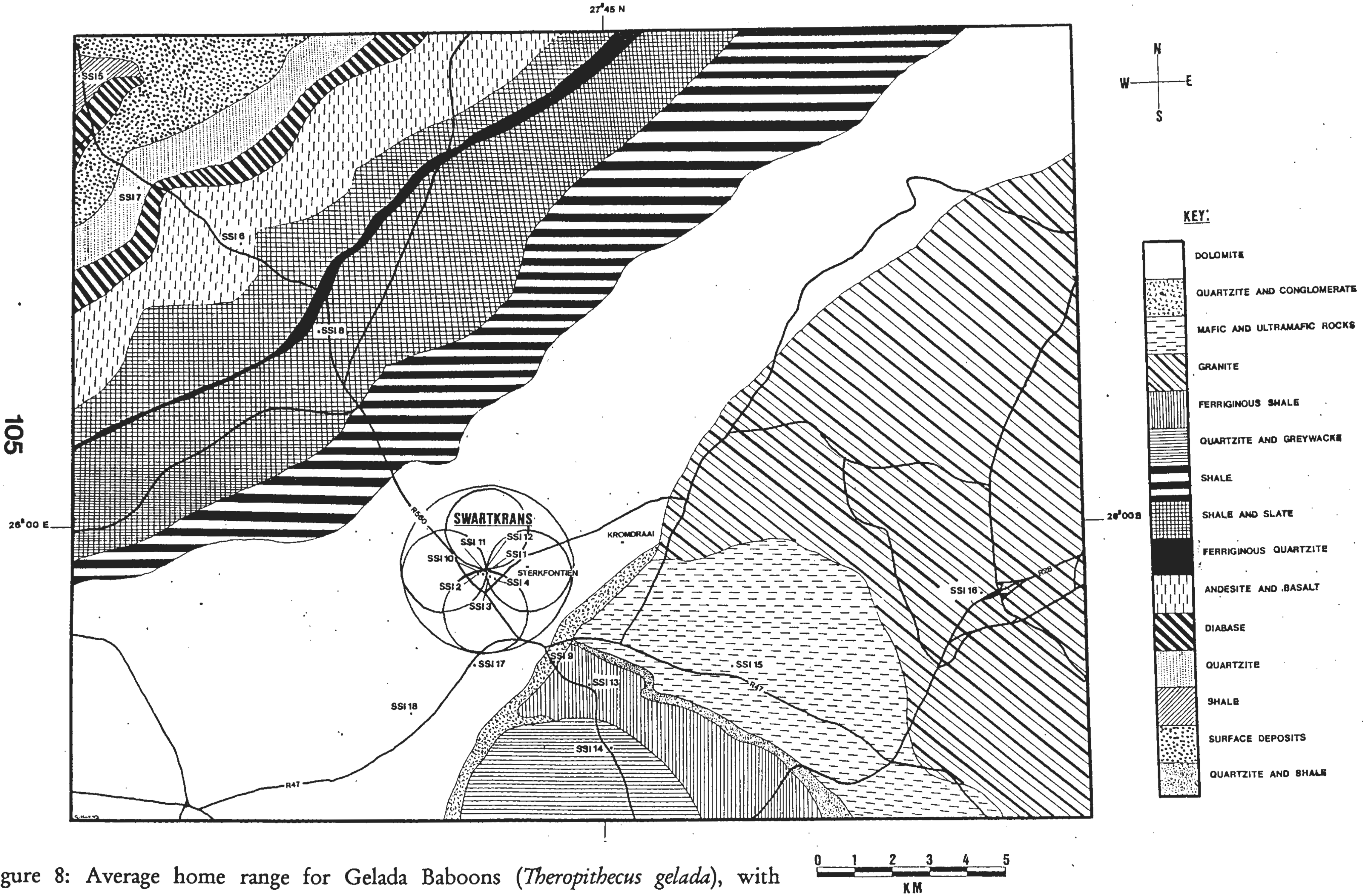

Figure 8: Average home range for Gelada Baboons (*Theropithecus gelada*), with Swartkrans as the point of origin.

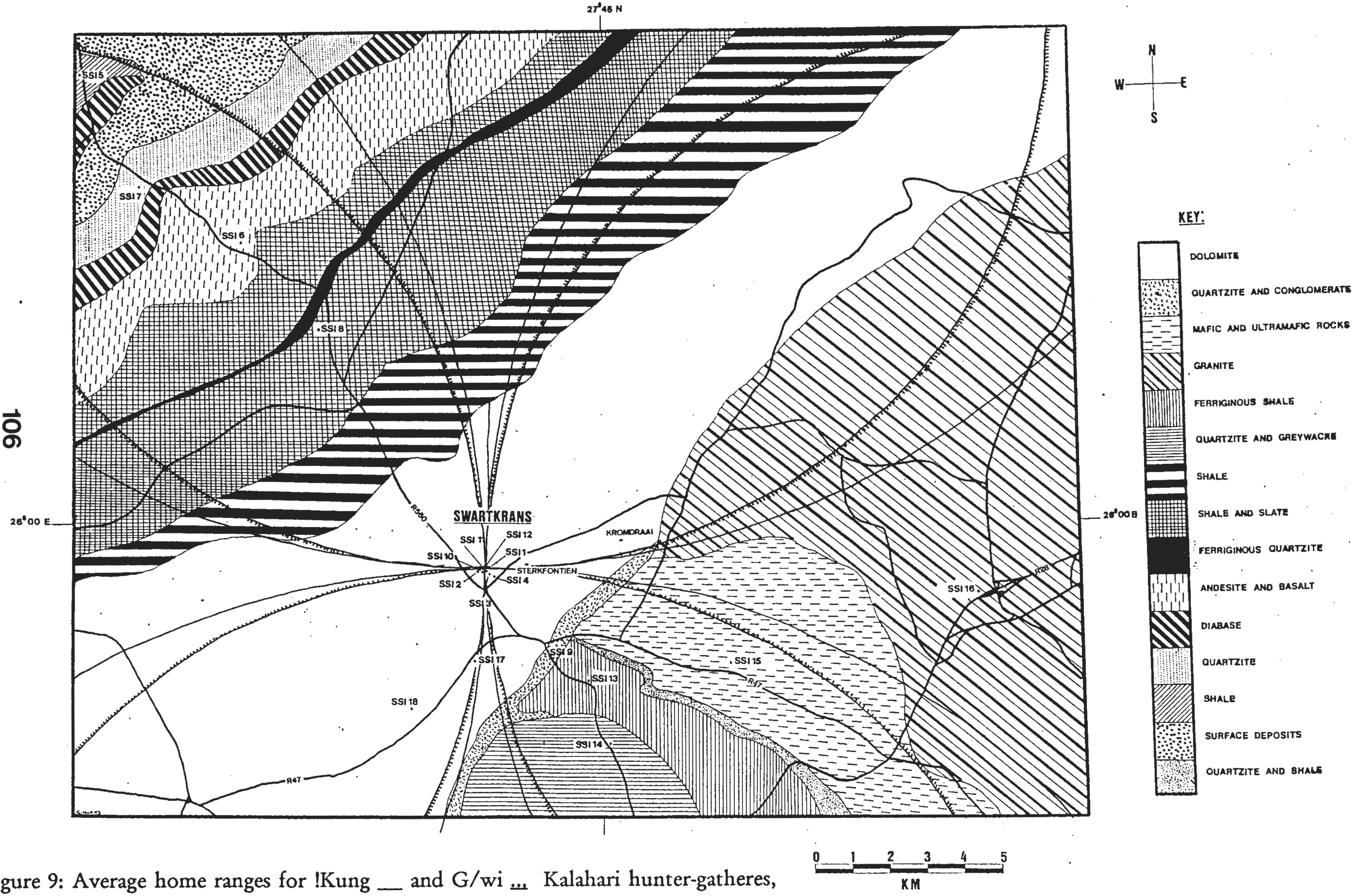

Figure 9: Average home ranges for !Kung __ and G/wi ... Kalahari hunter-gatheres, with Swartkrans as the point of origin.

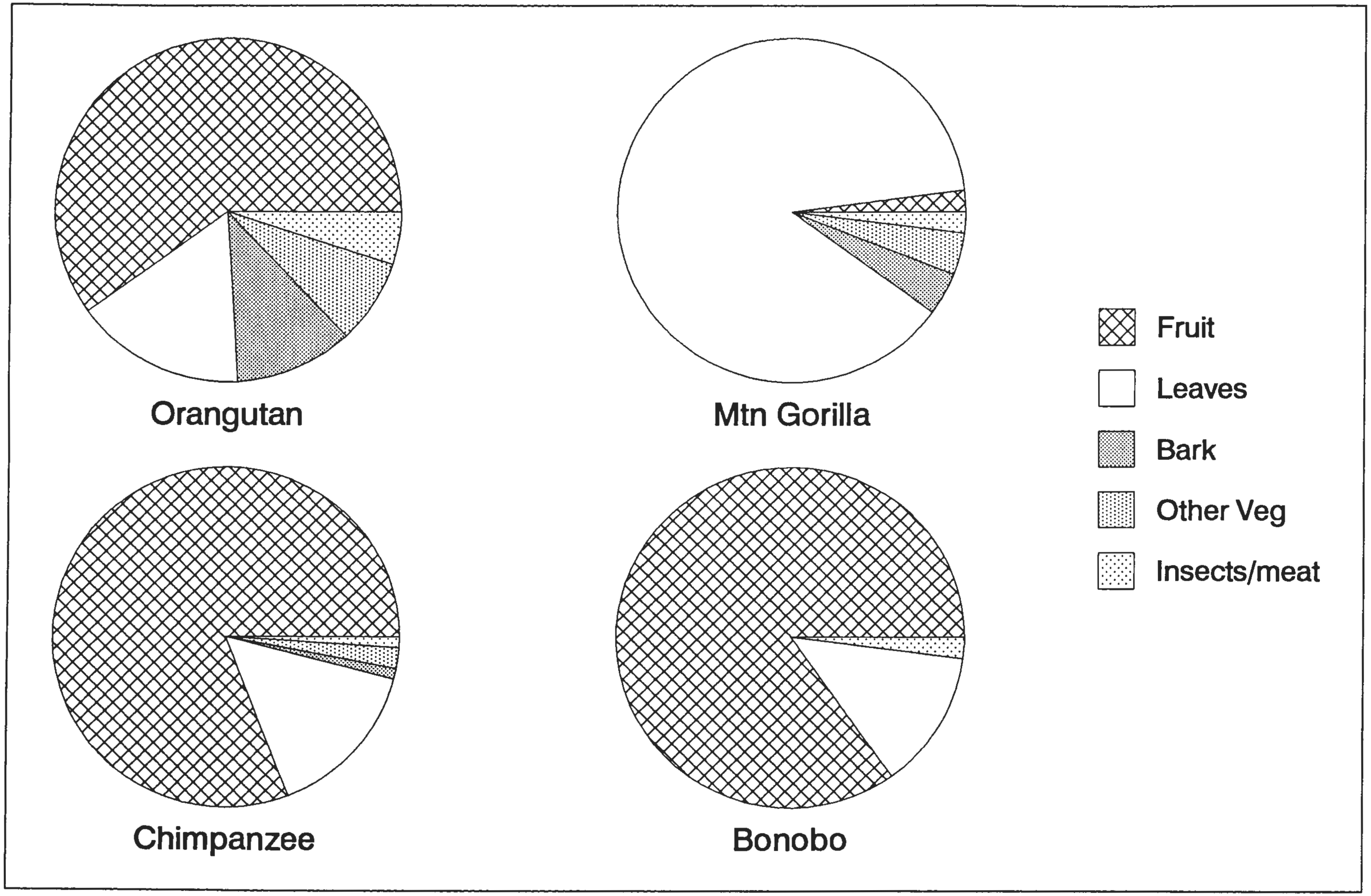

Figure 10: Dietary composition of orangutans, mountain gorillas, common chimpanzees and bonobos. Adapted from Ghiglieri (1987).

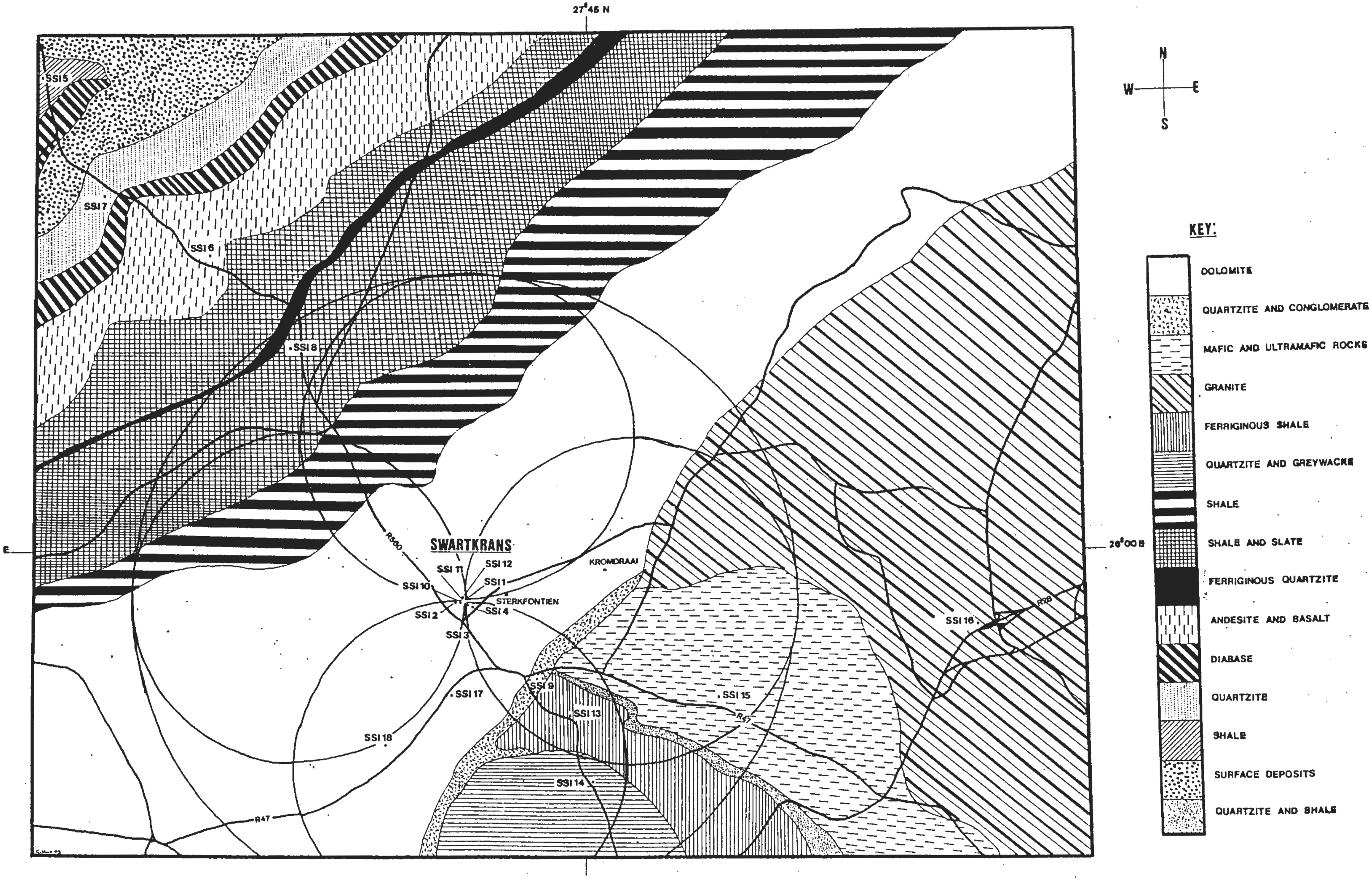

Figure 11: Average home range for Common Chimpanzees (*Pan troglodytes*) , with Swartkrans as the point of origin.

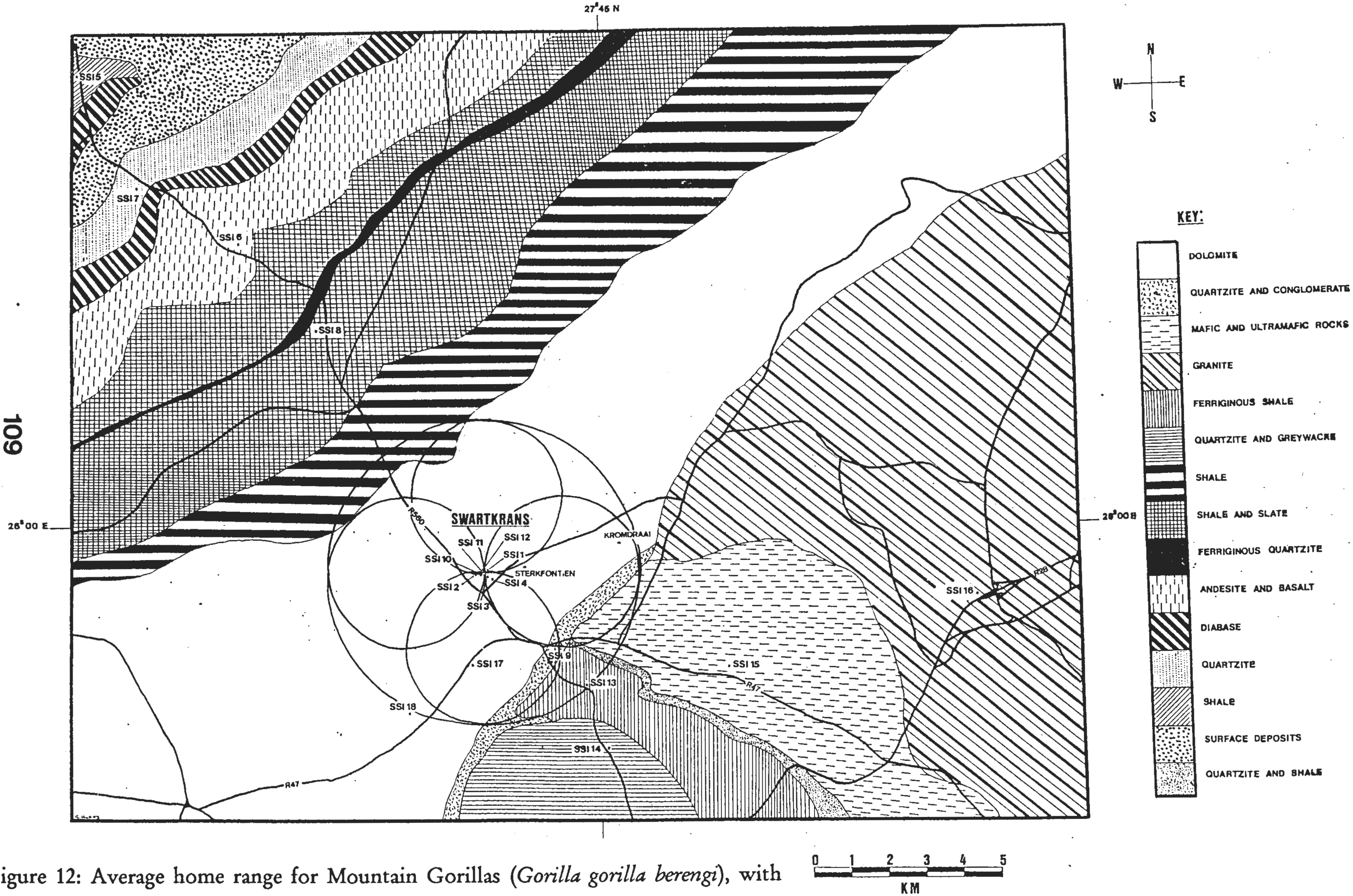

Figure 12: Average home range for Mountain Gorillas (*Gorilla gorilla berengi*), with Swartkrans as the point of origin.

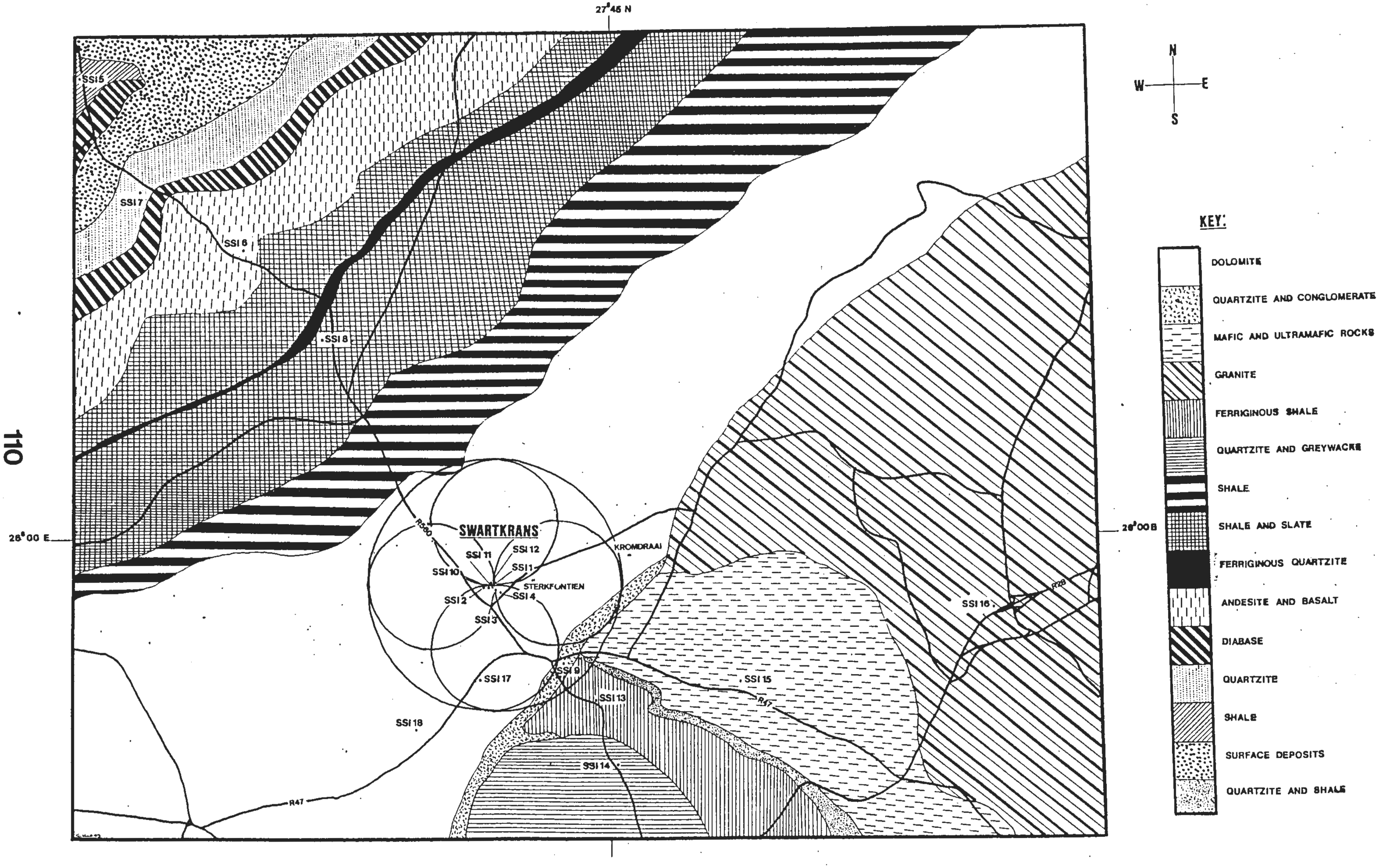

Figure 13: Average home range for Western Lowland Gorillas (*G.gorilla gorilla*), with Swartkrans as the point of origin.

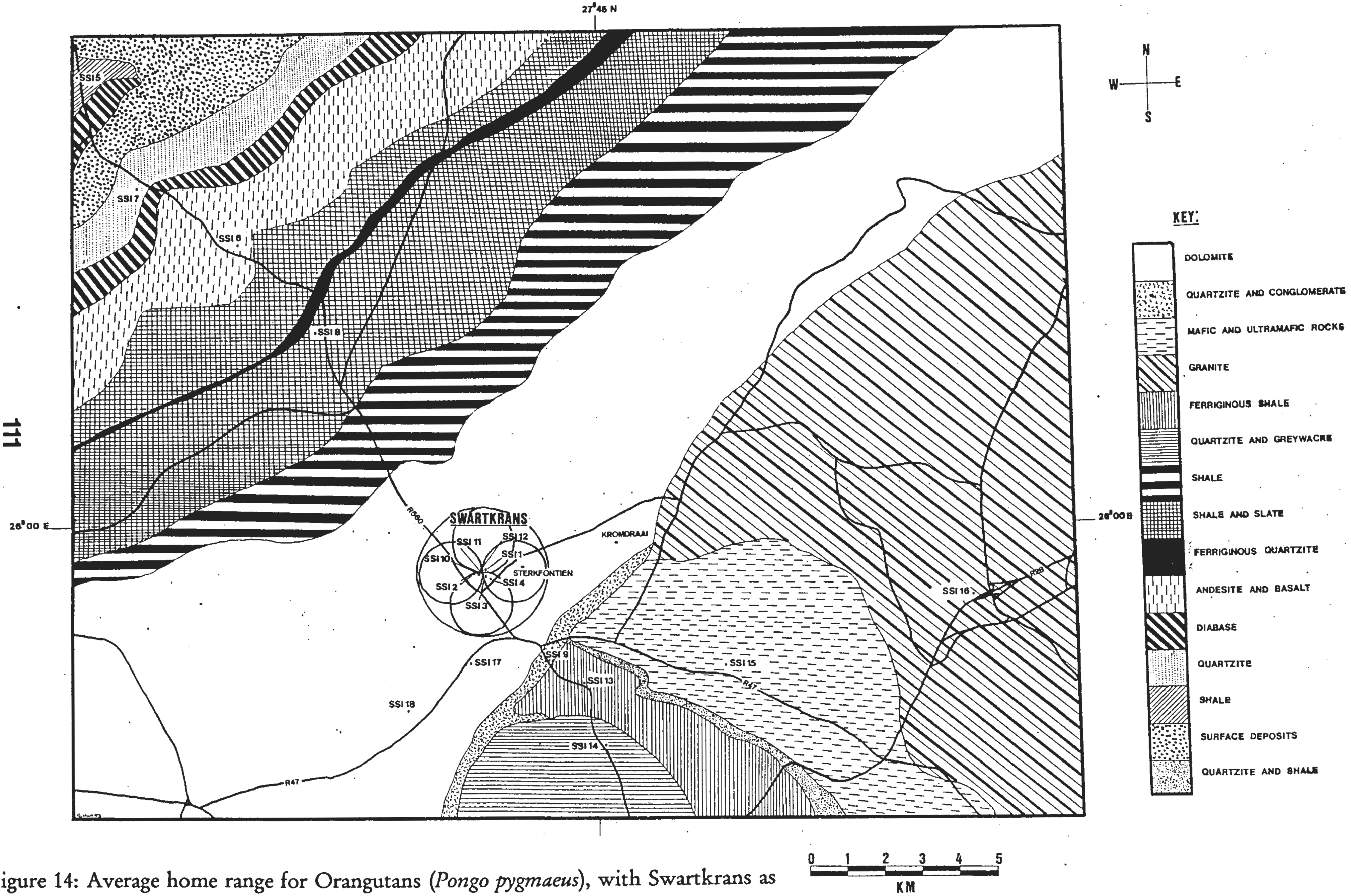

Figure 14: Average home range for Orangutans (*Pongo pygmaeus*), with Swartkrans as the point of origin.

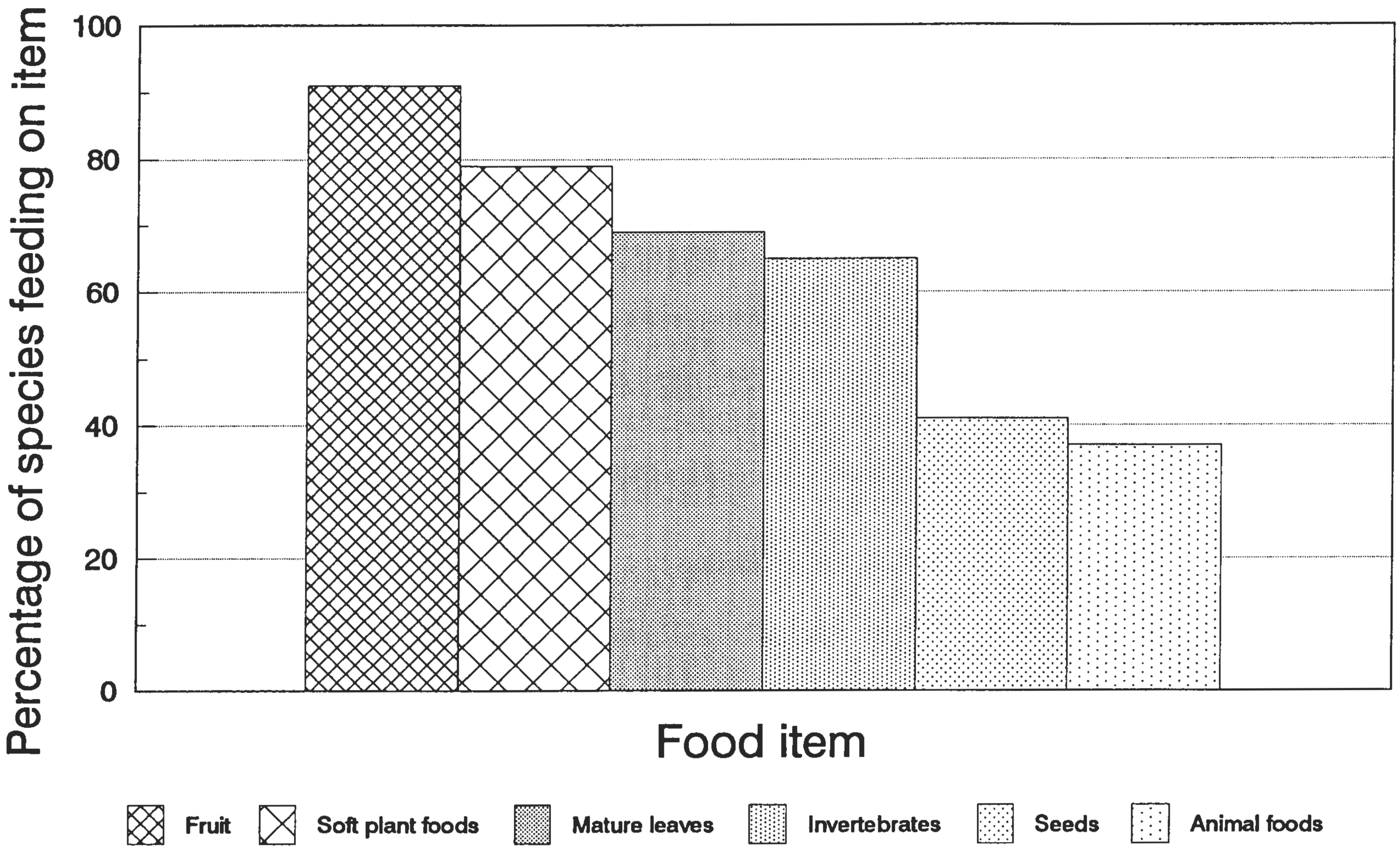

Figure 15: Percentage choice of 131 primate species for key food items. Adapted from Ghiglieri (1987).

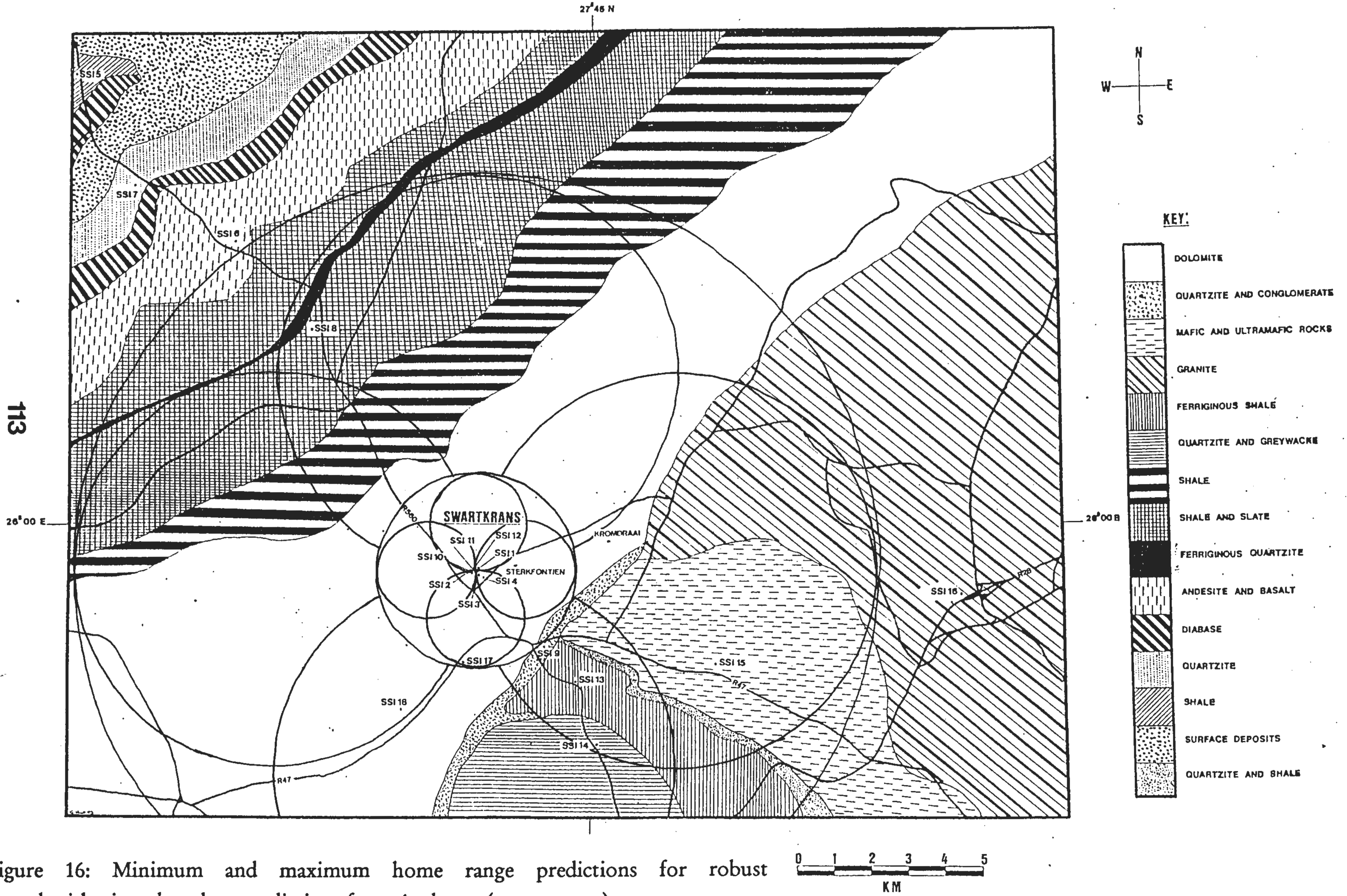

Figure 16: Minimum and maximum home range predictions for robust australopithecines, based on predictions from Ambrose (pers. comm.)

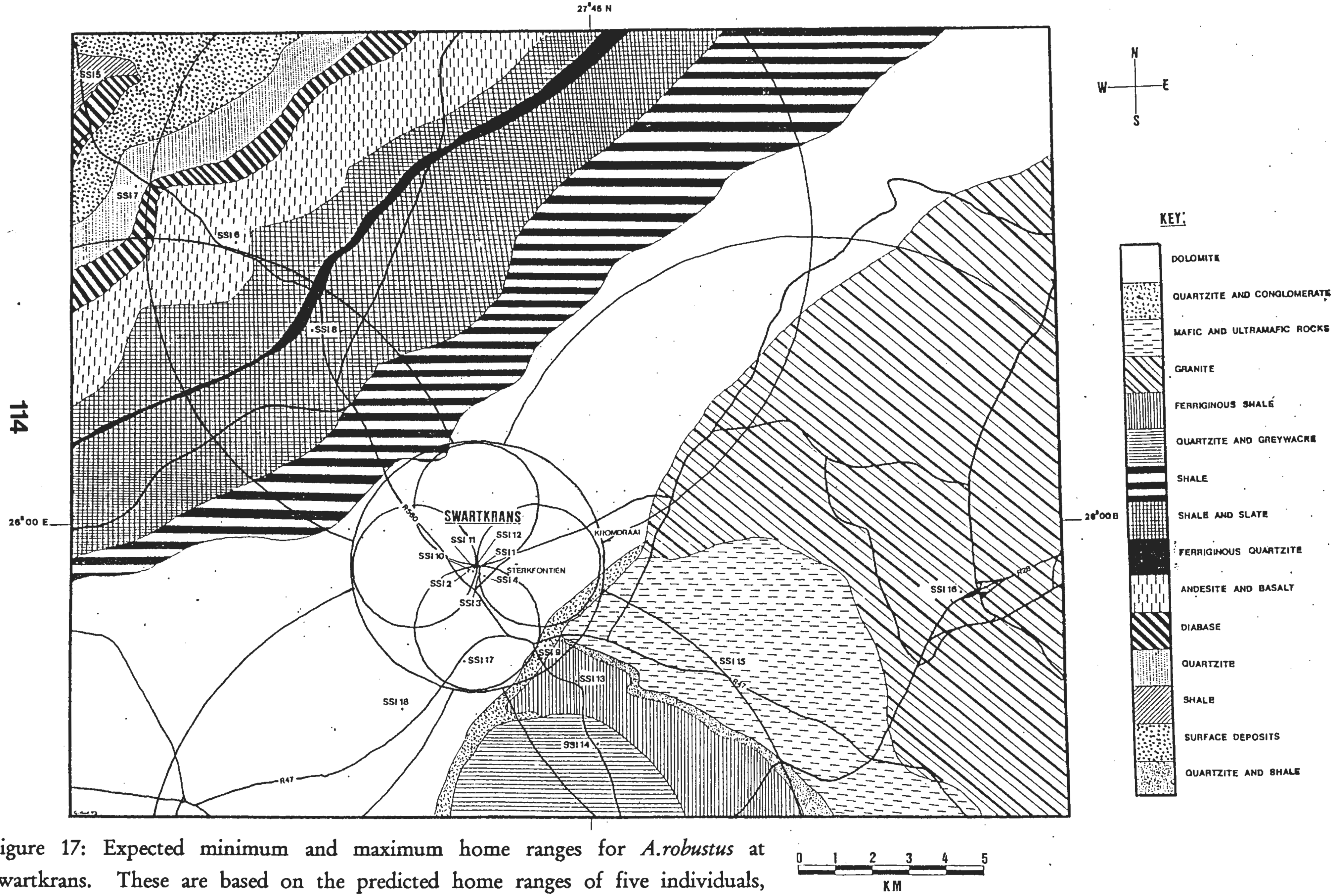

Figure 17: Expected minimum and maximum home ranges for *A.robustus* at Swartkrans. These are based on the predicted home ranges of five individuals, calculated by Milton and May's (1975) body weight formula.

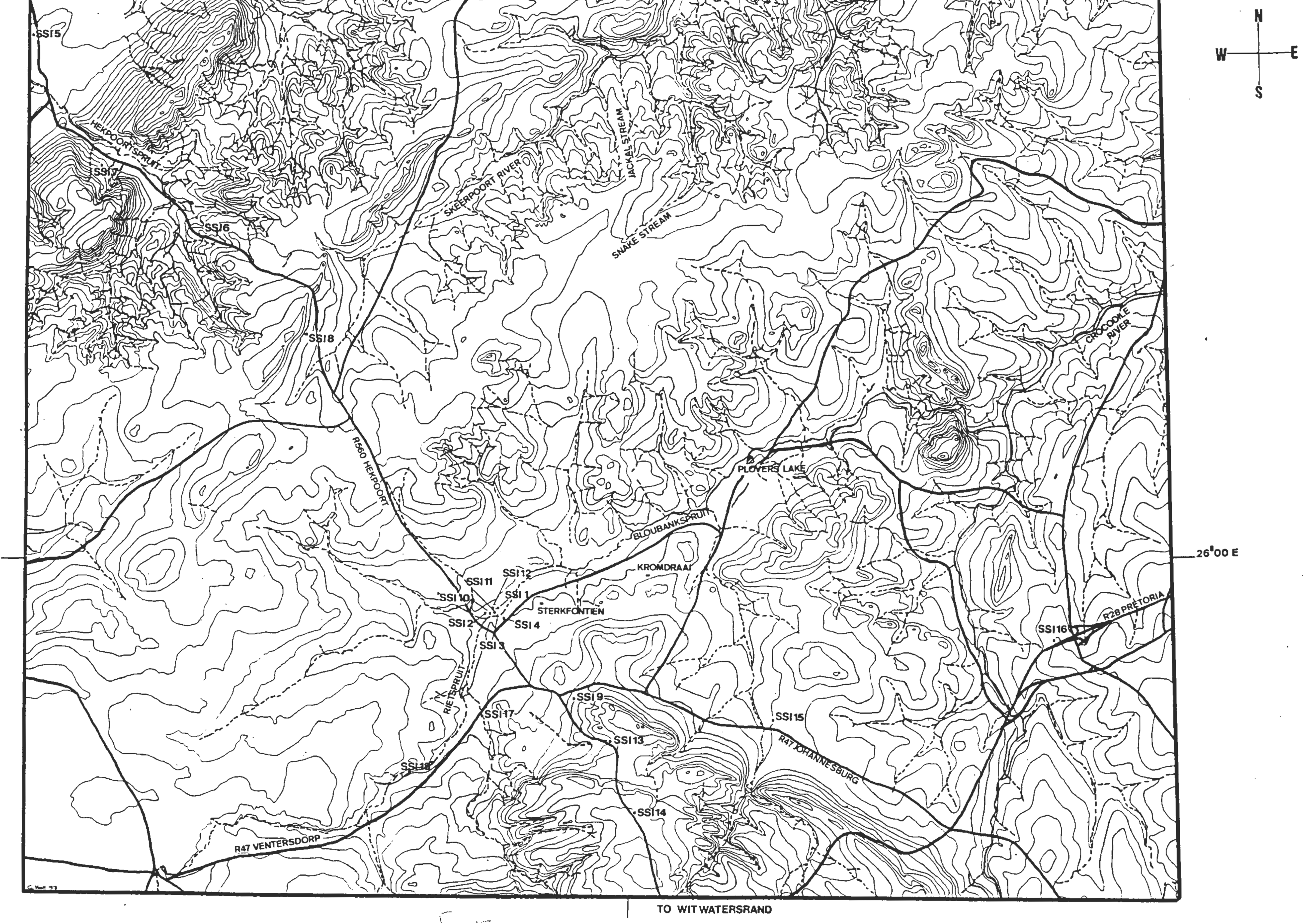

Figure 18: 1:50 000 topographical map of the Sterkfontein Valley and surrounding areas, indicating sample sites and drainage patterns. Contour intervals at 20m.

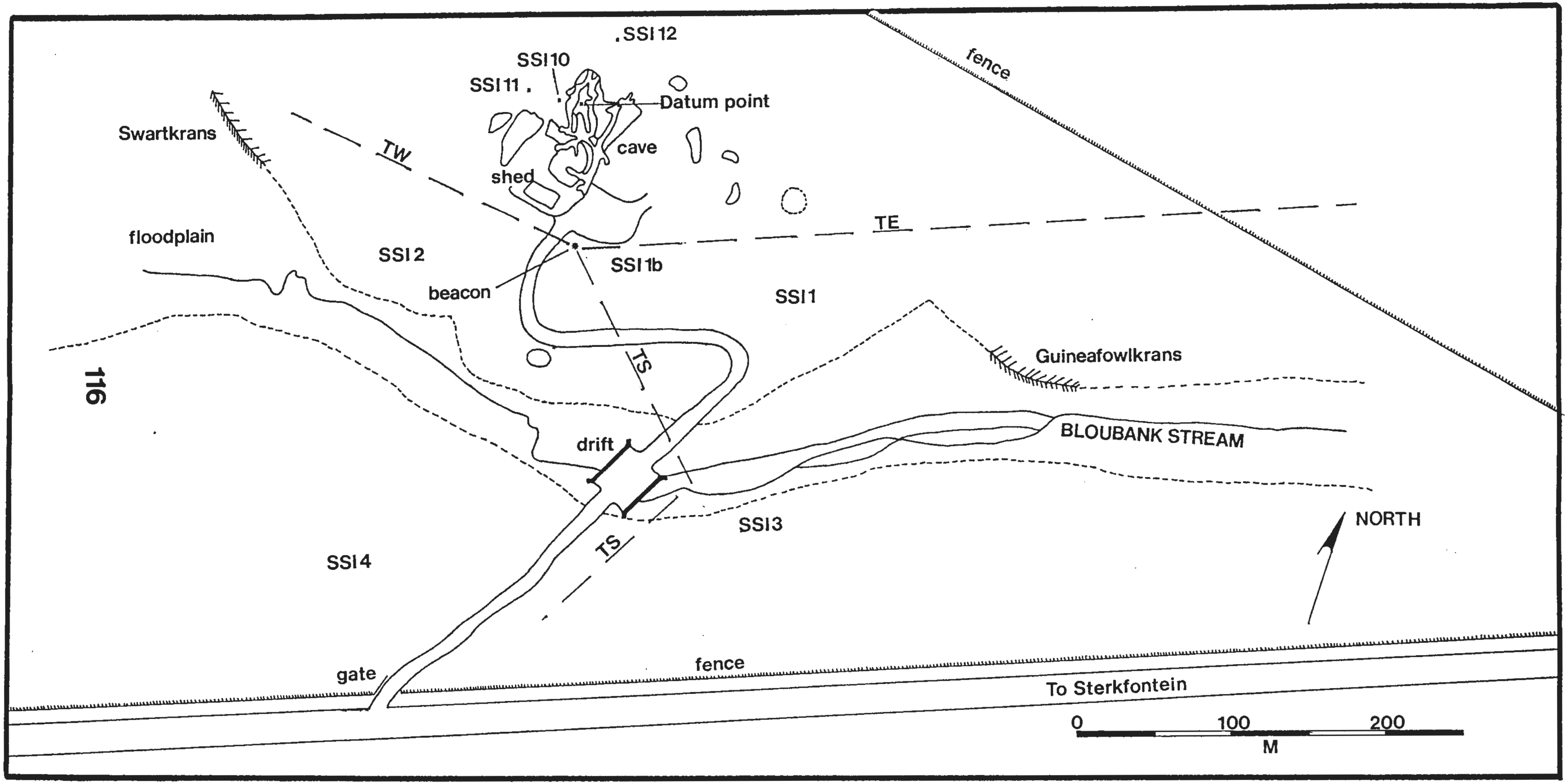

Figure 19: Detail of Swartkrans showing the location of key features and transects, with their origin at the beacon.

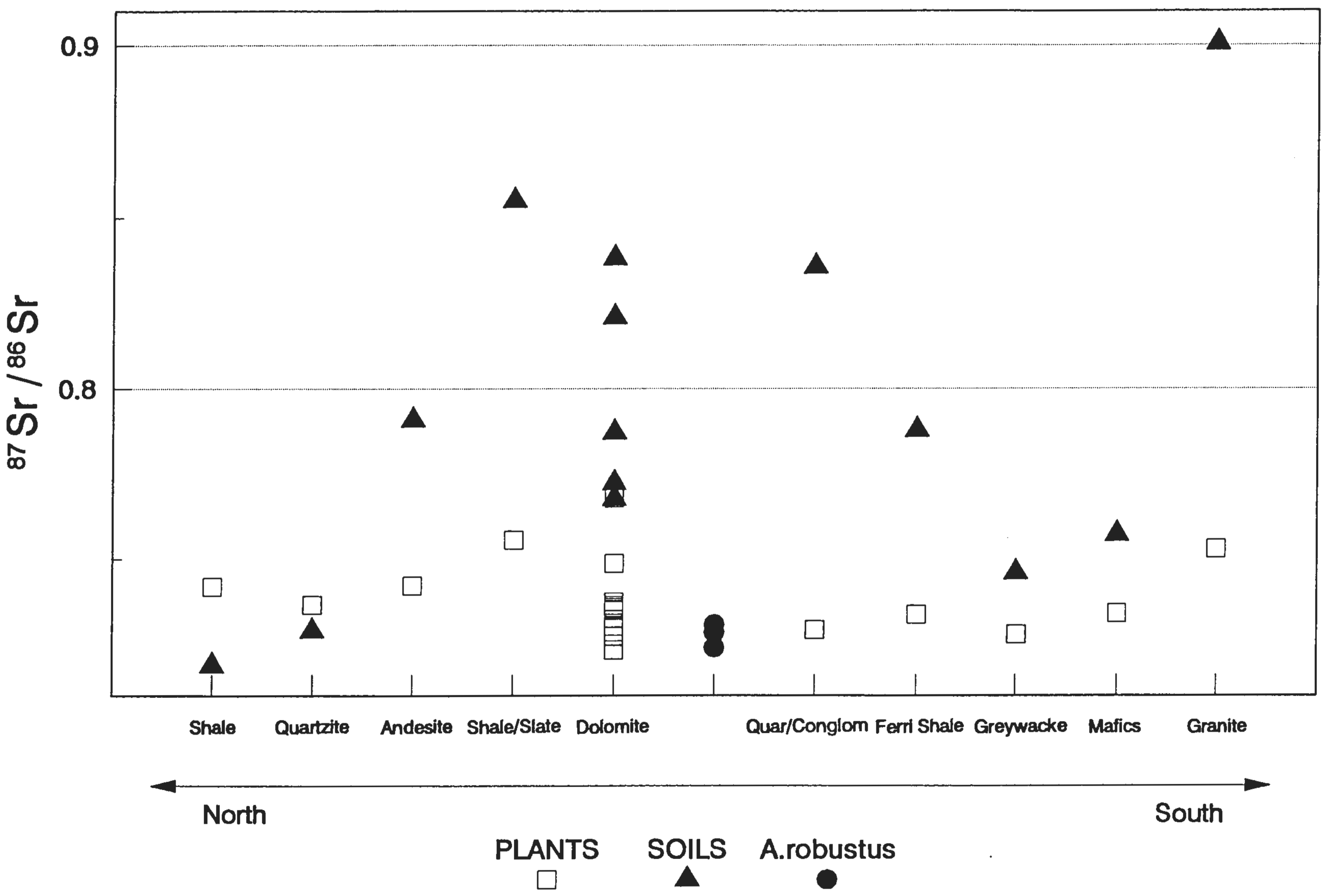

Figure 20: ^{87}Sr/^{86}Sr ratios for plant, total soil and 5 *A.robustus* individuals from sampled geological areas in the Sterkfontein Valley and immediate vicinity. Data are arranged as one moves from north to south across the study area. (*A.robustus* data from Sillen *et al* In press).

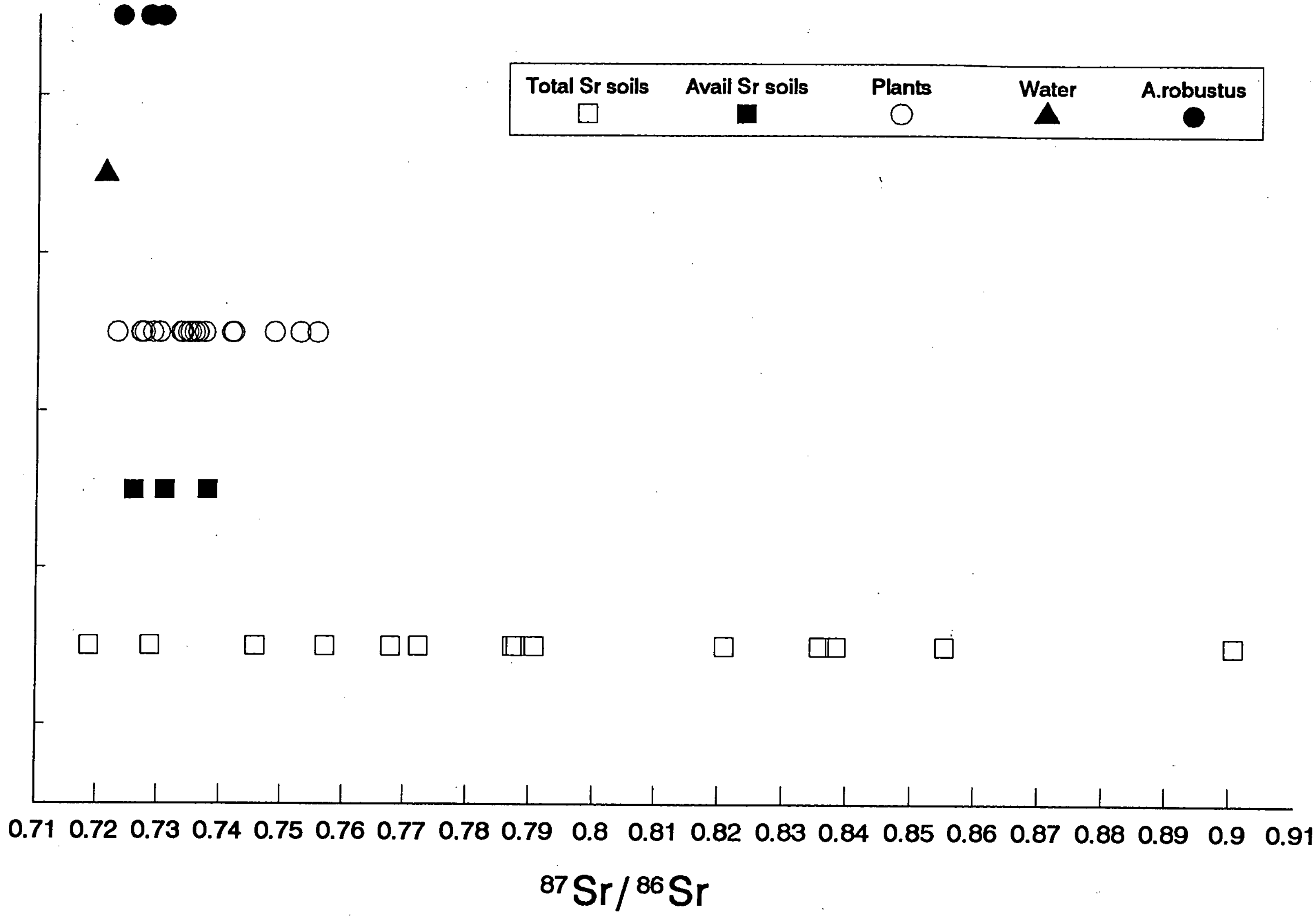

Figure 21: Total range of ^{87}Sr/^{8}6Sr ratios for plants, soils, water and 5 *A.robustus* individuals from the Sterkfontein Valley and immediate vicinity. (*A.robustus* data from Sillen *et al* In press).

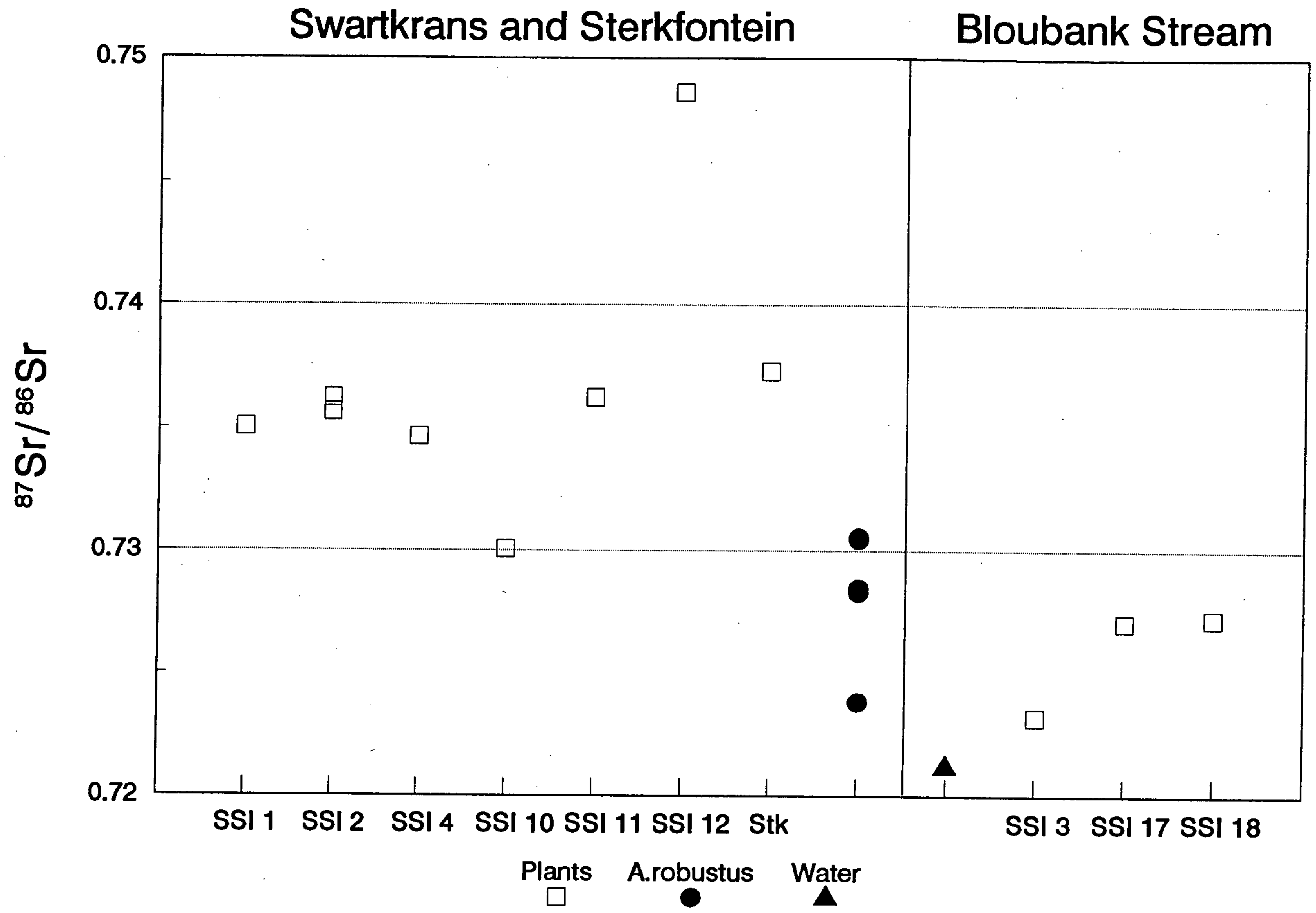

Figure 22: ^{87}Sr/^{86}Sr ratios for plants and water from dolomitic substrates in the Sterkfontein Valley. The *A.robustus* individuals are from Swartkrans Member 1 (Data from Sillen *et al* In press).

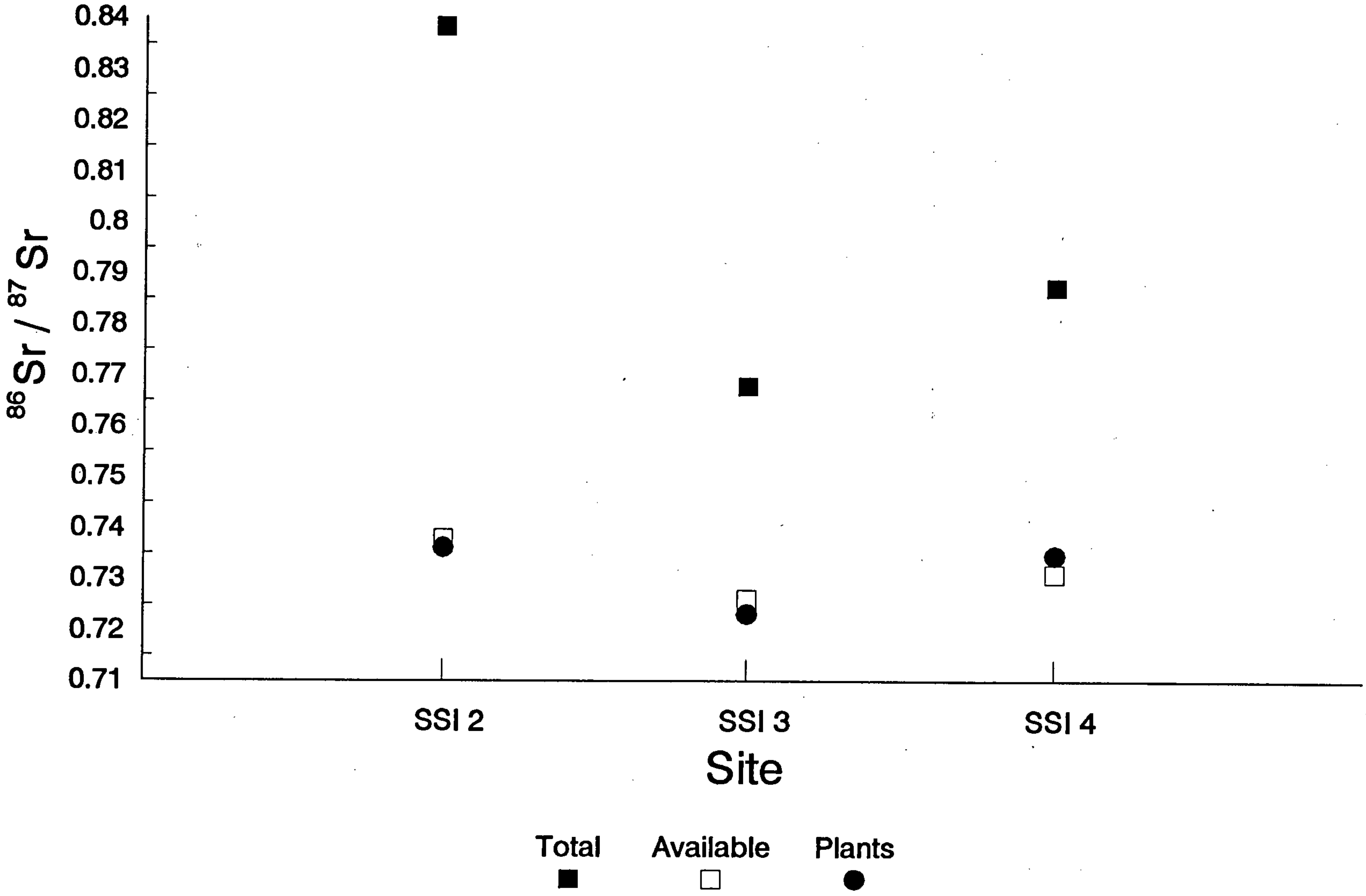

Figure 23: ^{87}Sr/^{86}Sr ratios for 3 plant and 3 soil samples from Swartkrans (dolomite), showing total and available soil strontium isotope ratios.

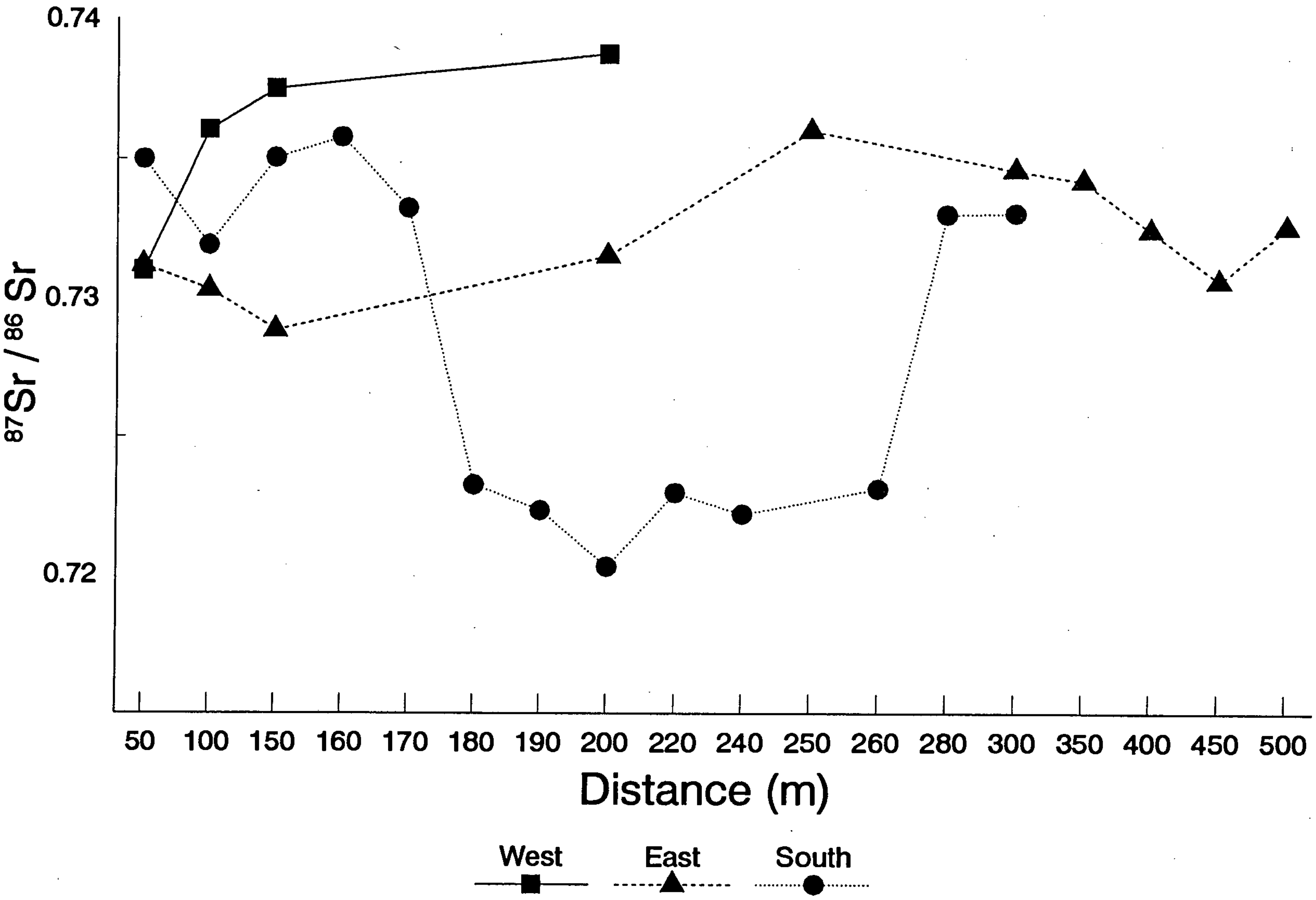

Figure 24: $^{87}Sr/^{86}Sr$ ratios for plant samples from three transects TE, TW and TS, taken around Swartkrans (dolomite). All three transects have a common point of origin at the beacon.

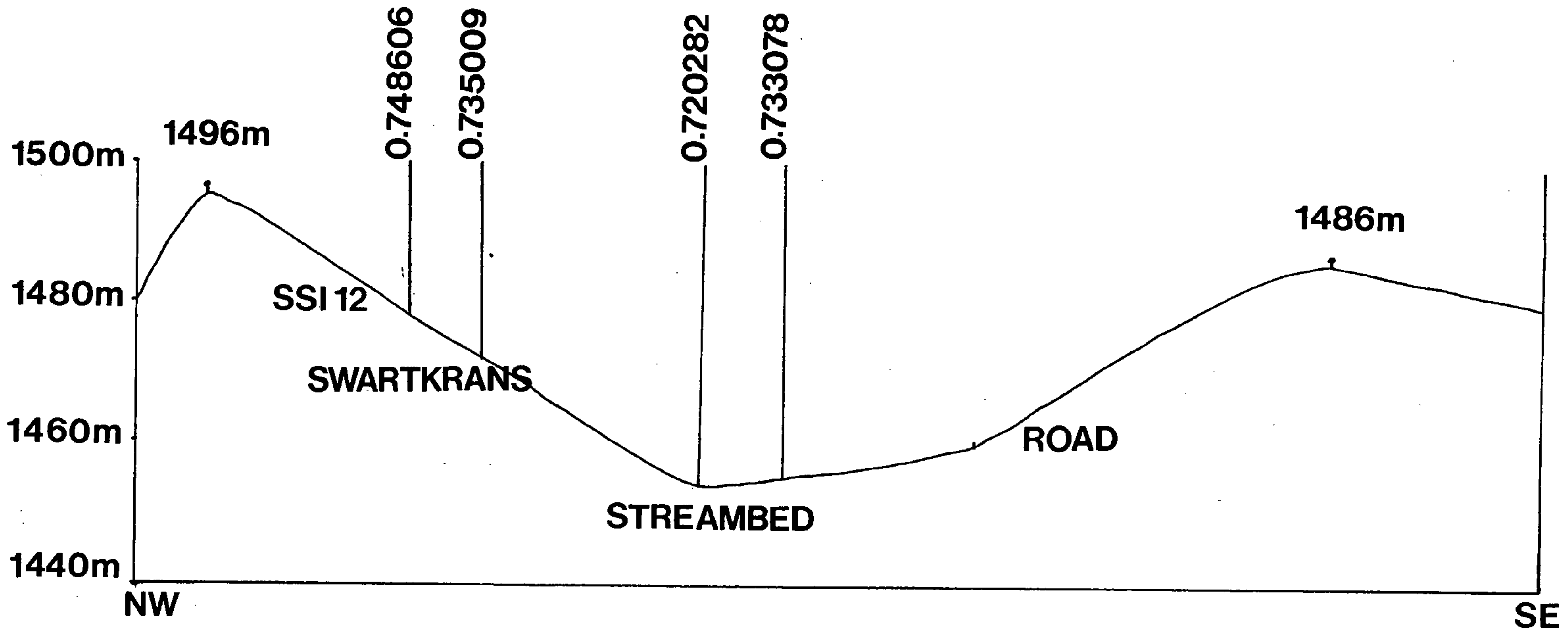

Figure 25: Cross-section (from NW to SE) of the Sterkfontein Valley , showing the variation in $^{87}Sr/^{86}Sr$ ratios from the highest point sampled (SSI 12) and the lowest point on the Bloubank streambed.

ROCK TYPE	MEAN ppm Sr
Basaltic rocks	465
Granitic rocks	100-410
Ultrabasic rocks	>1
Basic and sedimentary rocks	440-450
Neutral rocks	800
Acid eruptive rocks	300
Limestone (carbonated rocks)	610
Shale	300
Deep sea sediments	2075
Streams*	0.5-1.5
Groundwater*	0.2-36

Table 1: Mean Sr (ppm) content of the major rocks and freshwater sources (Adapted from Turekian and Kulp 1956; Skougstadt and Horr 1960*; Aubert and Pinta 1977).

ROCK TYPE	MEAN $^{87}Sr/^{86}Sr$
Volcanic rocks	0.7037
Granitic rocks	0.700 - 0.737
Alkalic rocks	0.7034 -0.749
Carbonatites	0.7034
Ultramafic and related rocks	0.704 - 0.729
Non-marine carbonates	0.712 -0.729
Oceans and marine carbonates	0.7093
Dolomites and limestones	0.7068 - 0.7092

Table 2: Mean $^{87}Sr/^{86}Sr$ ratios of the major rocks and the oceans (Adapted from Faure and Powell 1972; Graustein 1989).

MEMBER	TIME PERIOD
Member 1	1.6 to 1.8 mya
Member 2	Previous to 1 mya
Member 3	1.0 to 1.5 mya
Member 4	Middle Stone Age
Member 5	11 000 yrs (^{14}C date)

Table 3: Chronology for Swartkrans Members 1 to 5, based on bovid fossil assemblage composition (Brain *et al* 1993; Vrba 1975, 1985a).

Species 3	Member 1	Member 2	Member
Australopithecus robustus	13	17	9
Homo sp.	1	2	0
Papio hamadryas robinsoni	6	8	11
Theropithecus oswaldi danieli	1	1	4
Papio (Dinothepithecus) ingens	1	0	0

Table 4: Minimum Number of Individuals (MNI) for hominids and primates from Members 1, 2 and 3, Swartkrans (Adapted from Watson 1993).

SAMPLE	Sr RATIO
Liberia	0.71191
Sierra Leone	0.73314
Burkina Faso	0.71493
Kenya	0.71238
Kenya	0.71
Malawi	0.72683
Malawi	0.71101
Zambia	0.72155
Botswana	0.72126
Botswana	0.70649
Namibia	0.72426
Namibia	0.71646
Namibia	0.71928
Namibia	0.724338
Namibia	0.725462
Namibia	0.723448
Namibia	0.724681
Namibia	0.721813
Namibia	0.723087
Namibia	0.728249
Namibia	0.720615
Namibia	0.72159
South Africa:	
Kruger National Park	0.70799
Kruger National Park	0.71178
Kruger National Park	0.71562
Kruger National Park	0.72406
Kruger National Park	0.719014
Kruger National Park	0.720617
Kruger National Park	0.720915
Kruger National Park	0.72134
Kruger National Park	0.72253
Kruger National Park	0.710417
Kruger National Park	0.710528
Kruger National Park	0.713263
Kruger National Park	0.714848
Kruger National Park	0.711428
Kruger National Park	0.712864
Kruger National Park	0.713054
Addo Elephant Park	0.71154
Addo Elephant Park	0.711482
Addo Elephant Park	0.711562
Addo Elephant Park	0.711656
Addo Elephant Park	0.711442
Addo Elephant Park	0.711546
Addo Elephant Park	0.711484
Knysna Forest	0.710609
Knysna Forest	0.710281
Knysna Forest	0.710845
Knysna Forest	0.710676

Table 5: Strontium isotope ratios for elephant bone and tusks from Africa. Adapted from Van der Merwe *et al* (1990) and Vogel *et al* (1990).

Country	$^{87}Sr/^{86}Sr$	Sample
Liberia	0,71191	1
Sierra Leone	0,73314	1
Burkina Faso	0,71493	1
Zambia	0,72155	1
Kenya	0.71119	2
Malawi	0,71892	2
Botswana	0,71387	2
Namibia	0,722773	12
Kruger Park, S.A	0,715641	16
Addo, S.A	0,711530	7
Knysna, S.A	0,710602	4

Table 6: Mean $^{87}Sr/^{86}Sr$ ratios for elephant bone and tusk from Africa (adapted from van der Merwe *et al* 1990; Vogel *et al* 1990).

SAMPLE	Sr RATIO	Nd RATIO
NAMIBIA:		
Damaraland	0.71652	
Damaraland	0.71535	
Damaraland	0.71522	
Etosha Park	0.72143	
Etosha Park	0.72118	0.51175
Etosha Park	0.71902	
Etosha Park	0.71772	
Etosha Park	0.72	
Etosha Park	0.7196	0.51187
Etosha Park	0.71239	0.51181
Etosha Park	0.71562	
ZIMBABWE:		
Eastern Zambezi Valley	0.74495	
Eastern Zambezi Valley	0.72358	
Eastern Zambezi Valley	0.72351	0.51183
Eastern Zambezi Valley	0.7235	
Gonarezhou National Park	0.71168	
Gonarezhou National Park	0.71118	0.51229
Gonarezhou National Park	0.71309	
Gonarezhou National Park	0.70875	
Urungwe, Charara	0.7508	0.51163
Urungwe, Charara	0.73564	
Urungwe, Charara	0.74699	0.51166
Chizarira National Park	0.72594	0.51184
Chizarira National Park	0.73152	
Chizarira National Park	0.71936	
Chete Safari Area	0.72963	
Chete Safari Area	0.73447	0.51185
Chete Safari Area	0.72945	
Unknown Origin	0.7348	0.51173
Unknown Origin	0.75576	0.51097
Unknown Origin	0.74062	

Table 7: Strontium and neodymium isotope ratios for rhino horn from Namibia and Zimbabwe. Adapted from Lee-Thorp *et al* (1992).

SAMPLE	Sr RATIO	Nd RATIO
SOUTH AFRICA:		
Addo Elephant Park	0.71431	0.51212
Addo Elephant Park	0.71719	0.5122
Addo Elephant Park	0.7144	0.51218
Addo Elephant Park	0.71311	0.51213
Addo Elephant Park	0.71239	0.51219
Addo Elephant Park	0.71126	
Addo Elephant Park	0.71112	0.51224
Pilanesberg	0.70548	0.51165
Pilanesberg	0.70562	0.51171
Pilanesberg	0.70529	0.51161
Pilanesberg	0.70685	0.5116
Pilanesberg	0.70435	0.51162
Pilanesberg	0.7043	0.51162
Pilanesberg	0.71534	0.5113
Umfolozi Game Reserve	0.71694	
Umfolozi Game Reserve	0.71858	0.51214
Umfolozi Game Reserve	0.71663	0.51191
Umfolozi Game Reserve	0.71638	0.51189
Umfolozi Game Reserve	0.71643	
Umfolozi Game Reserve	0.7151	
Umfolozi Game Reserve	0.71656	0.51205
Umfolozi Game Reserve	0.71693	0.51205
Umfolozi Game Reserve	0.71642	
Umfolozi Game Reserve	0.7186	0.51178
Umfolozi Game Reserve	0.71737	
Umfolozi Game Reserve	0.71721	0.51184
Mkuze	0.7125	0.51244
Mkuze	0.71134	0.51242
Mkuze	0.71157	0.51243
Mkuze	0.7125	
Mkuze	0.71028	0.51247
Mkuze	0.71475	
Mkuze	0.71032	0.51249
Mkuze	0.71165	
Mkuze	0.71154	0.5121
Mkuze	0.71062	0.51216
Mkuze	0.71035	
Mkuze	0.7115	0.51216
Mkuze	0.71098	0.51214
Mkuze	0.71135	0.51215
Mkuze	0.71219	0.5121
Mkuze	0.71235	
Hluhluwe	0.7147	0.51202
Hluhluwe	0.71348	
Hluhluwe	0.71506	0.512
Hluhluwe	0.71098	0.51229
Hluhluwe	0.7172	0.51184
Hluhluwe	0.71678	0.5119
Hluhluwe	0.71656	0.51196
Hluhluwe	0.71611	
Vaalbos	0.71997	0.51189
Augrabies	0.73062	0.51217
Lapalala	0.74738	0.5108
Kruger National Park	0.70889	0.51232
Kruger National Park	0.709	0.51229
Kruger National Park	0.70911	0.51231
Kruger National Park	0.70882	0.51234
Kruger National Park	0.72978	0.51091
Kruger National Park	0.72954	0.51089

Table 8: Strontium and neodymium isotope ratios for rhino horn from South Africa. Adapted from Lee-Thorp *et al* (1992).

Country	$^{87}Sr/^{86}Sr$	$^{143}Nd/^{144}Nd$
South Africa:		
Addo Elephant Park	0,71339	0,51217
Pilanesberg	0,70674	0,51158
Umfolozi Game Reserve	0,71692	0,51195
Mkuze	0,71161	0,51227
Hluhluwe	0,71510	0,51200
Vaalbos	0,71997	0,51189
Augrabies	0,73062	0,51217
Lapalala	0,74738	0,51080
Kruger National Park	0,71585	0,51184
Namibia:		
Damaraland	0,71569	
Etosha Park	0,71837	0,51181
Zimbabwe:		
Eastern Zambezi Valley	0,72885	0,51183
Gonarezhou National Park	0,71117	0,51229
Urungwe, Charara	0,74447	0,51164
Chizarira National Park	0,72560	0,51184
Chete Safari Area	0,73118	0,51185
Unknown Origin	0,74372	0,51135

Table 9: Mean strontium and neodymium isotope ratios for rhino horn from Namibia, Zambia and South Africa (Adapted from Lee-Thorp *et al* 1992).

Marine system	**Coastal terrestrial**	**Inland**
^{87}Sr depleted	^{87}Sr depleted	^{87}Sr enriched
$^{87}Sr/^{86}Sr = 0,709$	$^{87}Sr/^{86}Sr \approx 0.709$	High $^{87}Sr/^{86}Sr$

Table 10: Model for strontium isotope patterning in the Southwestern Cape (Adapted from Sealy *et al* 1991).

Specimen	SK 97	SK 82	SK 3155	SKX 1084	SK 3981	Robust Austr.	Total Average
Body weight # Expected HR	55.8 to 65.2 9.5 to 11.5	45.6 to 52.1 7.4 to 8.7	37.1 to 42.2 5.8 to 6.8	57.5 to 88.6 9.9 to 16.8	* *	* *	49.0 to 62.0 8.1 to 10.8
Body weight @ Expected HR	56.5 to 60.8 9.7 to 10.6	55.1 to 57.8 9.4 to 9.9	* *	* *	* *	* *	55.8 to 59.3 9.5 to 10.3
Body weight Expected HR	52.7 8.9	49.8 8.3	* *	* *	36.1 5.6	* 5.5	46.2 7.5
Minumum HR $ Maximum HR $	10.32 334.6	8.86 246.1	6.3 124.7	13.36 559.9	5.6 98.6	5.5 95	9.24 268.2

Table 11: Predicted home range size for *A.robustus* individuals from Swartkrans based on body weight.

Jungers (1988) body weight caluclations using lower limb joint size.

@ McHenry (1988) body weight calculations using femoral shaft width.

$ These are based on averages of the combined Jungers and McHenry data set.

SPECIES	HABITAT	DAY RANGE (km	HOME RANGE (km2)	REFERENCE
Mountain Gorilla	Mnt rainforest	*	6.4 to 13.7	Dixon 1981
Mountain Gorilla	Mnt rainforest	*	4 to 25	Fossey and Harcourt 1977
Mountain Gorilla	Mnt rainforest	0.7 to 3.4	34	Goodall 1977
Mountain Gorilla	Mnt rainforest	variable	10.3 to 22	Schaller 1963
W. Lowland Gorilla	Lowland forest	*	6 to 12	Dixon 1981
Orangutan	Lowland forest/swamp	variable	5 to 6	Galdikas 1979
Orangutan	Kalimantan	0.3 to 0.8	0.42	Rodman 1977
Chimpanzee	Woodlands (Kasoje)	*	7 to 14	Collins and McGrew 1988
Chimpanzee	Woodlands (Gombe)	*	10 to 13	Collins and McGrew 1988
Chimpanzee	Gombe	Female 3	Male 9 to 12	Goodall 1986
Chimpanzee	Gombe	Male 5	Anest female 6 to 7	Goodall 1986
Chimpanzee	Gombe		Cycl female 8 to 11	Goodall 1986
Chimpanzee	Gombe		Comm 9.6 to 33	Goodall 1986
Yellow Baboon	Amboseli	4.83	24.08	Altmann and Altmann 1970
Papio anubis	Dry savanna	5.6	43.75	Barton et al 1992
Olive Baboon	Savanna	*	32.8	DeVore and Hall 1965
Chacma Baboon	Fynbos	*	33.7	DeVore and Hall 1965
Savanna Baboon	Savanna	*	7.7 to 40.1	DeVore and Hall 1965
Gelada Baboon	Grassland	1.5 to 3.5	3 to 4	Dunbar 1977
Hamadryas Baboon	Desert	4 to 19	Unknown	Kummer 1968
!Kung	Kalahari	31 to 36.2	2590	Lee 1965
G/wi	Central Kalahari	*	457 to 1036	Silberbauer 1981

Table 12: Habitat and home range size for the great apes, baboons and hunter-gatherers.

FOOD ITEM	WET SEASON	DRY SEASON
First ranked foods:		
Nut-like oil seeds	high	low/int
Second ranked foods:		
Mature fleshy fruits	high	low/int
Third ranked foods:		
Flowers (incl. pollen)	high	low
Dry fruits (excl. seeds)	int	low
Beans	low	high
Grass seeds	high	*
Nectar	some	few
Immature leaves/shoots	high	*
Deep USOs	high	low/int
Mushrooms	high	*
Fourth ranked foods:		
Gum	high	some
Cambium	*	*
Young stems/stalks/pith	high	*
Shallow USOs	high	high
Dicot seeds	high	low
Mature leaves (petioles)	high	*
Fifth ranked foods:		
Mature leaves (lamina)	high	int/high
Bark	*	*

Table 13: Ranking of food items, according to quality, for non-fire using hominids. Adapted from Peters, O'Brien and Drummond (1992).

	GORILLAS	ORANGUTANS	CHIMPANZEES	BONOBOS	HUMANS
1. Exogamy	females > males	female retentive	via females	via females	via females
2. Subadults	occassional tolerance of sons	subadults disperse	males stay in natal group	males stay in natal territory	male retention common
3. Female associations	due to silverback	adult females socialize with related females	due to kin-related males	due to kin-related males and resources	based primarily on marrige to female
4. Female bonds	no lasting bonds	kin related	weaker than bonds to males	very strong	weak
5. Social group	closed social harem	both males and females independant	stable closed community with day to day fussion -fission groups	pronouced fussion-fission based on resources	variable
6. Mating	polygynous	polygynous	community polygyny	community polygyny	mostly polygynous
7. Territoriality	not	not	communially	strongly	variable
8. Male aggression for females	strongly to strange males	very severe competion	intense between kin groups	between males	variable, may be even to the death
9. Infanticide	occassional	no	yes, if male from outside group	no	occassional
10. Male parental investment	very little	none	none	very little	more closely divided between males and females
11. Sexual dimorphism	strongly	strongly	less pronounced	less pronounced	less pronounced

Table 14: Summary of social structures of great apes and humans. Adapted from Ghiglieri (1987).

	Based on Jungers 1988		Based on McHenry 1988		
Species	Body weight	Expected HR	Body weight	Expected HR	Observed HR
Gorilla gorilla					
male	164.3 (7)	35.91	168.0 (3)	36.91	4 to 34
female	75.5 (4)	13.78	68.0 (1)	12.13	
Pan troglodytes					
male	56.6 (4)	9.68	44.9 (3)	7.28	7 to 33
female	40.1 (5)	6.34	35.6 (9)	5.47	
Pan paniscus					
male	46.3 (6)	7.56	43.3 (3)	6.96	*
female	33.2 (6)	5.02	33.7 (5)	5.12	
Pongo pygmaeus					
male	81.2 (8)	15.09	77.5 (9)	14.25	0.42 to 6
female	37.2 (11)	5.78	40.2 (8)	6.38	

Table 15: Expected and observed home range sizes for the great apes. Expected home ranges were calculated by Milton and May's (1975) body weight formula.

SITE No.	GEOLOGY	LOCATION
SSI 1	Dolomite	SE of SK excavation
SSI 2	Dolomite	NW of SK excavation
SSI 3	Dolomite	Streambed left of drift
SSI 4	Dolomite	N slopes opposite SK
SSI 5	Shale	Stoney Brook, 20km, R560N
SSI 6	Andesite/Basalt	Small kloof, 15km, R560 N
SSI 7	Daspoort Quartzite	L upper slope,12km,R560 N
SSI 8	Shale/Slate	Protea Inn, lower R560
SSI 9	Quartzite/Conglom	Ridge, 2km SE of SK ,R47
SSI 10	Dolomite	Mem 3 at Brain's datum
SSI 11	Dolomite	30m W of Brain's datum
SSI 12	Dolomite	50m N of Brain's datum
SSI 13	Ferriginous Shale	3,5 km from Zennex, R560S
SSI 14	Quartzite/Greywacke	4,4km S from R47/R560
SSI 15	Mafic/Ultramafic	Palaborwa Training, R47
SSI 16	Granite	0,5 km Zwartkops exit,R47
SSI 17	Dolomite	1st bridge, R47 Vdorp
SSI 18	Dolomite	Royal Engineering, R47
Sterkfontein	Dolomite	Left of Tearoom at Stk

Table 16: Location and geology of main sample sites in the Sterkfontein Valley and surrounding areas.

TRANSECT	DESCRIPTION
TW 1	50m due W of beacon
TW 2	100m due W of beacon
TW 3	150m due W of beacon
TW 4	200m due W of beacon
	Then descends into Bloubank stream
TE 1	50m due E of beacon
TE 2	100m due E of beacon
TE 3	150m due E of beacon
TE 4	200m due E of beacon
TE 5	250m due E of beacon
TE 6	300m due E of beacon, terrain opens up
TE 7	350m due E of beacon, terrain opens up
TE 8	400m due E of beacon, terrain opens up
TE 9	450m due E of beacon, over fence into grazed area
TE 10	500m due E of beacon, grazed area
TS 1	50m SE of beacon
TS 2	100m SE of beacon
TS 3	150m SE of beacon, margin of greenbelt
TS 4	160m SE of beacon, greenbelt
TS 5	170m SE of beacon, greenbelt
TS 6	180m due S through greenbelt
TS 7	190m due S through streambed
TS 8	200m due S through streambed
TS 9	220m due S through streambed
TS 10	240m due S through streambed
TS 11	260m due S through streambed
TS 12	280m due south to SE corner of drift
TS 13	300m due S to base of SSI 4

Table 17: Description of transects sampled around the Swartkrans Cave site.

SITE	GEOLOGY	Sr ISOTOPE RATIO
SSI 1	DOLOMITE	0.73503
SSI 2	DOLOMITE	0.73621
SSI 2	DOLOMITE	0.73566
SSI 3	DOLOMITE	0.72318
SSI 4	DOLOMITE	0.73466
SSI 5	SHALE	0.74170
SSI 6	ANDESITE/BASALT	0.742006
SSI 7	QUARTZITE	0.736298
SSI 8	SHALE/SLATE	0.75559
SSI 9	QUARTZITE/CONGLOMERATE	0.729005
SSI 10	DOLOMITE	0.73006
SSI 11	DOLOMITE	0.73623
SSI 12	DOLOMITE	0.748606
SSI 13	FERRIGINOUS SHALE	0.73353
SSI 14	GREYWACKE/QUARTZITE	0.72759
SSI 15	MAFIC/ULTRAMAFIC ROCKS	0.73383
SSI 16	GRANITE	0.752851
SSI 17	DOLOMITE	0.727036
SSI 18	DOLOMITE	0.72719
STERKFONTEIN	DOLOMITE	0.73730
STREAMBED	DOLOMITE	0.76778

Table 18: $^{87}Sr/^{86}Sr$ isotope ratios for whole plant samples from the Sterkfontein Valley and surroundings. The $^{87}Sr/^{86}Sr$ value for standard SRM 987 during the analytical period was 0.71020.

TRANSECT	DISTANCE (m)	Sr ISOTOPE RATIO
SSI TW 1	50	0.73100
SSI TW 2	100	0.73608
SSI TW 3	150	0.73754
SSI TW 4	200	0.73877
SSI TE 1	50	0.73119
SSI TE 2	100	0.730321
SSI TE 3	150	0.72885
SSI TE 4	200	0.73153
SSI TE 5	250	0.73604
SSI TE 6	300	0.73462
SSI TE 7	350	0.73424
SSI TE 8	400	0.73244
SSI TE 9	450	0.73061
SSI TE 10	500	0.73256
SSI TS 1	50	0.735009
SSI TS 2	100	0.731923
SSI TS 3	150	0.73506
SSI TS 4	160	0.735800
SSI TS 5	170	0.733249
SSI TS 6	180	0.723247
SSI TS 7	190	0.722322
SSI TS 8	200	0.720282
SSI TS 9	220	0.722948
SSI TS 10	240	0.722183
SSI TS 11	260	0.723100
SSI TS 12	280	0.733020
SSI TS 13	300	0.733078

Table 19: $^{87}Sr/^{86}Sr$ isotope ratios for whole plant samples from western, eastern and southern transects at Swartkrans. The $^{87}Sr/^{86}Sr$ value for standard SRM 987 during the analytical period was 0.71020.

SITE	GEOLOGY	Sr ISOTOPE RATIO
SSI 1	DOLOMITE	0.820858
SSI 2	DOLOMITE	0.838306
SSI 3	DOLOMITE	0.767701
SSI 4	DOLOMITE	0.787265
SSI 5	SHALE	0.718738
SSI 6	ANDESITE/BASALT	0.79073
SSI 7	QUARTZITE	0.728804
SSI 8	SHALE/SLATE	0.855211
SSI 9	QUARTZITE/CONGLOMERATE	0.835794
SSI 13	FERRIGINOUS SHALE	0.787843
SSI 14	GREYWACKE	0.745772
SSI 15	MAFIC/ULTRAMAFIC ROCKS	0.757129
SSI 16	GRANITE	0.900582
STERKFONTEIN	DOLOMITE	0.772283
BLOUBANK STRE	DOLOMITE	0.721169

Table 20: $^{87}Sr/^{86}Sr$ isotope ratios for total soil strontium and Bloubank Stream water from the Sterkfontein Valley and surroundings. The $^{87}Sr/^{86}Sr$ value for standard SRM 987 during the analytical period was 0.71020.

SAMPLE	GEOLOGY	Sr ISOTOPE RATIO
SSI 2	DOLOMITE	0.737888
SSI 3	DOLOMITE	0.726032
SSI 4	DOLOMITE	0.730959

Table 21: $^{87}Sr/^{86}Sr$ isotope ratios for available soil strontium from three dolomitic soil samples from Swartkrans. The $^{87}Sr/^{86}Sr$ value for standard SRM 987 during the analytical period was 0.71020.

Specimen	Age	$^{87}Sr/^{86}Sr$
SK 1588	19 ±2	0.73046
SK 876	28 ±4	0.72383
SK 46	34 ±3	0.73057
SK 57	25 ±2	0.72846
SK 54	Juvenile	0.72829

Table 22: 87Sr/86Sr isotope ratios for 5 *A.robustus* individuals from Swartkrans Member 1. The ratios are pooled for washes 16 to 20. (Data from Sillen *et al* In press).