

## Chapter 7

# *Australopithecus* from Sterkfontein Caves, South Africa

Ronald Clarke

**Abstract** Since the discovery by Robert Broom of the first adult *Australopithecus* at Sterkfontein in 1936, a large quantity of fossil remains of this genus, consisting of crania, teeth and postcranial bones, has been excavated from those cave infills. They have generally been considered as belonging to one species, *Australopithecus africanus*, but there is now abundant proof that a second species is represented by many of the fossils. This second species should be classified as *Australopithecus prometheus*, the name given by Raymond Dart in 1948 to such fossils from Makapansgat (MLD 1 and MLD 2). *A. prometheus* is distinguished from *A. africanus* by having a more vertical occiput, larger, bulbous-cusped cheek teeth, a flatter face, lower frontal squame, and sagittal crest in the males. An almost complete skeleton of *Australopithecus* (StW 573) from an early deposit in the cave belongs to this second species, and for the first time this discovery made it possible to indisputably associate postcranial anatomy with specific cranial anatomy. It is also now possible to clearly distinguish males and females of each species, and to state with conviction that StW 53, a cranium excavated in 1976 and widely identified as *Homo habilis*, is in fact a male *A. africanus*, virtually the same as the TM 1511 cranium found by Broom 40 years earlier.

**Keywords** *Australopithecus prometheus* • *Homo habilis* • Makapansgat • StW 53 • Taxonomy • Taung

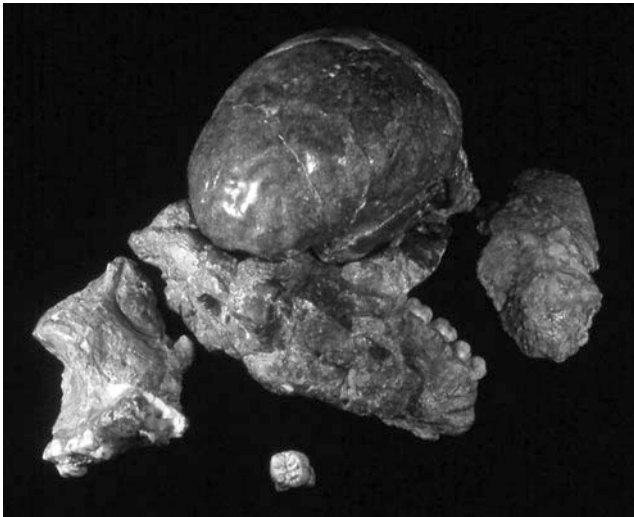
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R. Clarke (✉)  
Institute for Human Evolution, University of the Witwatersrand,  
Private Bag 1, WITS, Johannesburg, 2050, South Africa  
e-mail: Ronald.Clarke@wits.ac.za

## Introduction

It was on 17th August 1936 that Dr. Robert Broom discovered at Sterkfontein Caves, South Africa, the first known adult *Australopithecus* cranium to add to the only other *Australopithecus* known at that time, which was the child skull from Taung, the type specimen of *Australopithecus africanus*. Broom (1936) placed his specimen (TM 1511) into a new species, *Australopithecus transvaalensis*, but following his discovery in 1938 of a child symphyseal fragment (TM 1516 with canine Sts 50), he created a new genus, *Plesianthropus*, for the Sterkfontein fossils (Broom 1938) and with subsequent discoveries (Broom and Schepers 1946; Broom et al. 1950) suggested that there were large-toothed males (e.g., Sts 7) and smaller-toothed females (e.g., Sts 5, TM 1512) represented in the assemblage. Robinson (1954) placed all the Sterkfontein specimens into *A. africanus* and, later still, Robinson (1972) was to include them in the genus *Homo* as *Homo africanus*, a move that has not gained acceptance.

The first adult *Australopithecus* (TM 1511), from Sterkfontein, was badly crushed and its main contribution to the understanding of *Australopithecus* morphology has been its natural endocranial cast (Sts 60), its facial structure and its cheek teeth (Fig. 7.1). The incisors and canines were missing, but recently the missing left third molar and right second premolar (Fig. 7.2) were recovered from a lime miner's dump (Clarke 2007, Clarke and Partridge 2010). With the discovery of more *Australopithecus* fossils, Broom and Robinson had to counter the arguments of some colleagues that the fossils were merely a variety of ape that had nothing to do with human ancestry. Hence they had to emphasize their human-like features. They also considered the fossils all to belong to one species that came from one Sterkfontein stratum, the Lower Breccia of Robinson (1962), now called Member 4 of the Sterkfontein Formation (Partridge 1978). It was further assumed that all of the hominid postcranial bones that were found in that deposit belonged to that same species (*Plesianthropus transvaalensis*, now termed



**Fig. 7.1** TM 1511 with Sts 60 endocranial cast. The first discovered adult *Australopithecus*



**Fig. 7.2** Dentition of TM 1511 *Australopithecus africanus* with the recently discovered left M<sup>3</sup> and right P<sup>3</sup>

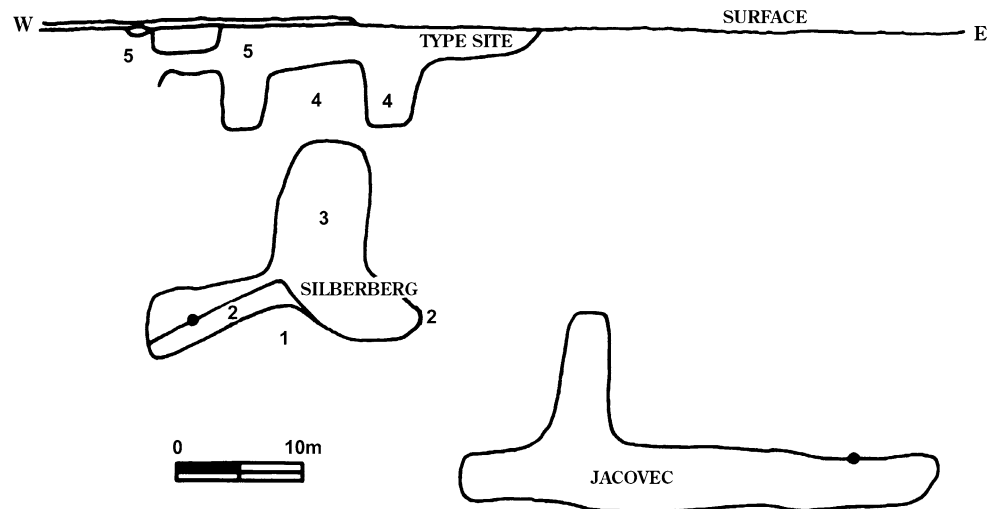
*A. africanus*). This lumping of all the fossils into one species has led over the years to three different perceptions of the phylogenetic position of *A. africanus* (see also Grine 2013). Some researchers concentrated on the *Homo*-like features and saw them as ancestral to *Homo* (Robinson 1967, 1972; Olson 1985), others concentrated on the larger teeth and jaws within the sample and saw them as ancestral to *Paranthropus* (Johanson et al. 1981; Rak 1983), and the third view was that *A. africanus* was ancestral to both *Homo* and *Paranthropus* (Tobias 1980; Skelton et al. 1986). The one-*Australopithecus*-species concept for Sterkfontein has been the accepted view until recently. However, excavations at Sterkfontein since 1966 have now revealed that there are at least three *Australopithecus*-yielding infills apparently of different ages—Member 4, Member 2, and Jacovec Cavern

(Partridge 1978; Partridge et al. 2003; Clarke 2006) (Fig. 7.3)—with at least two different species of *Australopithecus*. The main infill, Member 4, which is at least 8 m thick, could cover a long time-span of perhaps 300 kyr (Partridge and Watt 1991) and has provided a large sample of more than 500 *Australopithecus* fossils. It has been claimed that in addition to *A. africanus* there is a second distinct species of *Australopithecus* present in Member 4 (Clarke 1985, 1989, 1994a), and one of the lower infills (Member 2) contains an *Australopithecus* skeleton (StW 573) that appears not to belong to *A. africanus* but rather to the second species (Clarke 1998, 2008). The *Australopithecus*-bearing deposits of Sterkfontein possibly cover a period from about 3.3 to 2.14 Ma (Partridge 2005).

## Member 4

This massive infill of breccia has yielded hundreds of *Australopithecus* fossils (Broom and Schepers 1946; Broom et al. 1950; Deloison 2003; Pickering et al. 2004a; Moggi-Cecchi et al. 2006). When Broom first visited Sterkfontein in 1936, the lime miners were working in a surface quarry and blasting out fossil-rich breccia of what is now known as Member 4 of the Sterkfontein Formation (Partridge 1978). It was from this quarry area that the type specimen of *A. transvaalensis* (TM 1511) was recovered by Broom on the 17th of August 1936 (Figs. 7.1, 7.2). Hence the quarry locality later became known as the Type Site to distinguish it from other Sterkfontein cave localities. Many *Australopithecus* specimens, as well as other fauna, were recovered during ensuing years from this quarry site. In 1937, four other specimens were recovered from an area of solid breccia that was lower than and slightly to the east of the Type Site, but which appears to be the same body of breccia (Fig. 7.4): a well-preserved right maxillary fragment (TM 1512), a distal femur (TM 1513), a left maxilla (TM 1514) and a capitate (TM 1526). Here the lime miners had begun blasting in the area that now forms the exit chamber from the tourist route through the caves. After 1966, A. R. Hughes and P. V. Tobias began systematic excavations and recovered more *Australopithecus* specimens from dumps of lime miners' breccia that derived from Member 4. Their in situ excavations in the Type Site, as well as in the decalcified breccia adjacent to and southwest of the Type Site, produced a large sample of *Australopithecus* fossils, as well as other fauna and fossil wood that have provided information on the environment of *Australopithecus* (Bamford 1999). The fossils of Broom and Robinson are housed in the Transvaal Museum, Pretoria (with catalogue numbers prefixed by TM, Sts, and Se), and those of Tobias and Hughes in the School of Anatomical

**Fig. 7.3** Schematic West–East section of the main Sterkfontein fossil deposits to show relative positions of the stratigraphic Members 1–5, as well as the Type Site, Silberberg Grotto and Jacovec Cavern. Positions of the Member 2 and Jacovec hominids are shown by *large dots*. Other *Australopithecus* fossils occur throughout Member 4



**Fig. 7.4** TM 1512 maxilla (*top left*), TM 1513 distal femur (*bottom left*), TM 1514 crushed maxilla (*top right*), and TM 1526 capitate (*bottom right*)

Sciences of the University of the Witwatersrand, Johannesburg (with catalogue numbers prefixed by StW). When all of these hominid fossils are considered, they provide a wealth of information on *Australopithecus* anatomy, including variation within the cranial sample. Some of this variation most reasonably represents males and females of *A. africanus*, whilst other variation represents males and females of a second, larger-toothed, flatter-faced species of *Australopithecus* (Clarke 1989, 2008).

The type specimen of *A. africanus* is the child skull from Taung (Dart 1925), and when the *Australopithecus* cranial fossils from Member 4 are compared to this type specimen, there are some that clearly match the morphology, such as Sts 5 cranium, Sts 52 maxilla and mandible, and TM 1512 and StW 391 maxillary portions (Fig. 7.5). Of these, Sts 5 and TM 1512 have small canines and thus appear to be female, whilst Sts 52 and StW 391 have larger canines and appear to represent males (Fig. 7.6).

There are other specimens, however, that do not fall within this *A. africanus* morphology, and Clarke (1985, 1989, 1994a, 2008) has suggested that they represent a second, larger-toothed species of *Australopithecus*. These are well represented by Sts 71 cranium, Sts 1 maxilla, StW 183 maxillary portion, StW 252 cranium, StW 498 maxilla and mandible, StW 384 mandible, Sts 36 mandible and StW 505 cranium (Fig. 7.7). There are several other specimens within the Sterkfontein sample that undoubtedly belong in this second species. Clarke (1989) noted that the differences between the large-toothed and small-toothed *Australopithecus* are not simply a matter of size and cannot be attributed to sexual dimorphism (Fig. 7.8). First, there are morphological differences in the teeth, in that the larger teeth have more inflated, bulbous cusps, approaching the *Paranthropus* morphology. A geometric morphometric study on the maxillary molars by Fornai (2009; Fornai et al. 2010) confirmed that there are indeed two distinct

morphologies. Secondly, the larger-toothed cranium represented by StW 252 has a thin brow ridge, whereas the smaller-toothed cranium represented by Sts 5 has a thicker brow ridge. Among primates, including humans, the large-toothed males have more prominent brow ridges whilst the smaller-toothed females have less pronounced, or thinner, brow ridges. The larger-toothed *Australopithecus* has more anteriorly situated cheekbones that give it a flattened, or slightly hollowed nasal region (Sts 71 and StW 252). This contrasts with the more posteriorly situated cheekbones in the smaller-toothed form, such as Sts 5. The larger-toothed cranium has an incipient supraglabellar hollowing and a more vertical, rounded occiput. Broom et al. (1950) noted that whilst their skull number 6 (Sts 17) agreed closely with skull number 5 (Sts 5), skull number 7 (Sts 71) differed considerably. They observed that, in side view, the latter skull was relatively short and the occipital region was rounded rather than angled. However, they thought that this different morphology was probably due to slow post mortem crushing. Whilst it is true that such crushing does occur with some Sterkfontein fossils, this does not seem to be the case with Sts 71, especially as the uncrushed StW 252 shows the same morphology. Conroy et al. (2000) made CT scans of Sts 71 in order to digitally reconstruct the cranium and calculate the endocranial capacity. They found that the high resolution CT scans through the occipital confirmed the observation by Broom et al. (1950) that there was no obvious breakage of the bone. Thus one would have to postulate slow plastic deformation to account for the rounded profile of the occipital if one does not accept it as normal morphology. Conroy et al. (2000) did not refer to the work of Clarke (1990) where, following his cleaning and some reconstruction of the cranium, he observed that Sts 71 “differs from Sts 5 in being less prognathic, having a thinner supraorbital margin, flat upper nasal region, more bulbous cheek region, less of a step from the anterior malar



**Fig. 7.5** *Australopithecus africanus* child from Taung (left), adult female TM 1512 and adult male StW 391 (upper right), and adult male Sts 52 (lower right)—not all to same scale. Note the similarity of the

facial profiles and note the larger canine and canine socket in the males Sts 52 and StW 391 respectively





**Fig. 7.6** Palatal view of TM 1512 female *A. africanus* (left) and StW 391 male *A. africanus* (right). Note the larger canine socket and wider premolars in the male

surface to the canine root eminence, more medially-directed temporal lines, and a larger canine socket. The canine socket is 7.5 mm in mesiodistal diameter, whereas the Sts 5 canine socket is 5.6 mm.” In all of these features, which cannot be ascribed to plastic deformation, Sts 71 corresponds with the morphology of StW 252. Thus it is highly likely that the more vertical, rounded occiput, which also corresponds with StW 252 morphology, is a feature characteristic of this second species.

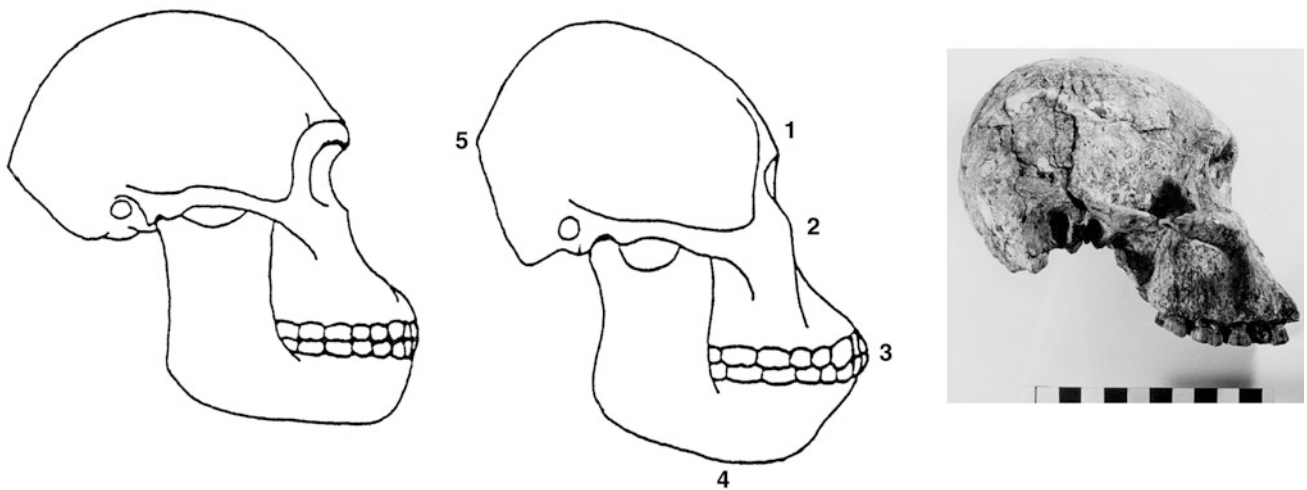
The existence of this second species was actually recognized at Makapansgat by Dart (1948a–c). The first *Australopithecus* from there was an occiput, MLD 1, which Dart found to be different from that of Sterkfontein “*Plesianthropus*.” Although, at the time, this may have seemed an insufficient basis on which to create a new species, it does currently seem that Dart was correct, as the occiput more closely resembles those of the second species such as StW 252 and Sts 71 than it does Sts 5 (*A. africanus*). Furthermore, the temporal lines approach each other so closely that there was probably a sagittal crest on the

parietals, as there is in StW 505 (a male of the second species) and the StW 573 skull, which also seems to belong to this species, as discussed later on. The second *Australopithecus* found at Makapansgat was the juvenile mandible MLD 2, which has the typical large bulbous-cusped molars characteristic of the Sterkfontein second species. Dart named this Makapansgat species *Australopithecus prometheus*. Although this name has not been generally used in many years, it was I believe a valid name and should be used for the second species, as tentatively suggested by Clarke (1994a).

There is a reluctance of some researchers to accept that two species of one genus of hominid (*Australopithecus*) could be living in the same location and be preserved as fossils in the same breccia. However, such a scenario is not unusual in the animal kingdom, for example lion (*Panthera leo*) and leopard (*Panthera pardalis*) being two species of one genus of carnivore live in overlapping territories and both are preserved as fossils in the Sterkfontein Member 4 and Post-Member 6 (Kuman and Clarke 2000; also called



**Fig. 7.7** Comparison of dentition of *A. africanus* mandible Sts 52 (far left) and mandible of large-toothed species StW 384 (left), as well as maxillae of large-toothed species Sts 1 and StW 183 (right and far right)



**Fig. 7.8** Reconstructed profiles of *A. africanus* female based on Sts 5 (left), and second species male based on StW 252 (center), with female cranium of second species Sts 71 (right). Numbers indicate major features of second species to contrast with *A. africanus*. 1 Thin

supraorbital margin and incipient supraglabellar depression. 2 Anteriorly situated cheekbone. 3 Large canines and large anteriorly projecting incisors in male. 4 Large but slender-bodied mandible. 5 Vertical, rounded occiput

“Post-Member 5” breccia in Turner 1997 breccias and in Swartkrans Member 2 (Brain 1981). Furthermore, we know that among the primates, two species of *Parapapio* (*Parapapio broomi* and *Parapapio jonesi*) inhabited the same areas and were preserved as fossils in the Sterkfontein Member 4 breccia (Brain 1981).

The dental differences between *A. africanus* and the second species of *Australopithecus* are such that they suggest different feeding strategies, and indeed some dental and cranial similarities of the second species to *Paranthropus* indicate the possibility that it could well be close to the ancestral stock from which *Paranthropus* evolved. Aguirre

(1970) was so impressed with the *Paranthropus*-like morphology of the MLD 2 dentition that he even proposed placing it in that genus. However, the large canines and incisors of the second species, together with the cranial morphology, show that although it is *Paranthropus*-like it belongs within *Australopithecus*.

In addition to the many dental, maxillary and mandibular fossils of *Australopithecus* from Member 4, there are several adult and sub-adult partial crania and one near-complete cranium (Sts 5). The partial crania are TM 1511 (crushed and with endocranium), Sts 17 (face, palate and parietal), Sts 19 (cranial base with StW 73 palate), Sts 52 (lower face with palate and mandible), Sts 67 (calvaria), Sts 71 (right side of cranium), StW 13 (crushed face with maxilla and left parietal), StW 53 (fragmented cranium with teeth), StW 252 (fragmented cranium with teeth), StW 498 (mandible, maxilla and parietal fragments) and StW 505 (face with left side of braincase). Of these, the StW 53 cranium requires some detailed explanation because it is a very important specimen and has frequently, but erroneously, been referred to in the literature as *Homo habilis* from Member 5 (see also Grine 2013).

In 1976, at the southwestern end of his Sterkfontein excavation, Alun Hughes recovered hominid teeth and cranial fragments of one individual (StW 53) from the decalcified breccia within a solution pocket. The right posterior portion of the braincase was embedded in solid breccia in the wall of the solution pocket, thus indicating the exact location and breccia type from which the other fragments had been decalcified and scattered. The breccia at that western end was, at the time, thought to be all Member 5 with an overlying exposure of Member 6 in a small area on the northern side. As Member 5 had yielded abundant early stone tools, and as no stone tools whatsoever had occurred in Member 4, Hughes and Tobias (1977) believed that StW 53 must be a cranium of early *Homo*. Subsequently, it was frequently referred to as *H. habilis* because of its supposed similarity to the OH 24 “*Homo habilis*” from Olduvai Gorge Bed 1 (Leakey et al. 1971; Clarke 1985). Later stratigraphic investigation by Clarke (1994b) showed that StW 53 did not in fact come from tool-bearing Member 5, but from a hanging remnant of Member 4 (Kuman and Clarke 2000). Furthermore, at a conference in Orce, Spain, in 1995, Clarke (1999a) observed that StW 53 and supposed *H. habilis* specimens OH 13, OH 24, and KNM-ER 1813 had small brains and flat noses like those of *Australopithecus*, and in these respects differed greatly from the much larger-brained OH 7 type specimen of *H. habilis*, as well as from KNM-ER 1470 *H. habilis* which has a prominent nasal skeleton. He also referred to the work of Spoor (1993; Spoor et al. 1994) who found that the bony labyrinth of the StW 53 temporal was unique among hominid fossils and had similarity to large cercopithecoids, suggesting arboreality. In other words, there was nothing in its anatomy

to suggest that StW 53 was anything but an *Australopithecus* and it certainly came from the non-tool-bearing Member 4, just like the other *Australopithecus* fossils from Sterkfontein (Kuman and Clarke 2000).

Clarke (1985) made a reconstruction of the StW 53 cranium “based solely on anatomical considerations and symmetry.” This was the only reconstruction of StW 53 Clarke ever made (see below), but Curnoe and Tobias (2006) incorrectly claimed that Hughes and Clarke had made two reconstructions differing from each other, and Curnoe and Tobias used this imaginary discrepancy to justify their making a “new reconstruction.” Clarke (2008) published a detailed criticism of their methods, their incorrect claims, and their results. Some of the main points made were that they had widely separated a near-contact, unrealistically flexed joints and bone contacts, and unnaturally extended the gap between front and back to produce a braincase that is wider, higher, and longer than it should be. Furthermore, the cranium was now deformed. Thus their construction is not a reconstruction because it has not followed the anatomical guidelines and contours and therefore does not reflect the original form of the cranium. It is a construct of how they considered it should be, rather than a reconstruction of how it actually was. In their own words, Curnoe and Tobias (2006) admit that “our reconstruction differs in important respects from the earlier one, especially in terms of neurocranial length, breadth, and height. However, given that StW 53 exhibits extensive damage, these dimensions are most likely prone to much error in reconstruction.” Despite this, they have still maintained that the maximal cranial length of their “reconstruction” is virtually identical to the *H. habilis* cranium KNM-ER 1470 (their Fig. 18) and their overall conclusion based on their artificially enlarged and deformed StW 53 braincase, as well as their interpretation of the anatomy, is that it is a representative of *H. habilis*.

The Clarke (1985) reconstruction, which was based on anatomy and contours of the bones (which contra Curnoe and Tobias do not “exhibit extensive damage”), shows that the StW 53 cranial size and shape does not differ significantly from *A. africanus* in the form of Sts 5 (Fig. 7.9). The facial structure of the two is very similar with small, narrow muzzle, small nasal aperture and flat nasal skeleton, and both have a narrow, rectangular palate. The frontal bones of both resemble each other in size and form with a prominent metopic ridge. The StW 53 frontal bone fits very closely on the Sts 60 endocranial cast of the first adult *Australopithecus* TM 1511 and is very obviously not that of a large-brained *Homo*, but of a small-brained *Australopithecus*. The wider intermastoid breadth in StW 53 when compared to Sts 5 is undoubtedly because it is a male *A. africanus*, whilst Sts 5 is a female. This is indicated also in the dentition. Sts 5 has smaller canine and cheek teeth sockets than does StW





**Fig. 7.9** Clarke reconstruction of StW 53 male *A. africanus* (top left) compared to Sts 5 female *A. africanus* cast (top right), Endocranial casts of StW 53 (lower row left) and Sts 5 (lower row right)

53, which more resembles Sts 52 and StW 391. In its small canine and premolar sockets Sts 5 is similar to TM 1512 which is also undoubtedly a female. The larger canine socket in the apparent males has caused the socket to bulge more anteriorly, which can contribute to a less pronounced appearance of the premaxillary region.

There is in fact nothing in the anatomy of StW 53 to align it with *H. habilis* (in the form of OH 7, KNM-ER 1470, and OH 65) rather than with *Australopithecus* (see Blumenschine et al. 2003). The type specimen of *H. habilis* is Olduvai Hominid 7 (OH 7), consisting of the two parietals and mandible of a juvenile (Leakey et al. 1964). The parietals alone indicate a much larger-brained hominid than any *Australopithecus*, and these parietals match in size and shape those of the near-complete cranium KNM-ER 1470 (Leakey 1973). Hence, the 1470 cranium cannot be distinguished from *H. habilis*, and there is no justification for its having been placed in a separate species, *Homo rudolfensis* (e.g., Groves 1989; Wood 1992). The discovery of a complete dentition in the maxilla of OH 65 from Olduvai Gorge Bed 1 (Blumenschine et al. 2003) supports the placement of KNM ER 1470 in *H. habilis*. The maxilla of OH 65 matches in shape and size that of 1470, and the cheek tooth crowns, though small by comparison with *Australopithecus*, have widely-flaring roots like those of KNM-ER 1470. The palates of both fossils are broad and horseshoe-shaped, thus differing radically from the narrow, rectangular palates of *Australopithecus* Clarke (2012).

It is rather the smaller-brained, more *Australopithecus*-like fossils OH 13, KNM-ER 1813, and OH 24 which should be removed from the taxon *H. habilis* as they have no similarity to *H. habilis* as represented by the type specimen OH 7, the cranium KNM-ER 1470, and the maxilla OH 65. The question of whether the smaller-brained forms should be

classified as *Homo* or *Australopithecus* is debated. While most textbooks and research papers classify them as *H. habilis*, Richard Leakey (1974; Leakey et al. 1978; Leakey and Lewin 1992) classed them as *Australopithecus* (see also Leakey 1979). Ferguson (1995) made ER 1813 the holotype of his new species *Homo microcranous*.

## Member 4 Postcranial Fossils

In 1946, after the discovery of many cranial fossils from Sterkfontein, Broom (in Broom and Schepers 1946) wrote “it is very remarkable that, as in the caves in China, postcranial bones are very rare.” In spite of the wealth of *Australopithecus* fossils discovered since that time, the situation has not much changed. In other words, relative to the quantity and state of completeness of cranial and dental fossils, the postcranial fossils are few and mostly fragmentary. Considering that for one skull of a human skeleton there are 174 postcranial elements, one would normally expect a greater amount of postcranial fossils to accompany the numerous cranial specimens at Sterkfontein. Even allowing for fragmentation of long bones by carnivores and by the crushing effect of rocks in the talus cone of the cave, there should be a greater quantity of articular ends and of the smaller and more compact bones such as those of the wrist, hand, ankle and foot. The relative paucity of such elements compared to cranial and dental remains is a taphonomic question that needs further investigation (Clarke 2007). It is noteworthy that monkey postcranial fossils are much better represented.

Nevertheless, there are now several informative hominid postcranial fossils (Table 7.1). Notably, there are two partial skeletons, Sts 14 (Robinson 1972) and StW 431 (Kibii and Clarke 2003; Toussaint et al. 2003), from Member 4 (Fig. 7.10), some well-preserved articular ends of limb bones, and some complete foot and hand bones. Most importantly there is now a practically complete *Australopithecus* skeleton with skull (StW 573) from Member 2, providing a near-total *Australopithecus* skeletal morphology of a single individual against which the other fragmentary fossils can be compared (Clarke 1998, 1999b, 2002, 2008).

Broom (Broom and Schepers 1946) was so impressed by the human-like characters of a distal femur (TM 1513) and a capitate (TM 1526) that he raised the question of whether they might belong to a human rather than to *Australopithecus*. He concluded, however, that they were almost certainly those of *Plesianthropus* (i.e., *Australopithecus*). As the sample of cranial and postcranial fossils recovered from Sterkfontein Member 4 has increased over the years, it has become clear that there are no cranial or dental remains of *Homo* and that the postcranial bones are, as Broom said, almost certainly those of *Australopithecus*. However, the



**Table 7.1** *Australopithecus* postcranial fossils from Sterkfontein Member 4

Skeletal part	Catalog number(s)	Details/notes	
Partial skeleton	Sts 14	9 thoracic and 6 lumbar vertebrae, complete pelvis, proximal left femur minus head	
	StW 431	4 thoracic and 5 lumbar vertebrae, partial pelvis with partial sacrum and parts of both ilia, lateral half of right clavicle shaft, lateral margin of left scapula, distal half of right humerus and proximal halves of right radius and ulna	
Vertebra	Sts 73	Partial vertebra	
	StW 8/41	2 thoracic and 4 lumbar vertebrae conjoined	
	StW 642	Partial column of 12 thoracic and lumbar and 1 cervical vertebrae	
Clavicle	StW 616	Left shaft fragment	
	StW 582	Right shaft	
Scapula	StW 162	Left proximal portion	
	StW 366	Left spine of scapula	
	StW 612	Left spine of scapula	
Humerus	Sts 7	Right proximal portion	
	StW 124, 150	Left distal portions	
	Sts 7	Right head and proximal shaft	
	StW 328 and 517	Right heads	
Radius	StW 38, 182, 339, Sts 2198a	Right distal portions	
	Sts 68	Left proximal quarter	
	StW 626a	Left shaft	
	StW 627	Left shaft fragments	
	StW 46	Left distal end	
	StW 354	Left distal end with partial shaft	
	StW 348, 528	Right shafts	
	StW 105	Right proximal third of an adolescent	
	StW 139	Right proximal portion	
	Sts 2198b	Proximal fragment	
	StW 125	Fragment of a shaft	
	StW 516	Proximal portion	
	Ulna	StW 108, 398, 613, 632	Left proximal ends
		StW 113	Left proximal half
		StW 626b	Left shaft portion
StW 399 (398b)		Left distal end	
StW 380, 390		Right proximal third	
StW 571		Right proximal end	
StW 349, 577		Right shaft portion	
StW 326		Right shaft and distal end	
StW 125		Proximal end	
StW 340		Shaft portion	
Wrist	TM 1526, StW 624	Right capitate	
	StW 618	Left scaphoid	

(continued)

**Table 7.1** (continued)

Skeletal part	Catalog number(s)	Details/notes	
Metacarpals	StW 583	Left 1st, distal portion	
	StW 382	Left 2nd	
	StW 64	Left 3rd	
	StW 394	Left 3rd, distal portion	
	StW 330	Left 4th, missing distal epiphysis	
	StW 26, 292	Left 4th, distal portion	
	StW 63	Left 5th	
	StW 68	Right 3rd	
	StW 27	Right 3rd, distal portion	
	StW 65	Right 4th, proximal portion	
Hand phalanges	StW 293	Left 2nd, proximal portion	
	StW 294	Right thumb, distal portion	
	StW 331	Right 3rd, middle	
	StW 400	Right 3rd, proximal portion	
	StW 28	Right 5th, proximal	
Pelvis	StW 617	Thumb, distal portion	
	StW 29, 597	Proximal	
	StW 122	Proximal, eroded	
	StW 635	Phalanx	
	StW 611	Left ischium	
	Sts 65	Right ilium	
	Femur	TM 1513	Left distal end
		StW 522	Right neck and head
		StW 367	Right neck and shaft
		StW 99	Right head, neck and shaft
StW 614		Right distal end of shaft	
Sts 34		Right distal end	
StW 318		Right distal fragment	
StW 25, 30, 31, 361, 392, 527		Heads	
StW 403, 479, 501		Neck and head	
StW 610		Neck	
Tibia	StW 121, 448	Shaft	
	StW 615	Portion of shaft	
	StW 129	Distal end	
	StW 181	Left distal fragment	
	StW 358, 389	Left distal end	
Fibula	StW 396	Right proximal portion	
	StW 514	Proximal portion	
	StW 515	Distal portion	
	StW 356	Left shaft	
	StW 88, 102, 486	Right talus	
Ankle	StW 347, 363	Left talus	
	StW 352	Right calcaneum	
	StW 643	Right calcaneum fragment	
	StW 638	Right cuboid	
	StW 623	Left navicular	

(continued)

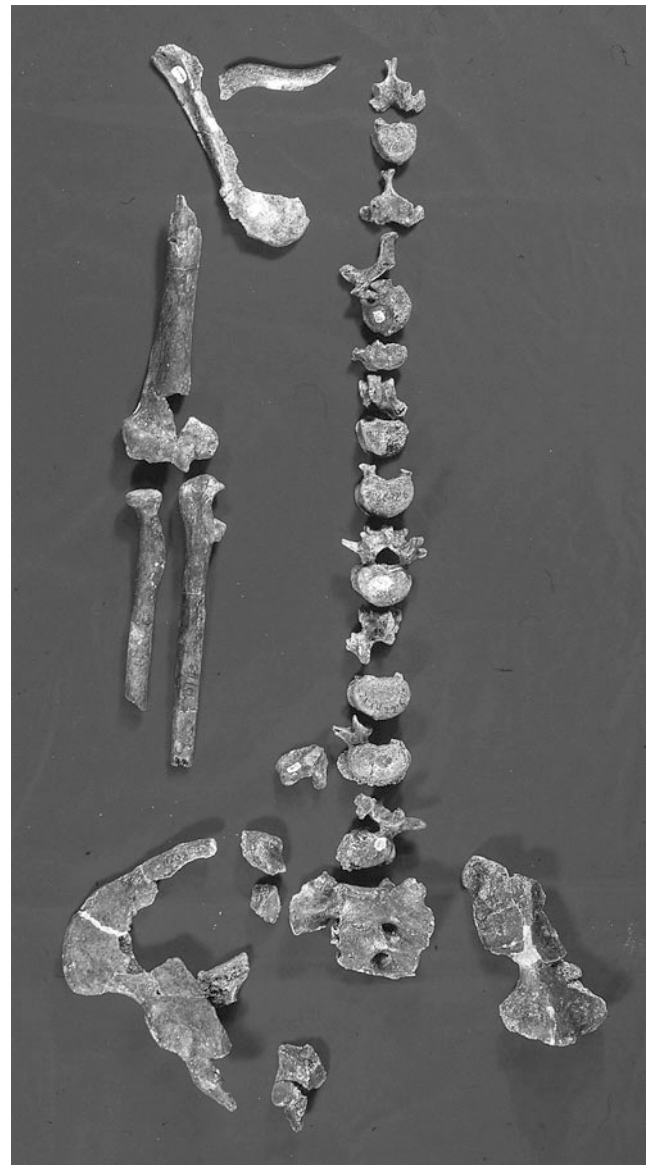
**Table 7.1** (continued)

Skeletal part	Catalog number(s)	Details/notes
Metatarsals	StW 89, 377	Left 2nd
	StW 477, 496	Left 3rd
	StW 387	Left 3rd, proximal half
	StW 485	Left 4th, proximal portion
	StW 634	Left 5th
	StW 562, 595	Right 1st
	StW 595c	Right 2nd
	StW 435	Right 3rd
	StW 388, 595d	Right 3rd, proximal half
	StW 596	Right 4th
	StW 114	Right 5th
	Foot phalanges	StW 478
StW 355		Proximal left of 2nd, 3rd or 4th ray
StW 470		Proximal right of 1st ray
StW 595b		Right proximal phalanx of hallux

question of association between cranial and postcranial fossils has to be considered in the light of the demonstration that two species of *Australopithecus* might be represented by the cranial remains.

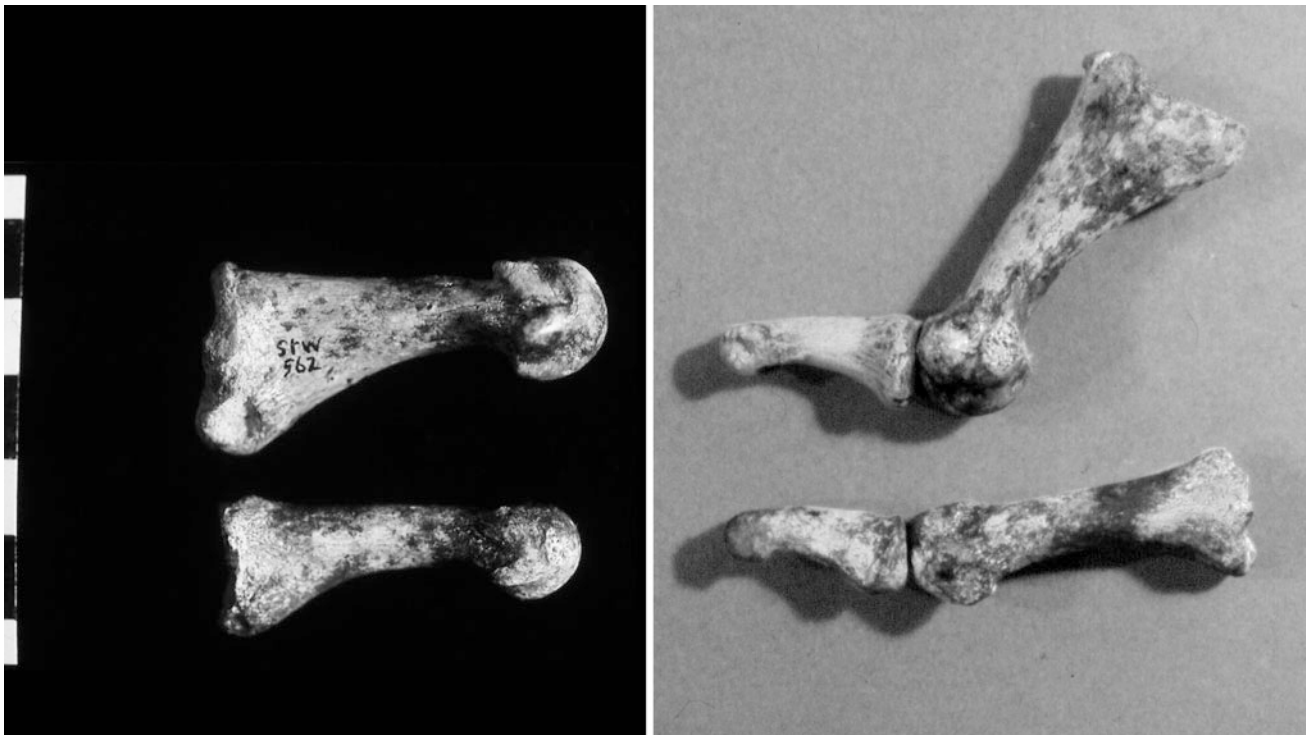
Two first right metatarsals that I excavated from Member 4 are relevant to this question because I observed that one (StW 595) is very ape-like, and the other (StW 562) has some more human-like characters. In particular, on StW 595, as in the chimpanzee, the articular surface for the first phalanx does not extend onto the dorsal surface, indicating that it could not toe off in walking. By contrast, StW 562 is rather less ape-like in morphology than StW 595 and has an articular surface for the first phalanx that does extend onto the dorsal surface, indicating that it could toe off in walking (Fig. 7.11). Hence there seem to be two types of locomotion represented in these foot bones of *Australopithecus*. If that is the case, then they would represent two species and clearly one cannot make assumptions about the postcranial anatomy and locomotive behavior of *A. africanus* until postcranial remains can be definitely associated with *A. africanus* cranial fossils. This is pertinent to the study by Proctor (2010).

When Robinson (1972) published his work on early hominid posture and locomotion, he noted that there was no known fossil material of the *Australopithecus* foot, but he went on to claim that the Olduvai foot and other fossils of *H. habilis* represent the same kind of creature as *Australopithecus*. From this he deduced that *Australopithecus* could “stand, walk and run essentially as man does” and that it “was probably capable of running and walking fast.” The two recently discovered foot bones just mentioned from Sterkfontein show that Robinson was not entirely correct in

**Fig. 7.10** StW 431 *Australopithecus* partial skeleton

this deduction and that at least one *Australopithecus* species had a foot anatomy that would not have permitted running. One can only make some general statements about the postcranial anatomy and locomotion of the genus *Australopithecus* at Sterkfontein. We can say, for example, that the two species of *Australopithecus* were both upright walkers and that they had hands proportioned like those of modern humans with a long, powerful, opposable thumb relative to short palm and fingers. This is further discussed below in the section on Member 2.

Surprisingly, despite the relative rarity of *Australopithecus* postcranial fossils at Sterkfontein, two important and informative postcranial bones represented the third and fifth *Australopithecus* specimens recovered from there. These were a



**Fig. 7.11** Two morphologically different right first metatarsals from Sterkfontein Member 4, StW 562 (top left) and StW 595 (bottom left). Same bones articulated with chimpanzee proximal phalanx and StW

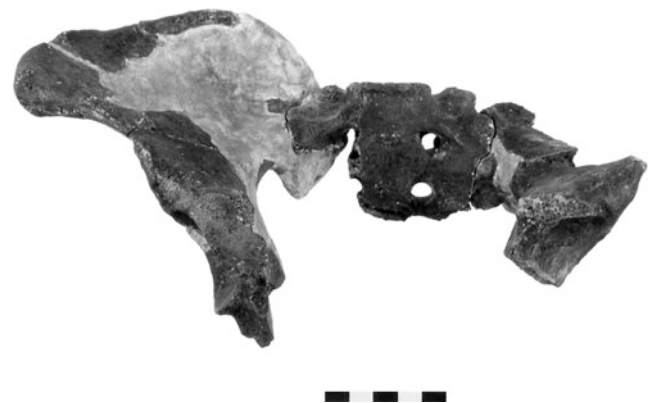
595b proximal phalanx at right to show that StW 562 can extend its big toe (top right), whilst StW 595 cannot (bottom right)

distal femur (TM 1513) and a capitate (TM 1526) found in 1937. Both of these were crucial elements in that they provided information on the locomotion of *Australopithecus*. Broom (in Broom and Schepers 1946) concluded that “the femur is that of an animal that walked as does man, entirely or almost entirely on its hind feet.” Although Broom found that the capitate had some ape-like as well as human-like characters, he observed that the articulation for the second metacarpal was large and this suggested to him that, if the second metacarpal was better developed than that of an ape, then the thumb metacarpal would also have been better developed. He concluded that “as the proximal end of the second metacarpal must have been still more like that of man than that of the living anthropoids, we may not be wrong in suspecting that *Plesianthropus* had a useful thumb, or at least a better thumb than in any of the living anthropoids.” Subsequent discoveries of hand bones in Member 4 and in particular the discovery of a complete *Australopithecus* hand in Member 2 (Clarke 1999b) have shown that indeed Broom was not wrong in his deduction. *Australopithecus* did have a well-developed thumb.

The discovery of a complete pelvis in the partial skeleton (Sts 14) in 1947, as well as the partial pelvis of StW 431 and some finds of proximal femur fossils have confirmed Broom’s initial observation, based on the distal femur TM 1513, that *Australopithecus* walked bipedally, although not

in exactly the same fashion as modern humans. The ilia are more laterally flared (Fig. 7.12) and some femoral necks are long with relatively small heads. Furthermore, the legs of *Australopithecus* had not become as elongated relative to the body size as they are in modern humans.

The Sterkfontein *Australopithecus* fossils recovered by Broom and Robinson, including the Sts 14 partial skeleton, were studied in detail by Robinson (1972). The StW 431 partial skeleton has been described by Toussaint et al. (2003) and the StW 431 pelvis by Kibii and Clarke (2003).



**Fig. 7.12** Pelvis of StW 431 *Australopithecus* as reconstructed by Kibii and Clarke



In addition to various studies on different aspects of *Australopithecus* postcranial anatomy, which have included references to Sterkfontein fossils, there have also been detailed studies of *Australopithecus* hand bones by Ricklan (1988), thoracic and lumbar vertebrae by Benade (1990), the shoulder girdle by Berger (1994), foot bones by Deloison (1993, 2003), and distal humeri and proximal radii and ulnae by Menter (2002).

## Member 2

Member 2, exposed in the Silberberg Grotto, represents (with the Jacovec Cavern) one of the oldest major fossil-bearing deposits at Sterkfontein and contains a near-complete *Australopithecus* skeleton, StW 573, initially dated by paleomagnetism to 3.3 Ma (Clarke 1998; Partridge et al. 1999; see “Dating”). It was discovered in situ in 1997, and subsequent excavation has revealed a complete skull



**Fig. 7.13** StW 573 *Australopithecus* skull and left humerus

(Fig. 7.13), complete left arm and hand (Fig. 7.14), crushed and broken right arm and hand, complete right scapula and clavicle, crushed pelvis and scattered ribs and vertebrae, both legs complete though broken (Fig. 7.15), and a partial left foot and one right lateral cuneiform (Clarke and Tobias 1995; Clarke 1998, 1999b, 2002; Deloison 2003). At present, some of the skeleton is still embedded in concrete-like breccia and is being slowly uncovered whilst parts of the skeleton including the left arm and the skull have been lifted in blocks so that final cleaning can be done in a laboratory with the aid of microscopes. Thus, only general observations can be made. The skull differs from those of *A. africanus*. It has a deep anterior zygomatic arch, prominent nuchal crest and inion, and a posterior sagittal crest. It has resemblance to StW 505, a large male *A. prometheus*. The hands are proportioned like those of modern humans, with short palm and fingers and long thumb. There is a strong curvature to the phalanges and powerful muscle attachments. The arms are of approximately equal length to the legs, i.e., not proportioned like either apes (with long arms relative to legs) or humans (with long legs relative to arms). The complete right scapula has some human-like and some ape-like features. The foot bones have a mixture of ape and human characters, and in particular, the big toe shows slight divergence and some mobility at the metatarsal-cuneiform articulation (Clarke and Tobias 1995). All of this indicates that *Australopithecus* at Sterkfontein was adept at tree-climbing in an upright posture and that hominids (meaning *Australopithecus*, *Paranthropus*, *Homo*, and related forms, excluding apes) did not evolve from a knuckle-walking ancestor (contra Richmond and Strait 2000) but were upright in the trees and walked upright on the ground (Clarke 1999b). The Laetoli footprints of bipedal *Australopithecus afarensis* show that the foot had some ape-like characters, including a slightly divergent big toe (Deloison 1991, 1993), and the foot bones of StW 573 from Sterkfontein Member 2 have the kind of anatomy that could have made the Laetoli footprints (Clarke 1999b).

## Jacovec Cavern

In 1995, a Sterkfontein deposit in the Jacovec Cavern separate from, but adjacent to, the main Sterkfontein deposits (Wilkinson 1983; Kibii 2000, 2004) began yielding *Australopithecus* fossils that seemed to be of similar age to the skeleton of Member 2 (Partridge et al. 2003). These specimens include a partial cranium (StW 578) with a temporal bone that again differs from *A. africanus* and is more like that of *A. afarensis*, and a partial clavicle (StW 606) that is more ape-like than either *A. africanus* or *A. afarensis*, both of which are similar to modern humans. A proximal left



**Fig. 7.14** StW 573 *Australopithecus* left forearm and hand, with hand enlarged at bottom right

femur (StW 598) from this deposit is the best preserved *Australopithecus* femur from Sterkfontein (Fig. 7.16). Similarly, a complete distal left humerus (StW 602) is the best preserved of *Australopithecus* from Sterkfontein (Partridge et al. 2003). The Jacovec fossils were recovered partly from in situ breccia (part of the cranium) and partly from a debris cone of collapsed material (other fragments of the cranium and other hominid fossils). This cone seems to be of considerable depth and has yielded other faunal material including *Chasmaporthetes* limb bones in very good condition. There is thus much potential for the recovery of more well-preserved *Australopithecus* fossils, including highly informative postcranial material.

## Dating

Until recently, the only way of dating the Sterkfontein *Australopithecus* fossils was by general comparison of the fossils of Members 4 and 5 and the stone tools of Member 5

with the well-dated deposits of East Africa. Thus if the early Acheulean and *Homo ergaster* of Member 5 date to about 1.6 Ma and the Oldowan tools and *Paranthropus* teeth of lower Member 5 date to nearly 2 Ma, it could be proposed that the *Australopithecus*-bearing Member 4 deposit beneath, with no stone tools and no *Homo* fossils, is probably older than 2 Ma. Through consideration of the stratigraphy it was further estimated that the *Australopithecus* of Member 2 could be 3–3.5 Ma, and Partridge et al. (1999) provided a paleomagnetic date of 3.3 Ma. Now various other dating methods have been applied to the breccias. One of the methods (cosmogenic nuclide burial dating) has given dates for Member 2 and Jacovec Cavern that seem too old, ca. 4 Ma (Partridge et al. 2003), and another (uranium-lead dating) has given dates for Member 2 that seem too young, 2.2 Ma (Walker et al. 2006; Pickering and Kramers 2010). A paleomagnetic date for the top of Member 4 (Partridge 2005; Herries 2013) has provided an age of 2.14–2.15 Ma, which is a reasonable age when stratigraphy and faunal comparisons are taken into account. If one then considers the 16 m of cave breccia between this dated





**Fig. 7.15** StW 573 *Australopithecus* left lower leg and foot and right lower leg

horizon and the much lower Member 2 skeleton, an age of around 3 Ma for the skeleton seems quite reasonable (but see Herries 2013 and also Grine 2013). Although under certain conditions rapid infill of an underground cavern could be possible, it seems unlikely in the case of Sterkfontein which, during *Australopithecus* times, was most probably no lower than the surrounding terrain. The landscape was heavily vegetated with gallery forest (Bamford 1999). The combination of these features would have made for a more stable land surface, not prone to fast infilling of caverns through surface erosion. A major problem with both the paleomagnetic dating and the uranium-lead dating of Member 2 is that they were based on the flowstones, and it is clear that the flowstones around the skeleton were formed after a collapse that took place, displacing parts of the hominid and leaving cavities that were subsequently filled with flowstone. Thus a date on the flowstone does not give a date for the skeleton. This fact is particularly well



**Fig. 7.16** *Australopithecus* fossils from Jacovec Cavern: StW 606 lateral half of left clavicle (top right), StW 598 proximal half of left femur (left), StW 600 5th lumbar vertebra (center middle), StW 605 hand phalanx (lower middle), and StW 602 distal end of left humerus (lower right). Note long neck and small head of femur and chimpanzee-like morphology of clavicle

emphasized by the formation of flowstone on the wall of the Silberberg Grotto and the surface of Member 2 that began only in January 1999 and which has been increasing every year during the rainy season. It is obvious a date on this flowstone would not give the age of Member 2.

## Paleoenvironment

Hundreds of fragments of fossil wood were recovered from Member 4 in association with *Australopithecus*. Many of these have been sectioned and shown to belong to a liana, *Dichapetalum mombuttense*, that grows now only in tropical forests of central and western Africa (Bamford 1999) and which requires large trees for support. Such a forest



scenario for *Australopithecus* accords with the presence in the deposit of many large monkeys (*Parapapio* and *Cercopithecoides*), as well as the fossils of *Makapania*, a bovid with skull and feet similar to those of the takin (Pickering et al. 2004b), which inhabits woodland in the Himalaya foothills. The fauna of Member 4 contrasts with that of the succeeding Member 5 that contains elements such as horse, spring hare, and ostrich indicative of a more open grassland environment (Vrba 1976; Reed 1997; Kuman and Clarke 2000; Luyt 2001; Luyt and Lee-Thorp 2003; Kibii 2004).

## Taphonomy

In 1950, Broom, Robinson, and Schepers wrote: “There seems to be little doubt that the quarry which yielded our best *Plesianthropus* specimens is the upper part of a large cave which for many years had been the lair or lairs of sabre-tooths and that the bones had been introduced by them.” The extensive excavations since that time have shown that such an explanation does not fit the facts. First, the entrances to the caves during the time of *Australopithecus* were vertical shafts and the caves were not accessible for use as dens until the talus infill had nearly reached the roof. Secondly, we know that there were many other

large carnivores in the vicinity at that time, e.g., leopards, lions, hyenas, and the long-legged hunting hyena *Chasmaporthetes*. Any or all of these, in addition to the sabretoothed cats could have been a contributing factor to the bone accumulation. If an *Australopithecus* did fall prey to a carnivore, then it would have been consumed on the surface and some of its bones could have entered the cave either through slope wash or by being dropped by cats feeding in overhanging trees. However, to judge from the paucity of tooth marks on the Sterkfontein hominid remains (Pickering et al. 2004a), this was probably not the main reason for their accumulation. Another way in which animal and hominid remains entered the caves is by natural death trap, i.e., by falling into one of the vertical shafts. The Member 2 deposit in the Silberberg Grotto is a particularly good example of this, where articulated skeletal parts of carnivores and monkeys have been recovered (Pickering et al. 2004b), in addition to the complete *Australopithecus* skeleton (Fig. 7.17). A similar death trap area was excavated by this author in Member 4 in the 1990s consisting of several partial skeletons and skulls of monkeys. It is indeed possible that natural death traps contributed to much of the *Australopithecus* accumulation in Member 4 but that subsequent disturbance of the talus through roof fall and partial collapse into lower chambers and movement of the talus slope resulted in the breaking up and scattering of once-complete skeletons (Clarke 2007).



**Fig. 7.17** Sketch by R.J. Clarke of StW 573 *Australopithecus* body in Member 2 talus slope, based on position of fossilized skeletal elements in the breccia



**Fig. 7.18** Internal aspect of right posterior braincase of StW 53, as exposed by decalcification in the breccia. Arrow points to sharp-edge chert block in the area of the zygomatic arch. Note many chert blocks surround the cranium

Raymond Dart's (1949a, b, 1957) concept of *Australopithecus* as a bone-tool using cannibalistic killer has in recent years been discounted because it has been shown that the so-called osteodontokeratic bone tool culture of Makapansgat had nothing to do with hominids but resulted from hyena and porcupine activity (Hughes 1954, 1961; Brain 1981). Similarly, the damaged monkey skulls from Taung which Dart originally attributed to *Australopithecus* activity have been shown to have been damaged by eagle beaks and talons (Berger and Clarke 1995). No stone tools have been found in association with *Australopithecus* at Sterkfontein (Kuman and Clarke 2000), even though *Australopithecus* had the manual ability to make them and in East Africa stone tools occur as long ago as 2.6 Ma, which was the time when *Australopithecus* was living in southern Africa.

This issue is particularly relevant to the case of StW 53, an *Australopithecus* cranium originally classed as early *Homo* (Hughes and Tobias 1977) but which I have demonstrated (Clarke 2008) to be a male *A. africanus*. This hominid comes from upper Member 4 and is said to bear cut marks (Pickering et al. 2000). Those authors have presented a case for considering them as manmade cut marks. In the context of the Sterkfontein breccias, different sized blocks of stone, including sharp quartz and chert can be forced against bone surfaces either during talus formation or during collapse episodes. A Member 4 *A. prometheus* mandible, StW 498, also has cut marks similar to those of StW 53. Thus one could question whether cut marks made by a handheld flake would differ from cut marks made by a natural stone forced against the bone in a debris slope.



In fact, the cut marks on StW 53 were, I believe, produced naturally by a small chert block in the area of the zygomatic arch and which moved against the bone under pressure in the talus slope. A block was there when the cranium was discovered and can be seen in a cast made at the time (Fig. 7.18). Although there is no proof of stone tools made by *Australopithecus*, there still remains an intriguing question of whether any of the *Australopithecus* remains could have resulted from predation by hominids. We know that in parts of Africa humans have had the habit of killing and eating chimpanzees (Himmelheber and Himmelheber 1958), and thus it would not be surprising if early *Homo* killed and ate *Australopithecus*. So perhaps we need to look again at Dart's early hypothesis, not to resurrect the osteodontokeratic, but to consider whether there could have been, on occasion, the possible involvement of hominids in the accumulation of other hominid remains.

## Conclusion

The picture we have of *Australopithecus* at Sterkfontein is that between 3.5 and 2.14 Ma, in what was generally a forest-fringe environment, there were at least two species represented. The earliest representative of one species, *A. prometheus* from Member 2, dates to probably about 3 Ma. Then in Member 4, dating between 2.5 and 2.14 Ma, *A. prometheus* and *A. africanus* are represented.

It is apparent from the anatomy of *Australopithecus* from Sterkfontein that it shared with modern humans the following attributes: (1) a similar though larger dentition with relatively small canines compared to those of the apes; (2) upright posture with a similar pelvis to that of humans and a foot with some human-like modifications; (3) a basically unspecialized hand with short palm and fingers but with a relatively long thumb which is specialized for opposability. All of these features uniting *Australopithecus* and *Paranthropus* with humans differ from those of the apes. As Hooton (1931: 132) stated: "The possession of a human foot makes an animal a man." The apes do not have a human foot, do not have a human hand, and do not have human teeth, and therefore it is highly misleading and confusing to classify them with the human-like forms as Hominidae. Hence there seems no justification for the current trend in paleoanthropology to group the apes together with humans and australopithecines in the family Hominidae, and I prefer to retain that family name only for the human-like primates.

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