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STONE AGE INSTITUTE PUBLICATION SERIES
*NUMBER 2*
*Series Editors Kathy Schick and Nicholas Toth*

# BREATHING LIFE INTO FOSSILS:

## Taphonomic Studies in Honor of C.K. (Bob) Brain

*Editors*

**Travis Rayne Pickering**
University of Wisconsin, Madison

**Kathy Schick**
Indiana University

**Nicholas Toth**
Indiana University

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*COVER CAPTIONS AND CREDITS.*

*Front cover, clockwise from top left.*

*Top left:*
*Artist's reconstruction of the depositional context of Swartkrans Cave, South Africa, with a leopard consuming a hominid carcass in a tree outside the cave: bones would subsequently wash into the cave and be incorporated in the breccia deposits. © 1985 Jay H. Matternes.*

*Top right: The Swartkrans cave deposits in South Africa, where excavations have yielded many hominids and other animal fossils. ©1985 David L. Brill.*

*Bottom right: Reconstruction of a hominid being carried by a leopard. © 1985 Jay H. Matternes.*

*Bottom left: Photograph of a leopard mandible and the skull cap of a hominid from Swartkrans, with the leopard's canines juxtaposed with puncture marks likely produced by a leopard carrying its hominid prey. © 1985 David L. Brill.*

*Center: Photo of Bob Brain holding a cast of a spotted hyena skull signed by all of the taphonomy conference participants. © 2004 Kathy Schick, Stone Age Institute.*

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# CHAPTER 1

# FIFTY YEARS OF FUN WITH FOSSILS: SOME CAVE TAPHONOMY-RELATED IDEAS AND CONCEPTS THAT EMERGED BETWEEN 1953 AND 2003

**C.K. BRAIN**

## ABSTRACT

During the last 50 years, African cave taphonomy has been established as a discipline in its own right, capable of informing us about the lives and deaths of animals whose remains are preserved in the caves concerned. It all started with Raymond Dart who, shortly after his interpretation and description of *Australopithecus africanus* in 1925, began to speculate about what the faunal remains, associated with the child skull, could tell us about the circumstances in which our early ancestors lived and died. Twenty years later, when Dart became interested in fossils from the Makapansgat Limeworks cave in the northern Transvaal, he made a pioneering study of over 7,000 fossil bone pieces that had been laboriously chipped from the rock-hard breccia matrix. He concluded that the vast fossil bone accumulation in this cave had been collected by *Australopithecus* for use as tools and weapons. In his view these hominids were undergoing a "predatory transition from ape to man" and were already mighty hunters, capable of killing the most powerful animals of their time and making use of an "osteodontokeratic culture." He put forward these ideas in a series of 39 publications, making use of dramatic and provocative prose that was intended to stimulate and provoke others to take the issues further. In my case, his provocation and encouragement was so great that I spent 40 years examining southern African caves and their associated fossil assemblages, in particular the Swartkrans one, as well as documenting contemporary taphonomic processes. In the paper that follows, some of the facts, concepts and ideas that emerged from this work are discussed. They are:

1. Understanding skeletal part disproportions in bovid bone assemblages.
2. The complication of bone pseudo-tools.
3. "Head-hunters" and "professional decapitators"?
4. "The myth of the bone-accumulating hyena"?
5. The comparative vulnerability of primate and bovid skeletons to carnivore damage.
6. Stone tools in the South African early hominid bone accumulations.
7. The finding and interpretation of bone tools.
8. The importance of cave-form to taphonomic reconstructions.
9. The effects of progressive Cainozoic cooling on African habitats and fauna.
10. Evidence for the management of fire at Swartkrans.
11. Evidence from Swartkrans for predation on early hominids.
12. The significance of predation to the evolution of intelligence in hominids and much older ancestral animals.
13. The pleasure of seeing taphonomic themes being carried forward from their early beginnings.

## THE EARLY DAYS OF TAPHONOMY IN AFRICA

The emerging discipline of vertebrate taphonomy, with particular reference to Africa, received a major boost in July 1976 when the Wenner Gren Foundation of New York, under the enthusiastic research direction of Lita Osmundsen, sponsored a symposium entitled *Taphonomy and Vertebrate Paleoecology, with special reference to the Late Cenozoic of Sub-Saharan Africa*.

*Figure 1. In 1976, Lita Osmundsen was Director of Research at the Wenner Gren Foundation in New York and her enthusiasm was of critical importance in developing the new discipline of taphonomy.*

This was held at the Foundation's Conference Centre, the castle of Burg Wartenstein, in the Austrian Alps and was attended by 17 delegates from a wide variety of disciplines. The meeting was organised by Anna K. Behrensmeyer, Andrew P. Hill, Alan Walker and myself, while the proceedings appeared thereafter in book form, *Fossils in the Making–Vertebrate Taphonomy and Paleoecology*, edited by Behrensmeyer and Hill (1980). This volume served to place vertebrate taphonomy on a secure footing, that was reinforced by other highly significant books that appeared thereafter, such as Pat Shipmans's *Life History of a Fossil. An Introduction to Taphonomy and Paleoecology* (1981), Lewis Binford's *Bones: Ancient Men and Modern Myths* (1981) and Kathy Schick and Nick Toth's *Making silent stones speak: Human evolution and the dawn of technology* (1993).

## RAYMOND DART - THE PROVOCATIVE PIONEER OF AFRICAN CAVE TAPHONOMY

The sub-discipline of *African Cave Taphonomy* had its roots a long time ago, although it was initially not designated as such. It started with Raymond Dart who described the child skull from Taung (Dart, 1925a) as *Australopithecus africanus*, the southern ape of Africa, claiming that it showed features intermediate between those of apes and humans. A few years later (Dart, 1929) started to speculate about the significance of all the other fossil bones found in association with the child skull. He wrote:

> "Examination of the bone deposit at Taungs shows that it contains the remains of thousands of bone fragments. It was a cavern lair or kitchen-midden heap of a carnivorous beast. It was not a water-borne deposit and the Taungs remains could not have been washed into the cavern from the surface. The bones are chiefly those of small animals like baboons, bok, tortoises, rodents, rats and birds. Egg shells and crab shells have also been found. This fauna is one that is not characteristic of the lair of a leopard, hyaena or other large carnivore, but is comparable with the cave deposits formed by primitive man. The deposit was, therefore, formed by primitive man or by Australopithecus, an advanced ape with human carnivorous habits. As no human remains have been found there, as no Australopithecus remains have been found elsewhere in known Pleistocend deposits, I am of the opinion that the deposit was formed by the Taungs sub-man himself."

*Figure 2. Delegates at the symposium on Taphonomy and Vertebrate Paleoecology, with Special Emphasis to the Late Cenozoic of Sub-Saharan Africa, held at the Wenner Gren Foundation's Conference Centre of Burg Wartenstein in the Austrian Alps during 1976. It can be said that Taphonomy crystallised as a significant new discipline at this meeting.*

This opinion was strengthened by Dart's observations, published a few years later (Dart, 1934) concerning the damage that baboon skulls from Taung had suffered, in particular the holes and fractures he observed in their brain-cases. He concluded that these had been caused by blows from clubs and stones wielded by the ape-men. But it was only when Dart became preoccupied with the vast fossil deposits at the Makapansgat Limeworks that his ideas on the hunting ability of the ape-men were really formulated. His attention was drawn to the fossil potential of the Makapansgat Limeworks Cave by a local school teacher, Wilfred Eitzman, during the early 1920s. Among the numerous fossils that Eitzman sent to Dart at that time were several blackened bones, enclosed in the calcified cave earth, that Dart suspected had been burnt. He arranged for chemical analyses of the bones to be done and these showed the presence of free carbon, suggesting that the bones had indeed been in a fire. On the strength of this evidence, together with that of the broken bones from a wide variety of animals, Dart (1925b) concluded that Makapansgat had been "a site of early human occupation." Subsequently, following a University of the Witwatersrand student expedition, led by Phillip Tobias in 1945, new fossils were found at the Limeworks that encouraged Dart to visit there the following year. Dart immediately recognised the importance of the cave as a potential early hominid locality and employed James Kitching, Alun Hughes and their helpers to sort the lime-miners' dumps. This resulted in the finding of the first Makapansgat hominid fossils (Dart, 1948) which Dart named *Australopithecus prometheus*, assuming that they had been responsible for the burning of blackened bones found in the deposit. Subsequent research on this topic by Kenneth Oakley (1956) failed to confirm the presence of free carbon in the bones and the conclusion was reached that the blackening was caused by the presence of manganese dioxide. It has been suggested that the carbon initially detected in the first samples may have come from the blasting activities of the lime-miners.

The long-term operation of sorting miners' dumps at Makapansgat also produced very numerous blocks of highly fossiliferous grey breccia that had been blasted from the lower levels of the cave. Dart arranged for many of these blocks to be transported to the University in Johannesburg, where the individual fossil bones were manually chipped from their matrix.

At the Third Pan-African Congress on Prehistory, held at Livingstone in 1955, Dart (1957a) presented the results of his taphonomic investigation of the Makapansgat grey breccia (now termed Member 3) fossil assemblage. His sample consisted of 7,159 pieces of fossil bone of which, 4,560 were found to be sufficiently complete to allow allocation to skeletal part and taxon, while the remaining specimens consisted of bone flakes and fragments. Dart found that 91.7% of the identifiable fossils were of bovid origin, 4.0% came from non-bovid ungulates and the rest were from non-ungulates, such as primates and carnivores. Among the 293 individual antelope represented, 39 were large such as kudu. 126 were medium-sized, 100 were from gazelle-sized antelope and 28 were from small species such as duiker. Non-bovid ungulates were represented by four equids, six chalicotheres, five rhinos, 20 pigs, one hippo and six giraffids. Among the primates, there were remains of 45 baboons and five australopithecines, together with a variety of other animals that included 17 hyaenas, a sabre-toothed cat, porcupines, as well as other small mammals and reptiles, including terrapins. Non-ungulate mammals were typically represented by skull-parts only, but the antelope had contributed a wide variety of skeletal parts which, however, showed striking and unexpected disproportionate representations. Most common of all parts were skull pieces, particularly mandibles; neck vertebrae, especially the atlas and axis, were well represented, but thoracic vertebrae were scarce and those from the tail were absent. Among the limb bones, disproportions were most striking of all: in the case of the humerus, for instance, the distal ends were ten times more common than were the proximal ends.

Dart also made a detailed study of the damage that the fossil bones had suffered. He described how, in his opinion, broken antelope cannon bones had been pounded with a pointed object, perhaps a bovid calcaneus, converting them into scoop-like tools. As would be the case in a contemporary taphonomic investigation, Dart

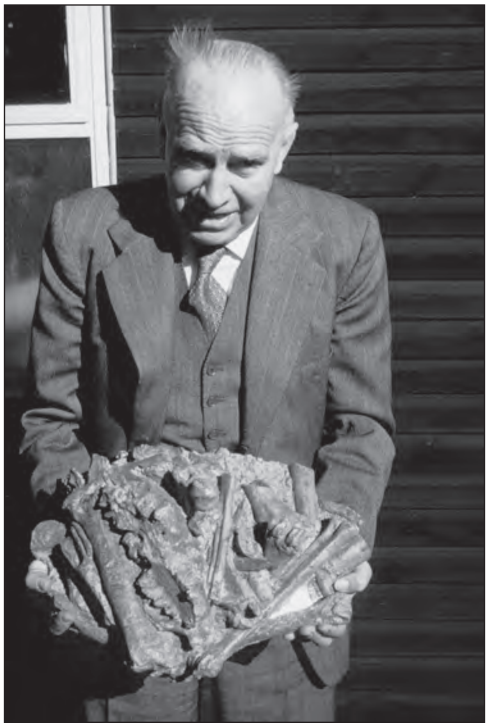

*Figure 3. Raymond Dart in 1965 with a block of richly fossiliferous grey breccia from the Makapansgat Limeworks Cave. It was on the basis of fossils from this site that he developed his concept of the Osteodontokeratic Culture of* Australopithecus.

speculated on the possible agents of accumulation for the collection of bones in the cave and the behaviour of the animals involved. Since the early conclusions of William Buckland (1822) about the role of hyaenas as bone collectors in the Kirkdale Cave of Yorkshire, it had been customary to implicate these scavengers in the accumulation of fossil assemblages elsewhere. Dart (1956a), however, dismissed this concept in his paper on "the myth of the bone-accumulating hyaena." He concluded instead that the entire accumulation of bones in the grey breccia, running to many hundreds of thousands, had been taken to the cave by hominids, who ate the meat and then used the bones as a variety of tools and weapons. The implication was that australopithecines were powerful hunters as Dart (1956b) made clear:

> "The fossil animals slain by the man-apes at Makapansgat were so big that in 1925 I was misled into believing that only human beings of advanced intelligence could be responsible for such manlike hunting work as the bones revealed ... These Makapansgat protomen, like Nimrod long after them, were mighty hunters."

In his 1957 monograph, Dart elaborated his theory of the "osteodontokeratic" (bone, tooth and horn) culture of *Australopithecus prometheus*. He explained the striking disproportions in skeletal parts apparent in the Makapansgat assemblage in terms of deliberate selection of certain bones in view of their potential as tools and weapons. Parts of antelope skeletons not suitable for these purposes were simply left at the kill sites, hence their absence from the cave. Uses were suggested for virtually all the bones in the fossil assemblage: the tooth-rows of mandibles made good saws, for instance, while the distal ends of humeri served as convenient clubs. Early in the investigation, Dart (1949) had suggested that humeral clubs had been responsible for the depressed fractures he observed on the calvaria of baboons and hominids from the caves of Taung, Sterkfontein and Makapansgat. In the case of fossil animals, such as baboons and carnivores, where only skulls are found in the Limeworks assemblage, Dart suggested that the exclusive presence of these, too, represented deliberate selection, concluding that the hominids had been "head-hunters" and "professional decapitators."

In the course of the 20-year-long duration of his Makapansgat project, Dart published 39 papers, the text of which often contained powerful provocative prose. For instance, in his paper "The predatory transition from ape to man" (1953), he wrote:

> "On this thesis, man's predecessors differed from living apes in being confirmed killers: carnivorous creatures that seized living quarries by violence, battered them to death, tore apart their broken bodies, dismembered them limb from limb, slaking their ravenous thirst with the hot blood of victims and greedily devouring livid writhing flesh."

As this style of writing struck me as unusual in a serious scientific context, I asked Dart what he hoped to achieve by using it. He replied without a moment's hesitation. "That will get 'em talking!" he said, and he certainly succeeded in his objective. His highly provocative ideas and style of presentation sparked heated discussion in scientific circles in many parts of the world, while the American dramatist, Robert Ardrey, was so impressed with Dart's theme of "the blood-bespattered archives of humanity" that he wrote a series of five widely-read books on the subject, starting with *African Genesis* in 1961.

My own imagination was so captivated by Dart's ideas on the behaviour of our early ancestors that I spent 40 years developing the new discipline of Cave Taphonomy, in the hope that fossils in African caves could be interpreted with ever increasing confidence. This included a long-term investigation of the Swartkrans cave in the Sterkfontein valley where Robert Broom and John Robinson had worked between 1948 and 1951, and had recovered numerous fossils of robust australopithecines and demonstrated, for the first time, the co-existence of these hominids with early humans. This co-existence has subsequently been confirmed in many parts of Africa.

But as the principles of cave taphonomy became established, alternative interpretations emerged for almost all the observations that Dart had made on his Makapansgat fossil assemblage. His concepts of the "mighty hunters," the "predatory transition from ape to man" and the "osteodontokeratic culture" all gave way to other ideas which, although less dramatic, are probably more realistic. As each of these ideas surfaced, I made a particular point of telling Dart about them. For instance, when I found that a collection of goat bones from the Namib Desert showed skeletal disproportions very similar to those that he had encountered at Makapansgat (see below), and that such disproportions had a very simple explanation, Laura Brain and I took the collection over to Dart's laboratory in Johannesburg. There I explained that it was no longer necessary to suggest that hominids had deliberately selected certain skeletal parts for tools and weapons and had left others at the kill sites, but that such disproportions were to be expected in any assemblages worked over by carnivores or scavengers. When Dart realised this, he was silent for a few minutes. Then his eyes lit up and he said "This is wonderful—at last we are getting closer to the truth!" A few days later he nominated me for an award! But despite the fact that Dart was always willing to accommodate alternative viewpoints, I doubt if he ever really gave up his conviction that our pre-human ancestors had been bloodthirsty killers. For instance, when we found bone tools with the early hominid remains at Swartkrans, we showed them to Dart before describing them. He was over 90 years old at the time and his eyesight was failing, but he felt the smooth, tapering points with his fingers. Then he said: "Brain, I always told you that *Australopithecus* made bone tools, but you never believed me! What were these used for?" I

*Figure 4. In 1981, Raymond Dart and his wife Marjorie visited the Transvaal Museum to examine bone tools from Swartkrans. They were delighted to see evidence of bones being used as tools by early hominids.*

replied that I thought that they had been used for digging in the ground. Dart slumped back in his chair with a look of total disbelief on his face. "That" he said "is the most unromantic explanation I have heard of in my life!" He than grabbed the longest of the bone points and stuck it into my ribs saying, "Brain, I could run you through with this!"

It was Dart's generosity of spirit that added greatly to the pleasure I experienced from my varied taphonomic studies in the early hominid field that had sprung from Dart's stimulation and provocation. And like Dart, I too made various assumptions in the course of my research that proved to be false. For instance, when I was doing my Ph.D. project 50 years ago, on the cave deposits from which South African hominid fossils came, I spent a lot of time trying to reconstruct past climatic conditions at the times that the cave entrances were admitting surface-derived sediments. I found that the older sediments, that had been laid down at Makapansgat and Sterkfontein, contained significant proportions of aeolean sand and therefore suggested that the climate and environment at that time was more desertic than it was when the later deposits at Kromdraai and Swartkrans accumulated. Some years later, Karl Butzer (1976) pointed out that my assumption that surface-derived sediment, entering an underground cave, was a valid indicator of climatic conditions at that particular time, was false. He said that, during the Pliocene, much of the southern African interior surface consisted of the African Peneplain, on which thick deposits of Kalahari desert sand had been laid down in earlier times. This meant that the presence of aolean sand grains in the cave deposits could not be used to infer desert conditions at the time of their entry to the caves. They could be reflections of much more ancient desiccation. It was only when continental uplift disrupted the old African surface and resulted in the downcutting of streams and rivers, that the residual aeolean sediment was eroded away. By the time of Swartkrans Member 1, for instance, the surface-derived sediment entering the cave appears to have been in equilibrium with conditions at the time. Thus, my deduction that sediments at Makapansgat and Sterkfontein indicated arid conditions, at the time of their deposition, was completely at variance with subsequent evidence from plant and animal fossils that reflected lush riverine vegetation.

What follows now is a brief overview of some facts, ideas and concepts that emerged during the 50 years of personal taphonomic involvement.

## 1. Understanding skeletal disproportions in bovid bone assemblages

Today it is taken for granted that any ancient bone assemblage is likely to contain certain parts of the skeletons of the animals that contributed to it, but not others. But, at the time that Dart did his analysis of the fossil assemblage from the Makapansgat grey breccia this likelihood had not been appreciated. Consequently, when Dart found that some skeletal parts were present to the partial or complete exclusion of others, he came up with his imaginative explanation, implicating the hominids in deliberating selecting and preserving some useful bone pieces, while ignoring others.

Unexpected insights to this question came my way, unexpectedly, in the Namib Desert. At Gobabeb, on the banks of the normally dry Kuiseb River bed, 96 km inland from Walvis Bay in southwestern Africa, the Transvaal Museum built a Desert Ecological Research Station in 1963. Two years later I visited this spot to set up a bone-weathering experiment in an arid environment and noticed that there was an abundance of goat bones, lying on the desert sand in the nearby villages occupied by Nama Hottentot people. Out of sheer curiosity I picked up a sample of these bones and laid them out at the research station as an exercise in osteology. It struck me at once that some skeletal parts were well represented, while others were rare or absent. Distal humeri, for instance, that had been so important in Dart's osteodontokeratic cultural concept, were common but, search as I might, I could not find a single proximal end of a humerus. The explanation was not difficult to find: the bones represented the resistant residue of goat skeletons, able to survive the treatment they had received. But what was this treatment? Inquiries and observations during the following week showed that goats were virtually the only source of meat for these rural people. When a goat was slaughtered, its body was treated in a traditional manner and those parts that the people found inedible were tossed to the dogs. When they, in turn, were finished, the parts unchewable by person or dog were left on the desert surface, where recovery was easy for me, as the sand was devoid of vegetation in the villages. Apart from occasional crows, no other carnivores or scavengers were involved.

After the initial reconnaissance in 1965 (Brain, 1967a), I returned the following year to collect all the available bones and to investigate the circumstances in greater detail. On this occasion, I was accompanied by Trefor Jenkins who undertook a thorough genetic and demographic study of the Nama population there. We found that the total population of the lower Kuiseb valley was 133 people who lived in eight separate villages. Between them they had 40 dogs and 1754 goats, while the spacing of the villages along the riverband was determined by the number of goats kept at each, since grazing could only take place in the riverbed and the extent of a village's pasturage was measured in a linear fashion (Brain and Jenkins, 1967).

*Figure 5. A Nama Hottentot village in the Namib Desert of Namibia, on the bank of the Kuisib River bed, inland from Walvis Bay. The discarded goat bones from here, shown in the foreground, provided valuable information on the survival and disappearance of skeletal parts in 1965.*

The treatment of goat carcasses, slaughtered by these Nama people has been described elsewhere (Brain, 1969, 1981). All meat eaten by the people was cooked before it was eaten, either by boiling in large metal pots or direct roasting over the fire. The horns were broken at their bases from the skulls by sharp blows from an axe and were discarded. The dogs chewed the horn-core bases before rejecting them. The complete head was then boiled for several hours in a pot, standing over a fire. All edible meat was picked from it and eaten, after which the braincase was smashed in the occipital region with a hammerstone for the removal of the brain. The skull and mandibles were passed to the dogs. As eating progressed, all marrow-containing bones were broken by the people, by being held on a rock anvil and hammered with another stone. Neither the anvil nor the hammerstone were artefacts in the usual sense of the word, as they were simply suitable pieces of rock that happened to be lying around. These Hottentots habitually ate while squatting on the ground and, apart from their anvils and hammerstones, their only utensils were pocket knives. Their feeding behaviour seems to be a mixture of long-standing tradition and European influence.

Once discarded by the people, the goat bones were gnawed for many days by the dogs, all of which were about the size of jackals. When lying on the sandy surface, the bones became bleached and de-greased in about three months. The collection made in the villages consisted of 2,373 pieces which included 385 horns and horn-core pieces from an estimated number of 190 individuals, estimated on these elements. However, it was clear that horns survived the weathering effects of the arid desert climate much better than did other bony pieces and in long-deserted villages, these were the only parts to be found. Therefore, in the final estimation of the number of animals involved, horns were excluded in favour of the next most abundant element, which happened to be mandible pieces, as in Dart's Makapansgat sample. I found that the 188 fragments could be divided into 53 left and 64 right half-mandibles, indicating a minimum of 64 individual goats that contributed to the sample. On known tooth-eruption and wear criteria, it transpired that there was one goat in the sample under 6 months of age, 23 between 9 and 12 months, 7 between 15 and 30 months, and 35 more than 30 months in age. The goats had therefore been slaughtered largely when either just under a year in age or when fully mature. The village people confirmed that this was their usual practice, the

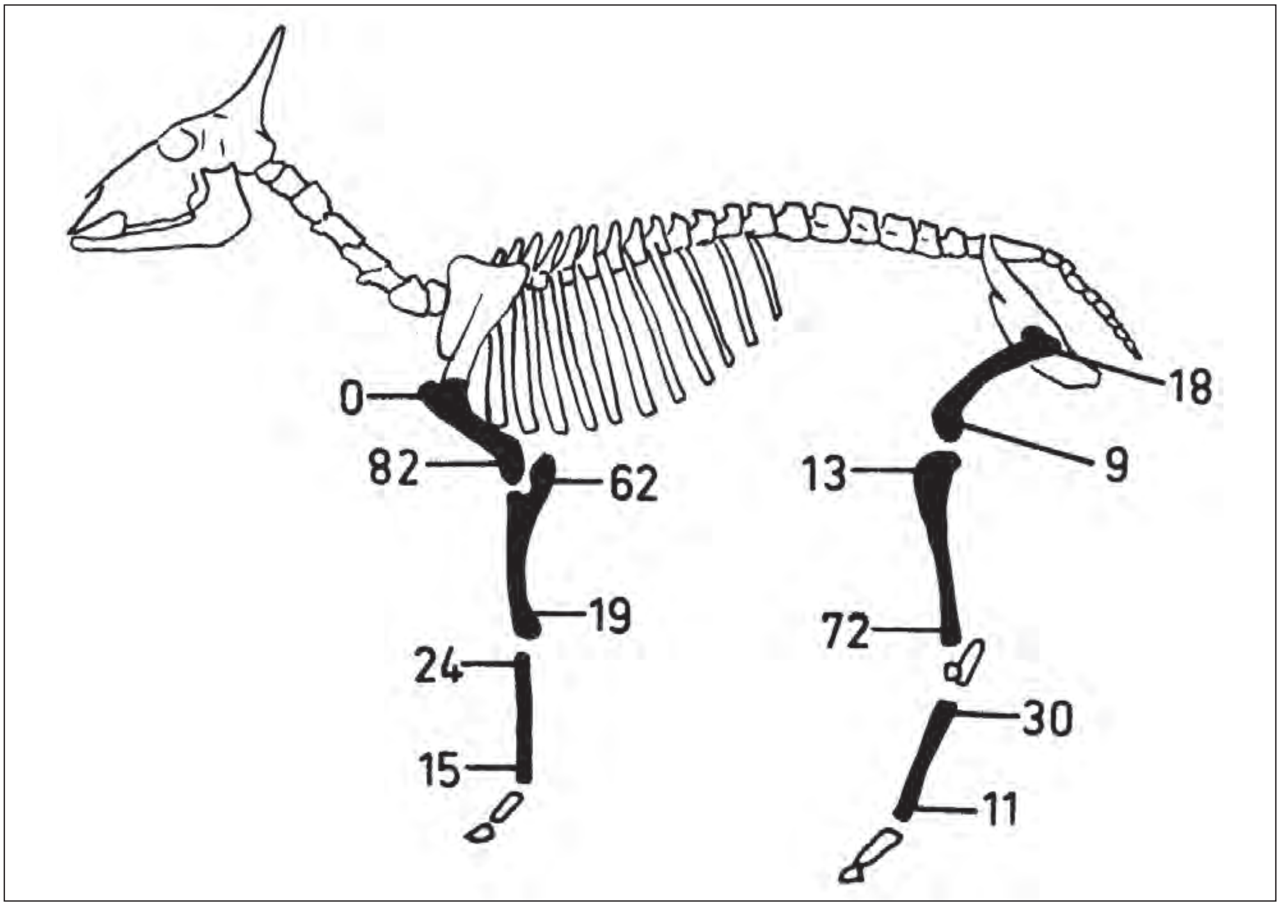

*Figure 6. Diagram of a goat skeleton published in 1967. The numbers refer to ends of long bones present in the sample collected in the Namib Desert.*

yearlings usually being the surplus males.

After mandible pieces, the most commonly preserved skeletal element was the distal humerus, followed by the distal tibia, proximal radius and ulna and so on. Parts absent altogether were caudal vertebrae and proximal humeri. So it became clear that the parts of the goat skeleton that survive best are the unchewable ones. In the course of this study it occurred to me that, in a sample derived essentially from immature animals, the survival of limb-bone ends could be related to the time at which the epiphysis of that bone fused to its shaft. Consider the humerus for instance, in which survival of the proximal end is nil but that of the distal end amounts to 64%. The proximal epiphysis is likely to fuse to the shaft at about 36 months, whereas the distal epiphysis is fully fused by 12 months. An unfused epiphysis is linked to its shaft by a cartilaginous interface that is easily broken, making the two pieces vulnerable to damage. This means that, when a year-old goat is eaten, the distal end of the humerus will be fully ossified and unchewable, while the proximal end remains chewable. But, in addition to fusion times, structural considerations are very important. The proximal end of the humerus is wide, thin-walled and filled with spongy bone; the distal end is comparatively narrow and compact. Such qualities may be expressed in terms of specific gravity of each end of the bone. When I made the necessary measurements, I found that the proximal end of a goat humerus had a specific gravity of about 0.6, while that of the distal end was approximately 1.0. There turned out to be a clear and direct relationship between the specific gravity of the end of a long bone and its percentage survival. In fact, percentage survival of a part is related directly to the specific gravity of that part, but inversely to the fusion time expressed in months. The conclusion to be drawn is simply that survival is not haphazard, but is related to the inherent qualities of the parts (Brain, 1981, p. 21).

In contrast to the goat-bone sample, Dart's Makapansgat sample was made up of remains from 293 antelopes, ranging in size from large species (39 individuals), medium (126 individuals), small (100 individuals) and very small antelopes (28 individuals). Using the total number of 293 individuals, it was possible to calculate the percentage survival of various parts of the skeletons as was done for the Namib goat bones. When listed and plotted in descending order of survival, the Makapansgat bones showed a remarkable similarity to those from the goats, despite the fact that the fossil bones came from such a wide species and size range and that they could have been subjected to a variety of destructive processes. So, what the goat-bone study did show, is that skeletal-part disproportions are extremely likely to occur in an assemblage and that they can inform us on the destructive influences that the contributing skeletons had suffered.

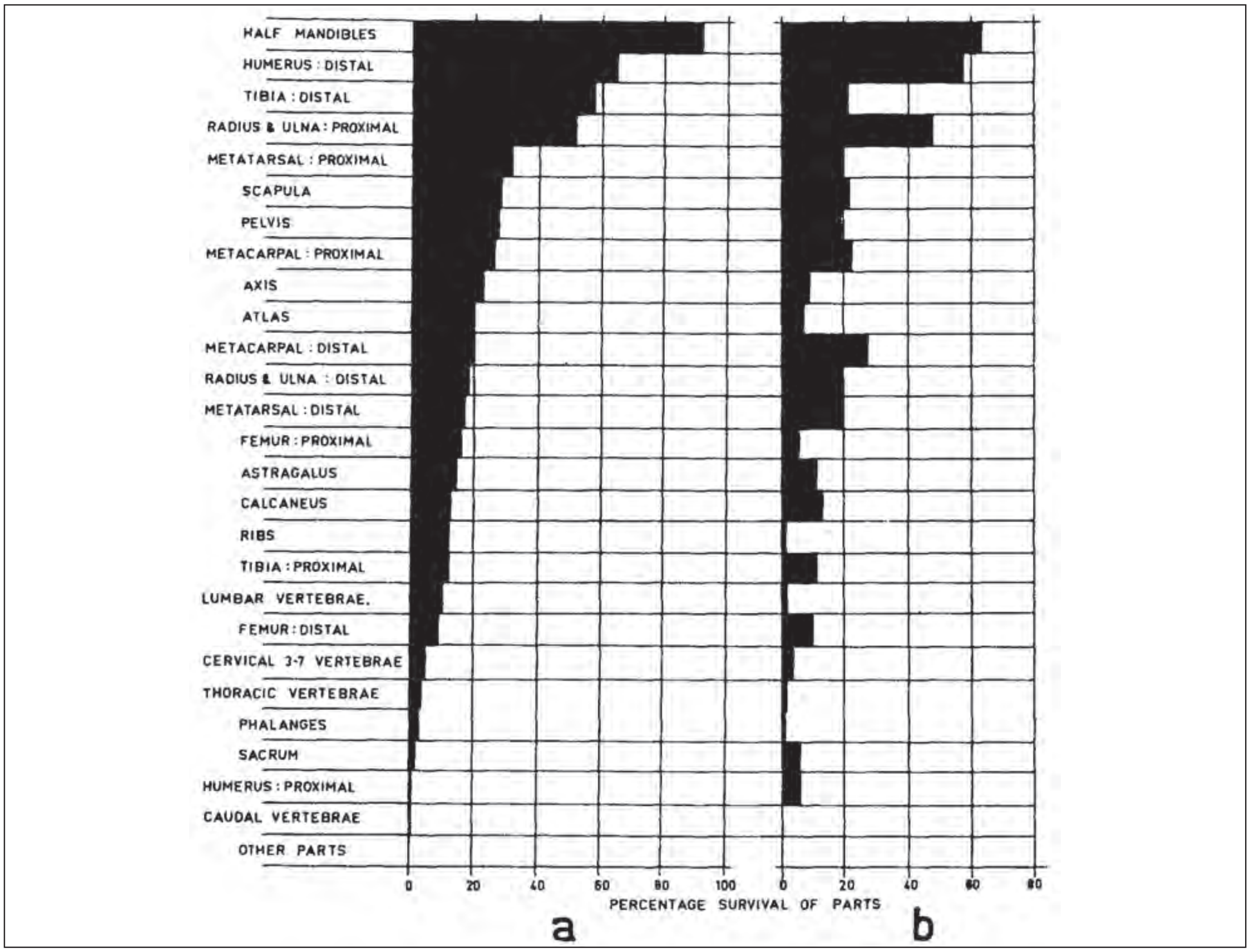

*Figure 7. A diagram published in 1969. (a) Histogram showing percentage survival of parts of goat skeletons from the Kuisib River villages. Calculations are based on a minimum of 64 individuals. (b) Percentage survival of parts of fossil bovid skeletons from Makapansgat, arranged in the same order as for (a).*

## 2. The complication of bone "pseudo-tools"

Another unexpected insight into the interpretation of Dart's Makapansgat fossil assemblage came with the finding of "pseudo-tools," which showed overall wear and polish. Similar specimens from the Makapansgat assemblage were thought by Dart to have acquired their surface modification by hominid handling and use. In connection with the Namib evidence, I wrote (Brain, 1981, p.15):

> "While collecting bone fragments from the vicinity of the Hottentot villages, I was surprised to find many pieces that appeared to be bone tools. They tapered to points and showed wear and polish that had surely resulted from human use. In reply to my queries, the Hottentots denied that they made use of bone tools at all, and I had to find a different explanation for the remarkably suggestive appearance of these 'pseudotools.' Further observation showed that the worn and polished bones were specially abundant in areas regularly used by men and animals, such as around the Ossewater water hole, where 460 goats converge daily to drink, in the immediate vicinity of goat kraals, and along paths used by the Hottentots and their goats in the riverbed. If protected among rocks, for instance, the bones would develop their characteristic chalky surfaces but would lack signs of wear and polish. The mechanism of pseudotool production was therefore clearly related to the disturbance of the sand in which the bones lay by the feet of animals and men (Brain, 1967c). The process may therefore be summarized as follows: bones come to rest on the sand, and their surfaces weather to a chalky consistency. Regular disturbance of the sand by the feet of animals abrades the chalky surface as it forms, leading to bones that are both worn and polished. If the whole piece of bone is lying in the disturbed sand zone, it is likely to acquire wear and polish on all surfaces, but if some part of it is buried deeper this will remain protected, and only a part of its surface will be converted into a pseudotool. Selective abrasion of this kind has been observed on a number of metapodial and other limb-bone pieces that have been buried with their long axes vertical, or at least inclined. This meant that parts of such bones were

> buried too deep to be affected by superficial sand movements, so that wear and polish occurred on one end only. Pseudotool production is not restricted to arid environments like that of the Kuiseb River, and the mechanism should be borne in mind when any interpretation of a bone assemblage is undertaken."

With respect to the Makapansgat situation I wrote (Brain, 1981, p.264):

> "Over the years, a picture has developed in my mind of how the Limeworks cave may have looked when the bones were accumulating there. I visualize an extensive amphitheatre that had resulted from a collapse of part of the cavern system's roof, while from this amphitheater openings to the cavern system we know today led downward. I visualize, too, a permanent water hole in the amphitheatre, perhaps at the point where the Makapansgat stream descended into the subterranean chambers. Finally, I visualize large numbers of animals regularly visiting the water hole and some of them being killed there by carnivores that perhaps included hominids. Their bones would lie about in abundance within the catchment area of the cavern's mouth. Some would be modified by australopithecines, all would be worked over by scavengers, and large numbers would be transported to the inner recesses of the cavern by breeding hyaenas and resident porcupines. While lying in the much disturbed sand around the fringes of the water hole, some of the bones would acquire the wear and polish so characteristic of certain specimens in the gray breccia assemblage. Like all other fossil assemblages in caves, the Makapansgat bones could be taphonomically interpreted with assurance only if they were excavated with due regard to subtle detail. I have no doubt that if an in situ deposit of bone-rich gray breccia could be stripped of its overburden and if the individual fossils could then be chipped out as they lay in a carefully controlled grid system, it would be possible to assess with confidence the accumulation pattern that originally operated. Such a task would be difficult, but it would be highly rewarding in the interpretation of a situation that has excited the imagination of paleontologists for years."

Fortunately detailed work is progressing at the site on various fronts, such as that of Latham, Herries and Kuykendall (in press), and the results are anticipated with great interest.

## 3. "Head-hunters" and "professional decapitators?"

As mentioned earlier, Dart was intrigued to find in his Makapansgat fossil assemblage that the remains of non-ungulate animals such as hominids, other primates and carnivores were typically represented by little more than their skulls. He thought that this might have been the result of deliberate selection, for trophy purposes, on the part of hominid hunters.

Early in my taphonomic career I made a detailed study of several contemporary caves that had been used for many years by leopards (Brain, 1981, p. 85-93) as breeding and feeding lairs. These were on the farms Valencia and Portsmut in the Hakos Mountains of Namibia, about 160 km southwest of Windhoek where their owner, Atilla Port, was very enthusiastic about such projects. We found that the leopards frequently fed on *Procavia* hyraxes in these caves, invariably eating the entire body of each, with the exception of the heads, the anterior parts of which accumulated in the lairs. Similar observations were made on a captive leopard that we caught and confined in a cage on Valencia, until it managed to escape one night. Feeding experiments with captive cheetahs there confirmed that they, too, only leave the stomach and the head, when feeding on hyraxes.

But, considering the bone-crushing ability of hyaenas, it came as a complete surprise to find that brown hyaenas (*Parahyaena brunnea*) frequently leave the skulls of their smaller prey animals undamaged. When these hyaenas have cubs in a breeding lair, they tend to kill a variety of small animals, including other carnivores, which they take back to the lair for the young to feed on. The cubs typically leave the skulls of these prey animals and, it seems as if the adults have an inhibition against themselves eating any of the food they provide for their cubs. For instance, food remains collected from brown hyaena breeding lairs in the Kalahari Gemsbok National Park (Mills and Mills, 1977) contained the virtually undamaged skulls of 6 black-backed jackals, 11 bat-eared foxes, 4 caracal, 1 aardwolf and 1 ratel (Brain, 1981, p. 295). Observations in the Kruger National Park have shown that baboons are also killed by brown hyaenas for the feeding of young.

So, if the Makapansgat cave was originally a hyaena lair, as will be discussed shortly, there is no need to suggest, as Dart did, that skulls of non-bovid animals had been collected there by head-hunting hominids.

## 4. "The myth of the bone-accumulating hyena?"

Since Dart published his paper with this title in 1956, important observations have been made by numerous people in various parts of Africa on the bone-collecting behaviour patterns of Spotted, Brown and Striped hyaenas. There is now no question that all three species collect significant numbers of bones at their lairs which, might well be in caves. At Makapansgat, the hyaenas represented in the fossil assemblage are Striped Hyaenas, *Hyaena hyaena*, which do not occur at present in southern Africa, but are found further north on the continent and in the Middle East. Various studies have been made on the bones found in their feeding and breeding lairs, both in East Africa and Israel and there is now no

*Figure 8. The discovery of stone artefacts by Bob Brain at Sterkfontein in May 1956. Shown here in the West Pit, close to the main Type Site quarry, are (left-right) Ben Grobbelaar, Daniel Mosehle and Absalom Lobelo.*

question that this species can accumulate vast numbers of bones in the caves that they use. The current consensus opinion appears to be that, during Member 3 grey breccia times, the low-roofed parts of the cavern served as breeding and feeding lairs for Striped hyaenas, that collected the bones for adult and cub consumption. Additional input was made by porcupines and other carnivores, such as leopards.

Following his detailed taphonomic study of the fossil assemblages from Sterkfontein Member 5 West, Travis Pickering (1999, p. 159) wrote:

> "The weight of taphonomic evidence presented here–bone surface modifications, the presence of juvenile hyena remains, and to a lesser degree, bovid skeletal part ratios–indicates that hyenas probably played a significant role in the accumulation of Member 5 West faunal assemblage. Furthermore, consideration of species-specific behavioral adaptations implicates brown hyenas as the most likely primary collectors of bone at the site. Porcupines also contributed to the accumulated assemblage, in addition to possibly spotted hyenas. The serial use of single den sites by brown hyenas, spotted hyenas and porcupines is well documented in modern habitats (e.g., Mills and Mills, 1977). Considering the presumably much longer accumulation period of the Member 5 West assemblage, alternating occupation of the site would not be surprising."

*Figure 9. May 1956. One of the newly-discovered stone artefacts, made on a quartzite pebble, still embedded in the breccia of the Sterkfontein West Pit.*

## 5. The comparative vulnerability of primate and bovid skeletons to carnivore damage

When I analysed the composition of the available fossil assemblages from the various hominid-bearing cave deposits in the 1960s, it became apparent that antelope were represented by a far wider range and abundance of skeletal parts than were primates. In fact, postcranial remains of hominids, baboons and monkeys were rare in comparison with cranial ones, whereas bovid postcranial fossils were comparatively common. The reason for this was not immediately apparent, but some light was thrown on the question when I made a study on the feeding behaviour and food-remains of cheetahs. My reason for studying these topics was that I thought cheetahs might tell us something about the food remains of sabre toothed cats, the dentition of which was specialized for the cutting and slicing of meat, as is the case, albeit to a lesser extent, in cheetahs.

On the Valencia Ranch in Namibia, mentioned above, Attila Port caught several wild cheetahs for me and put them in a large enclosure, where they were fed mainly on karakul sheep and the occasional springbok. It was clear that the cheetahs could do little damage to the skeletons of these animals, apart from some chewing on the ventral ends of the ribs, vertebral processes and the blades of the scapulae. But, on one memorable day we were unable to find a springbok so Attila shot, instead, a large male baboon that had been taunting us from the top of a nearby cliff. The baboon was offered to the cheetahs with unexpected results, as is reflected in this extract from my field notes (Brain, 1981, p.24):

> "20 March 1968: The body of an adult male baboon weighing 29.5 kg was placed in the enclosure at 9:05 a.m. It was immediately taken by the two male cheetahs and carried by its arms to the shade of a tree. All three cheetahs started to feed on the ventral surface of the abdomen; the viscera were removed and part of the intestine eaten. The rib cage was quickly chewed away and the vertebral column simply crunched up and swallowed—quite unlike the antelope situation. As the vertebral column was destroyed, the pelvis and both hind limbs were removed by one cheetah and carried a short distance away. The sacrum was eaten so that the femurs, still articulated into the innominates, were separated. One cheetah left the baboon after 1hr. 10 min., the others remained 15 min. longer, then left, but all three returned intermittently throughout the day."

When the remains were removed and photographed the next day we found that the entire vertebral column, from atlas to first caudal, had disappeared, as had most of the ribs. The innominate bones showed damage round the edges, and both knee joints had been disarticulated and chewed. The disappearance of the vertebral column in this baboon carcass came as a complete surprise and suggested that a primate backbone was less resistant to carnivore chewing than its bovid counterpart. To test this suspicion, an adult sheep of almost exactly the same liveweight as the baboon was fed to the cheetahs when they showed equivalent signs of hunger. Once again the vertebral column was left intact, apart from the tail that had been eaten, while slight damage was done to the innominates and ends of the ribs.

Little new information on the reasons for the comparative durability of primate and bovid skeletons came to light in recent years until the research of Travis Pickering and Kristian Carlson was undertaken on "intrinsic qualities of primate bones as predictors of skeletal element representation in modern and fossil carnivore feeding assemblages" (Carlson and Pickering, 2003). This publication was preceded by one (Pickering and Carlson, 2002) in which the question of "bulk bone mineral density" (bulk BMD) was addressed in baboon and bovid skeletal elements on the assumption that such measurements would provide an indication of the durability of the parts involved. They concluded that the differences in bulk BMD between bovid and baboon skeletal parts were not always sufficient to explain the presence and absence of parts in the Swartkrans fossil assemblages, and that "factors other than bone density—such as bone size, length, shape, and/or the relative palatability of surrounding soft tissue on bones" would have to be implicated. This certainly seems to be the case. In the cheetah feeding experiments, for instance, several of the baboons had their hands and feet completely chewed away. This could never have happened in the case of a bovid, with its resistant hooves and lack of palatable meat in those parts.

## 6. Stone tools in the South African early hominid cave deposits

At the time that I started my Ph.D. project on *The Ape-Man-Bearing Cave Deposits* (Brain, 1958), stone artefacts were not known from any of these sites. So, in 1955 I was excited to find a number of dolomite pieces in the Makapansgat Limeworks deposit that, in my opinion, had been artificially chipped. These came from the stony breccia, now known as Member 4, overlying the grey breccia from which Dart's fossil assemblages came. I showed these to Dart and to the well-known archaeologist of that time, C. van Riet Lowe, who said that he had no doubt that they were artefacts. An illustrated report appeared in *Nature* (Brain, van Riet Lowe and Dart, 1955) entitled "Kafuan stone implements in the post-australopithecine breccia at Makapansgat." Subse-

*Figure 10. One of the Swartkrans bone tools, showing how the smooth wear is restricted to the tip.*

*Figure 11. One of many experiments in which bone pieces were used to dig edible plant food from the contemporary hillside at Swartkrans. Here Conrad Brain digs out a tuber of a* Hypoxis *lily, using a bone flake from a wildebeest humerus generated by hyena feeding, while Bob Brain looks on. Photograph by David Brill.*

quent to this, australopithecine fossils were found in this Member 4 breccia also (Dart, 1955), suggesting that the time interval between it and the underlying grey breccia (Member 3) was not very great. A problem was that all these presumed artefacts were made on dolomite pieces and critics argued that they would not be convinced of their authenticity as tools until some were found made of quartzite.

In May 1956, I was writing up my doctoral thesis and, in the Sterkfontein chapter, I had a heading “Cultural material from the deposit,” but found that I had nothing to report. Despite the fact that I had spent many weeks working through the Sterkfontein profiles that were available for study at that time, I decided to devote that particular day looking specifically for stone artefacts. To my considerable surprise, when I re-examined the breccia walls of the “West Pit” on the hilltop, a few metres from the west wall of the Type Site, where so many hominid fossils had been found, I was amazed to find a number of unquestionable *in-situ* artefacts, made of pieces of quartzite and diabase that must have been selected from the river gravels in the vicinity. There were also many artefacts in pieces of breccia on the miners’ dumps surrounding the West Pit. Several of these were illustrated in my thesis (Brain, 1958, p.72-73). This find prompted John Robinson to re-open excavations in the West Pit area, after Revil Mason and I had shown that the artefact-containing breccia was continuous with that in the west wall of the Type Site, beneath a soil overburden that contained Middle Stone Age artefacts. Robinson’s excavation proceeded for two years and produced 58 stone artefacts, one bone tool and several hominid teeth (Robinson and Mason, 1957; Robinson, 1959).

Further excavations in the West Pit area by Alun Hughes, Ron Clarke, and their team revealed stratigraphic complexity that had not previously been suspected, while Kathy Kuman showed that while the artefacts from the West Pit were Early Acheulean, there were also Oldowan artefacts to be found in the lower levels of the Member 5 infill (Clarke, 1994; Kuman, 1994a and b; Kuman and Clarke, 2000; Kuman, 2003).

In my early taphonomic interpretation of the Sterkfontein Member 5 assemblages (Brain, 1981, p. 217) I wrote: “The remarkable density of artefacts in the excavated part of Member 5 strongly suggests that the cave was intensively occupied during this accumulation phase. It would therefore be remarkable if the bone pieces associated with the artefacts did not represent hominid food remains.” The later work of Travis Pickering (1999) and Kathy Kuman (2003) does not support this conclusion. They point out that the virtual absence of cut-marks on the bones, and the weathered state of many of the artefacts, imply that the latter were left outside the cave for a considerable time before being washed into it. Human involvement in the bone accumulation process might well have been negligible.

## 7. The finding and interpretation of bone tools

As the Swartkrans excavation proceeded between 1979 and 1986, a total of 68 fossil bones were found that appeared to have been used as tools. Of these, 17 came from the Lower Bank of Member 1, 11 from Member 2 and 40 from Member 3. They typically tapered to smooth points and some of them showed superimposed polish. Most of these specimens were bone flakes, although there were several horn cores and other skeletal parts represented. The wear was very reminiscent of that suffered by the metal screwdrivers that we used when excavating the lightly calcified cave earth in various parts of the Swartkrans cave, so it seemed possible that the bone pieces had been used for digging in the ground. I had often watched baboons digging edible bulbs and tubers from the ground with their hands, about 20km north of Swartkrans, but they were only able to do this in the reasonably soft alluvial soils at the bottom of the valleys. The plants most commonly involved were a lily, *Scilla marginata*, and two species of “African potato,” *Hypoxis costata* and *H. rigidula*, all of which were particularly common on the rocky dolomite hillsides, although the baboons could usually not dig them out there. It seemed conceivable that, had the hominids access to digging tools, they would have been able to extract the bulbs and tubers from the rocky situations as well. A series of digging experiments were therefore carried out, using bone flakes from the limb bones of a wildebeest, killed by lions in the Kruger National Park, the bones of which were worked over by spotted hyaenas. These flakes were used for between four and eight hours of digging on the rocky Swartkrans hillside, where we found it possible to extract a *Scilla* bulb or *Hypoxis* corm in 14 to 30 minutes, depending on the stoniness of the ground.

Wear similar to that seen on the fossil bones could be caused in four hours of digging, while subsequent wear proceeded more slowly.

I was familiar with the work that Pat Shipman was doing on worn bones from Olduvai (Shipman and Rose, 1988; Shipman, 1989), so took the collection of Swartkrans specimens, as well as two experimental bone tools, over to the Department of Cell Biology and Anatomy of the Johns Hopkins University Medical School in Baltimore. Here, Pat Shipman replicated selected parts of the specimens, using silicone-based dental impression material to make negative impressions, in conjunction with epoxy resin used to make positive casts, according to the method described by Rose (1983). The surfaces of these were then examined with a scanning electron microscope.

The similarity of wear-patterns on the experimental digging tools and the Swartkrans fossil specimens was striking, leading us to conclude that the latter specimens had, in fact, been used for digging by the hominids about one million years ago. But, in addition to this, three of the fossil specimens showed a polish, superimposed on the characteristic wear and scratch-marks. Our suggested interpretation was that the digging tools had been used also for rubbing a soft substance, presumably animal skin. Of interest in this regard is the description of a bone tool by Robinson (1959) from his excavation of Sterkfontein Member 5. It was made on a bone flake with a natural point and has a well-defined worn facet, showing fine linear scratching and a high polish. Robinson's interpretation was that the bone had been repeatedly rubbed on a soft substance, presumably animal hide.

Another bone tool, from Swartkrans Member 3, is also suggestive of use on animal hides. It is a delicate awl-like artefact (SKX 37052) that consists of a thin flake of bone tapering to a worn point and showing longitudinal and circumferential scratching, together with polish. This tool may have been used for piercing holes in skins or other soft materials, as similar microscopic wear has been documented on experimental awls (Olsen, 1984).

The evidence discussed here suggests that the Swartkrans hominids may have made simple carry bags from animal skins, in which they transported their tools and possibly their gathered food. This could explain the evidence for the apparent use of the same tools over successive days or weeks.

More recently, Lucinda Backwell (2000) completed a Masters project at the University of the Witwatersrand on "A critical assessment of southern African early hominid bone tools." She has since progressed to a Ph.D. on this topic, with her research supervised by Francesco d'Errico of Bordeaux. While they concur that these are genuine bone tools, they conclude, on the basis of image analysis of the marks and striations on the bones, that they were used for digging in termite mounds, rather than in the stony soil of the dolomite hillsides (Backwell and d'Errico, 2001; d'Errico, Backwell and Berger, 2001).

More recently, Backwell and d'Errico (2004) have identified another 16 bone pieces from the Swartkrans assemblage that they regard as being bone tools. Most of these had been looked over earlier by Pat Shipman and myself, but they had not been included in the original sample as they lacked proper stratigraphic documentation, or, in our opinion, could have been pseudo-tools. The possibility that the Swartkrans hominids had augmented their diet with termites, dug out with bone tools is an exciting one.

*Figure 12. Pat Shipman making molds of Swartkrans bone tools in her laboratory at the Johns Hopkins University Medical School in Baltimore during 1987.*

## 8. The importance of original cave-form to taphonomic reconstructions

All of the South African early hominid cave sites have suffered considerable surface erosion, and in some cases mining, since the bones originally found their way into the caves. But, if we are to interpret the bone accumulating agencies with confidence, it is important that the original form of the cave be reconstructed. In the case of the Taung site, for instance, the fossils occur in secondary infillings of cavities in a massive travertine boss that had been laid down by lime-rich water flowing over the edge of a dolomite cliff. However, mining of this boss has seriously complicated the reconstruction of the time that bones accumulated.

In the 1980s, I had the opportunity of examining a series of very similar, but undamaged, travertine deposits, set in the wild and natural environment of the Namib-Naukluft Park of Namibia. Here it is possible to observe travertines forming and eroding, while natural taphonomic processes may be studied in the numerous secondary cavities within the travertine masses themselves. The travertines are currently forming outward over a cliff in a steep-sided valley in Precambrian dolomite, where it is possible to see how closely the formation of carapace travertine is linked to the presence of moss and algae. The steeply-inclined carapace layers are formed where water flows or seeps slowly over living moss, often in the form of hanging curtains. Quite apart from the natural evaporation of this lime-rich water, it is the photosynthesis of the moss and algae that removes carbon dioxide from the water, leading to the precipitation of calcium carbonate. Moss-banks in various stages of calcification may be seen in such places and it is not unusual to find natural cavities behind hanging curtains of moss. These usually have an opening at one end, leading into a chamber perhaps four metres high, five metres wide, and up to 30 metres long. These are probably the sort of places into which the Taung fossils, including the numerous baboon skulls and that of the *Australopithecus* child found their way. Examination of the bones currently accumulating in the Naukluft travertine caves show that the expected taphonomic accumulating processes are at work there. Some bones have been accumulated by porcupines; others show unmistakable signs of leopard feeding activity—this is to be expected as leopards may be observed in the immediate vicinity (Brain, 1985).

Where normal dolomite caves are concerned, as at Sterkfontein, Swartkrans and Makapansgat, it is important to try to reconstruct their form at the time that the fossiliferous sediments were accumulating. For instance, was the entrance to the cave a death-trap situation, meaning that if an animal fell into it, it would not be able to escape? If the cavern was accessible to animals, was the roof high or low? This is important, as hyaenas and porcupines, for instance, definitely favour low-roofed chambers for their feeding- and breeding-dens, whereas baboons prefer more open situations for their sleeping sites. This may have been the case for hominids as well.

## 9. Effects of progressive Cainozoic cooling on African habitats and fauna

In the 1960s, people interested in reconstructing past climatic and environmental conditions in Africa were working with the concept that, during the last one to two million years, there had been three pluvial and three non-pluvial episodes. At that time, Waldo Meester and I speculated as to how these might have served as biological isolating mechanisms (Brain and Meester, 1965, pp. 332-340), with particular reference to small mammals and the vegetation they required in their habitats. But, as I gradually unravelled the complicated stratigraphy of the Swartkrans cave, it became apparent that there had been numerous episodes of deposition of the cave sediment, interspersed with others, during which erosion took place. It seemed inevitable that such episodes were climatically induced, and we were fortunate in that Swartkrans proved to be a sensitive indicator of climatic change. The reason for this was that the cavern had been linked upward to the hillside surface with several openings, but also downwards to lower caverns. The main cave would rapidly fill up with sediment and then, in a successive climatic cycle, parts of this filling would be eroded and carried away to the lower caverns. It seemed that the infilling processes had been relatively rapid, compared to the much longer intervals when erosion took place.

It seemed likely to me that such depositional/erosional cycles must have been climatically induced, but also that changing temperature was more likely to be the primary factor than was rainfall. I was invited by the Geological Society of South Africa to give the 17th Alex L. Du Toit Memorial Lecture in 1979 and, for this, decided to look into the evidence then available for temperature changes during the last few million years. In the published version of the lecture (Brain, 1981) I wrote:

> "The aim of this lecture is a simple one—*to draw the attention of those interested in human evolution to a remarkable record of past global temperatures that has recently become available, and to point out that certain low temperature episodes, reflected in this record, could well have served as stimuli for critical steps in hominoid evolution*. The record of past global temperatures, to be described here, is based largely on isotope compositions of foraminiferal tests preserved in deep-sea sediments. Fluctuations in global temperature are regarded as *primary environmental changes*, which then led to *secondary effects*, such as rainfall and vegetation changes. In the case of many African habitats, the secondary effects could well have been more important as evolutionary stimuli than were the primary temperature fluctuations."

The deep-sea temperature record, for the southern oceans, showed a progressive cooling trend during the last 50 million years, and it seems that this trend, involving about 12 degrees C, could be attributed largely to conti-

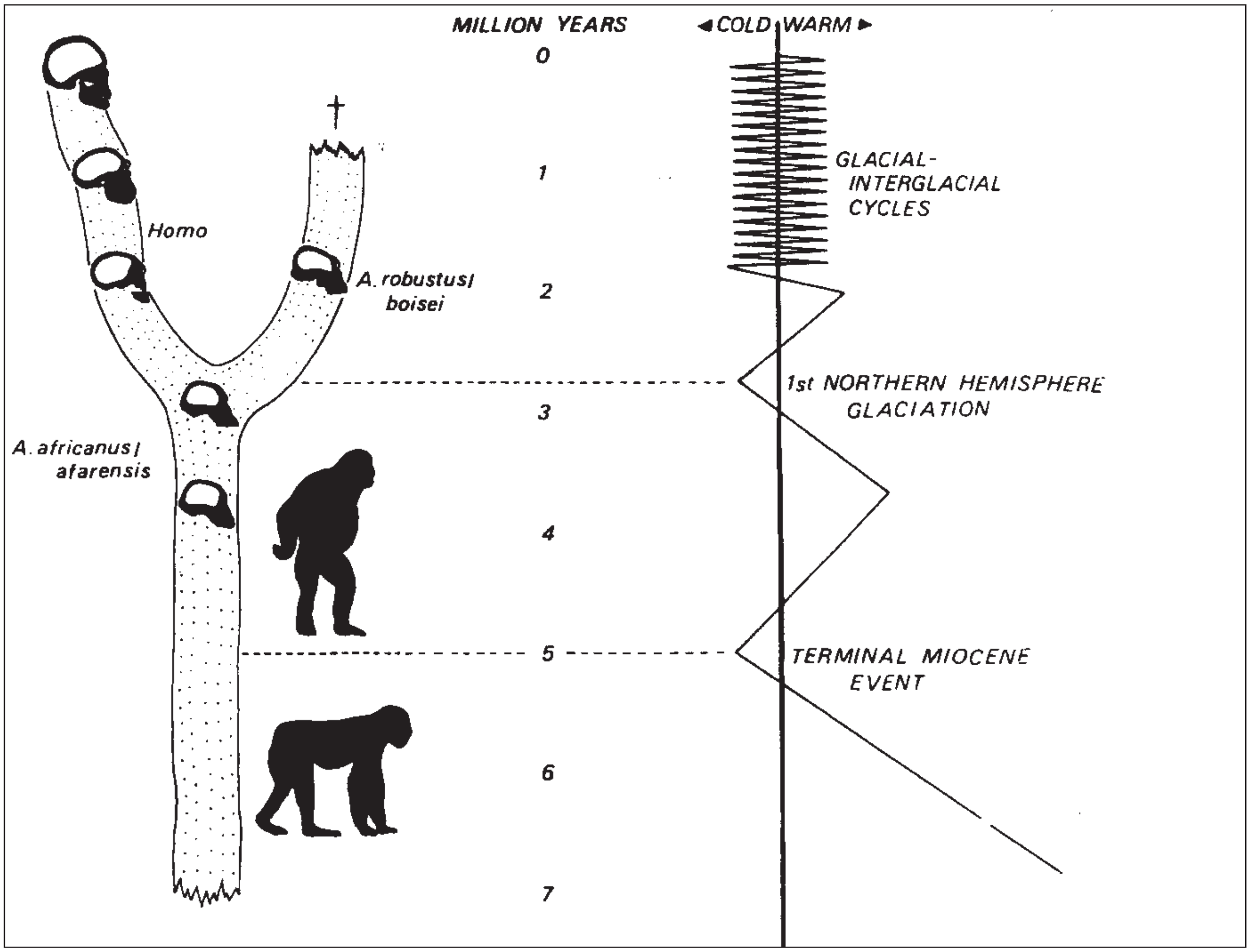

*Figure 13. An early attempt in 1979 (Brain, 1981) to correlate events in hominid evolution with low-temperature global climatic episodes. This was prompted by the realization that the Swartkrans cave filling reflected repeated cycles of deposition and erosion.*

nental drift, following the breakup of the supercontinent Gondwanaland, that initially embraced South America, Africa, Antarctica, and Australia. When Antarctica took up its south polar position, other continents drifted away from it to the north, and an open seaway was created around its periphery. This started the Circum-Antarctic Current, driven by the rotation of the earth and the resultant westerly winds. Once this happened, the thermal isolation and refrigeration of Antarctica began.

As far as African habitats go, the global cooling trend seems to have crossed a critical threshold about 6.5 million years ago with the "Terminal Miocene Event." At about this time, a widespread sea-level drop has been recorded and this, in addition to tectonic movements in the Gibralter area, resulted in the isolation of the Mediterranean from the Atlantic. The seawater in the Mediterranean basin then dried out completely, depositing over one million cubic kilometres of sea salt, which, as Ryan (1973) pointed out, constitutes about 6% of the dissolved salts in the world's oceans; its removal from circulation must have resulted in a significant freshening of sea water that would have facilitated the formation of sea-ice near Antarctica. This *Messinian Salinity Crisis* had striking physical and biological consequences, as was first described by Hsu et al. (1977). For instance, a dry-land connection was opened between Africa and Europe, facilitating the free exchange of fauna and flora, while the cool, arid climate around the desiccated Mediterranean might well have promoted an early expansion of African savannahs (Brain, 1984). The evidence further suggested that the connection between the Atlantic Ocean and the Mediterranean basin was re-established abruptly at about five million years ago, which brought the salinity crisis to an end.

It has long been surmised that the Terminal Miocene Event was precipitated by the sudden establishment of the west Antarctic ice-cap, and its link-up with the long-standing east Antarctic equivalent. While this concept still seems to be current, the situation has been complicated by evidence of tectonic activity, active rifting and the rise of the Trans-Antarctic Mountains (Denton, 1995; Cande et al., 2000).

The next important event in the cooling trend was the onset of the first Northern Hemisphere glaciation, which is currently placed at about 2.54 million years ago (Clark et al., 1999). This trend was accompanied by the regular glacial-interglacial cycles that have been such a feature of more recent times, first with a periodicity of 41,000 years until about one million years ago, followed by the establishment of the 100,000 year cycles, in which we are still currently locked. In Africa, the effects of cooling on habitats was greatly enhanced by volcanic activity and tectonic movement; in East Africa, combined effects of the Rift valley development, associated volcanoes and regional uplift was striking, while, in southern Africa, uplift of between 600 and 900 metres along the eastern regions may have had as much effect itself as the superimposed global cooling trend (Partridge et al., 1995).

So, in 1979, when I tried to correlate some of the features of hominid evolution with global low temperature events, it seemed reasonable to assume that the dramatic breakup of tropical evergreen forest areas at the time of the Terminal Miocene Event, between six and five million years ago, could be related to the acquisition of bipedal posture in our hominid ancestors. Following that, the next major low temperature event, at about 2.5 million years, seems to coincide with a split in the hominid lineage, with one line leading to humans and the other to the robust australopithecines, whose strategy for coping with ever more difficult environmental challenges did not, in the end, succeed. By contrast, adaptations in our own lineage proved to be more viable.

Since then, the regular glacial/interglacial cycles must have been very important in the spread of grasslands, at the expense of woodlands, the shrinking and breakup of tropical lowland forest areas (Hamilton, 1976), and the fragmentation of other habitats. Such effects must surely have promoted allopatric speciation in a variety of animals; in fact, Elisabeth Vrba has documented the first appearance of 37 new African antelope species, many of them open country grazers, between 2.7 and 2.5 million years ago, at the time when the robust australopithecine lineage split from that leading to *Homo*.

In September 1982, Elisabeth Vrba organised a symposium at the Transvaal Museum in Pretoria on "Species and Speciation," at which I again emphasized the significance of *Temperature-induced environmental changes in Africa as evolutionary stimuli* (Brain, 1985, pp. 45-52). The following year an international symposium was held by the South African Society for Quaternary Research in Swaziland, where I again drew attention to *The Terminal Miocene Event: a critical environmental and evolutionary episode* (Brain, 1984, pp. 491-498). At this meeting, Elisabeth Vrba took up the temperature/evolution theme with her usual energy and enthusiasm. She teamed up with George Denton, Tim Partridge, and Lloyd Burckle to organise a series of workshops on palaeoclimate and evolution at the Lamont-Doherty Earth Observatory, Palisades, New York in September 1984; at Sun City, South Africa in February 1985, and again at the Lamont-Doherty Earth Observatory in May 1985. The proceedings were published as extended abstracts in three dedicated issues of the South African Journal of Science (vols 81(5), 1985; 82(2), 1986 and 82(9), 1986). Finally a conference was held in Airlie, Virginia, in May 1993 under the title *Paleoclimate and evolution, with emphasis on human origins* where many important topics were addressed. Here I discussed *The influence of climatic changes on the completeness of the early hominid record in southern African caves, with particular reference to Swartkrans* (Brain, 1995), stressing that the fossiliferous infills of caves such as Swartkrans, probably reflected only the interglacial periods of the last two million years. The much longer glacial episodes were probably not represented at all in the deposits.

## 10. Evidence from Swartkrans for predation on early hominids

Early on in the analysis of the fossil assemblage from Swartkrans, it became apparent that, although the numerous hominid individuals were well represented by cranial fossils, post-cranial bones were very rare, and I was confronted with "the mystery of the missing bodies," as we called it then. In addition to the hominids, four baboon species were represented and we found that, the larger the body-size of these, the more juvenile remains appeared in the assemblage. An obvious conclusion to draw was that we were dealing with the food remains of a predator, which had preference for prey of a particular body-size. Leopards immediately came to mind, as they are well-known to select prey within preferred limits and this suspicion was confirmed by the specific damage that some of the bones had suffered (Newman, 1993). One well-known specimen, the calvaria of a hominid child, was found to have two punctures in its parietal bones and the distance between these was matched by the spacing of the canines of a fossil leopard from the same part of the cave. The reconstruction that I suggested was that the child had been killed by a leopard, perhaps by the usual throat-bite method, and that it had then been picked up by its head, as leopards are inclined to do, and dragged off to a feeding place in the dark recesses of the cave. This carrying behaviour, observed in contemporary leopards with monkey or baboon prey, results in the upper canines gripping the face of the prey, while the lower canines penetrate the back of the skull (Brain, 1969, 1974, 1981).

The detailed taphonomic analysis of the fossil assemblages from Swartkrans Members 1 and 2 suggested that hominids and baboons came to shelter within the entrance area of the cave on cold winter nights and that they were preyed upon there by leopards and sabre-tooth cats. The predators took their victims to the lower parts of the cave and ate them; what scraps survived their attention, and that of scavengers such as hyaenas—whose coprolites in the deposits testify to their visits—contributed to the fossil assemblage (Brain, 1993).

In broad perspective, my impression is that the life of hominids in environments such as that of the Sterkfontein valley, one and a half million years ago, would have been a hazardous one, calling for continual vigilance against a wide variety of predatory threats, day and night. In my opinion, such threats must have represented a significant selective pressure in favour of any advance in intelligence and resulting technology that could have reduced the threat.

Figure 14. Part of a juvenile australopithecine cranium (SK 54) with two round holes in it, from the Swartkrans Hanging Remnant. The spacing of these holes is matched closely by that of the lower canines of a fossil leopard from the same deposit.

## 11. Evidence for the management of fire at Swartkrans

As mentioned above, there can surely be no doubt that humans eventually established their current dominance in the natural world through intelligence and its product, technology. But were the initial steps along this path also mediated in this way? I have the impression that some of the evidence from the Swartkrans cave confirms this possibility. Excavation revealed that the Member 3 deposit accumulated in a roofed erosional gully, about 20 m long and up to 5 m wide, running between the west wall of the cave and an eroded vertical bank of older sediments on the east side of the gully. Initially I was not aware that the calcified sediment in this gully was different from that further to the east, but when pieces of burnt bone started turning up with regularity, suspicions were aroused and a near-vertical unconformable contact became apparent between the contents of this gully and what surrounded it. The excavation proceeded to a depth of 850 cms and produced 59,488 pieces of fossil bone, including nine fossils of robust australopithecines and 270 pieces of bone that showed signs of having been burnt. Careful chemical analyses were undertaken at the University of Capetown by Andy Sillen, while we measured the temperatures attained in a number of experimental fires, using different kinds of wood. We then made thin sections of bones heated to such temperatures in a kiln fitted with a very precise temperature regulating device. After all this, we were able to estimate the approximate temperatures to which each of the fossil pieces had been heated. (Brain and Sillen, 1988; Sillen and Hoering, 1993; Brain, 1993b)

It is to be expected that natural grass fires passing the entrance to a cave should burn any pieces of bone lying around, and that these could later make their way back into the lower parts of the cave. In fact, three pieces of fossilised burnt bone had turned up, among 153,781 other fossils in the Lower Bank of Member 1, and one may assume that the burning could have happened in this way. But when pieces of burnt bone made their appearance in 17 excavation grid squares (1 m × 1 m), and in up to 23 vertical excavation spits (each 10 cms thick) in

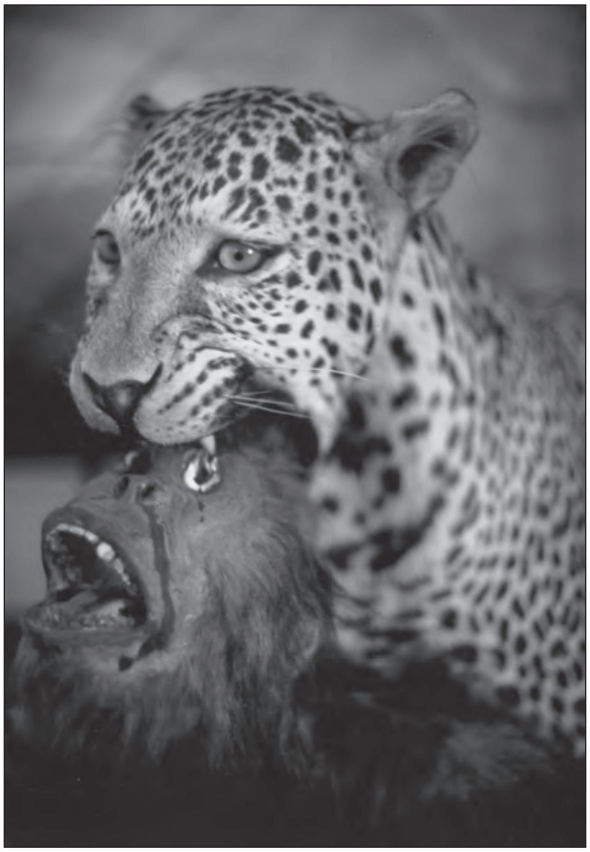

Figure 15. A reconstruction in the Transvaal Museum of the Swartkrans ape-man child suggesting that it had been killed by a leopard and then carried to a feeding lair in the cave. The lower canines of the leopard are in the back of the child's head, while the upper canines are in its face.

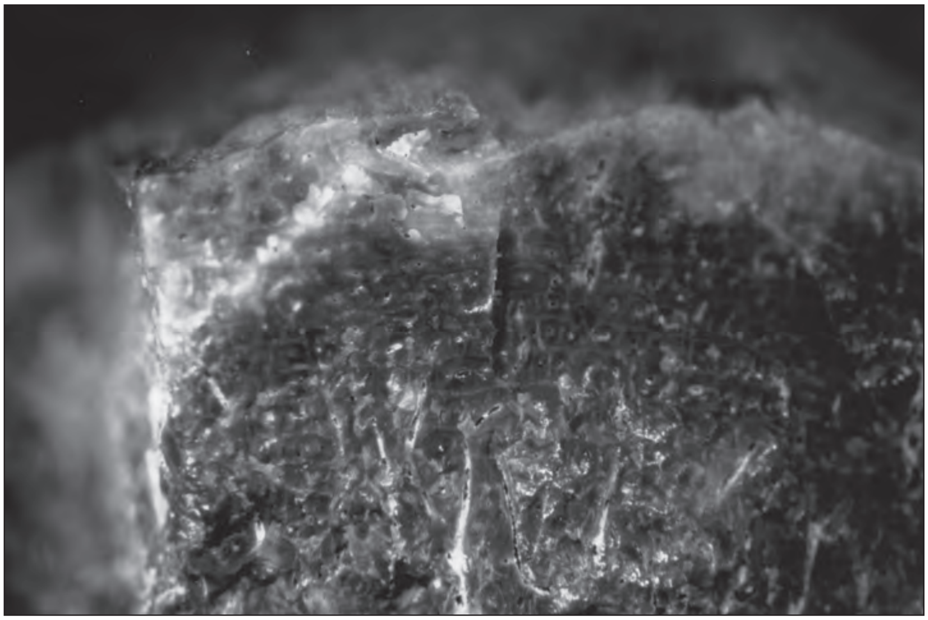

*Figure 16. A piece of fossil burnt bone, one of many found in the Member 3 sediments at Swartkrans cave. The dark interior of this particular bone had been carbonized, while the pale exterior was calcined.*

the newly exposed Member 3 deposit, one was obviously dealing with a different situation. The interpretation that we proposed was that fires had been tended in the entrance area of the Member 3 gully repeatedly during the accumulation period of this sedimentary profile, and that pieces of bone heated in these fires had made their way down the talus slope to their final repository. There is no evidence that people at this time had mastered the technique of *fire making*, but had presumably collected burning branches from natural, lightning-induced grass fires—that are very much a feature of the highveld grassland in early summer—and brought this fire back to their sleeping place. If Member 3 is about one million years old, hundreds of thousands of years would probably have had to pass before the deliberate making of fire became a reality. But whatever the source of the fire, its presence in the cave entrance would have given these early human groups some measure of protection from the ever-present danger of waiting leopards. In addition to the burnt bones, we also recognised 16 pieces in the Member 3 assemblage with cut- and chop-marks on them. Since then, many others have been recognised in the collection through the careful work of Travis Pickering and his colleagues. Such damage has not been seen on any of fossils from Members 1 and 2, suggesting that hominid meat-eating at the cave, presumably round a camp-fire, became a reality in the cold interval between Members 2 and 3. Presumably, without the protection af-

*Figure 17. An experimental camp fire at Swartkrans, using the local* Celtis *wood, in 1985. Here Virginia and Tim Brain measure temperatures within the fire, using a long thermocouple proble, linked to a digital thermometer.*

forded by fire, it would have been too dangerous to bring meat to the cave for fear of attracting the attention of other carnivores. In my view, fire-management of this kind, must have represented a critical early step in human emancipation from subservience to more powerful carnivores that ultimately led to their domination.

As a result of further intelligence-driven technology, humans then went on to become highly effective social hunters and predators in their own right. The selective pressures driving this process were presumably similar to those that had allowed the human emergence from a former subservient role. Among the variety of selective pressures that drove the evolution of the large human brain, it can be argued that the demands of predation, first in surviving its dangers and later in the successful practice, were ever-present and powerful in their effects.

## 12. The significance of predation to the evolution of intelligence in hominids and much older ancestral animals

By any standards, the increase in brain size relative to that of the body in our human ancestors during the last two million years was a remarkable zoological event. When the earliest known members of the *Homo* lineage appeared on the scene, in the form of *H. habilis* or *H. rudolfensis*, their average brain-capacity was about 654 cc; this had risen to about 850 cc in *H. ergaster* and *H. erectus*, and to 1400 cc in archaic *H. sapiens* towards the end of the Middle Pleistocene. As Leslie Aiello and Peter Wheeler (1995) pointed out, this event is all the more remarkable because a brain is built of “expensive tissue”—although a human brain may only make up 2 to 3% of the weight of the whole body, it uses 16-20% of the energy consumed by the resting body. To double the size of the brain, relative to that of the body, would usually mean that the basic metabolic rate of the animal would have to be substantially increased. Oddly enough, this has not been observed in humans, in comparison to related primates, and this prompted Aiello and Wheeler to conclude that human brain expansion occurred at the expense of the size of the gut, that has apparently shrunk during the course of human evolution. To be able to function with a much smaller gut implies that ancestral humans changed to a diet of higher quality, such as one including animal protein, and they would have done this by scavenging and active hunting. There is, in fact, good evidence for this behaviour among the 2.5-million-year-old Bouri hominids of Ethiopia, as Tim White and his colleagues have pointed out (de Heinzelin et al., 1999).

Clearly, a greatly increased brain-size is not a luxury to be acquired lightly. It is something that would only have evolved under strong selective pressure. For many years it has been suggested that brain expansion, and the benefits that it brings to humans, has been linked to the problems of making a living in the changed and more open habitats that characterized Africa during the last two million years. Frequently cited is the need to cope with the more complex foraging strategies than had been the case when ancestral hominids lived in evergreen forests. I have no doubt that this need would have been one of the factors. But, as I have discussed above, I believe that it was also the need to survive the ever-present threat of predation by carnivores in these more open and alien habitats that provided the needed selective pressure (Brain, 2001a).

At the end of my Swartkrans project in the early 1990s, I thought it would be fun to find out more about the ancient roots of predation in the animal lineage. These would have been among ancestral invertebrates, some of which were very small, and I was attracted to them as I have had a long-standing interest in living micro-invertebrates in African fresh waters. These have included testate amoebae, rotifers and planarians, which I had the chance to study intensively while serving as Curator of Invertebrates at the Transvaal Museum between 1991 and 1995. But, to gain any insights on the ancient roots of predation, one has to turn to the fossil record, going back at least 600 million years to Terminal Proterozoic times. Some of the best evidence in this regard can be found in sediments belonging to the Nama Group of Namibia, that were accumulating in a shallow sea on the western edge of the Kalahari craton at the time of the assembly of Gondwanaland (Brain, 1997b). It is to the fossil record from the Nama Group, as well as from the somewhat older Otavi Group on the Congo Craton further to the north, that I have given my attention in the last few years.

Late proterozoic times, when animals first left abundant traces in the fossil record, were preceded by several very severe glacial periods. Glacial deposits from two of these episodes, each with their very distinctive “cap-carbonates,” have been recognised in northern Namibia (Hoffmann and Prave, 1996), as well as elsewhere in the world. Based on these, the “snowball earth” scenario has been invoked (Hoffman et al, 1998), addressing the problem of low-latitude glaciations, as are indicated by the Namibian evidence. It proposes that the oceans froze over and that biological productivity collapsed for some millions of years. It was only through the abundant production of carbon dioxide by active volcanoes that a “greenhouse” situation developed, rapidly melting the global ice and swinging the climate to an opposite extreme, as indicated by the cap carbonates, immediately above the glacial sediments.

The period following the last of these glacials, starting at about 580 million years, saw two remarkable radiations of animal life. The first is known as the Ediacaran radiation and involves soft-bodied organisms whose impressions are typically preserved in sandstones. The first evidence of these turned up in the Nama Basin of southern Namibia as early as 1908, and was described by Gürich in 1933. These organisms were typically flat or leaf-like with a very characteristic quilted structure, reminiscent of an air-mattress, but there were also circular medusoid-like structures. A similar fauna came to light during 1946 in the Ediacara Hills of South Australia and it is from this locality that the radiation gained its name. Since then, similar fossils have become known from at least 30 localities on five continents (Narbonne, 1998).

The remarkable structure shown by these organisms prompted Adolf Seilacher (1992) to create a new Kingdom, the Vendobionta, for them, although their affinities have been the subject of vigorous debate during the last 20 years. But, whatever they actually were, it is now clear that this fauna existed for about 55 million years, showing maximum diversity during the last 20 million of their existence. The Ediacaran community was apparently composed of sedentary or very slow-moving individuals, luxuriating in a tranquil "Garden of Ediacara," as Mark McMenamin (1986) has called it. Also attached to the shallow sea's "biomat" of that time were small cone-in-cone structures, originally described by Gerard Germs from the Nama Basin as *Cloudina*. These have since been found in many parts of the world and are regarded as a Terminal Proterozoic index fossil. The cones presumably housed a filter-feeding metazoan, of at least cniderian-grade organisation, with tentacles protruding from the top. Of particular interest is the fact that many fossils from China studied by Bengtson and Zhao (1992), showed evidence of having been bored into by predators. Recently, I came across similarly bored *Cloudina* tubes from the Nama Basin (Brain, 2001b) and the hunt is now on for fossils of the predator that caused the damage. But whatever the zoological affinity of this first predator might be, recent molecular evidence suggests strongly that the animal lineages would have gone back far further in time than currently known fossils might indicate. For this reason, I am working these days on micro-invertebrate fossils from Otavi Group limestones in northern Namibia, that date from between the two snowball earth glacials, 720–590 million years ago. This project is very labour-intensive, necessitating the preparation of hundreds of acetic acid residues of the limestones as well as the cutting and grinding of thin-sections that Laura Brain does on the back verandah of our home. But we have found a limestone succession where preservation of these small, soft-bodied creatures is exceptionally good, even though interpretation of the fossils that we find is fraught with problems (Brain et al., 2001). Some of these interpretive problems are now being overcome (Brain et al., 2003) and future prospects are exciting. So the fun with fossils continues!

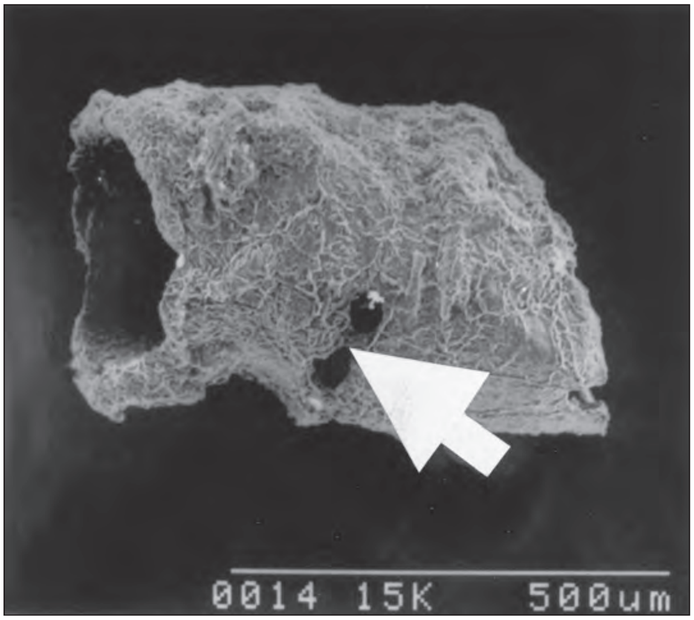

*Figure 18. The calcified tube of an ancestral animal,* Cloudina*, preserved in 550 million year-old Nama limestones of Namibia. It is thought to have been a coelenterate, with tentacles protruding in life from the open upper end of the tube. But in this specimen, a predator has drilled holes (arrow) through the wall of the tube, to gain access to the soft-bodied interior. This provides very early evidence for predatory activity.*

Returning to the theme of the appearance of the first predators, it is clear that this anticipated the demise of the tranquil Garden of Ediacara. The end came with the second major radiation of those times, the "Cambrian explosion of animal life," so well documented in the fossils of the Burgess Shale and other sites such as those at Chengjiang in China. These fossils suggest that within a brief period of geological time, representatives of almost every known phylum of animal life made their appearance in Middle Cambrian seas. Among these animals were, of course, burrowers and grazers, that rapidly destroyed the microbial biomats that had been such a feature of shallow seas for three billion years. But of particular relevance here was the appearance, with the Cambrian radiation, of the first effective predators that the world had seen. By definition, an animal is a multicellular heterotroph–an organism that feeds on other living things or their remains, while predators form but a subset of these. To feed on other true animals will generally require active pursuit and the overpowering of reluctant prey. For this, coordinated mobility and the ability to locate evasive prey are required. In other words, mobility and sense organs are needed.

Predators obviously rely on a variety of senses, but for the present purpose, let us consider just one—that of sight. The largest and most fearsome of Cambrian predators was *Anomalocaris*, growing up to 50 cms long and known now from a variety of localities in different parts of the world. The expanded lateral lobes along the length of the body made it an active swimmer, while the two powerful appendages anterior to the mouth must have been effective in the capture of prey, such as trilobites. These appendages had, in fact, been described (Whiteaves, 1892) many years before the entire animal was recognised and each was thought to represent a phyllocarid crustacean in its own right, although the "heads" of these could never be found, hence the name *Anomalocaris*. Now that the entire animal can be examined in fossil form (Collins, 1996), it is clear that two very large eyes were one of its striking features, each providing information to a central coordinating nervous system.

Eyes that are even more remarkable can be seen in fossils of another Burgess Shale organism of uncertain affinity, known as *Opabinia*, According to the reconstruction and interpretation provided by Briggs *et al*. (1994), *Opabinia* had five large eyes at the front of the head and a long flexible proboscis that ended in an array of grasping spines used to capture prey as the animal swam rapidly over the seafloor, relying on its lateral lobes for propulsion and using its tail as a stabilizer.

Throughout 500 million years of animal evolution, every advance that a predator could make to its effectiveness as a hunter had to be countered by comparable improvements in the survival ability of its prey, if one or the other were to avoid extinction. In this way, sense organs and coordinating neural systems were under constant selective pressure to promote their improvement. Cranial expansion, improved intelligence and the use of technology by hominids, faced with completely new and unprecedented predatory challenges, appears to have been one of the solutions. The fact that robust australopithecines did not follow this route of cranial expansion, may well have contributed to their disappearance from the merciless African savannah.

## 13. The pleasure of seeing taphonomic themes being carried forward from their early beginnings

The overview of my taphonomic career that I have provided here has obviously been retrospective. But writing it has made me realise what I appreciate most about my current situation. It lies in observing how many of the themes with which I have been concerned, are now being carried forward by young and enthusiastic taphonomists, like Travis Pickering and his colleagues, in ways that I could not have imagined (Pickering et al., 2004 a, b; Egeland et al., 2004). They bring new enthusiasms, insights and skills to the quest, and all my good wishes go with them.

I currently serve as Chief Scientific Adviser to the Palaeo-Anthropology Scientific Trust, or PAST, a South African organisation that, for the last ten years has provided financial support to students, researchers and educators, formerly in palaeo-anthropology, but now also in the wider field of palaeontology (Brain and Read, 2002a and b; Brain, 2003). A real pleasure in this is that I am brought into contact with students and others in the palaeo-field, throughout southern Africa, and am able to follow the progress of their interesting projects.

## ACKNOWLEDGEMENTS

It is with particular gratitude that I plan to participate in this meeting and thank Travis Pickering, Nick Toth and Kathy Schick for their invitation, and for all the hard work that they have put into its organisation. I would like to wish them and their colleagues at CRAFT every success with their work in the wonderful new facilities at Indiana University.

By way of acknowledgement, I also wish to record that much of my early work in this field was supported by the Wenner Gren Foundation and, in particular, by the interest of its then Director, Lita Osmundsen. Subsequently, generous research grants from the National Research Foundation in South Africa made my scientific work possible and this support is gratefully acknowledged. In the topics outlined above I have had the encouragement and support of many colleagues, without which the work could not have been done. For instance, Francis Thackeray started helping me at Swartkrans when he was 16 years old, and I was joined by Ron Clarke and Clark Howell in the description of new *Homo* remains from there, as long ago as 1970. My gratitude goes to many such people.

Fossil projects have provided me with a great deal of fun over the last 50 years, due largely to the presence of Laura Brain who, with our four children, have participated so enthusiastically. Finally, the encouragement and generosity of spirit shown to me by Raymond Dart is something for which I will always be grateful.

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