

CHAPTER 4

4.1. OVERVIEW OF SOUTH AFRICA'S FOSSIL HOMINID SITES: Temporal, geological, environmental context and hominid taxonomy.

Hominid evolution during the Plio-Pleistocene in southern Africa is best documented from the stratigraphically complex cave breccia deposits hosted in the Pre-Cambrian dolomites of the Sterkfontein Valley. To date, there are eleven Pliocene and/or Pleistocene hominid sites recognized in South Africa. In addition, there are an extended number of fossil sites with large and varied faunal assemblages, but which have not yielded hominid remains to date. The hominid bearing caves in the order in which discoveries were made are: Taung, Sterkfontein, Kromdraai, Coopers, Swartkrans, Makapansgat, Gladysvale, Gondolin, Drimolen and Plovers Lake. In addition, there is a single molar reported from Bolts Farm, but there is no factual information to support this claim.

The total number of hominid species recognized in South Africa's Plio-Pleistocene varies from four to six. The generally accepted species are: *Australopithecus africanus*, *Paranthropus robustus*, *Homo habilis* and *H. ergaster*. Two other potential species have been proposed but these are not accepted by all scholars. The first of this species is *P. crassidens* (Broom 1950; Howell 1978; Grine 1982) from Swartkrans. The other is a species as yet un-named but purportedly present in Sterkfontein (Clarke 1988). Additionally, the most complete *H. habilis* specimen known from South Africa (Hughes & Tobias 1977; Clarke 1988) has been classified as *Australopithecus* by some (Kuman & Clarke 2000).

The stratigraphy of Sterkfontein, Makapansgat, Swartkrans and Kromdraai has been formally defined in stratigraphic units or Members which as a whole define a Formation (e.g. Partridge 2000). The temporal period covered by these sites is

significantly difficult to assess due to the lack of datable volcanic materials inside the cave deposits (Rightmire 1984, Berger *et al.*; 2002). Thus, traditionally the deposits have been dated via biochronological methods. Originally, ages for these sites were proposed by Vrba (1985, 1995), Delson (1984) and White and Harries (1978) using bovids, monkeys and pigs respectively. Over time, some of these have been reconsidered while others however, have reasonably stood the test of time. The latter pertain mostly to the *Paranthropus* sites for which dates no older than 2.0 Ma and no younger than 1.0 Ma have been argued. The *Australopithecus* sites in the contrary have recently been re-evaluated, specially the older Members of Sterkfontein. Newly proposed dates of *Australopithecus* fossils from this site have been assigned to the Early and Middle Pliocene (Partridge 2000; Partridge *et al.*; 2003). This view has been strongly contested by Berger *et al.*; (2002) but this issue remains unresolved.

A short review of the hominid taxa present at each site and its geological and environmental context is presented below. This review will only consider the sites for which specimens are available for the present study: Sterkfontein, Swartkrans and Kromdraai. These sites were chosen because they contain the largest samples of broken teeth. The Drimolen collection was not available for study at this stage.

4.2. GEOLOGICAL SETTING OF THE CAVE SITES

4.2.1. Sterkfontein

Cooke (1938) provided the first study dealing with the geology of this site, and since this time the stratigraphy of the deposits have been the focus of several studies, beginning with a number of broad descriptive classifications (e.g. Haughton, 1947; King 1951; Robinson 1952). Brain (1958) gives the first detailed description of the stratigraphy and sedimentology of the site and Wilkinson (1973) included some aspects of the cave fill in

a geomorphological study of the cave system. These works provided the standard lithostratigraphic subdivision of the site prior to the work of Partridge (1978).

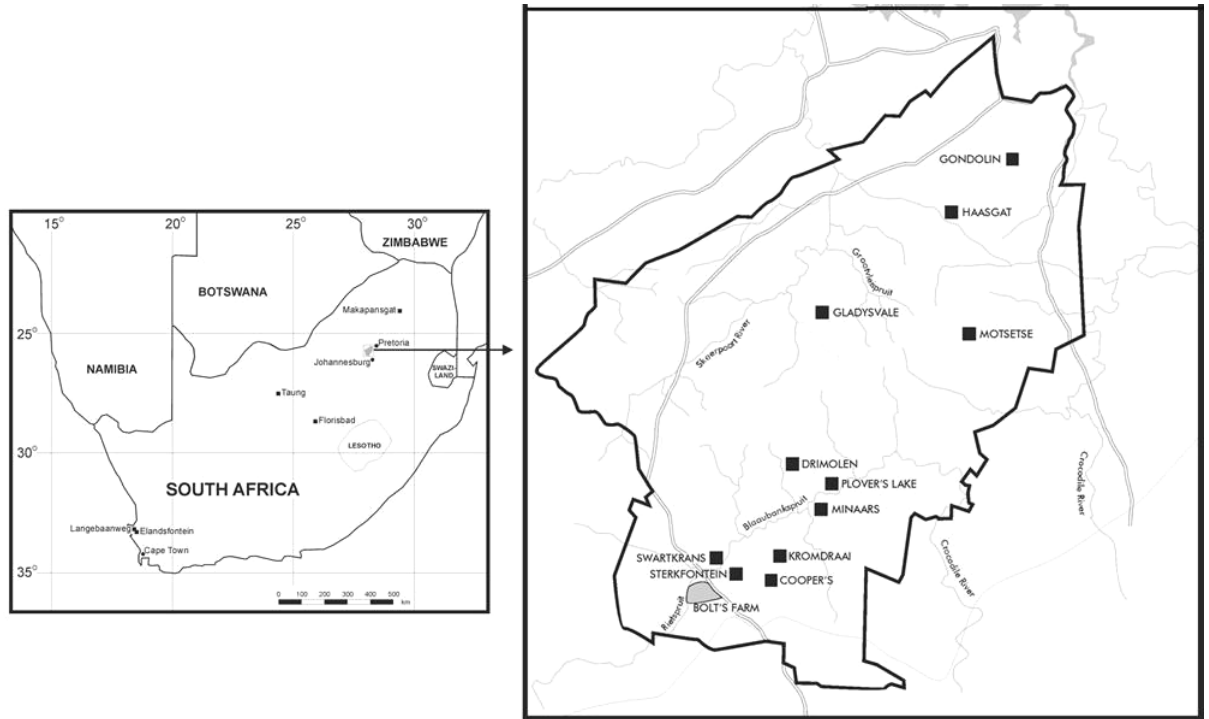


Figure 4.1 Map of Southern Africa showing the location of the most relevant fossil sites, specifically the sites discussed in this study where the fossil hominids derived. The thick line on the right side map marks the borders of the World Heritage Site- Cradle of Humankind.

Partridge (1978) re-appraised the lithostratigraphy of the sequence at Sterkfontein, documenting six Members, comprising the Sterkfontein Formation. The work of Wilkinson (1983) proposed that the fossiliferous deposits at Sterkfontein had a continuous vertical extent of more than 50m, which contradicted the earlier findings of Partridge (1978) and was the catalyst for a drilling program that began in 1989. This work helped to clarify the issue of the thickness of the deposits, and elucidated the stratigraphic relationships of the various members, as well as providing some three-dimensional control on the deposits (Partridge & Watt, 1991). Clarke (1994) proposed some modifications to the scheme of Partridge and Watt (1991), focusing on Members 4

and 5. Kuman and Clarke (2000) subdivided the Member 5 deposit (formerly known as the Extension Site) into three discrete infills, terming them the Oldowan Infill, the Stw 53 infill, and the Sterkfontein Member 5 West infill.

The Sterkfontein Formation as currently described (Partridge 2000) averages 20 m in thickness, reaching a maximum thickness of 30 m in places. Member 4 (subunits A-D) comprises a succession of debris cones and some of these sub-units are preserved at the Type Site area where Broom undertook his early excavations, and from where specimens such as Sts 5 originated (Partridge 2000). In fact most of the early hominid specimens from Sterkfontein are attributed to Member 4. The majority of these hominid specimens have been assigned to *Australopithecus africanus*, though Clarke (1988) has suggested that a second species ancestral to *Paranthropus* might also be present. This Member has also yielded more than 300 fragments of fossil wood (Bamford 2000).

4.2.2. Kromdraai

The site of Kromdraai is situated some 1.5 km to the East of Sterkfontein, adjacent to the Coopers cave deposits. The first fossils from Kromdraai were discovered by Broom in 1938, including a fragmented skull and some associated post-cranial remains ascribed to *Paranthropus robustus*. Two main sites are recognized, Kromdraai A (the faunal site) and Kromdraai B (the hominid site), the latter divided into five Members (Partridge 2000). A third excavation trench is known as Kromdraai C. Although originally subdivided into these three different units (A-C), recent excavations have shown that Kromdraai B and C are continuous beneath a shallow soil cover and are interconnected with Kromdraai A (Partridge 2000). The Kromdraai deposits occur in an East-West striking structurally controlled solution fissure or (grike). Kromdraai B is presumed to have accumulated rapidly via storms, when vegetational cover was discontinuous, bringing surface material and soil into the cave (Partridge 2000).

4.2.3. Swartkrans

Swartkrans is situated approximately one kilometer to the west-northwest of Sterkfontein. The cave site occurs on the intersection of two fault traces that trend roughly East-West and North-South (Brain 1995). Most of the original roof of the cave has been removed by erosion and as presently preserved, the cave is somewhat irregular in plan view, measuring a maximum of 45 m in both east-west and north-south directions.

The earliest palaeontological work at Swartkrans dates to 1948 when Broom, at the request of the University of California African Expedition, began collecting fossils. Broom worked at the site until his death in 1951, and, followed by John Robinson, recovered a large amount of hominid material. This material included the first recorded co-occurrence of more than one hominid species in a single deposit, *Paranthropus robustus* and a type of early *Homo* (Broom & Robinson, 1950, 1952). Robinson continued work until 1953, when the site was abandoned. Some years later, Brain (1958) described the main deposits of Swartkrans into two main units: the orange and brown breccia. In 1965, Brain, then of the Transvaal Museum, resumed activity at the site, which continued for the next 21 years. Brain's excavations involved sampling *ex situ* breccia blocks, as well as the first *in situ* excavations at the site.

Brain (1976) began *in situ* excavations of the sedimentary strata of Members 1, 2 and 3. This work provided a number of insights into the complexity and nature of the fill, and led to the development of a five-member stratigraphy for the site, with each member separated from its older counterpart by an erosional discontinuity (Brain 1993). These are: Member 1, which includes the Hanging Remnant and Lower Bank, Member 2 and 3, and the non fossiliferous Member 4. Member 5, or the Bondi channel, is the youngest deposit dated to about 11 ky, but contains some mixed materials (de Ruiter 2001).

4.3. Dating the sites

Historically, South African cave sites have been dated using faunal correlations with East African sites; however, some problems are inherent to this methodology.

Geomorphic evolution in South Africa's hominid-bearing sites during the Plio-Pleistocene has been regionally influenced by the evolution of the Great Escarpment and subsequent local erosional factors in the Sterkfontein Valley (Partridge *et al.*; 1995). The taphonomic and depositional environments in the East and South African sites are known to be different. Most known Plio-Pleistocene fossil localities in east Africa are lacustrine or riverine in nature, while in southern African localities the depositional environment is restricted to cave sites within karstic landscapes. Here, different agents of accumulation play a role in the representation of the fossil taxa in a given assemblage (Brain 1981). It is therefore likely that any attempt to correlate faunas from distantly placed localities through time will be influenced by a combination of differing ecological parameters, taphonomic factors and regional endemism. However, faunal exchanges between Africa and Eurasia, as well as movement along different regions within the African continent, have shown that broad patterns can nonetheless be discerned (Bromage & Schrenk 1995; Turner 1990; Turner & Wood 1993; Vrba 1995).

4.4. Faunal correlations

Different taxonomic groups have been used to correlate the faunas from South Africa to East Africa. Vrba (1974) first correlated the bovids from South Africa with Olduvai Gorge and East Rudolf. She estimated that Sterkfontein Member 5 and Kromdraai B were approximately 0.5 Mya, Kromdraai A was 1.0 Mya, Swartkrans Member 1 was 1.5 Mya, Sterkfontein Member 4 was 1.5 – 2.0 Mya, and Makapansgat was just over 2.0 Mya. Her later work (Vrba 1995) suggested that Sterkfontein Member 4 was roughly 2.0 – 2.5 Mya, and Makapansgat was probably closer to 2.5 – 3.0 Mya. In her most comprehensive study of the age of the South African hominid sites, Vrba (1982) again

revised her estimates, indicating the following ages: Makapansgat: 3.0 Mya, Sterkfontein Member 4: 2.3 – 2.8, Taung: 1.0 – 2.5, Kromdraai B: 1.0 – 2.5 but probably around 2.0, Swartkrans 1: 1.5 – 1.8, Sterkfontein Member 5: 1.5 and Swartkrans 2: 1.0 million years in age. Vrba's (1995) most recent evaluation of the dates indicated that Sterkfontein Member 4 was probably about 2.5 my, and for simplicity, we use this age to contextualize the hominids from Member 4 included in this study.

Delson (1984, 1988) attempted to correlate the east and South African faunal assemblages using the abundant primate material recovered from the various sites. Delson constructed a series of biozones based on the longer, stratigraphically controlled sequences of east Africa, and then compared the South African materials to the geochronologically dated east African fossils. He concluded that Makapansgat was probably the oldest site at roughly 3.0 Mya; Sterkfontein Member 4, Taung and Pit 23 of Bolt's Farm fell somewhere between 2.0 – 2.5 Mya; Swartkrans, Kromdraai, Coopers A and Pit 6 of Bolt's Farm were approximately 1.65 – 1.9 Mya (Delson 1984, 1988).

Brain (1995) following Vrba's work suggested the following ages for the different Members at Swartkrans: Member 1 to about 1.8 my, Member 2 to about 1.6 and Member 3 to about 1.0 to 1.5 my. Hominids are found throughout these three members, although in Member 3, only *Paranthropus* is found, paradoxically, this is the member where Brain (1993) documented the presence of burnt bones. More recently, Turner (1997) indicated that based on the carnivore fossil remains recovered from Member 3 of Swartkrans, there appear to be no differences in taxonomic representations with the older Members of that Formation. This suggests an age of about 1.5 my for this deposit.

4.5. Other dating methods

Several attempts to date the South African cave sites using palaeomagnetism have produced mixed results (Brock *et al.*; 1977; McFadden 1980; McFadden *et al.*; 1979; Partridge 1982; Partridge *et. al.*; 2000). Kromdraai was tentatively associated with the

Matuyama reversed epoch 0.73 – 2.58 Mya, and Sterkfontein Members 2, 3 and 4 with the Gauss normal epoch 2.58 – 3.58 Mya (Jones *et al.*; 1986; Partridge 1986). Most recent palaeomagnetic study of Kromdraai by Thackeray *et al.*; (2002) indicated an age of 1.9 my for this deposit.

Sterkfontein Member 4 has been dated by palaeomagnetism to about 2.1- 2.2 my (Thackeray *et al.*, 2004), which has been confirmed by Partridge (2005).

Recent attempts at dating the South African fossil localities employing electron spin resonance have met with some success (Schwarz *et al.*; 1994; Curnoe *et al.*, 2001; Schmid 2002), though problems relating to reworking of materials have not yet been satisfactorily resolved (Blackwell 1994). Curnoe *et al.* (2001) produced an age estimate of 1.6 – 2.1 Mya for the Hanging Remnant of Swartkrans, a number that accords well with previous faunal estimates for the deposit (Delson 1984; Vrba 1982, 1985a,b). A study of the ESR of Sterkfontein 4 produced an average estimate of 2.1 Mya, though it was noted that the distribution was bimodal, possibly indicating admixture of younger Member 5 materials into the older Member 4 deposit (Schwarz *et al.*, 1994). The discrete age estimates produced (1.7 and 2.4 respectively) still compare well with the faunal age estimates of the site, and even the average estimate of 2.1 Mya was noted to not be beyond the potential age of the site (Schwarz *et al.*, 1994).

More recently, Partridge *et al.*; (2003) and Walker *et al.*; (2004) have made use of more innovative methods ranging from cosmogenic nuclides to Uranium series methods. Success of the former is questionable, but appears that the latter method shows more reliability in that independent laboratories have replicated similar results.

4.6. Environments

The African faunas as a whole appear to have undergone a general turn-over beginning at about 2.8 to 2.5 my (Turner & Wood 1993; Vrba 1995; Bobe & Eck 2001). Palaeontological and chronological data has indicated that at that time, a drying trend

developed in the African landscapes (e.g. Vrba *et al.*; 1995). While there maybe some documented exceptions to the punctuated nature of this phenomenon (e.g. McKee 2001), it appears that between 2.5 to 2.0 my, there was a marked faunal change based on species representation in both East and South Africa (Vrba 1995; Bobe & Eck 2001)

In the southern African landscapes, the assemblages dated to the Pliocene (Makapansgat and Sterkfontein Member 4) record a wetter phase of climatic conditions based on the presence of primate, bovid and suid faunas which were more adapted to this type of environment (Vrba 1995; Reed 1996). Taxa such as the antelope *Makapania* and a high percentage of browsing antelopes reflected the presence of closed environments at Sterkfontein Member 4. In contrast, sites dated to late Pliocene and early Pleistocene (e.g. Kromdraai; Swartkrans and Member 5 Sterkfontein) have shown a greater percentage of faunas associated with more open environments (Vrba 1974, 1995; Reed 1997). Especially relevant is the increase in the abundance of Alcelaphine taxa in these later sites, which Vrba (1995) interpreted as an indication of the presence of more open areas near the caves.

This indicates that climatic conditions during the time of *A. africanus* environments were characterized by abundant tree cover. This maybe reflected in the postcranial morphology of this species (McHenry & Berger 1998). During the times of *Paranthropus* and early *Homo*, more open areas dominated the landscapes of Southern Africa. However, small differences have been recorded between the environments of Swartkrans and Kromdraai whereby the latter appears to indicate a slightly less open environment than the former (Vrba 1974; Kuman & Clarke 2000), although this is based on very limited faunal evidence.

4.7. Taxonomy of the South African Hominids

The taxonomy of the southern African hominids is characterized by a series of appearance and disappearances of genera and species names since the first hominid was discovered in 1924. As many as three genera and five species were recognized by Broom (1950). Some years later, Robinson (1953, 1954) simplified Broom's taxonomy encompassing all taxa into two genera and two species of australopithecines. However, sub-specific distinctions are retained for both *A. africanus* (the Taung was considered a different subspecies from the Sterkfontein and Makapansgat material) and *P. robustus* (the Swartkrans and Kromdraai samples are considered only different subspecies). The genus *Telanthropus* was originally used by Broom and Robinson (1950) to refer to the mandible (SK 15) recovered from Swartkrans. This genus was later subsumed into *Homo* by Robinson (1961).

Some controversy has surrounded the generic distinction between the "gracile" and the "robust" South African hominids. The status of the genus *Paranthropus* informally regarded as a "robust" form has been questioned by some authors who have claimed that it has been wrongly separated from the more "gracile" *Australopithecus* (Brace 1969; Wolpoff 1971, 1974). Allometric growth within a single lineage was the argument employed by these authors to disregard the generic separation. Tobias (1967) indicated that the differences seen between these two hominid groups, only deserves specific distinction and should be subsumed within the same genus. However, it appears that there is ample and widely accepted evidence supporting not only morphological differences, but also ecological differences between *Australopithecus* and *Paranthropus* (Robinson 1956; Grine 1981; Ungar and Grine 1991).

At present, there are no records that indicate the co-occurrence of *Paranthropus* and *Australopithecus* at any of the temporally distinct units within each of the different sites (but see Aguirre 1970, this author considered that *Paranthropus* was present at

Makapansgat specifically by the mandible MLD 2). There is also no evidence supporting the temporal co-occurrence of *Australopithecus* and *Homo* in the South African cave deposits. However, *Paranthropus* co-occurs with *H. ergaster* at the site of Swartkrans (Robinson 1953) and it's possibly coeval with the genus *Homo* at Kromdraai and Sterkfontein Member 5 (Kuman & Clarke 2000; Braga & Thackeray 2003).

For simplicity, in this study we have made use of the terms *Paranthropus* to refer to the “robust” Swartkrans and Kromdraai samples; and *Australopithecus* to refer to the Sterkfontein derived sample.

4.7.1. Genus *Australopithecus*

The earliest recognized species derived from the southern African caves was that represented by the type specimen of *A. africanus*, the Taung child (Dart 1925). Subsequently, this species has been found at Sterkfontein, Makapansgat and Gladysvale. Originally, the discoveries at Sterkfontein by Broom were referred to as *Australopithecus transvaalensis*, a name later changed to *Plesianthropus transvaalensis*. Dart's *Australopithecus* from Makapansgat was described as *A. prometheus* (Dart 1948). However, Robinson (1953, 1954) subsumed all the Taung, Makapansgat and Sterkfontein (Type Site) hominids into *A. africanus*. Although some claims were put forward concerning the presence of *A. africanus* in east Africa (e.g. Olson 1985; Tobias 1980), it is generally considered that *A. africanus* is an endemic South African species. This species is one of the better known and one of the most abundantly represented in the African Plio-Pleistocene record. However, some authors have indicated that the range of morphological variation encompassed within the presently known hypodigm is very large. Based on cranio-dental variation, Clarke (1988; 1994) has indicated the presence of a second species. A list of potential specimens attributed to this “second” species has been provided (Clarke 1988), but no formal specific designation has been proposed. Lockwood (1997) indicated that there was high

variability on the cranial morphology of *A. africanus*, specifically that of the parietals, and suggested the presence of a second species in the Member 4 hypodigm. Recently, Moggi-Cecchi (2003) analysed the dental remains derived from Member 4 of Sterkfontein and indicated that the coefficient of variation (CV) values of the length and breadth is similar to values for other fossil hominid species, providing no evidence for the presence of a second species.

Fossils recently derived from Member 2 as well as from the Jacovec cavern of Sterkfontein have been claimed to have a very primitive morphology (Clarke & Tobias 1995; Clarke 1999; Partridge *et al.*; 2003). The specimens have been referred to the genus *Australopithecus*, but no species designation has yet been proposed. White (2002), however, indicated that the Member 2 skeleton differs in morphological features from the Member 4 material. For the purpose of this study, the Sterkfontein Member 4 hypodigm is regarded as belonging to a single species, *A. africanus*.

4.7.2. Genus *Paranthropus*

A new genus and species was proposed by Broom (1938) to designate fossil hominids derived from the site of Kromdraai. Its cranio-dental morphology was clearly distinct from the known *A. africanus* specimens from the neighbouring site of Sterkfontein. Broom and Robinson (1952) regarded the discoveries of a similar hominid from Swartkrans to the new species *P. crassidens*. Although this distinction between the hominids derived from the sites of Kromdraai and Swartkrans are generally not recognized by most scholars, others like Howell (1978), Grine (1981) and Grine and Martin (1988) support Broom and Robinson (1952) original denominations. Grine (1981) provided morphological and ecological evidence in support of this specific distinction. Special reference was made to the deciduous dentition. Additionally, Grine and Martin (1988) indicated that the microanatomical features of one teeth of each hominid supported the species separation.

The hominids, *P. robustus/crassidens* (here referred to as *P. robustus* for simplicity without inferring any species preference) are South African endemics with no confirmed records of these taxa outside the Sterkfontein Valley (but see Olson 1988). However, it is one of the best known hominids of Africa due to its relatively large abundance at its wide distribution in the cave assemblages from this area. At present, *P. robustus* is recognized from Kromdraai, Swartkrans, Coopers, Drimolen and also from Sterkfontein Member 5 (Broom 1938, Broom & Robinson 1952, Grine 1993; Keyser 2000; Kuman & Clarke 2000; Berger *et al.*; 2003).

4.7.3. Genus *Homo*

The earliest record of this genus in South Africa is represented by a mandible (SK 15) recovered from Swartkrans brown breccia (now Member 2). This specimen was originally classified as *Telanthropus* but later subsumed into *Homo* (Robinson 1961). Additional specimens of this genus have been recovered from the same site. The most complete cranial material was described by Clarke (Clarke 1987) as SK 847, regarded as *H. ergaster* and very similar to the more complete cranium KNM-ER- 3733 (Wood 1991). Early *Homo* occurs at Members 1 and 2 of Swartkrans (Brain 1993).

From the Sterkfontein Member 5 assemblage, Hughes and Tobias (1977) described an incomplete cranium assigned to *H. habilis*. This specimen remains as the only confirmed record to date of this taxon in the southern African cave sites. Clarke (1988) initially confirmed the similarities between the Member 5 specimen (Stw 53) with other better known *H. habilis* material from Olduvai (OH 24). However, a recent interpretation of Stw 53 indicated that it maybe more correctly regarded as an australopithecine (Kuman & Clarke 2000). In addition to Stw 53, some isolated teeth from the same area of Sterkfontein have been classified as *Homo* (Tobias 1965).

Other specimens attributed to *Homo* have been identified at Drimolen, Kromdraai and Gladysvale (Schmid & Berger 1997, Keyser 2000; Braga & Thackeray 2003). It is

interesting to note that the specimen referred to by Grine and Martin (1988) as *P. robustus* from Kromdraai, has been identified as representing *Homo* by Braga and Thackeray (2003).

4.8. Phylogenetic relationships of South African Hominids

Meaningful interpretations of tempo and mode of human evolution require that fossils are classified in taxonomic groups, and that these groups are correctly placed in a chronological context. In the sections above, it was noted the complex nature of the dating to which the fossil rich cave sites of South African have been subjected, and the broad ages resulting from these studies. However, and given that most age estimates do not place *Paranthropus* and *Australopithecus* in South Africa within the same temporal range, this scenario leaves open the possibility that the latter genus gave rise to the former. The phylogenetic relationships between these groups appears complicated nevertheless (e.g. Tobias 1980; White *et al.*; 1981; Skelton & McHenry 1992; Strait *et al.*; 1997). It must be noted that the recognition of *Paranthropus* as a valid genus is still accepted with reservations by some (e.g. White 2002) and in some classifications, *Paranthropus* is synonymized with *Australopithecus*.

Two main schools of thought dominate the debate about early hominid relationships. The majority of the comparative or cladistic analyses discussed below employ large sets of individual cranio-facial and dental traits present in the various taxa. These are too large to be detailed here. On the one hand, it maybe possible that *A. africanus* gave rise to *P. robustus* (White *et al.*; 1981) and in the other, the possibility exists that *Paranthropus* from south Africa derives from an East African lineage and thus its evolution its independent from *A. africanus* (e.g. Strait *et al.*; 1997), but this has not yet been unequivocally demonstrated. Before these scenarios are further described, we present a summary of features that characterize the morphology of *A. africanus* and *P.*

robustus. This summary is deliberately concise and is largely based on White's (2002) list of characters.

4.8.2. Morphological characters of *A. africanus* and *P. robustus*.

4.8.2.1. *A. africanus*: Cranial average capacity of about 440 cc, cranium more globular than *A. afarensis*, prognathic face with canine pillars, post-canine teeth relatively larger than *A. afarensis*, canine morphology less primitive than *A. afarensis*, thick enamel molars, large anterior tooth size and body proportions different to other hominids but presumed biped (McHenry & Berger 1998).

4.8.2.2. *P. robustus*: cranial capacity 530 cc, dished face, high and forwardly placed zygoma, ectocranial crests, presence of frontal trigone and marked post-orbital constriction, incisors small and set on bicanine line, robust and tall mandibular corpus, large postcanine teeth, very thick enamel and molarized deciduous molars. No unequivocal associated postcrania are known for this species, but most elements preserved from Swartkrans and Kromdraai are thought to belong to this species and indicate habitual bipedality.

Since the discovery of the taxon *A. afarensis* (Johanson *et al.*; 1978), some 54 years after the discovery of *A. africanus*, it was suggested that its phylogenetic position rests at the base of the hominid family tree, a consideration that even today appears the most generalized evolutionary proposal (e.g. Lovejoy 2005). In this scheme, *A. afarensis* gave rise to all later hominids (White *et al.*; 1981), including *A. africanus*, which until then had occupied this position (e.g. Tobias 1980). However, only some time later, Tobias (1980) strongly argued for the morphological homogeneity of the Hadar-Laetoli hominids, regarded as *A. afarensis* (Johanson *et al.*, 1978) with those of the already known south African taxon *A. africanus* (Dart 1925). In Tobias (1980) interpretation, the morphological differences observed by Johanson and co-workers were only regarded as indicating sub-specific consideration, and thus, Tobias (1980) suggested that the Hadar-

Laetoli material could be included in the species *A. africanus*, the basal stock leading to *A. (P). robustus* and *Homo*. However, White *et al.*; (1981) detailed study of comparison of cranio-dental and functional aspects between the two taxa, supported the validity of the taxon *A. afarensis*, now widely recognized, primarily based on the more primate sets of traits present in this species coupled with its greater antiquity. In addition, White *et al.*; (1981) indicated that the modifications observed in the masticatory system of *A. africanus* were already too specialized towards the *Paranthropus* line, and therefore *A. africanus* was excluded as the possible ancestor of *Homo*. In a cladistic analysis of *A. afarensis* and *A. africanus*, Wood (1985) noted that there were characters found in one of the two taxa and not in the other, or if they were present in both, they were found in at least other early hominid taxa. Wood (1985) concludes this analysis indicating that *A. africanus* was the most likely candidate for the appearance of *Homo* and that *A. afarensis* formed a sister group with *Paranthropus*. This observation was also confirmed by McHenry (1985) and McHenry & Skelton (1985). However, in the latter study it was observed that *A. africanus* was also most similar to *Paranthropus*. This paradox was explained as possibly the result of homoplasy. Later studies by these authors (McHenry & Skelton 1986; Skelton & McHenry 1992), after the discovery of the best preserved skull of *P. aethiopicus* (Walker *et al.*; 1986), continued to support a phylogenetic line where *A. afarensis* gave rise to *A. africanus*, which in turn gave rise to both *Paranthropus* and *Homo*. In this scheme, *P. robustus* formed a cluster with *P. boisei*. More recently, Strait *et al.*; (1997) cladistic study of these relationships supported Skelton and McHenry (1992) analysis.

However, during the last decade or so, a whole new array of fossil hominid taxa has come to light from East and Central Africa, expanding the chronology of the hominid clade to between 6-7 my, and suggesting new links in the hominid family tree. The first of these hominids, found in Ethiopia, was originally placed in the genus

Australopithecus, but was later transferred to the new genus *Ardipithecus* and the species *A. ramidus* dating to about 4.4 my (White *et al.*, 1994). The following year, a new species of *Australopithecus* was described by Leakey *et al.*; (1995) from Kenya and dated between 3.9 and 4.2 my. This taxon, *A. anamensis* was regarded as the potential ancestor of *A. afarensis* and later hominids. In 1999 and from Ethiopia, *A. garhi* was described by Asfaw *et al.*; (1999) and placed at the important chronological point of 2.5 my. The authors identified this specimen as a descendant from *A. afarensis* and the taxon which possibly gave rise to *Homo*. From Kenya, Senut *et al.*; (2001) described a new hominid of great antiquity, about 6 my, placed on a new genus and species, *Orrorin tugenensis*. The same year, Leakey *et al.*, (2001) described a new genus and species which was said to be the direct ancestor of the genus *Homo*. This new taxon, *Kenyanthropus platyops*, has been dated to about 3.5 my (Leakey *et al.*; 2001). A year later, a 6-7 million year old cranium was described as *Sahelanthropus tchadensis* by Brunet *et al.*; (2002). The last addition to the hominid family tree was that of *Ardipithecus kadabba* (Haile-Selassie *et al.*; 2004) which was originally described as a subspecies of *Ar. ramidus* (Haile-Selassie *et al.*; 2001). The disparity of fossil taxa from the Late Miocene/ Early Pliocene (*Sahelanthropus*, *Orrorin* and *Ardipithecus*) has been interpreted by Haile-Selassie *et al.*; (2004) as representing variants of the genus *Ardipithecus*.

It must be noted that taxonomic classifications used by all authors and their co-workers detailed above, used large sets of cranio-dental features present in the respective fossils studied. However, a recent study of Collard and Wood (2000) indicated the limitations of this method when taxonomic classifications based on morphological characters are compared to molecular data. However, this conclusion has been brought into question by McCollum and Sharpe (2001).